

# Neighborhood matters: high phylogenetic diversity of experimental plant assemblages improves community performance

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## Research Article

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# Abstract

## Background and Aims

Although the role played by phylogeny in the assembly of plant communities remains as a priority to complete the theory of species coexistence, experimental evidence is lacking. It is still unclear to what extent phylogenetic diversity is a driver or a consequence of species assembly processes. We experimentally explored how phylogenetic diversity can drive the community level responses to drought conditions in annual plant communities. To this end, we manipulated the phylogenetic diversity of the species assemblages and the water availability in a common garden experiment with two treatments: average natural rainfall and drought.

## Methods

We recorded plant survival and the numbers of flowering and fruiting plants per species in each assemblage. High phylogenetic diversity favored species coexistence over time with higher plant survival and more flowering and fruiting plants, especially under severe drought.

## Key Results

. Our results demonstrate the existence of niche complementarity and the convergence of water economy strategies as major mechanisms for promoting species coexistence in plant assemblages in semiarid Mediterranean habitats.

## Conclusions

Our findings point to high phylogenetic diversity among neighboring plants as a plausible feature underpinning the recent “united we stand” framework, which states that diffuse positive interactions may promote mechanisms for the persistence of rare species in the community. We suggest that the large species number in the regional species pool may be the consequence of assembly processes occurring at small spatial scales, because the success of each species in terms of surviving and producing offspring was greater when the phylogenetic diversity was higher. Our study is a step forward to understand how phylogenetic relatedness is connected to the mechanisms determining the maintenance of biodiversity.

# Introduction

The current theoretical framework and evidence suggest that both stochastic (Hubbel, 2001; Rosindell *et al.*, 2012) and deterministic mechanisms (Diamond, 1975; Chase and Leibold, 2003; Götzenberger *et al.*, 2012; HilleRisLambers *et al.*, 2012; Adler *et al.*, 2013) operate simultaneously on the assembly of plant communities (Lortie *et al.*, 2004; Vellend *et al.*, 2010, 2014; Escudero and Valladares 2016).

Environmental filters (abiotic and biotic) are the main drivers of species assembly and usually act hierarchically in semiarid systems (Luzuriaga *et al.*, 2012). Plant trait-based community ecology is recognized as an invaluable tool for elucidating these processes because it provides morphological or

physiological trait-based indices in order to identify the role played by each species at the community level in a niche complementarity context (Kraft *et al.*, 2015). Thus, a species will become part of a realized species assemblage only if it possesses suitable traits to pass through the filters imposed by restrictive environmental conditions and it reduces niche overlap with neighbor species (Shipley, 2010).

In the last two decades, the toolbox of community ecologists has incorporated analyses of the phylogenetic patterns of plant communities to understand assembly processes (Webb *et al.*, 2002; Pausas and Verdú, 2010). It is evident that historical and evolutionary mechanisms related to migration and speciation are critical for the formation of the regional species pool, but it is not clear how the phylogenetic diversity that describes the degree of relatedness among species can provide information about assembly processes that occur at the ecological time scale (Götzenberger *et al.*, 2012; Gerhold *et al.*, 2015). A phylogeny should summarize the ecological requirements of coexisting species because it synthesizes the morphological, physiological, and phenological changes in each species throughout evolutionary time in a reduced geographical domain (Kraft *et al.*, 2007; Emerson and Gillespie, 2008; Cavender-Bares *et al.*, 2009). However, phylogenetic distance among species could indicate not only niche differences, but also competitive inequalities (differences in species competitive abilities) which may drive competitive exclusion (Chesson 2000, Godoy *et al.*, 2014). If functional traits are phylogenetically conserved, the phylogenetic diversity can serve as a good proxy of functional diversity (Kraft *et al.*, 2007; Cadotte *et al.*, 2013; Tucker *et al.*, 2018), specially because many functional attributes may be hard or impossible to measure (Webb *et al.*, 2002; Bello *et al.*, 2017). Thus, phylogenetic diversity may represent the ecological differences in an assemblage better than the functional diversity itself (Cadotte *et al.*, 2009; Srivastava *et al.*, 2012; Cadotte *et al.*, 2012; Staab *et al.*, 2021; but see Mazel *et al.*, 2018).

Many studies have aimed to detect assembly mechanisms based on the observed phylogenetic diversities under field conditions (i.e. phylogenetic response) (Webb *et al.*, 2002; Kembel, 2009; Mayfield and Levine, 2010; Godoy *et al.*, 2014; Luzuriaga *et al.* 2020), but the results are not completely coherent and they do not indicate unambiguous relationships among phylogenetic diversity and assembly processes (Kraft *et al.*, 2007; Gerhold *et al.*, 2015). For instance, coexistence of phylogenetically close species is usually interpreted as a result of habitat filtering processes and may be indicative of habitat use as a conserved trait along phylogeny (Webb *et al.*, 2002; Valiente-Banuet and Verdú, 2007). However, these types of low phylogenetic diversity assemblages can also result from competition among species when the competitive ability under certain environmental conditions is associated with whole clades (Mayfield and Levine, 2010). By contrast, high phylogenetic diversity responses may be associated with facilitation among species (Valiente-Banuet and Verdú, 2007; Butterfield *et al.*, 2013), but also with competition processes when competitive exclusion occurs between close relatives with patent niche overlap (Webb *et al.*, 2002; Slingsby and Verboom, 2006; Cahill *et al.*, 2008). Furthermore, if functional convergence occurs among distantly related taxa, high phylogenetic diversity may also be observed in the resulting species assemblages under competitive scenarios (Cavender-Bares *et al.*, 2004).

Consequently, progress needs to be made in order to elucidate the causal relationships among phylogenetic diversity and assembly mechanisms by directly manipulating the phylogenetic diversity of whole assemblages (i.e., phylogenetic effect) together with the abiotic and biotic filtering conditions. This has rarely been attempted with vascular plants to the best of our knowledge (but see Feng *et al.* 2019; Galland *et al.*, 2019). A wide consensus exists on the need for experimental approaches to specifically analyze the mechanisms involved in the assembly of plant communities (Götzenberger *et al.*, 2012; HilleRisLambers *et al.*, 2012). Ephemeral plant communities are especially appropriate for this type of experiments (Peralta *et al.* 2019) because of the rich regional species pool comprising around 100 annual plant species in the central Tagus valley (Luzuriaga *et al.*, 2018), which naturally form high species density assemblages at fine spatial scales (up to 38 species per 0.25 m<sup>2</sup> in rainy years; see Luzuriaga *et al.*, 2012, 2015). In addition, the small size of individuals (average height = 10 cm) and their short and synchronized life cycles (from autumn to spring) makes it feasible to manipulate the entire community and establish species assemblages of known phylogenetic structure. These features allow the design and implementation of experimental communities containing selected species under controlled conditions in common gardens (Peralta *et al.*, 2019).

