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Research article

Functional traits determine plant co-occurrence more than environment or evolutionary relatedness in global drylands



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ABSTRACT

Plant–plant interactions are driven by environmental conditions, evolutionary relationships (ER) and the functional traits of the plants involved. However, studies addressing the relative importance of these drivers are rare, but crucial to improve our predictions of the effects of plant–plant interactions on plant communities and of how they respond to differing environmental conditions. To analyze the relative importance of – and interrelationships among – these factors as drivers of plant–plant interactions, we analyzed perennial plant co-occurrence at 106 dryland plant communities established across rainfall gradients in nine countries. We used structural equation modelling to disentangle the relationships between environmental conditions (aridity and soil fertility), functional traits extracted from the literature, and ER, and to assess their relative importance as drivers of the 929 pairwise plant–plant co-occurrence levels measured. Functional traits, specifically facilitated plants' height and nurse growth form, were of primary importance, and modulated the effect of the environment and ER on plant–plant interactions. Environmental conditions and ER were important mainly for those interactions involving woody and graminoid nurses, respectively. The relative importance of different plant–plant interaction drivers (ER, functional traits, and the environment) varied depending on the region considered, illustrating the difficulty

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of predicting the outcome of plant–plant interactions at broader spatial scales. In our global-scale study on drylands, plant–plant interactions were more strongly related to functional traits of the species involved than to the environmental variables considered. Thus, moving to a trait-based facilitation/competition approach help to predict that: (1) positive plant–plant interactions are more likely to occur for taller facilitated species in drylands, and (2) plant–plant interactions within woody-dominated ecosystems might be more sensitive to changing environmental conditions than those within grasslands. By providing insights on which species are likely to better perform beneath a given neighbour, our results will also help to succeed in restoration practices involving the use of nurse plants.

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Introduction

Plant–plant interactions influence the structure and composition of ecological communities, and therefore may play important roles in determining the distribution of species, secondary succession, ecosystem productivity and stability (reviewed in [Brooker et al., 2008](#); [McIntire and Fajardo, 2013](#); [Soliveres and Maestre, 2014](#)). Plants compete for resources, but also may improve the microclimate of their neighbours via shading, run-off capture or grazing protection ([Callaway, 2007](#)). Thus, both negative (competition) and positive (facilitation) effects of plants on their neighbours often co-occur in nature, with the net outcome of their interaction depending on species-specific and environmental factors ([Maestre et al., 2009a](#); [Soliveres et al., 2012a](#); [He et al., 2013](#)).

Although most research has focused on the behaviour of plant–plant interactions across environmental gradients, there is a lack of agreement on how such plant–plant interactions respond to environmental gradients (see [He et al., 2013](#); [Soliveres and Maestre, 2014](#) for last reviews in the topic). The most influential theory in this regard (the Stress Gradient Hypothesis; [Bertness and Callaway, 1994](#)) predicts a monotonic increase of the frequency of positive plant–plant interactions with environmental stress. However, unimodal relationships with a collapse of facilitative interactions under extreme stressful conditions have been also empirically observed and theoretically predicted ([Hacker and Gaines, 1997](#); [Tielbörger and Kadmon, 2000](#); [Maestre and Cortina, 2004](#)). A third scenario, moreover, has been recently suggested in which the relationship between plant–plant interactions and environmental conditions can be nil when variability in species' responses to the environment within the community is high (e.g., [Soliveres et al., 2011](#)).

Part of the controversy regarding the relationship between plant–plant interactions and environmental conditions may be solved when considering the specific features of the interacting species and their relationship with the prevailing environmental conditions ([Maestre et al., 2009a](#)). Whether environmental conditions are more or less important than species-specific (functional traits or evolutionary relatedness of the interacting species) attributes, or how do these different drivers relate to each other, is poorly known (but see [Gross et al., 2010](#); [Schöb et al., 2012](#); [Soliveres et al., 2012b](#); [Butterfield and Callaway, 2013](#)). Additionally, the different drivers of plant–plant interactions do not act in isolation, and thus they need to be studied together. Environmental conditions, functional traits and evolutionary relatedness among interacting species are strongly related to each other ([Webb et al., 2002](#)). For example, the prevailing environment determines to a certain degree the trait values or the evolutionary lineages present within a community ([Weiher and Keddy, 2001](#); [Cornwell and Ackerly, 2009](#)) and thus those that are able to interact with each other (but see [Schöb et al., 2012](#)). Evolutionary information, conversely, is often regarded as an indirect measure of important functional traits that could be either unknown to be important or unmeasured under the assumption of evolutionary conservatism

of important functional traits ([Webb et al., 2002](#); but see [Mayfield and Levine, 2010](#)). Indeed, although current literature suggests that environmental conditions are the main driver of plant–plant interactions (e.g., [He et al., 2013](#)), the combination of environmental measurements with phylogenetic information ([Soliveres et al., 2012b](#); [Verdú et al., 2012](#)) or functional traits ([Liancourt et al., 2005](#); [Schöb et al., 2012](#); [Gross et al., 2013](#)) has proven more useful to better predict the outcomes of pairwise plant–plant interactions. Thus, simultaneously studying the importance of environmental conditions, phylogeny and functional traits as drivers of plant–plant interactions will clarify how such interactions influence species distribution under changing environmental conditions. Furthermore, such a comprehensive approach would shed light on how plant–plant interactions affect the functional and phylogenetic diversity of plant communities. However, such a holistic framework has been rarely applied when studying the outcome of the variety of pairwise interactions existing within local communities, which range from strongly negative to strongly positive.

Here, we use a field study conducted in 106 drylands worldwide involving 929 pairwise plant–plant interactions (measured as their level of co-occurrence) to test the relative importance of species-specific features vs prevailing environmental conditions as drivers of plant–plant interactions. Specifically, we aimed to answer the following questions: (i) what is the relative importance of environment, evolutionary relatedness and functional traits as drivers of plant–plant interactions?, (ii) how do these drivers relate to, and co-determine the effects of, each other?, and (iii) does the relative importance of them vary with the geographical region studied? Apart from being one of the biomes in which facilitative interactions among plants have been more extensively studied ([Callaway, 2007](#); [Brooker et al., 2008](#)), drylands occupy a large proportion of the terrestrial surface, and provide ecosystem services that are essential for the maintenance of life on Earth ([Reynolds et al., 2007](#)). The use of facilitative interactions among plants has been invoked to restore dryland diversity in degraded environments ([Cortina et al., 2011](#)), which can help to mitigate negative impacts of climate change and desertification in these areas ([Maestre et al., 2012](#)). Therefore, solving the above-stated questions will further refine our predictions regarding how these interactions will respond to a changing environment, and will enhance the success of restoration practices involving the use of nurse plants.

Materials and methods

Study sites and sampling protocol

Field data for this study were obtained from 106 sites established across rainfall gradients within nine countries (Australia, Chile, Ecuador, Morocco, Peru, Spain, Tunisia, USA and Venezuela; see [Table 1](#)). The sites surveyed encompass the major vegetation types found in drylands: grasslands (Peru, Morocco, Spain, Tunisia and Venezuela), shrublands (Chile, Ecuador, Spain, USA) and open

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