SHORT COMMUNICATION

Restoring phylogenetic diversity through facilitation

Jose A. Navarro-Cano[1], Pablo P. Ferrer-Gallego[3,4], Emilio Laguna[3], Inmaculada Ferrando[3,4], Marta Goberna[1], Alfonso Valiente-Banuet[5], Miguel Verdú[1,2]

Phylogenetic diversity enhances ecosystem functioning but restoration ecology has not taken advantage of this knowledge. We propose plant facilitation as a mechanism to promote phylogenetic diversity in restoration practices. We planted three functionally different species (*Gypsophila struthium*, *Sedum album*, and *Limonium sucronicum*) in a degraded gypsum ecosystem in Spain and found that after 7 years, the species with nurse traits (*G. struthium*) survived longer and facilitated the establishment of new species forming phylogenetically diverse neighborhoods. These facilitation-driven phylodiverse communities may potentially produce a cascade of benefits on ecosystem functioning.

Key words: ecological restoration, ecosystem functioning, gypsophyte plant, phylogenetic diversity, restoration success

Implications for Practice

- Selecting the plantation species based on their nurse traits not only maximizes survival but also facilitates the recruitment of other species.
- The facilitated species are assembled in phylogenetically rich neighborhoods.
- Phylogenetically neighborhoods are also functionally diverse, what is intimately linked to ecosystem function enhancement.
- Facilitation-based restoration methods may be used to restore species but also ecosystem functions and services.

Introduction

Ecological restoration practices are currently moving from reconstructing the past ecosystem to restore ecosystem functions including flows of goods and services (Harris 2009; Wortley et al. 2013; Kettenring et al. 2014). Growing evidence indicates that ecosystem functions are enhanced when plant diversity is high, not only in number of species (Doherty et al. 2011) but also in terms of genetic (Hines et al. 2014), functional (Clark et al. 2012), and phylogenetic (Cadotte 2013) diversity. The inclusion of the phylogenetic dimension has improved our understanding of the relationship between biodiversity and ecosystem functioning (Tucker & Cadotte 2013; Liu et al. 2015). Phylogenetic diversity is a good proxy of ecosystem functioning when the functional traits responsible of the ecosystem functions are evolutionarily conserved and therefore phylogeny may inform about traits (Webb et al. 2002). Thus, phylogenetically diverse communities will tend to be composed by species covering a large spectrum of functional traits providing more ecosystem functions. For example, plant phylogenetic diversity has been shown to increase productivity in terms of plant biomass (Cadotte 2013) or soil microbial productivity (Navarro-Cano et al. 2014). Despite the predictive

power of phylogeny on the assembly of communities and the functionality of ecosystems, restoration based on phylogenetic information has been seldom performed (Verdú et al. 2012). As an example, the term "phylogenetic diversity" is rarely found in the journals "Restoration Ecology" (two papers between 1993 and 2015) or "Ecological Engineering" (11 papers between 1992 and 2015) (data consulted in May 2015). The use of phylogenetic diversity as a proxy of functionality has been strongly recommended as a cost-efficient measure to monitor restoration (Montoya et al. 2012).

A natural process concomitantly increasing plant phylogenetic diversity and ecosystem functions is plant facilitation, an ecological interaction in which one species (nurse) ameliorates the environmental conditions for other species to recruit (Valiente-Banuet & Verdú 2007). Plant facilitation increases not only the number of species in the community but also phylogenetic diversity because nurses tend to facilitate functionally (and hence phylogenetically) dissimilar species, thus promoting phylogenetically diverse neighborhoods. For example, nurse and facilitated plants tend to have different regeneration niches, the former characterized by early colonizer, and the latter by late colonizer traits (Valiente-Banuet et al. 2006). The ecosystem functions provided by plant facilitation are related to biotic and abiotic processes, such as seedling recruitment,

herbivore protection, trace metal removal, erosion control, and microbially mediated soil productivity (Gómez-Aparicio et al. 2004; Navarro-Cano et al. 2014; Wang et al. 2014). This potential has been recently applied in restoration practices (Castro et al. 2002; Gómez-Aparicio et al. 2004; Padilla & Pugnaire 2006; Siles et al. 2008; Rey et al. 2009). The main objective of these nurse-based restoration practices was to establish target species in the degraded ecosystem taking advantage of the improved environmental conditions provided by the nurse. The success of these restoration practices has been measured in terms of the survival, growth, and reproduction of the planted species (Gómez-Aparicio 2009). But the need to move from successfully establishing particular species to restore ecosystem functions requires practices improving phylogenetic diversity. We propose that facilitation is a good candidate mechanism to promote not only species richness but also phylogenetic and functional diversity by recruiting distantly related plants, a scenario that will ultimately result in a convenient cascade of ecosystem functions.

