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## Less is more: facilitation of biodiversity maintenance declines with increasing plant species richness

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SCHOLARONE™ Manuscripts Less is more: facilitation of biodiversity maintenance declines with increasing plant species richness

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Running head: facilitation of diversity function

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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, some variables can provide a means to both explore causation as factors and for similar measures to serve as a response 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 associated with the function of biodiversity maintenance for communities in dryland 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 interactions in these studies 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 frequency 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 diversity maintenance of plant communities because of concurrent increases in the likelihood of indirect negative interactions between protege species under shrubs.
  Foundation species in natural systems can thus provide a novel tool to examine trade-offs in ecosystem functions by differences in local plant diversity.

## 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 many 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 (Loreau et al., 2001; Tilman et al., 2014) - notwithstanding negative drivers such as exotic species although there are also similar hypotheses in this field as well (Braga et al., 2018; Stohlgren et al., 2003). Likely one of the most stunning applications of richness was the development of and work supporting the theory of biodiversity ecosystem function (Tilman et al., 2014). This set of literature honed our understanding of scale (Thompson et al., 2018), function (Pacala & Kinzig, 2002a), resilience (Harvey et al., 2017), and the value of individual species relative to the number of species in a given context (Downing & Leibold, 2002). This literature provides an opportunity to further not only biodiversity research per se but has begun to support conservation science particularly when it examines realistic extinction scenarios and underrepresented systems (Srivastava & Vellend, 2005) or tests different scales (Thompson et al., 2018). The wealth of interactions in a system are also a critical feature of ecosystems and significant declines are predicted that will precede the loss of the resident species (Valiente-Banuet et al., 2015). The focus of this synthesis is to examine whether a biodiversity-ecosystem framework can advance the theory of positive interactions relative to the local richness of a plant community. In turn, this will expand ecosystem theory by testing for biodiversity maintenance as measure of functional capacity in naturally assembled communities.

Facilitation or positive interactions inform many components of community structure and assembly. It has been extensively studied for over 20 years with consistent reported benefits to

biodiversity (Callaway, 2007; McIntire & Fajardo, 2014). This subset of interactions between plants in particular further ties into biodiversity theory and also to conservation. First, ecosystem function can be driven by community dynamics including species composition, species interactions, and evenness in addition to total richness (Brophy et al., 2017). Second, complementarity is a well-supported hypothesis for relative increases in function with increasing diversity (Loreau & Hector, 2001). Complementarity is typically described as resource partitioning or at times positive interactions between species that subsequently lead to increased total resource use. Recently, it has been proposed that complementarity is actually comprised of three distinct changes with diversity including resource partitioning, abiotic facilitation, and also biotic feedbacks (Barry et al., 2019). The latter two refinements perfectly link to facilitation research in plant communities. The facilitation of diversity of plant communities has been established in foundation-plant species studies such as those that use shrubs in arid and semi-arid ecosystems (Filazzola & Lortie, 2014; He et al., 2013). A foundation plant species can be a shrub that changes habitat and community composition or structure (Crotty et al., 2019; Ellison, 2019; O'Brien et al., 2020). Nonetheless, a collective assessment of the relative frequency that facilitation between plants enhances varied measures of diversity are relatively sparse (Flores & Jurado, 2003; He et al., 2013). Furthermore, it is not uncommon in ecology for a variable used as a response to be applied as a mediator of outcomes in other models particularly in applied contexts (Evans et al., 2012; Pennekamp et al., 2017). To this end, we examined the capacity for reported local plant species richness in a synthesis of the primary research literature to predict measures of community-level diversity associated with shrubs relative to open gap sites.