Shifts of assembly mechanisms in a regional species pool greatly depend on the harshness of the abiotic conditions (Pistón *et al.*, 2015), especially dealing with resource availability (Luzuriaga *et al.*, 2012; Matías *et al.*, 2018). Since water availability is the main limiting resource in semi-arid Mediterranean ecosystems (Miranda *et al.*, 2011), it strongly affects plant community dynamics (Chesson *et al.*, 2004), particularly species richness and composition (Luzuriaga *et al.*, 2012). Furthermore, species-specific interactions (i.e., competition and facilitation) that strongly determine species assemblages (e.g., Hart and Marshall, 2013) can shift depending on water availability (Armas and Pugnaire, 2011; Luzuriaga *et al.*, 2012). In the present study, we manipulated both the level of phylogenetic relatedness among coexisting plants and the level of water stress in a common garden experiment by reproducing realistic annual plant assemblages along a period that encompasses a complete life cycle of annual plants (see Methods). The plant emergence of species in these communities is highly synchronized, so we prepared different phylogenetic combinations at this early demographic stage for our experimental treatments (i.e. phylogenetic effect). We aimed to evaluate the effects of the phylogenetic diversity of assemblages on surrogates of community performance under different water availability scenarios (i.e. stressful levels). In each experimental common garden unit, we measured the number of species and the total abundance of surviving plants each week for the whole phenological window of the community. In addition, we evaluated how many plants of each species achieved the reproductive (flowering) stage and how many set fruits. In the coexistence theory context (HilleRisLambers *et al.*, 2012), community performance is the net sum of all the differences in fitness of the species that form an assemblage (Adler *et al.*, 2007). The fitness inequalities among species may cause some of them to disappear, and thus the decrease in the number of species per sampling unit registered throughout the experiment indicated the limitations imposed by the experimental treatments. The proportion of individuals that produced flowers or fruits per experimental unit were used to represent the fitness inequalities among species.

The two main hypotheses tested in this study are (see our conceptual framework in Fig. 1): (1) If phylogenetic relatedness at the beginning of the growing season predicts niche differences among species, then plants will coexist more readily in high phylogenetic diversity scenarios due to functional/niche complementarity. By contrast, if phylogenetic relatedness predicts the competitive ability of species, in the manner that closely related species can compete more efficiently for the same resources (Webb *et al.*, 2002), then species will be more likely to coexist in low phylogenetic diversity scenarios. Previous studies have suggested that the competition among closely related species is symmetric, i.e. competition intensity between close relatives is very similar for both competitors (Scheffer and van Nes, 2006; Lamb and Cahill, 2008), and thus it does not cause exclusion, which may enhance the coexistence among similar competitor species (Yan *et al.*, 2012). (2) Provided that the functional traits related to water economy are phylogenetically conserved, the effect of drought on the community and species level performance will be less intense in assemblages containing more resistant clades. Thus, in high diversity assemblages, a few species are expected to perform better than the rest, so the species richness will decline faster in these scenarios than in low phylogenetic diversity ones under severe drought treatments. By contrast, if the functional traits related to water economy are convergent among distantly related taxa, then we expect phylogenetically diverse assemblages to be more resistant to drought than those that are closely related.

## Materials And Methods

The target plant community comprised annual plant communities on gypsum soils in the Tagus valley, central Spain, which has a semiarid Mediterranean climate with mean annual temperatures around 14.5°C and mean annual precipitation of 400 mm m<sup>-2</sup> yr<sup>-1</sup>. Precipitation events occur mainly in the late autumn and early spring, and there is an intense summer drought (Aranjuez weather station, 40°4'2"N; 3°32'46"W, 540 m). The dominant vegetation comprises gypsophilous dwarf shrubs (e.g., *Lepidium subulatum* L., *Centaurea hyssopifolia* Vahl, *Gypsophila struthium* L., *Helianthemum squamatum* (L.) Dum. Cours., *Thymus lacaitae* Pau, *Herniaria fruticosa* L., and *Frankenia thymifolia* Desf.) scattered in a matrix of bare soil covered mostly with a biological soil crust and seasonal cover of annual plants (over 120 species in the regional species pool in the middle Tagus valley; Luzuriaga *et al.*, 2018). The annual plant community develops from the first autumn rainfall (October) until early summer (June) when seeds are set and subsequently dispersed.

From March to June during 2016 and 2017, we collected seeds from more than 40 individuals of 60 annual plant species that naturally co-occur in open areas in the field in three nearby locations (Aranjuez (40°02'11.7"N, 3°32'59.5"W; 591 m), Ciempozuelos (40°08'36.9"N, 3°37'00.0"W; 585 m), and Portalrubio de Guadamejud (40°17'34.4"N, 2°35'31.0"W; 755 m). Seeds were cleaned and submitted to a light hot thermal shock (15 days at 50°C) to simulate hot summer conditions to break the seed dormancy. We established 6 experimental scenarios, but we finally maintained 4 of them because two of the scenarios did not fulfill the requirements to enter the experiment (seed germination was not enough at each plot),

thus, we finally used 28 species to build the species assemblages (see below). We prepared a common garden experiment with 110 experimental assemblages and more than 7000 seedlings.