The microenvironmental amelioration produced by nurses tends to increase with plant size and can be very fast (Pugnaire et al. 1996). For example, the pioneer nurse *Ononis tridentata* increased 6-fold the total organic carbon of barren gypsum soils under semiarid conditions in only two decades (Navarro-Cano et al. 2015). It becomes clear that pioneer nurse plants with traits adapted to survive and grow in stressful habitats are good candidates to trigger the ecosystem functions associated with facilitation in these habitats.

Here, we illustrate with an experimental planting how the ecological knowledge linking facilitation and phylogenetic diversity may help to assess restoration achievement beyond the response of planted species. Specifically, we hypothesize that the species with nurse traits will have higher survival rates and will start to facilitate other species to increasing levels of phylogenetic and functional diversity. To test it, we evaluate a restoration activity performed in an Eastern Spain gypsum habitat, a threatened ecosystem harboring high levels of endemicity, and listed as a conservation priority in local, national, and international directives (Escudero et al. 2015) where three functionally different species (*Gypsophila struthium*, *Sedum album*, and *Limonium sucronicum*) were planted.

Methods

Study Site and Species

The restoration activity was performed in the European Natura 2000 Site Valle de Ayora y Sierra de Boquerón (Jalance, Valencia; 39°11′30″N 14′55″S, 416 m.a.s.l.). Climate is dry Mediterranean with a mean annual rainfall of 463 mm and mean annual temperature around 16°C (Ninyerola et al. 2005; precipitation data in Fig. 1 collected from the IVIA (Instituto Valenciano de Investigaciones Agrarias) database at http://riegos.ivia.es/datos-meteorologicos). Landscape is characterized by steeply sloping hills formed by gypsum outcrops. The vegetation of the study area is a mixed open *Pinus halepensis* woodland (40% pine cover) with gypsicolous
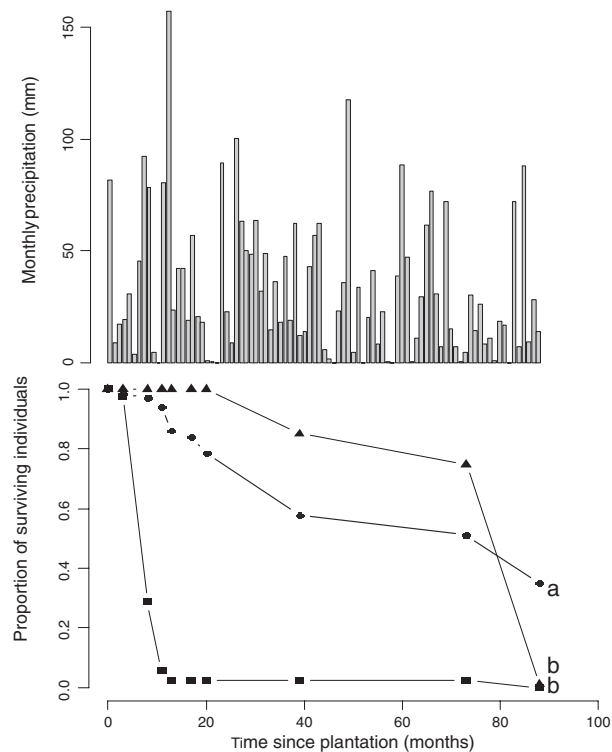

Figure 1. Survival rates of *Sedum album* (triangles), *Gypsophyla struthium* (circles), and *Limonium sucronicum* (squares) after 7 years as plantation is shown in the bottom panel. Monthly precipitation along the same period is shown on the top. Different letters in the plot indicate significant differences in survival rates after a post hoc Kruskal Nemenyi test.

shrubs dominated by *Gypsophila struthium*, *Ononis tridentata*, *Helianthemum squamatum*, and *Rosmarinus officinalis* (25% shrubland cover).

Following Meyer (1986), (1) gypsophiles are plants growing exclusively on gypsum soils, (2) gypsoclines have a preferential distribution on gypsum but are also found on other substrates, and (3) gypsovags grow both on and off gypsum soils. We selected three native species in the study area to assay a restoration activity in a gypsum slope: a gypsophile (*G. struthium*), a gypsocline (*Limonium sucronicum*) and a gypsovag (*Sedum album*) (Mota et al. 2003; Novák & Konvičkab 2011; Sánchez-Gómez et al. 2011). According to the regeneration niches, gypsophiles should behave as the best nurses in gypsum soils (Navarro-Cano et al. 2014).

Gypsophila struthium (Caryophyllaceae) is a 30–80 cm height chamaephyte with early summer blossoming. *Limonium sucronicum* (Plumbaginaceae) is a 20–40 cm height suffruticose chamaephyte or hemicryptophyte with late summer blossoming. *Sedum album* (Crassulaceae) is a 5–20 cm height succulent chamaephyte with spring blossoming. All three species have autochorous seed dispersal mechanisms.