## **Methods and Results**

A formal scientific synthesis workflow of the literature was used to test whether species richness locally for each experiment predicted the net of outcome of plant-plant interactions in shrubopen contrasts in arid and semi-arid ecosystems. The Web of Science bibliometrics resource was queried August 2020 using the terms shrub, facilitat\*, and positive (Analytics, 2020). A total of 593 peer-reviewed studies were returned and reviewed using the following criteria: plants, primary research, reported or visualized appropriate data, examined the facilitation of diversity at the community level (including native species richness, evenness, or reported a metric of diversity) for the plots under shrubs and in the open gaps, and listed total number of species (or provided a composite species list) for the local experimental site. This process produced a list of 19 studies for native plant species communities and a total of 141 unique experimental observations for synthesis. Studies were published between 2004 and 2020 in 13 different journals. The number of species reported for the sites was extracted for each instance and was independent of the reported mean diversity measures examined at the plot-level in the subsequent meta-analysis. Diversity measures included species richness for instance (Bai et al., 2019), evenness (Ruwanza, 2019), or indices of diversity for plots such as Shannon-Wiener estimates (Khosravi Mashizi & Sharafatmandrad, 2020). Gradients were not uncommon (Abdallah & Chaieb, 2010; Armas et al., 2011; Howard et al., 2012), and all extractable data from each study were used in the analyses. Full details of the review process and data extraction are provided here including a PRISMA figure (Moher et al., 2009) and the list of studies (Supplement Figure 1 and Table 1). The data and supporting code are also published openly (Lortie et al., 2020). A meta-analysis of the data was done in R version 4.0.3 (R-Development-Core-Team, 2020) using the packages meta (Schwarzer, 2020) and metafor (Purssell, 2015; Viechtbauer, 2017). The relative interaction intensity effect-size metric (i.e. RII) was used to

estimate the relative difference between shrub and open gap plots (Armas et al., 2004). A metaregression of RII against local plant species richness was used to explore whether increasing richness functioned to enhance the net positive interactions typically provided by foundation shrub species in these ecosystems. A meta-regression weights each observation by the respective variance associated with each effect-size estimate (Mengersen et al., 2013). Both linear and nonlinear models were fit and contrasted using information criterion scores (Aho et al., 2014) and permutation tests to determine best fit (Higgins & Thompson, 2004). 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 frequency of positive interactions declined linearly with increasing species richness (Figure 1, Metaregression, slope = -1.4841,  $r^2 = 0.67$ ,  $X^2 = 95.5023$ , p = 0.0001), and this trend was robust tested against different covariates and sources of potential between-study heterogeneity (see Supplement for full model outputs and sensitivity analyses). In summary, relatively fewer species locally at an experimental study site were associated with more consistent and intense positive effects of shrubs on the maintenance of diversity for the resident plant communities.

## **Implications**

Diversity can beget diversity in ecology. Within community interaction theory, intransitivity in competition can promote higher levels of species diversity and at times provide a buffer against a single winning species in mixtures (Maynard et al., 2017). Nonetheless, increasing richness need not necessarily increase all measures of function nor enhance all estimates of diversity mediated by plant-plant interactions. Here, the overarching net positive effect of shrubs most likely generated playing fields within their canopy understorey that subsequently produced a

competitive melee. Shrubs thus influenced protege diversity and their respective networks that in turn increased the relative frequency of indirect, and at times, negative interactions (Aschehoug & Callaway, 2015). This is akin to the finding that biodiversity-ecosystem functions can shift with successional stage as well (Mori et al., 2017). These are critical issues for the theory of biodiversity ecosystem function (particularly when the focus is on resilience and diversity responses) because naturally-assembled communities in relatively high-stress ecosystems can be structured by dominant plant species particularly at earlier successional stages. This is not the first instance of reductions detected in diversity at fine-scales because of the facilitation by foundation plant species (Kikvidze et al., 2015). Reductions in functions such as biodiversity maintenance strongly suggest that future observational and manipulative experiments exploring diversity-function outcomes should include tests for mediation by foundation species in relevant ecosystems.

