A global meta-analytic contrast of cushion-plant effects on plants and on arthropods.

Nurse plant facilitation is a commonly reported plant-plant interaction and is an important factor influencing community structure in stressful environments. Cushion plants are an example of alpine nurse plants that modify microclimatic conditions within their canopies to create favourable environments for other plants. In this meta-analysis, the facilitative effects of cushion plants was expanded from previous syntheses of the topic and the relative strength of facilitation for other plants and for arthropods were compared globally.The abundance, diversity, and species presence/absence effect size estimates were tested as plant responses to nurse plants and a composite measure was tested for arthropods. The strength of facilitation was on average three times greater for arthropods relative to all plant responses to cushions. Plant species presence, i.e. frequency of occurrence, was not enhanced by nurse-plants. Cushion plants nonetheless acted as nurse plants for both plants and arthropods in most alpine contexts globally, and although responses by other plant species currently dominate the facilitation literature,preliminary synthesis of the evidence suggests that the potential impacts of nurses may be even greater for other trophic levels.

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19   November 21st, 2013.

27   **Introduction**

28   Facilitation is a positive, non-trophic interaction that benefits at least one species (Callaway,

29   1995; Bruno et al., 2003). This interaction tends to occur in high-stress environments such as

30   deserts (Holzapfel & Mahall 1999) or arctic and alpine ecosystems (Antonsson et al., 2009). The

31   importance of facilitation tends to increase with environmental stress (Choler et al., 2001;

32   Brooker et al., 2008; le Roux & McGeoch, 2010). A commonly used tool to examine plant

33   facilitation in stressful environments is the use of nurse plants. Nurse plants modify

34   microclimatic conditions of stressful environments within their canopies and thus may increase

35   species richness (Nunez et al., 1999; Arroyo et al., 2003; Badano & Marquet, 2009), abundance

36   (Cavieres et al., 2002; Badano et al., 2007; Sklenar 2009), diversity (Badano & Marquet, 2009;

37   Butterfield et al., 2013), and species survival (Cavieres et al., 2007; Badano et al., 2007;

38   Cavieres et al., 2008). Less commonly, nurse plants can also increase seedling tolerance to

39   herbivory (Acuna-Rodriquez et al., 2006). Cushion plants are nurse plants that grow in alpine,

40   subalpine, arctic, and subarctic ecosystems. The physiology of cushion plants, including their low

41   height and compact form, makes them well adapted to stressful alpine environments. It also

42   allows them to alter microclimatic conditions within their canopies (Cavieres et al., 2006). The

43   canopy traps heat providing a warmer microclimate for other plants to grow in (Arroyo et al.,

44   2003; Molenda et al., 2012), increases soil water content by retaining moisture (Cavieres et al.,

45   2007; Schoeb et al., 2012; Anthelme et al., 2012), reduces wind (Cavieres et al., 2007; le Roux

46   and McGeoch, 2010), and increases litter accumulation which contributes to increased soil

47   nutrients (Cavieres et al., 2008; Schoeb et al., 2012; Anthelme et al., 2012). Consequently,

48   cushion plants are an excellent set of species to explore positive interactions in the alpine,

49   particularly for impacts on other plant species.

50

51 Most cushion plant facilitation studies have focused on the facilitation of other plants with few

52 examples of effects on arthropods (but see Molina-Montenegro et al., 2006; Sieber et al., 2011;

53 Lortie & Reid, 2012; Molenda et al., 2012). Accordingly, reviews of cushion plant facilitation

54 have also focused on plants (Arredondo-Nunez et al., 2009; Anthelme & Dangles 2012; Reid et

55 al., 2010). For instance, Anthelme and Dangles (2012) examined plant-plant interactions in

56 tropical alpine environments and compared them to other alpine environments. They found that

57 cushions have a similar facilitative effect in tropical alpine environments to other alpine

58 environments in that cushions modified microclimatic conditions within their canopies and

59 similarly facilitated other plant species. A review by Reid et al. (2010) compared publications on

60 nurse-plant shrubs to cushion plants and found that although there are fewer studies using

61 cushion plants, these nurses have many of the same effects as shrubs in terms of modifying

62 microclimatic conditions and enhancing plant species diversity. Cushions are thus an ideal model

63 in many respects to study the effects of facilitation on diversity in alpine or arctic ecosystems.