The experimental design consisted of manipulating the phylogenetic diversity of starting experimental assemblages together with water availability treatments. In order to select the high and low phylogenetic diversity scenarios, we calculated the phylogenetic species variability (PSV) index (Helmus *et al.*, 2007) and the Net Relatedness Index (NRI) index (Webb 2000). The PSV index indicates the degree of relatedness among different species in a community with values ranging from 0 to 1. It has low values when the species that form the assembly are closely related. The NRI is a standardized phylogenetic index that contrasts the observed MPD (Mean Pairwise Distance) to 1000 null models. The more positive NRI values indicate that species are close in the phylogenetic tree and the more negative NRI values that species are more dispersed in the phylogenetic tree (**Appendix 1**). Values for high phylogenetic diversity scenarios (PSV = 0.82 and 0.85; NRI = -0.53 and -0.17) were decided on the basis of those naturally observed in the field at this stage (PSV ~ 0.8; data from Luzuriaga *et al.*, 2012), while values for low diversity assemblages were experimentally diminished by choosing related species of the family Asteraceae (PSV = 0.24; NRI = 9.6;  $p < 0.001$ ) and species of the orders Brassicales and Malvales (PSV = 0.64; NRI = 2.5;  $p < 0.05$ ). These indices were calculated running the R packages “ape” (Paradis and Schliep, 2018) and “picante” (Kembel *et al.*, 2010) based on the phylogenetic tree for the 28 species involved in the experiment built using “V.Phylomaker” package, using *phylo.maker* function and the “scenario1” option to bind new tips (Jin and Qian, 2019) (**Appendix 2**). To control for the idiosyncratic effect of species identities, we established two different species combinations for each phylogenetic diversity level. Thus, four taxonomic combinations were constructed comprising two combinations of distantly related species (high phylogenetic diversity scenarios) and two of more closely related species (low phylogenetic diversity scenarios).

We established water availability treatments with two levels in a fully crossed factorial design: average precipitation vs. drought. The average precipitation treatment simulated the monthly average rainfall recorded between 1981 and 2010 in the study area, and the drought treatment used 33% of the average rainfall for each month. We established two phylogenetic diversity levels · two taxonomic combinations of species · two water availability treatments (eight experimental scenarios). Each scenario was replicated in 10 to 16 units, thereby resulting in 110 experimental assemblages.

A common garden experiment was conducted in a greenhouse at Rey Juan Carlos University (<https://urjc-cultive.webnode.es/> Móstoles, Madrid, Spain: 40°20'2"N, 3°52'00"W, 650 m) from October 2017 when the seeds were sown, until June 2018 when the last individuals were collected. We used round pots with a diameter of 30 cm and height of 10 cm, which were filled with seed-free gypsum soil from a gypsum quarry located close to the collection sites. We aimed to establish 10 plants of each seven coexisting species per pot, so we initially sowed 70 seeds per species in each one. Excess of emergent seedlings was periodically removed to ensure the planned abundance of species. We watered pots to the soil water-carrying capacity for the first 20 weeks to ensure the establishment of experimental assemblages at the emergence stage mimicking natural field conditions and then commenced the water availability

treatments, which were maintained for 19 weeks. Between February and June, we monitored plant survival per species and per pot (summing 7700 plants) every two weeks, and we recorded the numbers of flowering plants once a week. In addition, for each species and pot we registered the final number of plants that reached the fruiting stage.

Generalized linear models were employed to analyze species richness, plant survival and the numbers of flowering and fruiting plants per pot. We do not use generalized linear mixed models because the term “pot”, as a random factor, explained extremely tiny fractions of the variability ( $\text{var} < 0.008$  and  $\text{SD} < 0.09$ , in all cases), so we decided to remove it out of the models. The water availability and phylogenetic diversity were treated as fixed factors in all variables and time as a fixed covariate in species richness, plant survival and the number of flowering plants. We used the Poisson distribution as the error distribution function and the logarithmic link function in all models. Generalized linear models were generated using the “glm” function in the “stats” package in R (4.0.3 version) (R Core Team, 2020).

## Results

Phylogenetically more diverse assemblages favored species coexistence, especially under stressful environmental conditions (Table 1; Figs. 2 and 3). In particular, we found that the experimental assemblages formed of distantly related species exhibited higher survival at the plant level but also at the species level (i.e., species richness per pot) compared with assemblages with closely related species. This trend was exacerbated under dry experimental conditions where more plants flowered and fructified in distantly related assemblages compared with those that were closely related (Figs. 2 and 3). In addition, high phylogenetic diversity scenarios showed earlier flowering times both in control and drought conditions than low diversity ones. Thus, the experimental assemblages with high phylogenetic diversity were less sensitive to drought than the low phylogenetic diversity assemblages in terms of the plant survival, number of coexisting species, and numbers of flowering and fruiting plants in each experimental unit.

Table 1

Generalized linear models (GLMs) for the analyses of the numbers of species, surviving plants and flowering plants per pot and per sampling date, and for the number of fruiting plants per pot. Sampling date was used as a fixed covariate in the first three models to statistically control for the effect of time (it was always highly significant, not shown). We did not consider the sampling date to model the number of fruiting plants because this variable was not measured over time, it was just the total cumulative number of fruiting plants per species in each pot. Phylogenetic diversity (PD) and water availability (W) were used as fixed factors. We used the Poisson distribution as the error distribution function and the logarithmic link function in all models. Chi-square values are indicated. \*:  $p < 0.05$ ; \*\*:  $p < 0.01$ ; \*\*\*:  $p < 0.001$ .

	Species richness	Surviving plants	Flowering plants	Fruiting plants
Phylogenetic diversity (PD)	11.65***	131.7***	328.2***	6.85**
Water availability (W)	23.93***	315.4***	789.6***	371.4***
PD · W	2.1	35.5***	135.0***	28.6***

## Discussion

As hypothesized phylogenetic relatedness among coexisting plants drives community level processes such as survival and reproduction. In particular, we found that assemblages formed of more distantly related species favored plant survival and consequently species coexistence, as shown by the reduced decay of the species richness throughout the whole life cycle of the annual plant experimental assemblages. Even more, plants not only were able to survive more successfully in phylogenetically diverse assemblages, but also more individuals completed the reproductive stage by setting flowers and fruits. In addition, we demonstrated the higher resistance of phylogenetically diverse assemblages to drought in terms of plant survival, number of coexisting species over time, and numbers of flowering and fruiting plants per species in the realized assemblages, which supports the hypothesis that phylogenetic relatedness predicts niche differences between species (Hypothesis 1a in Fig. 1).