From a conservation perspective, incorporating foundation species into diversity-function experiments can also address the call to increase the relevance of this theory for conservation efforts (Srivastava & Vellend, 2005). This work highlights the need for restoration strategies to manage and protect both native diversity and concomitantly address foundation plant effects directly through enhanced functions such as buffering (Eldridge et al., 2015; Swanson et al., 2019) and indirectly through their biodiversity effects (McIntire & Fajardo, 2014). In a related synthesis of naturally-assembled communities, the strength and direction of effects was also highly variable, and it was similarly concluded that other drivers of function can be even more important than direct biodiversity effects (van der Plas, 2019). The former synthesis was a systematic review and primarily examined relative reporting frequencies of the published studies

on both plot design and specific ecosystem function but supports the experimental innovation proposed herein that composition of certain species like shrubs can be significant levers of functional change.

Scale is important to biodiversity. Diversity declines at relatively larger global scales can reduce ecosystem functions, but increases in diversity at regional or local scales can be be occurring in some ecosystems in spite of global declines (Sax & Gaines, 2003). Hence, the ecosystem effects of increases in diversity at finer, local spatial scales is a critical issue. This synthesis study integrated data from two scales - from local sites to the relative plot-level mean effects of shrubs. The synthesis findings suggest that biodiversity maintenance as a function (Daily, 1997; Pacala & Kinzig, 2002b) must be balanced by a clear delineation of changes in number of species versus composition (Downing & Leibold, 2002). More refined prediction of the capacity of plant communities to respond to environmental change and sustain functions will thus benefit from studies at the microhabitat level with foundation species, and a unified framework that encompasses this scale to larger extents including stress gradients will enable more effective contrasts between species effects and responses (Soliveres et al., 2011). Furthermore, the scales that specific plants and animals experience in natural communities can be fine grained and to limited extents (Sandel, 2015), and studies that examine diversity scale-dependence at the microsite level for many plants (Guo, 1998) and some animals (Grimm-Seyfarth et al., 2017) will highlight tipping points and potential negative outcomes.

The value and statement of diversity as a functional outcome in addition to a driver in ecosystems at the scales of fine-scale community analyses relative to the local species pool is a

fundamental mechanism to better understand diversity-assembly processes. Naturally-assembled communities provide an ideal and wider set of processes to examine in situ relative to manipulated contexts, and given this, we cannot ignore foundation plant species that generate very different contexts for protege species. Effects can include numerous direct benefits (Filazzola & Lortie, 2014) but also indirect effects that can be negative (Sotomayor & Lortie, 2015). Facilitation is a critical ecological process that will better advance biodiversity ecosystem function theory and experimentation because it can mediate the structure and composition of plant communities that collectively provide emergent functions relevant to many scales including ecosystems. The resilience and stability of these positive interactions can also shift, and in some contexts, less is more. For instance, facilitation can collapse with increasing environmental stress because of changes in the effects of foundation plant species and in the strategies (and composition) of resident protege species needed to persist (Michalet et al., 2014). Interactions within plant communities can thus scale-up to influence ecosystems (Michalet & Pugnaire Francisco, 2016). These changes in facilitation will influence complementarity effects and mediate functions. Biodiversity maintenance is thus a key function and feedback, and changes in ecological interactions at different scales are a necessary component of deeper insights into ecosystem theory.

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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, JH, 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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A synthesis shrub facilitation studies testing for increases in community diversity estimates.

Knowledge Network for Biocomplexity. doi:10.5063/F147488H.

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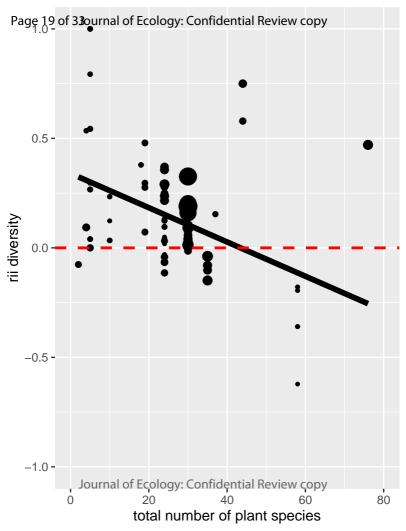
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**Figure 1.** A meta-regression of the relative interaction intensity (rii) of diversity estimates for plant communities by the total number of plant species. The rii estimate is an effect size measure contrasting the diversity measures reported in shrub relative to open-gap microsites in a synthesis of plant facilitation and positive interaction studies using shrubs. The total number of plant species was the total reported or listed number of species per study at the site level. The best fit line is linear (r2 = 0.67) weighted by the study variance with each effect size measure, and the red dotted line shows no net effect of the shrubs. Positive values are facilitation or enhancements in relative diversity in plots and negative values are decreases in the diversity of the plant communities. The size of points show reported variance for each observation.