64 However, these two reviews summarized cushion plant effects on understory species across

65 studies, and did not quantitatively assess these effects in terms of richness, abundance, survival

66 etc.

67 A pioneering meta-analysis by Arredondo-Nunez et al. (2009) quantitatively examined the effect

68 of cushion plants on plant species presence at high and low stress and concluded that facilitation

69 increased with environmental stress. This meta-analysis was very successful in quantitatively

70 demonstrating the facilitative effects of cushions on other plant species. However, the literature

71 available for synthesis at that time only examined plant-plant interactions in the Southern Andes,

72 and only tested plant species presence/absences a response variable in sufficient numbers (a total

73 of 9 studies). Hence, there is need for a quantitative synthesis update for these specific forms of

74 nurse plants.

75

76   In this meta-analysis, the effect of cushion plants will first be extended to assess effects on other

77   plant species globally by comparing the following three potential plant responses to nurses:

78   abundance, diversity, and presence/absence. The synthesis of facilitation literature will be further

79   extended by contrasting the responses of other plant species to nurses with the responses of

80   arthropods to nurses. These are critical extensions to the facilitation literature in general because

81   nurse plants may be foundation species for many trophic levels – not just other plants, and

82   identifying the appropriate responses to nurse plants may have important implications for

83   population and community dynamics of alpine plant populations. The following questions will be

84   addressed in this meta-analysis. (1) Is there significant evidence that cushion plants facilitate

85   plant abundance, diversity, and presence/absence globally? (2) Is there significant evidence that

86   cushion plants also facilitate arthropods? (3) Does the strength of evidence associated with

87   facilitation of plants and arthropods by cushion plants differ? Plants and arthropod responses to

88   cushions can be contrasted herein because the same effect size estimate is calculated and both

89   involve the same field of methodologies, i.e. contrasts of measures associated with cushion and

90   open microsites. This satisfies the best practices recommended for such meta-analytical contrasts

91   (Moayyedi, 20004; Borenstein et al., 2009; Jennions et al., 2013; Koricheva & Gurevitch, 2013)

92   when the efficacy of treatment is evaluated at larger scales.

93

94   **Methods**

95   *Study selection process*

96   A search was conducted using ISI Web of Knowledge for articles associated with cushion plant

97   facilitation. Three separate searches were performed in July 2013 on this topic and resulted in

98   613 articles (Table 1, search terms listed). These searches were refined in three stages with

99   increasing specificity in the inclusion criteria applied. The first stage limited articles to English

100   language publications and to the following Web of Knowledge search categories: plant science,

101   ecology, environmental sciences, geography physical, environmental studies, biodiversity

102   conservation, evolutionary biology, horticulture, entomology, biology, and mycology (Table 1,

103   432 articles remained). In the second stage of refinement, duplicate articles were removed, and all

104   publications were screened to determine if the study examined facilitation (retention of 52

105   articles). Only two taxa were reported in this set of publications, plants, and arthropods. The

106   third stage in the workflow inspected all studies for useable/extractable data and then sorted these

107   publications by response variables, i.e. abundance, diversity, and presence, and by plant or

108   arthropod species. This final refinement generated 16 studies for a total of 673 unique

109   experimental contrasts of nurse-plant cushion effects in the field (Table 2, N_{study} = 13 plants

110   responses, N_{study}= 2 arthropods, and N_{study} = 1 examined both taxa). A PRISMA flow diagram

111   was generated (Moher et al., 2009) outlining the publication selection process (Fig 1).

