**Less is more: facilitation of diversity declines with increasing local plant species richness**

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**Abstract**

1. The biodiversity ecosystem function literature provides a useful framework to examine many processes associated with species diversity in ecology.
2. In ecology, it is not uncommon for some variables to act as explanatory factors in some models and response variables in alternative models. Here, we used this concept to examine biodiversity-mediated interactions between plants on the net outcome of direct positive interactions amongst species for communities in arid and semi-arid shrub ecosystems.
3. A synthesis including a meta-analysis was used to compile nearly 600 papers on positive interactions mediated by shrubs in dryland plant communities (search terms: shrub, positive, facilitat\*) to examine whether the intensity of interactions changed with reported species richness. A total of 19 studies and 141 independent instances examined facilitation of diversity measures of the plant community and reported local species richness.
4. The net effect of increasing plant species richness was negative and shifted the relative intensity of interactions from positive or facilitative to negative with increasing number of species.
5. This relationship suggests that increases in richness do not always enhance functions associated with increasing diversity of plant communities, potentially because of concurrent increases in the likelihood of indirect negative interactions including apparent competition between protege species under shrubs. .

**Keywords**

Arid, biodiversity, ecosystem function, facilitation, foundation species, indirect interactions, positive interactions, semi-arid, shrubs, species richness.

**Introduction**

The rich get richer. This old adage is relevant to most key theories and hypotheses in ecology in some form. A richer and more varied set of species or interactions or processes or habitats can be associated with enhanced capacity of a natural system at various scales - notwithstanding negative drivers such as exotic species, although there are similar hypotheses in this field as well. Likely one of the most stunning applications of richness was the development of and work supporting the theory of biodiversity ecosystem function. This set of literature honed our understanding of scale, function, resilience, and the value of individual species relative to the number of species in a given context. This literature provides an opportunity to further not only biodiversity research per se but conservation science. For instance, conservationists tasked with increasing biodiversity have found success in promoting keystone or foundation species that in turn facilitate other species. Interaction webs are critical features of ecosystems, and disrupted interactions often precede loss of the resident species. The focus of this synthesis is to examine whether a biodiversity-ecosystem function framework focused on the intensity of positive interspecific interactions can can influence and be influenced by the local richness of a plant community. This framework capitalizes on the frequent use of species richness as both an explanatory factor and a response variable in studies of positive interactions in plant communities. Thus, the proposed framework will expand the scope of functions routinely associated with diversity as measure for capacity in naturally assembled communities.

Facilitation or positive interactions inform many components of community structure and assembly. Cite reviews here and explain in brief. Importantly, positive interactions are closely tied to fundamental biodiversity theory and also to conservation. Complementarity is a well-supported hypothesis for relative increases in function at the scale of ecosystems within increasing diversity (…). In short, the complementarity hypothesis attributes positive biodiversity-ecosystem function relationships to either niche partitioning or facilitation among species. For instance, in relatively unproductive systems such as deserts, shrubs and other foundation plants can strongly facilitate local biodiversity and ecosystem function by beneficially altering habitat and community composition or structure. Nonetheless, a collective assessment of how the relative intensity of positive interactions between plant species varies with measures of local diversity are relatively sparse. Furthermore, it is not uncommon in ecology for a variable used as a response in some models to be applied as explanatory in other models. To this end, we performed a synthesis of the primary research literature to examine the capacity for reported local plant species richness to predict the intensity of positive interactions mediated by foundation shrubs in dryland ecosystems globally.

**Methods and Results**

A formal scientific synthesis of the literature was used to test whether species richness locally for each study predicted the net of outcome of plant-plant interactions in shrub-open contrasts in arid and semi-arid ecosystems. The Web of Science bibliometrics resource was queried August, 2020, using the terms “shrub, facilitat\*, and positive”. A total of 593 peer-reviewed studies were returned and reviewed using the following criteria: protégé species were plants, primary research, reported or visualized appropriate data, examined the facilitation of diversity at the community level (including species richness, evenness, or other metric of diversity) for plots under shrubs and in open gaps, and listed the total number of species (or provided a composite species list) for the local study site. This produced a list of 19 studies and a total of 141 unique observations for synthesis. The number of species reported for the site was extracted for each instance and was independent of the reported mean diversity measures examined at the plot-level in the subsequent meta-analysis. Full details of the review process and data extraction are provided, including a PRISMA figure and list of studies included (Supplement Figure 1 and Table 1). The full data and supporting code are published openly (citation). A meta-analysis of the data was done in R version 4.0.3 using the packages meta and metafor (citations). The relative interaction intensity effect-size metric (i.e. rii) was used to estimate the relative difference in diversity between shrub and open gap plots (), and a meta regression of this response against local plant species richness was used to explore whether increasing richness functioned to enhance the net intensity of positive interactions typically provided by foundation shrubs. Both linear and non-linear models were fit and contrasted using information criterion scores and permutation tests to determine best fit (). The trends in effect sizes were best described by a linear fit (information criterion scores contrast p = 0.0352, and permutation tests z-score for linear model = —9.2717, p = 0.0010). The relative intensity of positive interactions declined linearly with increasing species richness (Figure 1, Meta-regression, slope = -1.4841, r2 = 0.67, QM Chi-square test statistic = 95.5023, p = 0.0001, and see Supplement for full model outputs). In summary, the positive effects of shrubs on the diversity of resident plant communities were greatest when the diversity of native plant communities was lowest.

**Implications**

Our findings suggest that increases in richness do not always enhance functions associated with increasing diversity of plant communities, potentially because of concurrent increases in the likelihood of indirect negative interactions (e.g., apparent competition) between protege species under shrubs. In this context, it is well established that diversity increases indirect interspecific interactions and attenuates the strength of direct interactions. Our findings also have critical implications for biodiversity conservation. Anthropogenic disturbances have degraded dryland biodiversity globally, and positive shrub-mediated interactions can be used to restore diversity to degraded drylands. We suggest that these restoration efforts may be most effective in the most species-poor communities, which is excellent news, as species-poor communities may have the greatest need of diversity restoration.

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**Authors’ contributions**

CJL, JL, and AF conceived the ideas and designed the methodology; all authors collected the data; CJL analyzed the data; AF reviewed the analyses; and CJL, JL, and AF led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

**Data availability**

All data and R code are publicly available at the Knowledge Network for Biocomplexity.

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**Literature Cited**