Planting Procedure

In October 2007, 135 seedlings of *G. struthium*, 87 of *L. sucronicum* and 87 of *S. album* were planted throughout

2.5 ha in a 30% gypsum slope. Seeds collected from the study site were grown in the nursery into 200 cm³ sheet pots filled with Kekkilä forest substrate with 3:2:3 NPK proportions. After 1 year in the nursery, plants were transplanted to the field in planting holes of 30 cm of diameter × 30 cm in depth. To distribute microenvironmental effects (i.e. slope inclination, moisture, erosion, and so on) homogenously across species, planting holes were spatially grouped in eighty-seven 2 m² plots, each plot containing all the species planted in three to four holes containing individuals of the three species. Plots were haphazardly distributed along the whole restoration area.

All plants were irrigated with 3 L of water 1 week after plantation and subsequently protected with galvanized mesh to avoid herbivory.

We surveyed mortality rates after 3, 8, 11, 13, 17, 20, 39, 73, and 88 months since plantation. At the final survey, we recorded the size of the surviving individuals as well as the species facilitated by them.

Plant size was estimated as:

$$\text{Plant size} = \pi \times \text{major radius} \times \text{minor radius} \times \text{height}$$

We identified and counted all the plants occurring beneath the canopy of the planted species. As an internal control of this nursing effect, we also counted the plants emerging in adjacent open ground plots. These plots had the same surface area compared to their adjacent, paired plots with planted species.

Statistical Analyses

The phylogenetic diversity of the plants recruiting under each planted nurse or on open ground plots was estimated as the mean phylogenetic distance between all pairs of coexisting plants. Phylogenetic distances were estimated after assembling a phylogenetic supertree based on the work of the Angiosperm Phylogeny Group (Stevens 2012) with the help of the program Phylomatic, as implemented in Phylocom version 4.2 (Webb et al. 2008) and BEAST 1.5.4 (Drummond & Rambaut 2007). We used the R20120829 reference tree to obtain the topology of the community phylogeny and subsequently we resolved polytomies and adjusted branch lengths with the help of BEAST (Drummond & Rambaut 2007) and the PolytomyResolver script (Kuhn et al. 2011). This branch length adjustment procedure follows a birth–death evolutionary model that is more realistic than traditional nonmodel-based approaches. Chronological constraints were posed for the nodes dated by Wikström et al. (2001), and the remaining nodes were dated by BEAST with the default settings specified in the PolytomyResolver script. Markov Chain Monte Carlo analyses were run for 10^6 iterations and trees were sampled every 10^3 iterations. A 25% burn-in was discarded and the maximum clade credibility tree recovered with the help of the TreeAnnotator v1.5.4 software (Drummond & Rambaut 2007).

The functional diversity of the plants recruiting under each planted nurse or on open ground plots was estimated as the mean phenotypic distance between all pairs of coexisting plants, as explained below. We characterized plant phenotypes with five traits that we considered to be relevant a priori for survival in gypsum soils:

1. Mean size: the average height (in cm) of each species from Mateo Sanz & Crespo Villalba (2009).
2. Rootq: root depth/spread quotient (from Guerrero-Campo 1998). It ranges from 1 to 7 and informs on how a root system explores the soil volume. Rootq = 1 indicates a plant with deep roots and low lateral root spread whereas Rootq = 7 indicates a plant with shallow roots and high lateral spread.
3. Rooti (from Guerrero-Campo 1998): root intensivity ranges from 1 to 7 and indicates the root system allocation between main and secondary roots in terms of density and biomass. A plant with Rooti = 1 has a low secondary root density and dominance of a taproot, like carrots whereas Rooti = 7 indicates the absence of a main root and high density of fine roots, like grasses.
4. Gypsophyly: 0: gypsovag (plants growing both on and off gypsum soils); 1: gypsocline (plants not only with preferential distribution on gypsum but also found on other substrates); and 2: gypsophile (plants growing exclusively on gypsum soils).
5. Xerophyly: 0: xerophytic plants (plants exhibiting morphological and physiological adaptations to cope with high water, temperature, and light stress, such as a reduction of surface area, tomentose leaves, succulent leaves, drought deciduous leaves, and so on) and 1: nonxerophytic plants.

Gower (1971) distance was used to compute phenotypic distances because it allows including quantitative and categorical traits in the trait matrix. For phylogenetic diversity to be a good proxy of functional diversity, functional traits have to be evolutionarily conserved, and therefore, we tested for the existence of a phylogenetic signal of these traits on the phylogenetic tree described above by using Pagel's lambda with the fitContinuous and fitDiscrete functions in the *geiger* package for R (Luke et al. 2008). The larger the value of lambda the higher the magnitude of phylogenetic signal and its significance was estimated through a likelihood ratio test against the null hypothesis that $\lambda = 0$.

Differences in mortality rates between species were tested through a Kruskal–Wallis test and post hoc comparisons were performed by means of the post hoc Kruskal Nemenyi test. A generalized linear model (glm) with Poisson distribution of errors was used to fit the relationship between the nurse size (log transformed) and the number of facilitated species. Similar glm models, but following Gaussian distribution of errors, were fitted to explain the relationship between functional and phylogenetic diversity of facilitated species and nurse size.