112

113   *Data Collection and Analyses*

114   Data for abundance, diversity and/or presence of plant and/or arthropod species were extracted

115   from tables, figures, or by contacting authors directly when not reported. All studies excepting

116   one included in the meta-analysis were observational (table 2). To compare results across studies,

117   the Relative Interaction Index (RII) effect size estimate was calculated as RII= $(B_w – B_o)/(B_w + B_o)$

118   where B_w is the value of species within the cushion, and B_o is the value of species without the

119   cushion (Armas et al., 2004). RII ranges from +1 to -1 with positive values indicating facilitation,

120   negative values indicating competition, and values not significantly different from zero indicating

121   neutral/no effects (Armas et al., 2004). Sets of meta-analytic contrasts were used to compare the

122   nurse effect of cushions on plants and to arthropods. The effect of cushions was determined by

123   comparing plant and arthropod responses within the cushion canopy to adjacent open areas

124   identical to the field methodology used to assess plant-plant interaction in most facilitation

125   studies (Brooker et al., 2008). These nurse plant-open pairs were extracted from each study and

126   used for each meta-analytic contrast resulting in 662 pairs for plants and 11 for arthropods.).

127   Pairs were first coded as a unique replicate/instance based on study number, cushion species,

128   elevation, and response variable reported within the study (i.e. abundance, diversity, or species

129   presence). However, to be very conservative, we chose not to model each field instance as fully

130   independent in our analyses. The mean RII values were calculated within each publication for

131   independent tests only, i.e. tested a different cushion species or a different elevation, for a total of

132   63 unique study cases for plants and 5 tests for arthropods. We first tested whether abundance,

133   diversity, and presence differed between plants on average. Next, we compared the composite

134   measure of all responses between plants and arthropods. Diversity data included raw species

135   richness and Shannon-Weiner diversity indices. Both meta-analyses were modeled as categorical

136   random effects. Heterogeneity tests (Q) were conducted to determine if the effect sizes calculated

137   in each meta-analysis were significantly different (Rosenberg et al., 2000). To determine if the

138   effect size was significantly different from zero and therefore significantly different from a

139   neutral effect, bias corrected confidence intervals were calculated. An effect size was

140   significantly different from zero if the confidence interval does not overlap zero (Cote &

141   Jennions, 2013). In order to explore bias, Rosenthal's fail-safe analyses were conducted for each

142   meta-analysis. To determine if the Rosenthal value for each meta-analysis is within the acceptable

143   range, we applied the bias rule of X=5k +10 where X = the Rosenthal value and k is the number

144   of studies (Moller & Jennions, 2001). An acceptable Rosenthal value for plants would be greater

145   than 80 whilst for arthropods it would be greater than 25. If the Rosenthal value of the meta-

146   analysis is greater than these values, then the results are generally considered robust (Moller &

147 Jennions, 2001). All univariate meta-analyses were conducted using Metawin 2.1 (Rosenberg et

148 al., 2000).

149

150 **Results**

151 Plant abundance was the most strongly facilitated response variable enhanced by cushions, and it

152 was significantly different from the other responses (Fig 2, different from 0 and non-overlapping

153 confidence intervals with either alternative response mean $RII_{abundance}$=0.434 ±0.144, mean

154 $RII_{diversity}$=0.130±0.081, mean $RII_{presence}$=0.095±0.166). Plant species diversity was also enhanced

155 by cushions whilst the presence plant response variable was not significantly different from zero

156 (Fig 2). Heterogeneity between groups was significantly different ($Q_{between}$ = 11.7, df = 2, p= 0.01)

157 with presence plant response having the highest levels of within group variation (presence

158 variance $_{pooled\ within\ group}$ = 0.13). The Rosenthal value for this meta-analytic comparison is 381

159 indicating robust results.