Our results can also be interpreted in terms of species niche complementarity (Chase and Leibold, 2003; Silvertown, 2004), which predicts that species with differences in terms of their resource use are more likely to coexist due to the reduced competitiveness among them (Pacala and Tilman, 1994; Chesson, 2000; Silvertown, 2004; Holt, 2008). Distantly related species are more likely to be phenologically and functionally complementary, and thus to suffer less from the effects of competition compared to living among conspecifics or close relatives in the neighborhood (Tilman *et al.*, 2001; Verdú *et al.*, 2009; Valiente-Banuet and Verdú, 2013). Closely related species are likely to have ecologically similar requirements (Lord *et al.*, 1995; Wiens and Graham, 2005), so they would share fundamental niches and be more prone to compete strongly for resources. Several mechanisms may promote niche complementarity, such as phenological differences among species (Pfennig and Murphy, 2002; Ashton *et al.*, 2010), different resource use traits (D'Antonio and Mahall, 1991; Jumpponen *et al.*, 2002; Miller *et al.*, 2007), or different root foraging activities (de Kroon and Mommer, 2006). Maynard *et al.* (2019) found that phenological differences among the species in a community could affect the competitive dynamics

to promote coexistence, thereby possibly leading to an increase in species richness at fine spatial scales, which may promote stabilizing dynamics. In our study, the distantly related species probably differed in terms of their phenology, resource uptake, and physiological efficiency, which could have reduced the intensity of the competitive interactions among them (Kraft *et al.*, 2015). This situation could have promoted individual plant survival and species richness, as well as higher plant fitness in high phylogenetic diversity assemblages (see also Violle *et al.*, 2011).

Remarkably, the beneficial effect of high phylogenetic diversity on community level performance was enhanced under severe drought, in terms of overall plant survival, coexisting species richness, as well as number of flowering and fruiting plants per experimental unit. This result supports the idea that drought resistance is a convergent strategy along phylogeny of annual plant species in our study system (Hypothesis 2b in Fig. 1). Our results also agree with García-Camacho *et al.* (2017) who did not detect phylogenetic conservatism in terms of the rainfall preferences of 111 annual plant species from an aridity gradient in Israel. Thus, the annual plant species in dryland areas have evolved over a long period under strong pressure due to drought events and highly unpredictable rainfall events, which may have resulted in the convergent adaptation of distantly related phylogenetic clades to cope with limiting water conditions. Clearly, a powerful abiotic filter such as severe droughts could have shaped the regional species pool over an evolutionary time scale. Consequently, regardless of phylogenetic relatedness, all the species in the community would be able to cope with water limitation, including when it occurs over an ecological time scale (Vellend, 2016).

Assembly processes that occur at the community level may affect the evolution of species over the long term (see also Cavender-Bares *et al.*, 2009; McPeck, 2017; terHorst *et al.*, 2018). Coexistence among closely related species can trigger character displacement to reduce competition intensity (Dayan and Simberloff, 2005) or character convergence to reduce competition asymmetry (Scheffer and van Nes, 2006). Community processes seem to exert crucial effects on evolution (McPeck, 2017), and provide a plausible explanation for the intriguing question regarding how so many annual plant species can coexist in the harsh conditions of semiarid gypsum systems. We suggest that the high species richness found at the regional scale (more than 120 annual species; Luzuriaga *et al.*, 2018) may be the consequence of assembly processes occurring at small spatial scales in a type of feedback process because the success of each species in terms of surviving and offspring production was greater when the phylogenetic diversity was higher. In this line, our findings may support the “united we stand” framework (Calatayud *et al.*, 2020), which states that rare species might remain in assemblages by establishing diffuse positive interactions. Such “diffuse positive interactions” could be related to high phylogenetic diversity among neighboring plants at fine spatial scales (see Chacón-Labela *et al.* 2016).

In conclusion, our results strongly demonstrate the existence of niche complementarity and the evolutionary convergence of water economy strategies as major mechanisms for organizing annual plant assemblages in semiarid Mediterranean gypsum habitats. Species that grow in assemblages of distantly related species are more likely to survive and fructify than those that grow in closely related ones. Importantly, we showed that this effect was exacerbated in drought conditions. Intense droughts occur

often in semiarid Mediterranean ecosystems (Miranda *et al.*, 2011; Luzuriaga *et al.*, 2012) and their intensity is expected to increase in the future (IPCC, 2014). Furthermore, the United Nations recently declared the next decade as “The Decade on Ecosystem Restoration” (United Nations Environment Programme, 2019), and they remarked the importance of understanding the drivers of community assembly. In this context, our study is timely since restoration strategies are moving beyond traditional restoration actions and adopting new tools that better describe the characteristics of species assemblies. In this way, we demonstrate that phylogenetic diversity is an excellent measure that can be used to understand species assembly processes. Furthermore, our study highlights that experimental approaches can provide new answers to old questions in community ecology by connecting assembly processes and patterns in a more robust causal framework. In particular, we show that species rich annual plant communities are excellent model systems for such investigations, due to the feasibility of manipulating species assemblages and the short time lapses needed to account for a complete generation.

## Declarations

**Author contributions:** AE and AL conceived the idea; AL, RC and PF collected seeds for the experimental set-up; AL and RC designed methodology; RC collected the data; RC and AL analysed the data; AL and RC led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## Ethical statement

Authors assure that legislation on seed collection has been accomplished.

Permission obtained from responsible authority to collect seeds.

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## References

Adler PB, Fajardo A, Kleinhesselink AR, Kraft NJB. 2013. Trait-based tests of coexistence mechanisms. *Ecology Letters* 16: 1294–1306.

- Adler PB, HilleRisLambers J, Levine JM. 2007. A niche for neutrality. *Ecology Letters* 10: 95–104.
- Armas C, Pugnaire FI. 2011. Belowground zone of influence in a tussock grass species. *Acta Oecologica* 37: 284–289.
- Ashton IW, Miller AE, Bowman WD, Suding KN. 2010. Niche complementarity due to plasticity in resource use: plant partitioning of chemical N forms. *Ecology* 91: 3252–3260.
- Butterfield BJ *et al.* 2013. Alpine cushion plants inhibit the loss of phylogenetic diversity in severe environments. *Ecology Letters* 16: 478–486.
- Cadotte MW, Albert CH, Walker SC. 2013. The *Ecology* of differences: assessing community assembly with trait and evolutionary distances. *Ecology Letters* 16: 1234–1244.
- Cadotte MW, Cavender-Bares J, Tilman D, Oakley TH. 2009. Using Phylogenetic, Functional and Trait Diversity to Understand Patterns of Plant Community Productivity. *PLoS ONE* 4(5): e5695.
- Cadotte MW, Dinnage R, Tilman D. 2012. Phylogenetic diversity promotes ecosystem stability. *Ecology* 93: S223–S233.
- Cahill JF, Kembel SW, Lamb EG, Keddy PA. 2008. Does phylogenetic relatedness influence the strength of competition among vascular plants? *Perspectives in Plant Ecology Evolution and Systematics* 10: 41–50.
- Calatayud J. *et al.* 2020. Positive associations among rare species and their persistence in ecological assemblages. *Nature Ecology and Evolution* 4: 40–45.
- Cavender-Bares J, Ackerly DD, Baum DA, Bazzaz FA. 2004. Phylogenetic overdispersion in Floridian oak communities. *The American Naturalist* 163: 823–843.
- Cavender-Bares J, Kozak KH, Fine PV, Kembel SW. 2009. The merging of community *Ecology* and phylogenetic biology. *Ecology Letters* 12: 693–715.
- Chacón-Labela J, de la Cruz M, Escudero A. 2016. Beyond the classical nurse species effect: diversity assembly in a Mediterranean semi-arid dwarf shrubland. *Journal of Vegetation Science*, 27: 80–88.
- Chase JM, Leibold MA. 2003. *Ecological Niches: Linking Classical And Contemporary Approaches* (University of Chicago Press).
- Chesson P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31: 343–366.
- Chesson P. *et al.* 2004. Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. *Oecologia* 141: 236–253.