## **Supplementary information**

Less is more: facilitation of diversity as a key ecosystem function that declines with increasing local plant species richness

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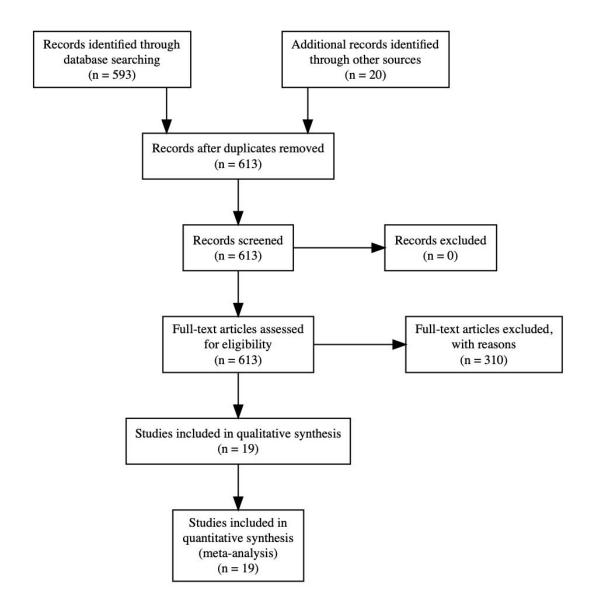
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**Supplementary Figure 1.** Preferred Reporting Items for Systematic Reviews and Meta-Analyses statement for the synthesis of shrub facilitation and the term positive. Web of Science was queried August 2020. See main text for full search details.



# Supplement Table 1. List of studies included in meta-analysis on the facilitation of diversity in shrub ecosystems.

Table 1

ID	year	authors	title	journal	DOI
6	2019	Bai, Yuxuan; Zhang, Yuqing; Michalet, Richard; She, Weiwei; Jia, Xin; Qin, Shugao	Responses of different herb life- history groups to a dominant shrub species along a dune stabilization gradient	BASIC AND APPLIED ECOLOGY	10.1016/j.baae.2019.06 .001
11	2019	Mashizi, Azam Khosravi; Sharafatmandra d, Mohsen	Assessing the effects of shrubs on ecosystem functions in arid sand dune ecosystems	ARID LAND RESEARCH AND MANAGEMENT	10.1080/15324982.201 9.1634655
32	2019	Ruwanza, Sheunesu	Nurse plants have the potential to accelerate vegetation recovery in Lapalala Wilderness old fields, South Africa	AFRICAN JOURNAL OF ECOLOGY	10.1111/aje.12536
64	2018	Zhang, Gefei; Zhao, Wenzhi; Zhou, Hai; Yang, Qiyue; Wang, Xiaofen	Extreme drought stress shifts net facilitation to neutral interactions between shrubs and sub- canopy plants in an arid desert	OIKOS	10.1111/oik.04630