160

161 Cushion plants facilitated both plants and arthropods (Fig 3, i.e. grand mean significantly

162 different from zero and positive grand mean= 0.278 ± 0.082). The facilitative effect of cushion

163 plants was significantly greater for arthropods compared to plants with arthropods having a RII

164 value more than 3.5 times greater than plants (Fig 2 mean RII_{plants} = 0.226 ± 0.079, mean

165 $RII_{arthropods}$= 0.830 ± 0.041). Heterogeneity between groups was not significantly different (Q

166 $_{between}$=3.3, df = 1, p=0.08) in spite of unequal sample sizes. The Rosenthal value was 461.8, and

167 this is 5 times greater than the threshold of 80 suggesting robust results.

168

169 **Discussion**

170 There is significant evidence that nurse-plant species function as foundation species in relatively

171 stressful ecosystems (Cavieres & Badano, 2009; Butterfield, 2009). Particularly in arid systems,

172 shrub nurse plants have been shown to positively influence many aspects of plant community

173 structure (Maestre et al., 2005), and this has been linked to restoration via synthesis, i.e. meta-

174 analysis (Gomez-Aparicio, 2009). However, in the alpine, the research is not as extensive but also

175 suggests that cushion plants can serve as foundation species with strong effects in driving the

176 frequency of occurrence of plant species within these communities (Arredondo-Nunez et al.,

177 2009). To update and extend this previous synthesis, we conducted a meta-analysis on the current

178 research examining cushions to include other plant responses, other alpine regions globally, and

179 to compare to effects on arthropods. Similar to the previous syntheses of nurse plants in general,

180 cushion plants facilitate other plant species and arthropods and are thus likely a foundational

181 species. Consequently, we propose that these species are an excellent model organism available

182 to ecologists to explore community dynamics and change in many alpine ecosystems.

183

184 There were several novel and sometimes contradictory findings in this synthesis effort relative to

185 previous reviews. In this meta-analysis, the abundance and diversity of plant species was

186 facilitated by cushion plants. This is a novel extension to the previous synthesis by Arredondo-

187 Nunez et al. (2009) wherein only frequency of occurrence, or as we termed here presence, was

188 examined. Increases in diversity and total abundance of plant species within the cushion

189 understory is not a surprising result given the above described mechanisms of abiotic stress

190 amelioration. Shelter in the alpine is a commonly assumed mechanism of facilitation for plants

191 (Carlsson, 1991; Cavieres et al., 2002; Cavieres & Sierra-Almeida, 2012). There is accumulating

192 support that cushions can enhance species richness in the alpine through higher rates of

193   addition/retention of species at the community level (Cavieres & Badano, 2009). This retention

194   by cushion plants has been shown to extend to reduced loss of phylogenetic diversity compared

195   to adjacent open areas in the alpine globally (Butterfield et al., 2013). Even more broadly,

196   facilitation can enhance diversity in many other ecosystems (Badano & Marquet, 2009;

197   Butterfield et al., 2013; McIntire & Fajardo, 2013). However, all species may not equally benefit

198   from nurse plants in alpine systems, and there are also instances of negative association of other

199   species with cushions (Fajardo et al., 2008) or different sets of species differentially associating

200   with cushions (Cavieres & Badano, 2009; Arredondo-Nunez et al., 2009). This synthesis thus

201   contradicted the previous synthesis of this topic (Arredondo-Nunez et al., 2009) in that the

202   presence, or frequency of occurrence, was not facilitated as was formerly detected. This

203   difference is likely due to several factors ranging from ecological to statistical. The current meta-

204   analysis included studies from a variety of alpine ecosystems because the cushion plant literature

205   has expanded in number and geographic scope since the former synthesis. This necessarily

206   introduces greater heterogeneity in the potential responses of plant communities to cushions

207   because very different alpine communities were sampled that likely differ in stability (Butterfield,

208   2009), net interactions (Callaway et al., 2002), and climate (Kikvidze et al., 2011) to name a few

209   important ecological considerations. Importantly, significant statistical heterogeneity was

210   detected for the presence plant response variable unlike the other responses tested suggesting

211   that this measure of community structure may be more sensitive the local ecological context