- D'Antonio CM, Mahall BE. 1991. Root profiles and competition between the invasive, exotic perennial, *Carpobrotus edulis*, and two native shrub species in California coastal scrub. *American Journal of Botany* 78: 885–894.
- Dayan T, Simberloff D. 2005. Ecological and community-wide character displacement: the next generation. *Ecology Letters* 8: 875–894.
- de Bello F, Smilauer P, Diniz JAF, Carmona CP, Lososova Z, Herben T, and Gotzenberger L. 2017. Decoupling phylogenetic and functional diversity to reveal hidden signals in community assembly. *Methods in Ecology and Evolution* 8: 1200–1211.
- de Kroon H, Mommer L. 2006. Root foraging theory put to the test. *Trends in Ecology and Evolution* 21: 113–116.
- Diamond JM. 1975. Assembly of species communities. In M. L. Cody, and J. M. Diamond (Eds.), *Ecology and evolution of communities* (pp. 342– 444). (Cambridge, MA: Harvard University Press 1975)
- Emerson BC, Gillespie RG. 2008. Phylogenetic analysis of community assembly and structure over space and time. *Trends in Ecology and Evolution* 23: 619–630.
- Escudero A, Valladares F. 2016. Trait-based plant *Ecology*: Moving towards a unifying species coexistence theory: Features of the special section. *Oecologia* 180: 919–922.
- Feng Y, Fouqueray TD, van Kleunen M. 2019. Linking Darwin's naturalisation hypothesis and Elton's diversity–invasibility hypothesis in experimental grassland communities. *Journal of Ecology* 107:794–805.
- Galland T, Adeux G, Dvořáková H, *et al.* 2019. Colonization resistance and establishment success along gradients of functional and phylogenetic diversity in experimental plant communities. *Journal of Ecology* 107: 2090– 2104.
- García–Camacho R, Metz J, Bilton MC, 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.
- Gerhold P, Cahill JF, Winter M, Bartish IV, Prinzing A. 2015. Phylogenetic patterns are not proxies of community assembly mechanisms (they are far better). *Functional Ecology* 29: 600–614.
- Godoy O, Kraft NJ, Levine JM. 2014. Phylogenetic relatedness and the determinants of competitive outcomes. *Ecology Letters* 17: 836–844.
- Götzenberger L. *et al.* 2012. Ecological assembly rules in plant communities—approaches, patterns and prospects. *Biological Reviews of the Cambridge Philosophical Society* 87: 111–127.

- Hart SP, Marshall DJ. 2013. Environmental stress, facilitation, competition, and coexistence. *Ecology* 94: 2719–2731.
- Helmus MR, Savage K, Diebel MW, Maxted JT, Ives AR. 2007. Separating the determinants of phylogenetic community structure. *Ecology Letters* 10: 917–925.
- HilleRisLambers J, Adler PB, Harpole WS, Levine JM, Mayfield MM. 2012. Rethinking Community Assembly through the Lens of Coexistence Theory. *Annual Review of Ecology, Evolution, and Systematics* 43: 227–248.
- Holt RD. 2008. Theoretical perspectives on resource pulses. *Ecology* 89: 671–681.
- Hubbel SP. 2001. *The Unified Neutral Theory Of Biodiversity And Biogeography* (Princeton).
- IPCC 2014: Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva, Switzerland, 151 pp.
- Jin Y, Qian HV. 2019. PhyloMaker: an R package that can generate very large phylogenies for vascular plants. *Ecography* 42: 1353–1359.
- Jumpponen A, Högberg P, Huss-Danell K, Mulder CPH. 2002. Interspecific and spatial differences in nitrogen uptake in monocultures and two-species mixtures in north European grasslands. *Functional Ecology* 16: 454–461.
- Kembel SW. 2009. Disentangling niche and neutral influences on community assembly: assessing the performance of community phylogenetic structure tests. *Ecology Letters* 12: 949–960.
- Kembel SW. *et al.* 2010. Picante: R tools for integrating phylogenies and Ecology. *Bioinformatics* 26: 1463–1464.
- Kraft NJ, Godoy O, Levine JM. 2015. Plant functional traits and the multidimensional Nature of species coexistence. *Proceedings of the National Academy of Sciences* 112: 797–802.
- Kraft NJB, Cornwell WK, Webb CO, Ackerly D. 2007. Trait Evolution, Community Assembly, and the Phylogenetic Structure of Ecological Communities. *The American Naturalist* 170: 271–283.
- Lamb EG, Cahill Jr JF. 2008. When competition does not matter: grassland diversity and community composition. *The American Naturalist* 171: 777–787.
- Lord J, Westoby M, Leishman M. 1995. Seed size and phylogeny in six temperate floras: constraints, niche conservatism, and adaptation. *The American Naturalist* 146: 349–364.
- Lortie CJ. *et al.* 2004. Rethinking plant community theory. *Oikos* 107: 433–438.