Table 1

ID	year	authors	title	journal	DOI
83	2017	Wang, Xiangtai; Michalet, Richard; Chen, Shuyan; Zhao, Liang; An, Lizhe; Du, Guozhen; Zhang, Xiaochen; Jiang, Xingpei; Xiao, Sa	Contrasting understorey species responses to the canopy and root effects of a dominant shrub drive community composition	JOURNAL OF VEGETATION SCIENCE	10.1111/jvs.12565
115	2016	Holthuijzen, Maike F.; Veblen, Kari E.	GRAZING EFFECTS ON PRECIPITATION- DRIVEN ASSOCIATIONS BETWEEN SAGEBRUSH AND PERENNIAL GRASSES	WESTERN NORTH AMERICAN NATURALIST	10.3398/064.076.0308
273	2013	Cuevas, Jaime G.; Silva, Sergio I.; Leon-Lobos, Pedro; Ginocchio, Rosanna	Nurse effect and herbivory exclusion facilitate plant colonization in abandoned mine tailings storage facilities in north- central Chile	REVISTA CHILENA DE HISTORIA NATURAL	10.4067/S0716- 078X2013000100006
294	2012	Abdallah, F.; Chaieb, M.	The influence of trees on nutrients, water, light availability and understorey vegetation in an arid environment	APPLIED VEGETATION SCIENCE	10.1111/j.1654- 109X.2012.01201.x

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ID	year	authors	title	journal	DOI
316	2012	Howard, Kimberley S. C.; Eldridge, David J.; Soliveres, Santiago	Positive effects of shrubs on plant species diversity do not change along a gradient in grazing pressure in an arid shrubland	BASIC AND APPLIED ECOLOGY	10.1016/j.baae.2012.02 .008
325	2011	Armas, Cristina; Rodriguez- Echeverria, Susana; Pugnaire, Francisco I.	A field test of the stress-gradient hypothesis along an aridity gradient	JOURNAL OF VEGETATION SCIENCE	10.1111/j.1654- 1103.2011.01301.x
356	2011	Soliveres, Santiago; Eldridge, David J.; Maestre, Fernando T.; Bowker, Matthew A.; Tighe, Matthew; Escudero, Adrian	Microhabitat amelioration and reduced competition among understorey plants as drivers of facilitation across environmental gradients: Towards a unifying framework	PERSPECTIVES IN PLANT ECOLOGY EVOLUTION AND SYSTEMATICS	10.1016/j.ppees.2011.0 6.001
379	2010	Madrigal- Gonzalez, J.; Garcia- Rodriguez, J. A.; Puerto- Martin, A.; Fernandez- Santos, B.; Alonso-Rojo, P.	Scale-dependent effects of pines on the herbaceous layer diversity in a semi- arid mediterranean ecosystem	COMMUNITY ECOLOGY	10.1556/ComEc.11.201 0.1.11
394	2010	Abdallah, Fathia; Chaieb, Mohamed	Interactions of Acacia raddiana with herbaceous vegetation change with intensity of abiotic stress	FLORA	10.1016/j.flora.2010.04 .009

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ID	year	authors	title	journal	DOI
477	2006	Tecco, PA; Gurvich, DE; Diaz, S; Perez- Harguindeguy, NP; Cabido, M	Positive interaction between invasive plants: The influence of Pyracantha angustifolia on the recruitment of native and exotic woody species	AUSTRAL ECOLOGY	10.1111/j.1442- 9993.2006.01557.x
485	2006	Holzapfel, Claus; Tielboerger, Katja; Parag, Hadas A.; Kigel, Jaime; Sternberg, Marcelo	Annual plant-shrub interactions along an aridity gradient	BASIC AND APPLIED ECOLOGY	10.1016/j.baae.2005.08 .003
514	2004	Wilby, A; Shachak, M	Shrubs, granivores and annual plant community stability in an arid ecosystem	OIKOS	10.1111/j.0030- 1299.2004.13085.x
522	2004	Pugnaire, FI; Armas, C; Valladares, F	Soil as a mediator in plant-plant interactions in a semi-arid community	JOURNAL OF VEGETATION SCIENCE	10.1111/j.1654- 1103.2004.tb02240.x
600	2020	Erfanzadeh, Reza; Shayesteh Palaye, Ali A.; Ghelichnia, Hassan	Shrub effects on germinable soil seed bank in overgrazed rangelands	PLANT ECOLOGY & DIVERSITY	10.1080/17550874.202 0.1718233

**Supplement supporting analyses.** Detailed meta-analysis visualization and model.

All code also published at Zenodo (DOI: 10.5281/zenodo.4058976).