212   versus regional drivers of change (Ricklefs, 2008). The inconsistency between this study and the

213   meta-analysis conducted by Arredondo-Nunez et al. (2009) is also due to purely statistical

214   reasons because the scope of inference differed. Herein, we fit random-effects statistical models

215   as we sought to describe global patterns whilst the former meta-analysis, quite appropriately, used

216   a fixed-effects model because they were describing a set of studies all from within the same

217   region, the Southern Andes. Random effects models estimate variance less conservatively

218   (Jennions et al., 2013), and we would thus expect that heterogeneity would be greater in some

219   instances. In summary, cushion plants have the capacity to shape many aspects of plant

220   community structure in the alpine, but research gaps associated with species specificity, scale,

221   and the sensitivity of different community-level responses to nurses can be further developed.

222

223   Although the facilitation of arthropods is an emerging field of research, arthropods were

224   facilitated by cushion nurse plants in the alpine in this limited set of studies conducted to date.

225   Interestingly, the strength of facilitation was significantly greater for arthropods relative to the

226   benefits accrued by other plant species. There are several explanations for this general finding.

227   Microclimatic modifications made by cushion plants may benefit arthropods even more

228   extensively than plants given their mobility and foraging behaviour. The canopy of cushions

229   provides a warmer and more stable microclimate (Cavieres et al., 2002; Arroyo et al., 2003;

230   Molenda et al., 2012). This may allow more arthropods to function and thermoregulate relative to

231   colder conditions outside cushions (Molina-Montenegro et al., 2006). If sets of arthropods seek

232   refuge within cushions, then the availability of prey may also be greater within cushions thereby

233   concentrating resources for other species (Lortie et al., 2012). Cushion plants also increase plant

234   abundance and diversity when compared to open areas in many instances (finding in this

235   synthesis and broadly reviewed in McIntire & Fajardo (2013)). This can provide arthropods with

236   a more diverse range of resources and niches in general (Molenda et al., 2012) particularly for

237   life-stages associated with colonization (Mysterud et al., 2010). Finally, pollinators have been

238   shown to benefit from cushions as they provide an increased availability of flowers (Reid &

239   Lortie, 2012). Hence, cushion plants likely have direct and indirect effects on arthropod

240   community dynamics related to both microclimate and to the other plant and arthropod species

241   present. The evidence to date strongly suggests that cushion nurse plant research should now

242   include and address multi-trophic perspectives (McIntire & Eliot, 2013; Van DerPutten, 2009;

243   Ferenc et al., 2009). In addition, decoupling direct and indirect interactions of cushion plants and

244   understory plant species is another important area of research. Biodiversity changes in the alpine

245   will be unavoidable given a changing climate and will not be restricted to plant species.

246   Therefore, understanding interactions that structure the greater community will be important in

247   determining the consequences of a rapidly changing climate in the alpine.

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Search terms used to select studies

Table 1. The search terms used in defining the scope of

studies used in this meta-analyses of nurse-plant cushions on other plant

species and arthropods. Web of Knowledge was the tool used to secure the

population of studies. Each workflow step of literature screening is described

in details in the methods, but in short, step 1 – all studies, step 2 –duplicates

removed and reported facilitation, and step 3 –useable data reported and sorted

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Table 1. The search terms used in defining the scope of studies used in this meta-analyses of nurse-plant cushions on other plant species and arthropods. Web of Knowledge was the tool used to secure the population of studies. Each workflow step of literature screening is described in details in the methods, but in short, step 1 – all studies, step 2 –duplicates removed and reported facilitation, and step 3 –useable data reported and sorted by response and taxa.