- Luzuriaga AL, Ferrandis P, Flores J, Escudero A. 2020. Effect of aridity on species assembly in gypsum drylands: a response mediated by the soil affinity of species. *AoB PLANTS* 12: plaa020.
- Luzuriaga AL, González JM, Escudero A. 2015. Annual plant community assembly in edaphically heterogeneous environments. *Journal of Vegetation Science* 26: 866–875.
- Luzuriaga AL, Sánchez AM, López-Angulo J, Escudero A. 2018. Habitat fragmentation determines diversity of annual plant communities at landscape and fine spatial scales. *Basic and Applied Ecology* 29: 12–19.
- Luzuriaga AL, Sánchez AM, Maestre FT, Escudero A. 2012. Assemblage of a semi–arid annual plant community: abiotic and biotic filters act hierarchically. *PLoS ONE* 7: 1–9.
- Matías L, Godoy O, Gómez-Aparicio L, Pérez-Ramos IM. 2018. An experimental extreme drought reduces the likelihood of species to coexist despite increasing intransitivity in competitive networks. *Journal of Ecology* 106: 826–837.
- Mayfield MM, Levine JM. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters* 13: 1085–1093.
- Maynard DS, Serván CA, Capitán JA, Allesina S. 2019. Phenotypic variability promotes diversity and stability in competitive communities. *Ecology Letters* 22: 1776–1786.
- Mazel F, Pennell MW, Cadotte MW, Diaz S, Dalla Riva GV, *et al.*, 2018. Prioritizing phylogenetic diversity captures functional diversity unreliably. *Nature Communications* 9: 2888.
- McPeck MA. 2017. *Evolutionary community ecology*. Princeton, NJ: Princeton Univ. Press.
- Miller AE, Bowman WD, Suding KN. 2007. Plant uptake of inorganic and organic nitrogen: neighbor identity matters. *Ecology* 88: 1832–1840.
- Miranda JD, Armas C, Padilla FM, Pugnaire FI. 2011. Climatic change and rainfall patterns: Effects on semi–arid plant communities of the Iberian Southeast. *Journal of Arid Environments* 75: 1302–1309.
- Pacala SW, Tilman D. 1994. Limiting similarity in mechanistic and spatial models of plant competition in heterogeneous environments. *The American Naturalist* 143: 222–257.
- Paradis E, Schliep K. 2018. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics* 35: 526–528.
- Pausas JG, Verdú M. 2010. The jungle of methods for evaluating phenotypic and phylogenetic structure of communities. *BioScience*, 60: 614–625.
- Peralta AM, Sánchez AM, Luzuriaga AL, de Bello F, Escudero A. 2019. Evidence of functional species sorting by rainfall and biotic interactions: A community monolith experimental approach. *Journal of*

*Ecology* 107: 2772–2788.

Pfennig DW, Murphy PJ. 2002. How fluctuating competition and phenotypic plasticity mediate species divergence. *Evolution* 56: 1217–1228.

Pistón N, Armas C, Schöb C, Macek P, Pugnaire FI. 2015. Phylogenetic distance among beneficiary species in a cushion plant species explains interaction outcome. *Oikos* 124: 1354–1359.

Rosindell J, Hubbell SP, He F, Harmon LJ, Etienne RS. 2012. The case for ecological neutral theory. *Trends in Ecology and Evolution* 27: 203–208.

Scheffer M, van Nes EH. 2006. Self-organized similarity, the evolutionary emergence of groups of similar species. *Proceedings of the National Academy of Sciences* 103: 6230–6235.

Shipley B. 2010. *From Plant Traits To Vegetation Structure: Chance And Selection In The Assembly Of Ecological Communities* (Cambridge University Press).

Silvertown J. 2004. Plant coexistence and the niche. *Trends in Ecology and Evolution* 19: 605–611.

Slingsby JA, Verboom GA. 2006. Phylogenetic relatedness limits co-occurrence at fine spatial scales: evidence from the schoenoid sedges (Cyperaceae: Schoeneae) of the Cape Floristic Region, South Africa. *The American Naturalist* 168: 14–27.

Srivastava DS, Cadotte MW, MacDonald AAM, Marushia RG, Mirotnick N. 2012. Phylogenetic diversity and the functioning of ecosystems. *Ecology Letters* 15: 637–648.

Staab M, Liu X, Assmann T, *et al.* 2021. Tree phylogenetic diversity structures multitrophic communities. *Functional Ecology* 35: 521–534.

terHorst CP, Zee PC, Heath KD *et al.* 2018. Evolution in a community context: Trait responses to multiple species interactions. *American Naturalist* 191: 368–380.

Tilman D. *et al.* 2001. Diversity and productivity in a long-term grassland experiment. *Science* 294: 843–845.

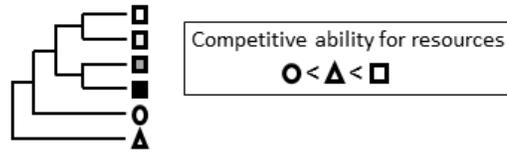
Tucker CM, Davies TJ, Cadotte MW, Pearse WD. 2018. On the relationship between phylogenetic diversity and trait diversity. *Ecology* 99: 1473–1479.

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

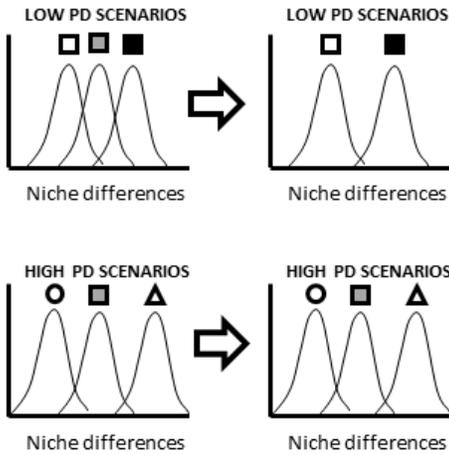
Valiente-Banuet A, Verdu M. 2013. Plant facilitation and phylogenetics. *Annual Review of Ecology, Evolution, and Systematics* 44: 347–366.