Mixed-Effects Meta-model Model (k = 87; tau^2 estimator: DL)

R Version 4.0.3

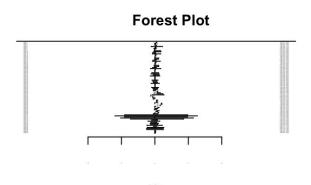
Meta and metafor packages to support analyses.

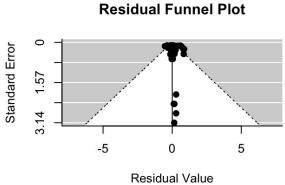
```
##
## logLik deviance
                       AIC
                                BIC
                                       AICc
## -23.0169 348.9753 54.0338 63.8974 54.5216
##
## tau^2 (estimated amount of residual heterogeneity): 0.0174 (SE = 0.0066)
## tau (square root of estimated tau^2 value):
                                                   0.1317
## I^2 (residual heterogeneity / unaccounted variability): 99.27%
## H^2 (unaccounted variability / sampling variability): 136.47
## R^2 (amount of heterogeneity accounted for):
                                                      67.79%
##
## Test for Residual Heterogeneity:
## QE(df = 84) = 11463.7988, p-val < .0001
##
## Test of Moderators (coefficients 2:3):
## QM(df = 2) = 95.5023, p-val < .0001
##
```

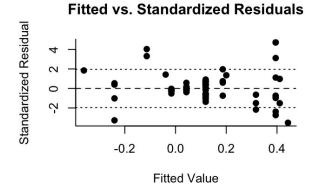
## Model Results:

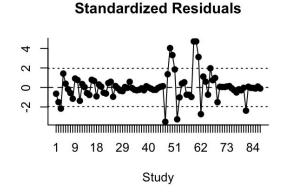
##

## ---









## Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

## Contrast of linear and non-linear meta-regression

### Permutation test for best fit model

```
## Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

## **Moderator tests**

## **Design of study**

## Manipulative - changed environment but not community (only three studies total)

```
Mixed-Effects Model (k = 87; tau<sup>2</sup> estimator: DL)
##
##
    logLik deviance
                           AIC
                                      BIC
                                               AICc
## -22.8865 348.7145 55.7730 68.1025 56.5137
##
## tau^2 (estimated amount of residual heterogeneity):
0.0165 \text{ (SE} = 0.0062)
## tau (square root of estimated tau^2 value):
0.1283
## I^2 (residual heterogeneity / unaccounted variability):
99.27%
## H^2 (unaccounted variability / sampling variability):
136.55
## R^2 (amount of heterogeneity accounted for):
69.46%
##
## Test for Residual Heterogeneity:
\#\# QE(df = 83) = 11333.5458, p-val < .0001
##
## Test of Moderators (coefficients 2:4):
\#\# QM(df = 3) = 105.0814, p-val < .0001
##
## Model Results:
##
##
                               estimate se zval
pval ci.lb
## intrcpt
                                    0.1680 0.1639 1.0249
0.3054 - 0.1533
## n species
                                    0.0017 0.0065 0.2668
0.7896 - 0.0110
                                  0.2763 0.1678 1.6465
## designobservational
0.0997 - 0.0526
## n species:designobservational -0.0148 0.0066 -2.2302
0.0257 - 0.0277
##
                                   ci.ub
## intrcpt
                                   0.4893
```

## Protege plant functional group

```
Mixed-Effects Model (k = 87; tau<sup>2</sup> estimator: DL)
##
    logLik deviance
                            AIC
                                      BIC
                                               AICc
   -9.4657 321.8729 40.9313 68.0563 44.4513
##
##
## tau^2 (estimated amount of residual heterogeneity):
0.0134 \text{ (SE} = 0.0053)
## tau (square root of estimated tau^2 value):
0.1158
## I^2 (residual heterogeneity / unaccounted variability):
99.10%
## H^2 (unaccounted variability / sampling variability):
110.54
## R^2 (amount of heterogeneity accounted for):
75.11%
##
## Test for Residual Heterogeneity:
## QE(df = 77) = 8511.5798, p-val < .0001
##
## Test of Moderators (coefficients 2:10):
\#\# QM(df = 9) = 173.7452, p-val < .0001
##
## Model Results:
##
##
                                   estimate
                                                  se
zval pval ci.lb
```