Workflow	Search Terms	$N_{initial}$	$N_{step\ 1}$	$N_{step\ 2}$	$N_{step\ 3}$
1	Cushion plant OR nurse plant AND facilitat* AND alpine OR arctic OR subarctic	30	30	27	13
2	Cushion plant OR nurse plant AND faciliatat*	54	53	12	2
3	Cushion plant	529	349	13	1

Table 2(on next page)

Article selection criteria for inclusion in the meta-analysis

Table 2. A summary of all articles included in the meta-analysis of nurse-plant cushions on plants and arthropods. Details of data extraction listed in detail in the methods ($N_{studies}$ = 16, n_{plants} = 662, $n_{arthropods}$ = 11).

Table 2. A summary of all articles included in the meta-analysis of nurse-plant cushions on plants and arthropods. Details of data extraction listed in detail in the methods ($N_{studies} = 16$, $n_{plants} = 662$, $n_{arthropods} = 11$).

Authors	Location	Elevation (m.a.s.l.)	Cushion species	Taxa	Response variable
Anthelme et al., 2012	00°28'S,78°09'W	4400, 4550, 4700	*Azorella aretioides*	Plants	Diversity, presence
Arroyo et al., 2003	50°48'S,73°10'W	700, 900	*Azorella monantha*	Plants	Presence
Badano et al., 2007	33°,70°W	3200, 3400, 3600	*Azorella monantha*	Plants	Abundance
Cavieres et al., 2002	50°48'S,73°10'W	700, 900	*Bolax gummifera*	Plants	Abundance, diversity, presence
Cavieres et al., 2006	33°20'S,70°16'W	2800, 3200	*Laretia acaulis*	Plants	Diversity, presence
Cavieres et al., 2008	33°20'S,70°16'W	3200	*Laretia acaulis, Azorella monantha*	Plants	Abundance, presence
Cavieres and Badano 2009		1900, 1600, 1900, 3200, 3600,4000, 4300	*Pycnophyllum bryoides, Adesmia suvterranea, Azorella madreporica, Laretia acaulis, Oreopolus glacialis, Discaria nana, Mulinum leptacapthum, Azorella monantha, Bolax gummifera*	Plants	Diversity
de bello et al., 2011	33°05′N, 78°27′E	5900	*Thylacospermum caespitosum*	Plants	Presence
Dvorsky et al., 2013	34°45'N, 77°35'E	4840, 5000,5100, 5300, 5600,5750, 5850	*Tylacospermum caespitosum*	Plants	Diversity, presence
Le Roux and McGeoch, 2010	46°54'S, 37°45'E	89, 97, 102	*Azorella selago*	Plants	Abundance
Molenda et al., 2012	50°15'N, 122°16'W	2160	*Silene acaulis*	Plants and arthropods	Abundance, diversity
Molina-Montenegro et al., 2006	33°20'S,70°16'W	3200	*Laretia acaulis, Azorella monantha*	Arthropods	Abundance
Quiroz et al., 2009	33°20'S,70°16'W	3200, 3580	*Azorella madreporica*	Plants	Abundance, diversity, presence
Schoeb et al., 2012	37°05'N,03°23'W	3240	*Arenaria tetraquetra*	Plants	Abundance, diversity
Sieber et al., 2011	46°31'N,09°43'W	3000	*Eritrichium nanum*	Arthropods	Presence
Yang et al., 2010	28°20'N,99°05'E	4500, 4700	*Arenaria polytrichoides*	Plants	Presence