Results

Mortality patterns differed across the three planted species (Fig. 1). *Limonium sucronicum* showed an abrupt early mortality because it was not able to survive the drought of the first summer. *Sedum album* showed late mortality, surviving at high rates for several years but suddenly dying after month 73,

Table 1. Generalized linear models testing the effects of the nurse (*Gypsophyla struthium*) size (log transformed) on the number and the functional and phylogenetic diversity of the facilitated species.

	Number of Species			Functional Diversity			Phylogenetic Diversity		
	Estimate ± SE	t	p	Estimate ± SE	t	p	Estimate ± SE	t	p
Intercept	1.74 ± 0.51	3.41	0.003	0.39 ± 0.14	2.83	0.014	380.5 ± 95.47	3.98	0.0007
Nurse size (cm^3)	0.17 ± 0.09	1.96	0.063	0.04 ± 0.02	1.77	0.092	39.88 ± 15.35	2.60	0.017
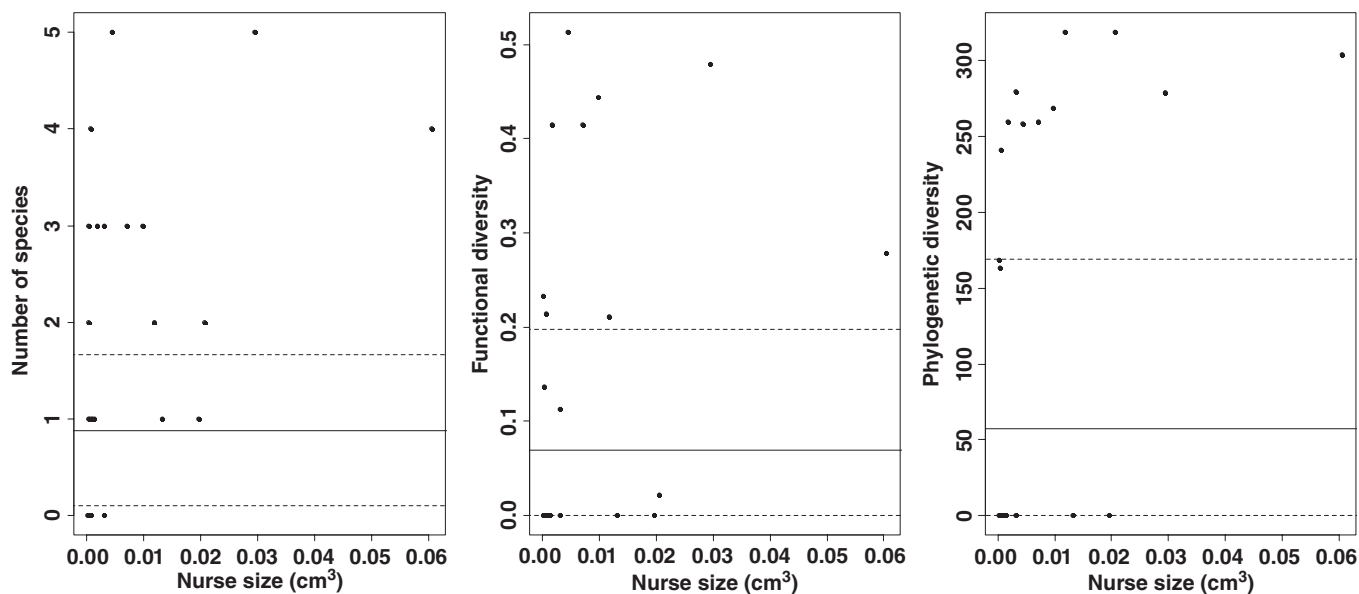
Figure 2. Number of species, functional, and phylogenetic diversity of facilitated species as a function of the nurse size reached after 7 years of nurse plantation. The mean ± SE values from open ground plots are represented with the solid and dashed horizontal lines, respectively.

coinciding with a severe drought period, when total precipitation was 42% less than that of the usual precipitation (Fig. 1, upper panel). *Gypsophyla struthium* showed a gradual mortality along the whole study period. The final survival rates differed between species (Kruskal–Wallis $\chi^2 = 58.8$, $df = 2$, *p* value $=1.7e-13$) with *L. sucronicum* and *S. album* showing null or negligible survival rates and *G. struthium* showing survival rates of 35%.

The most successful species in terms of survival (*G. struthium*) facilitated an increasing number of species as a function of its size, although this trend was marginally significant (Table 1; Fig. 2, left). Interestingly, the increasing number of facilitated species was not a phylogenetically random subset of species (Fig. 3) because phylogenetic diversity of the facilitated species significantly increased with nurse size (Table 1; Fig. 2, right). A small plant size like 0.02 cm^3, which roughly corresponds to 25–30 cm tall plants, was enough to increase phylogenetic diversity above the level found on the open ground.