```
## intrcpt
                                   0.4683 0.1573
2.9769 0.0029 0.1600
                                  -0.0059 0.0059 -
## n species
0.9985 0.3180 -0.0174
## protege pfgcommunity
                                  -0.3126 0.1802
1.7350 0.0827 -0.6657
## protege pfggrass
                                  -0.0067 0.1967
0.0340 0.9729 -0.3922
## protege pfgherb
                                  0.1040 0.1650
0.6302 0.5286 -0.2194
## protege pfgperennial
                                 -0.1901 0.1825 -
1.0419 0.2975 -0.5478
## n species:protege pfgcommunity 0.0015 0.0068
0.2132 0.8311 -0.0120
## n species:protege pfggrass
                             -0.0111
                                           0.0080
1.3814 0.1672 -0.0269
                                 -0.0074 0.0063
## n species:protege pfgherb
1.1636 0.2446 -0.0197
## n species:protege pfgperennial -0.0042 0.0062 -
0.6695 0.5032 -0.0164
##
                                  ci.ub
                                 0.7766 **
## intrcpt
## n species
                                 0.0057
## protege pfgcommunity
                                 0.0405
## protege pfggrass
                                 0.3788
## protege pfgherb
                                 0.4273
## protege pfgperennial
                                 0.1675
## n species:protege pfgcommunity 0.0149
## n species:protege pfggrass
                                 0.0047
## n species:protege pfgherb
                                 0.0050
## n species:protege pfgperennial 0.0081
##
## ---
## Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1
1 1 1
```

## Measure of diversity

```
Mixed-Effects Model (k = 87; tau<sup>2</sup> estimator: DL)
##
##
    logLik deviance
                           AIC
                                      BIC
                                               AICc
## -10.5595 324.0605 41.1190 65.7780 44.0137
##
## tau^2 (estimated amount of residual heterogeneity):
0.0178 \text{ (SE} = 0.0077)
## tau (square root of estimated tau^2 value):
0.1333
## I^2 (residual heterogeneity / unaccounted variability):
99.08%
## H^2 (unaccounted variability / sampling variability):
109.15
## R^2 (amount of heterogeneity accounted for):
67.02%
##
## Test for Residual Heterogeneity:
## QE(df = 78) = 8513.9411, p-val < .0001
##
## Test of Moderators (coefficients 2:9):
\#\# QM(df = 8) = 116.4573, p-val < .0001
##
## Model Results:
##
                                     estimate se
##
      pval ci.lb
zval
## intrcpt
                                       0.5646 0.1047
5.3915 < .0001 0.3593
                                      -0.0061 0.0186
## n species
0.3298 0.7416 -0.0426
                                      -0.5469 0.5043
## responseevenness
1.0845 0.2781 -1.5352
## responserichness
                                      -0.1955 0.1201 -
1.6277 0.1036 -0.4309
```

```
## responseShannon-Wiener
                              -0.3727 0.1578 -
2.3624 0.0182 -0.6820
                              -0.3750 0.4184 -
## responseSimpsons
0.8962 \quad 0.3702 \quad -1.1950
## n species:responseevenness 0.0057 0.0260
0.2208 0.8252 -0.0452
                              -0.0035 0.0187
## n species:responserichness
0.1863 0.8522 -0.0401
## n species:responseShannon-Wiener 0.0012 0.0192
0.0643 0.9487 -0.0364
##
                               ci.ub
                               0.7698 ***
## intrcpt
## n species
                               0.0303
## responseevenness
                               0.4415
## responserichness
                              0.0399
## responseShannon-Wiener -0.0635 *
## responseSimpsons
                              0.4451
## n species:responseShannon-Wiener 0.0389
##
## ---
## Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1
1 1 1
```