Figure 1

PRISMA diagram describing the search protocol used for the meta-analysis

Figure 1: PRISMA flow diagram depicting the search

protocol and workflow in determining the effective population of studies for

meta-analysis.
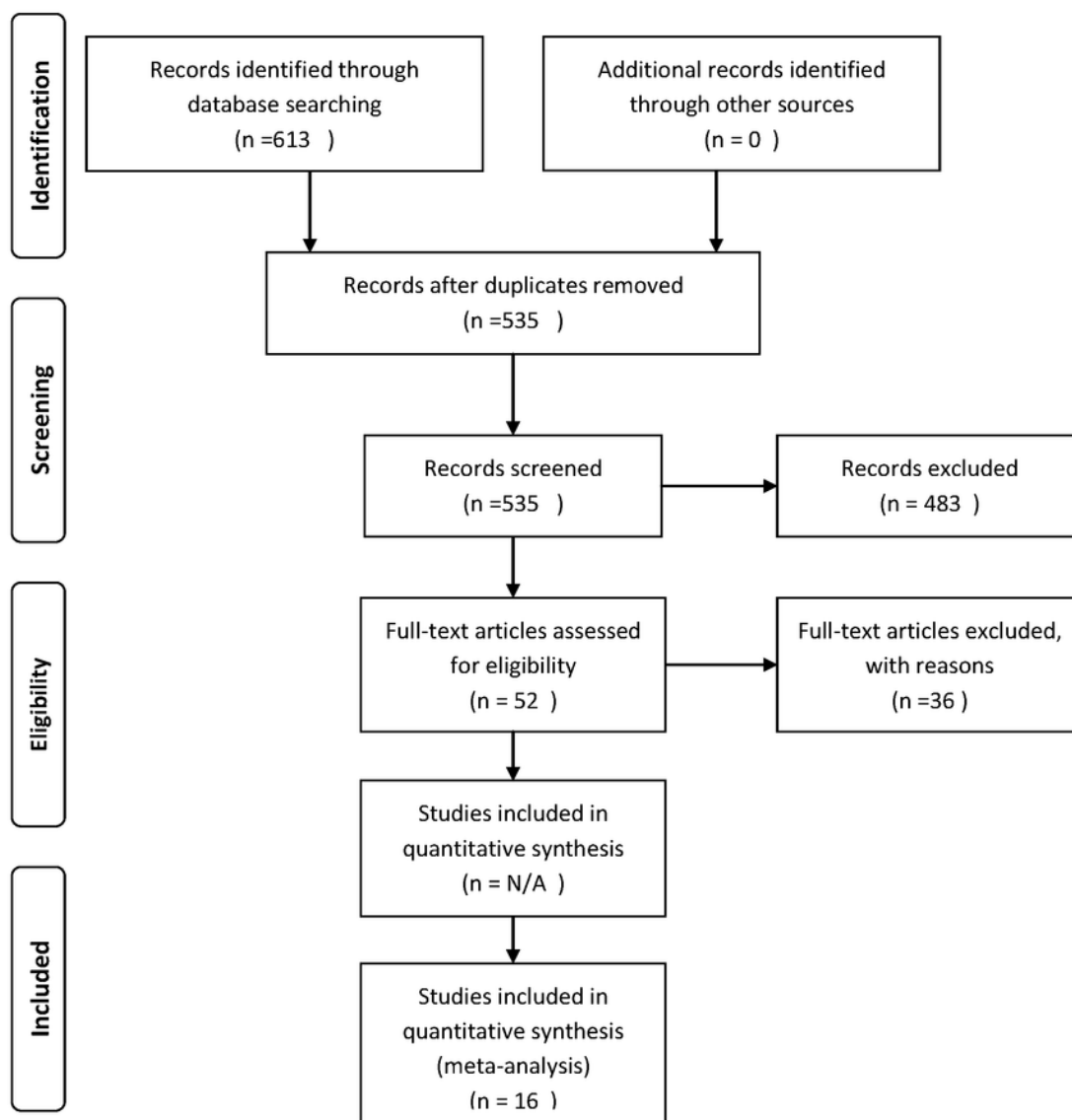
Figure 2

Mean RII values for the effect of cushion plants on the abundance, diversity, and presence of other plant species