Functional diversity of facilitated plants followed a similar pattern to that of phylogenetic diversity although it was marginally significant (Table 1; Fig. 2, center). Two out of five traits used to characterize plant functional diversity were phylogenetically conserved (Fig. 3, LRtest $= 4.81$; $p = 0.02$ for Rootq and LRtest $= 5.87$; $p = 0.01$ for gypsophyly).

Discussion

Here, we show that selecting the plant species with nurse traits ensures not only adult survival but also the recruitment of future generations of other, nonplanted, species. Furthermore, the facilitation-driven dynamics triggered by the nurse produces an increase on the plant phylogenetic diversity. Including phylogenetic information as a proxy of species traits may provide convenient shortcuts to select the appropriate traits, and therefore species, in restoration practices (Montoya et al. 2012). Ideally, traits maximizing both plant fitness (response traits) and ecosystem processes (effect traits) should be selected in restoration practices aimed to restore ecosystem functions in degraded habitats (Funk et al. 2008). Given the recent advances in biodiversity–ecosystem functioning research, our results imply that the benefits of planting the right species may cascade in future ecosystem functions provided by third species across different trophic levels like plant productivity (Cadotte 2013) and soil-mediated biogeochemical processes (Navarro-Cano et al. 2014).

Facilitation is an assembly mechanism acting worldwide (Valiente-Banuet & Verdú 2007) with an enormous potential in restoration ecology (Padilla & Pugnaire 2006). This potential goes beyond the reintroduction of one or a few species because facilitation can be used to restore community dynamics and
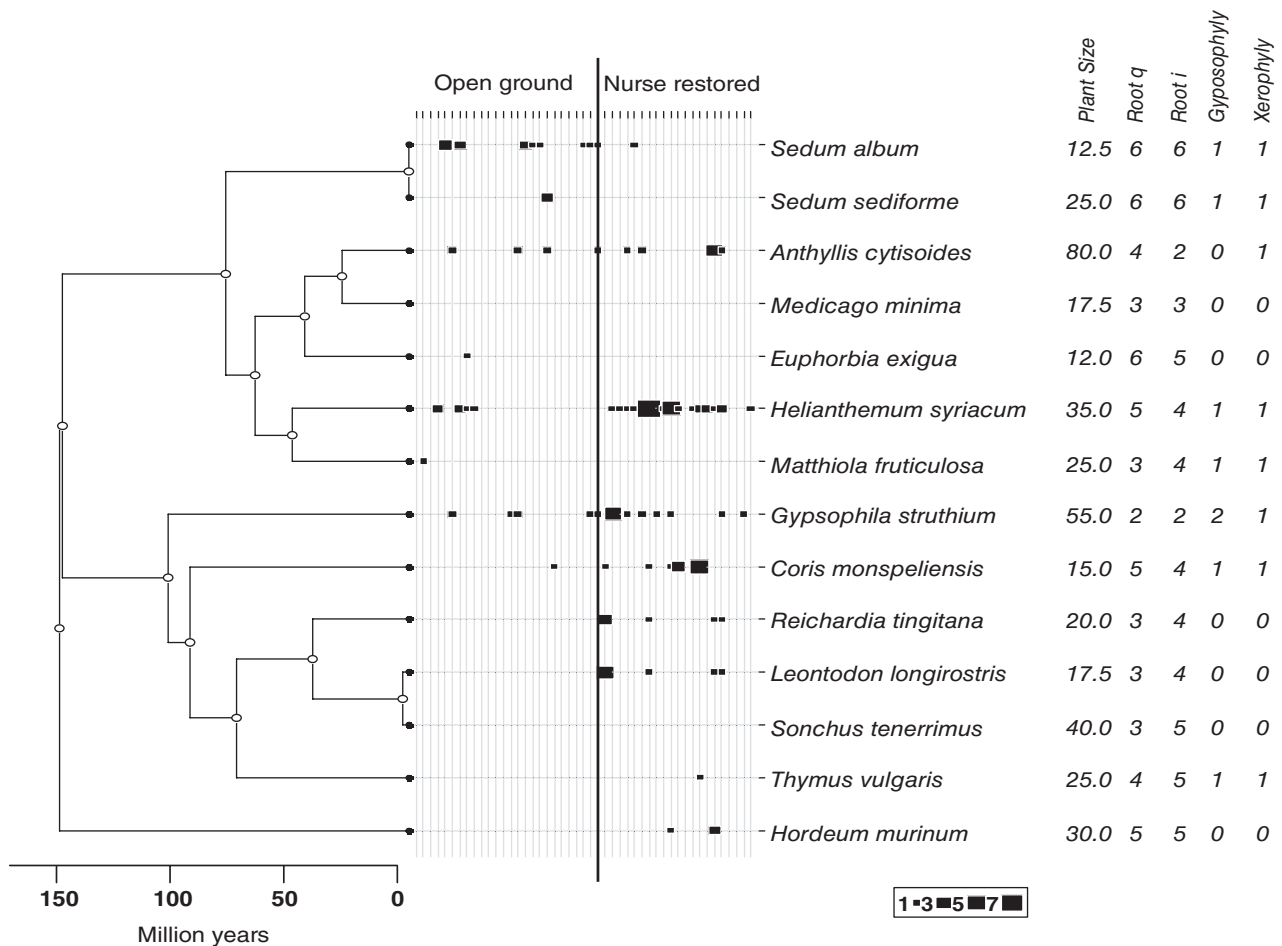
Figure 3. Phylogenetic relationships of the species found on the open ground plots and under the planted nurse. Square size is proportional to the number of individuals as indicated in the bottom right legend. Scale indicates divergence times in million years. Functional traits of species are shown after their names (see Methods section for explanation of trait values).