- Vellend M. 2010. Conceptual synthesis in community Ecology. *The Quarterly Review of Biology* 85: 183–206.
- Vellend M. 2016. *The Theory Of Ecological Communities* (Princeton University Press).
- Vellend M. *et al.* 2014. Assessing the relative importance of neutral stochasticity in ecological communities. *Oikos* 123: 1420–1430.
- Verdu M, Rey PJ, Alcantara JM, Siles G, Valiente-Banuet A. 2009. Phylogenetic signatures of facilitation and competition in successional communities. *Journal of Ecology* 97: 1171–1180.
- Violle C, Nemergut DR, Pu Z, Jiang L. 2011. Phylogenetic limiting similarity and competitive exclusion. *Ecology Letters* 14: 782–787.
- Webb CO, Ackerly DD, McPeck MA, Donoghue MJ. 2002. Phylogenies and Community Ecology. *Annual Review of Ecology and Systematics* 33: 475–505.
- Webb CO. 2000. Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. *The American Naturalist* 156: 145–155.
- Wiens JJ, Graham CH. 2005. Niche conservatism: integrating evolution, Ecology, and conservation biology. *Annual Review of Ecology Evolution and Systematics* 36: 519–539.
- Yan BG, Zhang J, Liu Y, Li ZB, Huang X, Yang WQ. *et al.* 2012 Trait assembly of woody plants in communities across sub-alpine gradients: identifying the role of limiting similarity. *Journal of Vegetation Science* 23: 698– 708.

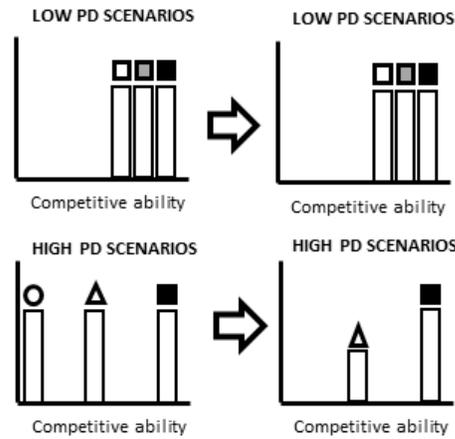
## Figures



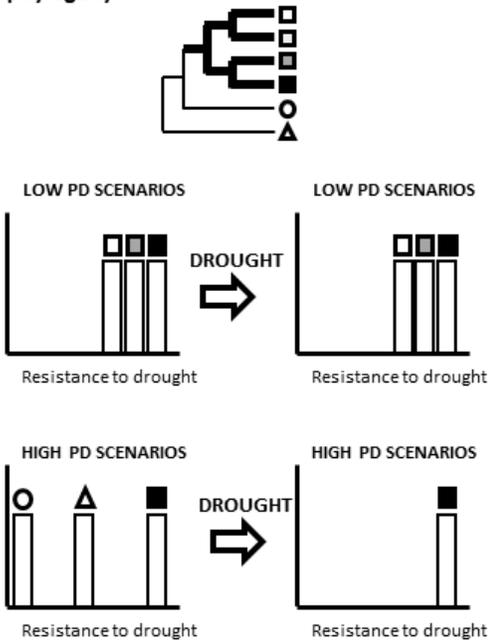
**1a) Phylogeny predicts niche overlap**



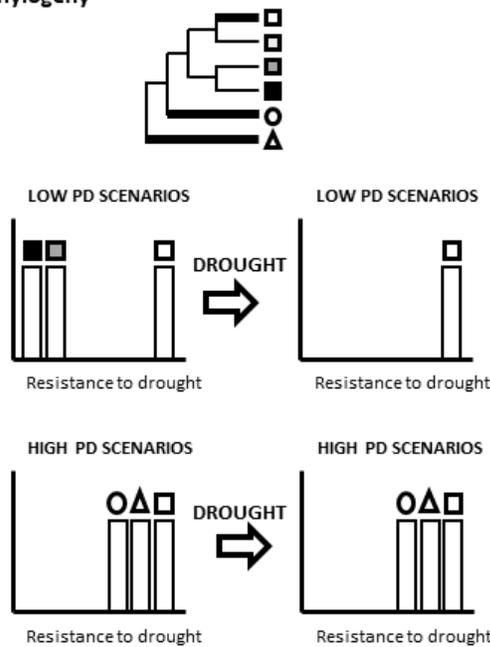
**1b) Phylogeny predicts competitive ability for resources**



**2a) Resistance to drought conserved in phylogeny**



**2b) Resistance to drought convergent across phylogeny**



**Figure 1**

Conceptual model illustrating the hypotheses on the mechanisms involved in the assembly of the annual plant community related to phylogenetic diversity. (1) If phylogenetic relatedness predicts the intensity of niche overlap-differentiation among species, then plants will coexist more readily in high phylogenetic diversity scenarios due to functional/niche complementarity. Conversely, if phylogenetic relatedness predicts the competitive ability of species, then coexistence will be more likely to occur in low

phylogenetic diversity scenarios (i.e., competition symmetry will enhance the coexistence among similar competitors). (2) If functional traits related to water economy are phylogenetically conserved, the response of plants to drought would be more heterogeneous in high diversity assemblages, resulting in a faster decline of species richness. In contrast, if water economy traits in the species pool are convergent among distantly related taxa, phylogenetically diverse assemblages will be more resistant to drought than those formed by close relatives.