Figure 2: The mean RII values for the effect of alpine cushion plants on the abundance, diversity, and species presence for other plants. Presence refers to presence/absence responses via associational pattern analyses in this literature. The bias-corrected 95% confidence intervals are shown.
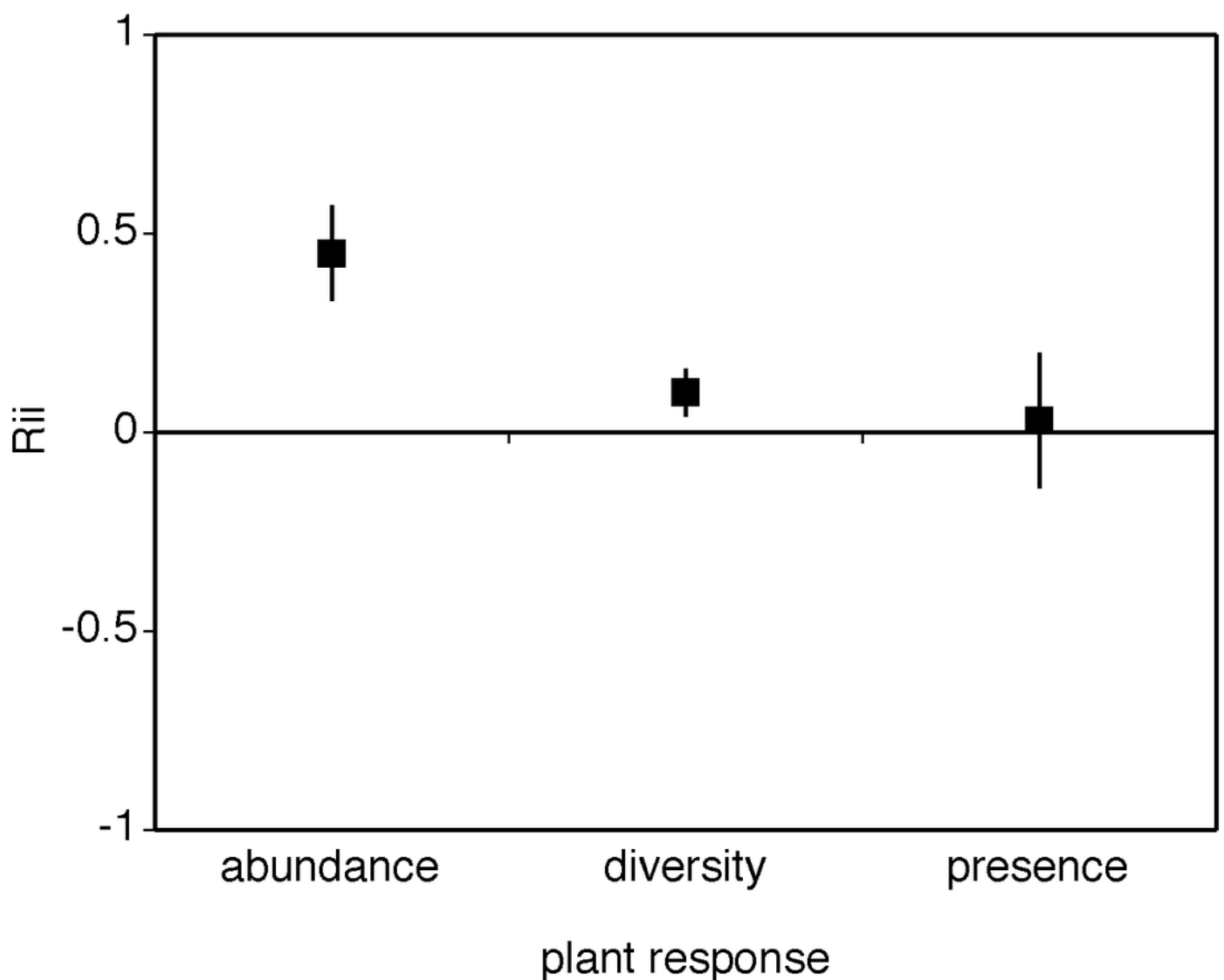
Figure 3

Composite mean RII values for plants, arthropods and the overall grand mean

Figure 3: A contrast of the composite mean RII values for plants
and arthropods. The overall or grand mean is the mean RII value for both plants
and arthropods. The bias-corrected 95% confidence intervals are shown.