ecosystem processes. For example, the long-term contribution of nurse plants to restoration of Mediterranean forests has been assessed through Markovian models that show that facilitation is fundamental for a secondary successional trajectory of vegetation dynamics (Siles et al. 2008). Plots with high frequency of facilitative interactions were projected to reach a steady state very similar to the reference community dominated by *Quercus ilex*, *Q. faginea*, *Pistacia lentiscus*, and *Crataegus monogyna*, at 58 years. Revegetation using the facilitative effect of nurses has been recommended to restore stressful semiarid grasslands because facilitation maintains the high nutrient content of top-soils (Pueyo et al. 2009).

Nurse-based restoration experiments have been locally (Siles et al. 2010) and globally successful (Gómez-Aparicio 2009; Verdú et al. 2012) especially when the appropriate combination of nurse and facilitated plant traits has been selected. The potential of a species to act as a nurse or as a facilitated plant can be easily defined through a simple trait, like regeneration niche, that encapsulates many morpho-functional plant characteristics (Valiente-Banuet & Verdú 2013a, 2013b). In stressful habitats like gypsum soils, facilitation tends to occur between a

gypsophyte plant acting as a nurse for non-gypsophyte species (Navarro-Cano et al. 2014). Previous research on abandoned gypsum quarries in southeastern Spain identified two groups of gypsophytes. The first group was constituted by *Gypsophila struthium* that was dominant in the early stages after abandonment whereas the second group was composed by the remaining gypsophytes, that appeared later, usually after 30 years of abandonment (Mota et al. 2003). For this reason, these authors considered that *G. struthium* is a good candidate to restore gypsum soils. Our results confirm that this gypsophile species survived longer than the other species with lower preference for gypsum soils. Specifically, the gypsocline *Limonium fruticosum* suffered an early mortality in the first summer, a common pattern described in Mediterranean climates, whereas the gypsovag *Sedum album* showed an abrupt mortality 7 years after plantation, coinciding with a severe drought episode. Seven-year-old plants are already senescent plants given the short lifespan of *S. album* (circa 10 years) and probably, more vulnerable to severe droughts.

In addition to early survival, early colonizers usually harbor traits conferring them good properties as nurse plants

(Valiente-Banuet et al. 2006), and therefore we expected that *G. struthium* would perform well not only in terms of survival but also as a nurse. Our results confirm that this species is able to facilitate functionally and phylogenetically diverse neighborhoods beneath its canopy in 7 years. There is a nonlinear effect of nurse size on species richness, functional and phylogenetic diversity, very strong at small and medium nurse sizes and asymptotic beyond a certain nurse size. Such effect was clearly marked in phylogenetic diversity. A similar result of a nurse plant (*Ononis tridentata*) increasing phylogenetic diversity of facilitated plants as a function of its size has been recently shown in gypsum soils (Navarro-Cano et al. 2014). The asymptotic relationship, stronger for phylogenetic diversity, may suggest that the positive effects of nurse size have a limited spatial extent. However, the evidence that facilitation increases phylogenetic diversity at the landscape scale (Valiente-Banuet & Verdú 2007) strongly suggests that the positive effect of nurse size on phylogenetic diversity in the small range of nurse sizes is enough to trigger an increase of phylogenetic diversity at larger spatial levels. However, a larger, replicated study would be necessary to get a more detailed picture of facilitation effects and phylogenetic/functional diversity at long temporal scales.

Phylogenetically diverse communities have been traditionally thought to be the result of coexistence of species with dissimilar traits, when such traits are evolutionarily conserved (Webb 2000; Cavender-Bares et al. 2004; Kembel & Hubbell 2006). Some of the functional traits we consider to be relevant for survival in gypsum soils are evolutionarily conserved, as shown the significant phylogenetic signal, and therefore, phylogenetic diversity may be used as a good proxy of functional diversity. Interestingly, phylogenetic diversity is reflecting not only our functional traits but also other unmeasured traits, and therefore, it may inform us about species functionality beyond the traits we have measured (Valiente-Banuet & Verdú 2013*a*, 2013*b*). Supporting the hypothesis that phylogenetic diversity enhances ecosystem functions, Navarro-Cano et al. (2015) showed that the most phylogenetically diverse neighborhoods under nurses were those with the highest soil fertility. This ecosystem function provided by the nurse plant was achieved very fast and reached its maximum level at the age of 38 years.