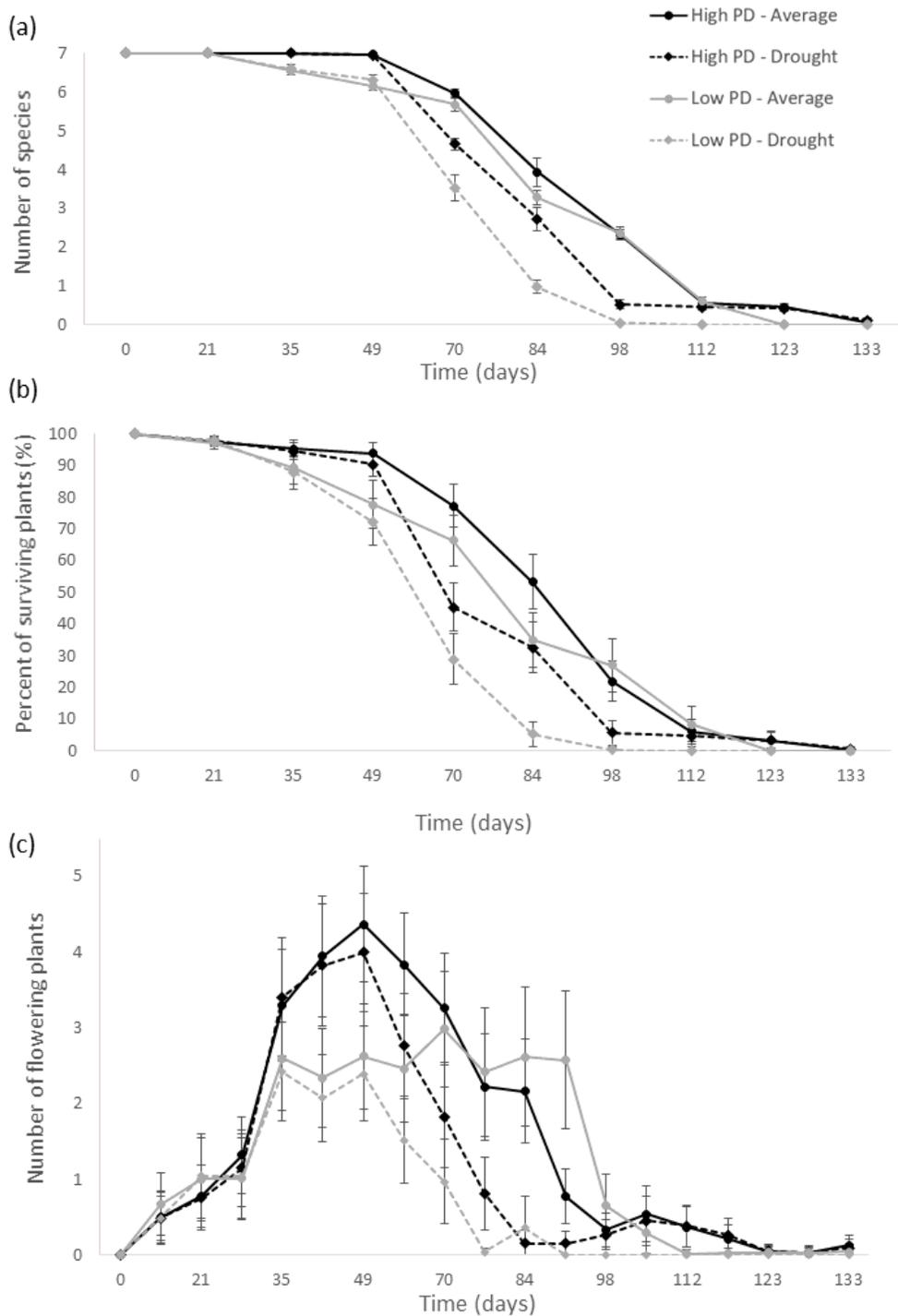
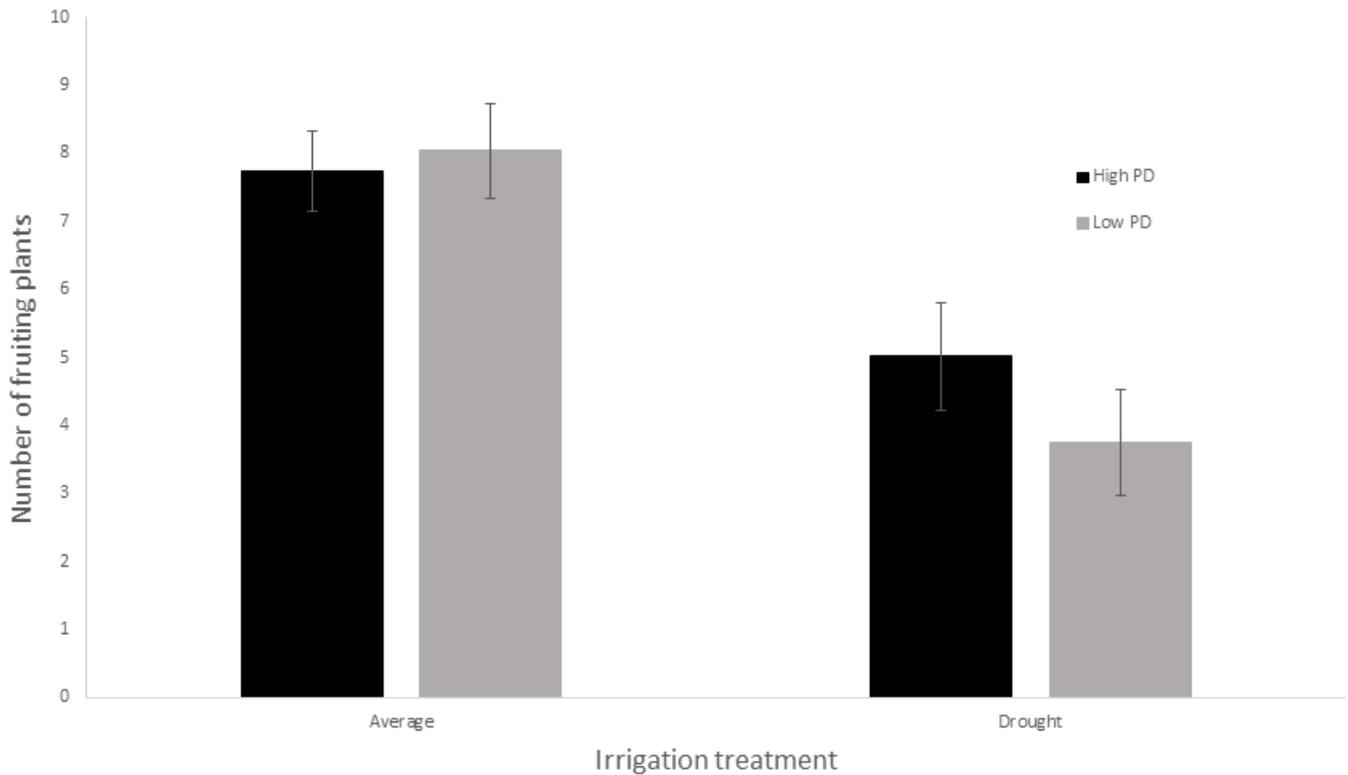


Figure 2

(a) Number of species, (b) number of surviving plants and (c) number of flowering plants, per pot on each sampling date. Black lines represent high phylogenetic diversity (PD) scenarios and grey lines denote low phylogenetic diversity scenarios. Solid lines represent the average precipitation treatments based on natural precipitation for 30 years, and spotted lines denote drought treatments (33% of the average precipitation). Vertical bars represent the standard error.



**Figure 3**

Average number of final fruiting plants per pot (see Table 1). Black bars represent high phylogenetic diversity scenarios and grey bars low phylogenetic diversity scenarios. Average precipitation treatments are based on natural precipitation for 30 years in the field and drought treatments represent 33% of the average precipitation. Vertical bars represent the standard error.

## Supplementary Files

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