This work, as most linking facilitation and ecosystem services, focuses on a single nurse species, but plant communities under severe stressful conditions can be depicted as complex networks of nurses interacting with facilitated species (Verdú & Valiente-Banuet 2008). The conservation of these networks and their ecosystem services should be a step forward in restoration ecology (Valiente-Banuet & Verdú 2013*a*, 2013*b*).

Acknowledgments

LITERATURE CITED

Cadotte MW (2013) Experimental evidence that evolutionarily diverse assemblages result in higher productivity. Proceedings of the National Academy of Sciences of the United States of America 110:8996–9000

Castro J, Zamora R, Hódar JA, Gómez JM (2002) The use of shrubs as nurse plants: a new technique for reforestation in Mediterranean mountains. Restoration Ecology 10:297–305

Cavender-Bares J, Ackerly DA, Baum D, Bazzaz FA (2004) Phylogenetic overdispersion in the assembly of Floridian oak communities. American Naturalist 163:823–843

Clark CM, Flynn DFB, Butterfield BJ, Reich PB (2012) Testing the link between functional diversity and ecosystem functioning in a Minnesota grassland experiment. PLoS ONE 7:e52821

Doherty JM, Callaway JC, Zedler JB (2011) Diversity–function relationships changed in a long-term restoration experiment. Ecological Applications 21:2143–2155

Drummond AJ, Rambaut A (2007) BEAST: Bayesian evolutionary analysis by sampling trees. BMC Evolutionary Biology 7:214

Escudero A, Palacio S, Maestre FT, Luzuriaga AL (2015) Plant life on gypsum: a review of its multiple facets. Biological Reviews 90:1–18

Funk JL, Cleland EE, Suding KN, Zavaleta ES (2008) Restoration through re-assembly: plant traits and invasion resistance. Trends in Ecology & Evolution 23:695–703

Gómez-Aparicio L (2009) The role of plant interactions in the restoration of degraded ecosystems: a meta-analysis across life-forms and ecosystems. Journal of Ecology 97:1202–1214

Gómez-Aparicio L, Zamora R, Gómez JM, Hódar JA, Castro J, Baraza E (2004) Applying plant facilitation to forest restoration in Mediterranean ecosystems: a meta-analysis of the use of shrubs as nurse plants. Ecological Applications 14:1128–1138

Gower JC (1971) A general coefficient of similarity and some of its properties. Biometrics 27:857–871

Guerrero-Campo J (1998) Respuestas de la vegetación y de la morfología de las plantas a la erosión del suelo: Valle del Ebro y Prepirineo Aragonés. CPN, Zaragoza, Spain

Harris J (2009) Soil microbial communities and restoration ecology: facilitators or followers? Science 325:573–574

Hines J, Reyes M, Mozder TJ, Gessner MO (2014) Genotypic trait variation modifies effects of climate warming and nitrogen deposition on litter mass loss and microbial respiration. Global Change Biology 20:3780–3789

Kembel SW, Hubbell SP (2006) The phylogenetic structure of a neotropical forest tree community. Ecology 87:S86–S99

Kettring K, Mercer K, Reinhardt-Adams C, Hines JE (2014) Putting genotypic diversity-ecosystem function relationship in context: toward effective wetland restoration. Journal of Applied Ecology 51:339–348

Kuhn TS, Mooers AØ, Thomas GH (2011) A simple polytomy resolver for dated phylogenies. Methods in Ecology and Evolution 2:427–436

Liu J, Zhang X, Song F, Zhou S, Cadotte MW, Bradshaw C (2015) Explaining maximum variation in productivity requires phylogenetic diversity and single functional traits. Ecology 96:176–183

Luke HJ, Weir JT, Brock CD, Glor RE, Challenger W (2008) GEIGER: investigating evolutionary radiations. Bioinformatics 24:129–131

Mateo Sanz G, Crespo Villalba MB (2009) Manual para la determinación de la flora valenciana, edición 4. Monografías de Flora Montiberica 5, Librería Compás, Alicante, Spain

Meyer S (1986) The ecology of gypsophile endemism in the Eastern Mojave Desert. Ecology 67:1303–1313

Montoya D, Rogers L, Memmott J (2012) Emerging perspectives in the restoration of biodiversity-based ecosystem services. Trends in Ecology & Evolution 27:666–667

Mota JF, Sola AJ, Dana ED, Jiménez-Sánchez ML (2003) Plant succession in abandoned gypsum quarries in SE Spain. Phytocoenologia 33:13–28

Navarro-Cano JA, Goberna M, Valiente-Banuet A, Montesinos-Navarro A, García C, Verdú M (2014) Plant phylodiversity enhances soil microbial productivity in facilitation-driven communities. Oecologia 174:909–920

Navarro-Cano JA, Verdú M, García C, Goberna M (2015) What nurse shrubs can do for barren soils: rapid productivity shifts associated to a 40 year ontogenetic gradient. Plant and Soil 388:197–209

Ninyerola M, Pons X, Roure JM (2005) Atlas Climático Digital de la Península Ibérica. Metodología y aplicaciones en bioclimatología y geobotánica. Universidad Autónoma de Barcelona, Bellaterra, Spain

Novák J, Konvičkab M (2011) Proximity of valuable habitats affects succession patterns in abandoned quarries. Ecological Engineering 37:1796–1803

Padilla FM, Pugnaire FI (2006) The role of nurse plants in the restoration of degraded environments. Frontiers in Ecology and the Environment 4:196–202

Pueyo Y, Alados CL, García-Ávila B, Kéfi S, Maestro M, Rietkerk M (2009) Comparing direct abiotic amelioration and facilitation as tools for restoration of semiarid grasslands. Restoration Ecology 17:908–916

Pugnaire FI, Haase P, Puigdefábregas J, Cueto M, Clark SC, Incoll D. (1996) Facilitation and succession under the canopy of a leguminous shrub, Retama sphaerocarpa, in a semi-arid environment in south-east Spain. Oikos 76:455–464

Rey PJ, Siles G, Alcántara JM (2009) Community-level restoration profiles in Mediterranean vegetation: nurse-based versus traditional reforestation. Journal of Applied Ecology 46:937–994

Sánchez-Gómez P, Vera JB, Jiménez JF, Catalán A, López-Donate JA, Mota JF (2011) Yesos de la Manchuela albacetense. Pages 424–429. In: Mota JF, Sánchez-Gómez P, Guirado JS (eds) Diversidad vegetal de las yeseras ibéricas: el reto de los archipiélagos edáficos para la biología de la conservación. ADIF-Mediterráneo Asesores Consultores

Siles G, Rey PJ, Alcántara JM (2010) Post-fire restoration of Mediterranean forests: testing assembly rules mediated by facilitation. Basic and Applied Ecology 11:422–431

Siles G, Rey PJ, Alcántara JM, Ramírez JM (2008) Assessing the long-term contribution of nurse plants to restoration of Mediterranean forests through Markovian models. Journal of Applied Ecology 45:1790–1798

Stevens P.F (2012) Angiosperm Phylogeny Website. Version 12, http://www.mobot.org/MOBOT/research/APweb/ (accessed 5 May 2015)

Tucker CM, Cadotte MW (2013) Unifying measures of biodiversity: understanding when richness and phylogenetic diversity should be congruent. Diversity and Distributions 19:845–854

Valiente-Banuet A, Verdú M (2007) Facilitation can increase the phylogenetic diversity of plant communities. Ecology Letters 10:1029–1036

Valiente-Banuet A, Verdú M (2013a) Plant facilitation and phylogenetics. Annual Review of Ecology, Evolution, and Systematics 44:347–366

Valiente-Banuet A, Verdú M (2013b) Human impacts on multiple ecological networks act synergistically to drive ecosystem collapse. Frontiers in Ecology and the Environment 11:408–413

Valiente-Banuet A, Vital A, Verdú M, Callaway R (2006) Modern quaternary plant lineages promote diversity through facilitation of ancient tertiary lineages. Proceedings of the National Academy of Sciences of the United States of America 103:16812–16817

Verdú M, Valiente-Banuet A (2008) The nested assembly of plant facilitation networks prevents species extinctions. American Naturalist 172:751–760

Verdú M, Gómez-Aparicio L, Valiente-Banuet A (2012) Phylogenetic relatedness as a tool in restoration ecology: a meta-analysis. Proceedings of the Royal Society of London B: Biological Sciences 279:1761–1767

Wang J, Ge Y, Chen T, Bai Y, Qian BY, Zhang CB (2014) Facilitation drives the positive effects of plant richness on trace metal removal in a biodiversity experiment. PLoS One 9:e93733.

Webb C (2000) Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. American Naturalist 156:145–155

Webb CO, Ackerly DD, Kembel SW (2008) Phylocom: software for the analysis of phylogenetic community structure and character evolution. Bioinformatics 24:2098–2100

Webb CO, Ackerly DD, McPeek MA, Donoghue MA (2002) Phylogenies and community ecology. Annual Review of Ecology, Evolution, and Systematics 33:475–505

Wikström N, Savolainen V, Chase MW (2001) Evolution of the angiosperms: calibrating the family tree. Proceedings of the Royal Society of London B: Biological Sciences 268:2211–2220

Wortley L, Hero J-M, Howes M (2013) Evaluating ecological restoration success: a review of the literature. Restoration Ecology 21:537–543