

1 **Spatial scale influences the associational effects of neighbor plants on mammal herbivory.**

2 **Insights from a meta-analysis**

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11

## 12 **Abstract**

13 There is high intra-specific variability in susceptibility of plants to herbivores with potential  
14 effects on the population dynamics of species, community composition, structure and function.  
15 This variability can be partly explained by vegetation assemblages, i.e. associational effects, but  
16 it is still unclear how the spatial scale of plant associations modulates foraging choice of  
17 herbivores; an inherently spatial process in itself. Using a meta-analysis, we investigated how  
18 spatial scale modifies associational effects of neighboring plants on the susceptibility to  
19 browsing by herbivores with movement capacities similar to deer. From 2496 articles found in  
20 main literature databases, we selected 46 studies providing a total of 168 differences of means in  
21 damage or survival with and without neighboring plants. We tested the impact of spatial scale,  
22 estimated as the distance between the focal plant and its neighbors, and the type of association  
23 effect on the effect sizes reported in these studies using a meta-analysis mixed model. The  
24 strength of associational effects slightly increases from 0 to 1 m and decreases at scales larger  
25 than 1 m. Associational defence (i.e. decrease in susceptibility with avoided neighbors) had  
26 stronger effects than any other type of associational effects, but was not more frequent. Our  
27 study is the first addressing the magnitude of change in associational effects with spatial scale.  
28 Further empirical studies should test associational effects between plants at multiple spatial  
29 scales simultaneously. The high remaining heterogeneity between the studies suggests that  
30 untested factors modulate associational effects, such as nutritional quality of focal and  
31 neighboring plants and/or timing of browsing. Associational effects are already considered in  
32 multiple restoration contexts worldwide, but a better understanding of these intratrophic  
33 relationships could improve and generalize their use in conservation and exploitation.

34 Keywords: neighboring effects, attractant-decoy hypothesis; associational resistance; plant-  
35 herbivore relationships, spatial scale, meta-analysis

## 36 **Introduction**

37 Selective herbivory can modify the composition, structure and functions of ecosystems (Hester et  
38 al. 2006). There is high variability in the susceptibility of different plant species and individuals  
39 to herbivory. This variability is driven by forage selection that in itself is determined the  
40 nutritional requirements of the herbivores (Pyke et al. 1977), by intrinsic (e.g. nutritive quality,  
41 Pyke et al. 1977), and by extrinsic characteristics of both the plants and the environment (e.g.  
42 vegetation assemblage, Atsatt and O'Dowd 1976). Multiple studies have demonstrated the  
43 influence of vegetation assemblage on forage selection, a process named neighboring or  
44 associational effects (Milchunas and Noy-Meir 2002, Barbosa et al. 2009), yet the conditions in  
45 which a specific plant assemblage will increase or reduce susceptibility to herbivory are still  
46 unclear. The distance between neighboring plants could explain part of the residual variability  
47 observed in associational effects (Underwood et al. 2014). Associational effects can be exploited  
48 as a management tool to alleviate the effect of herbivores; for example, Perea and Gil (2014)  
49 recommend planting seedlings under shrubs as to reduce damage to the seedlings by browsers.  
50 Other recent studies (Noumi et al. 2015, Stutz et al. 2015, Torroba-Balmori et al. 2015) explored  
51 the application and limits of associational effects for the restoration of plant species. A better  
52 understanding of these intratrophic relationships could improve and generalize their use in  
53 restoration, conservation and forestry activities.

54 Four different types of associational effects on plant susceptibility to herbivores have been  
55 described in the literature (Table 1), mostly depending on whether the neighboring plant appears  
56 to increase herbivory on a focal plant, i.e. the plant for which herbivory is measured (Thomas  
57 1986, Hjältén et al. 1993), or decreases it (Tahvanainen and Root 1972, Atsatt and O'Dowd  
58 1976). Associational susceptibility is the increase of herbivory damage to the focal plant in the

59 presence of a preferred neighboring plant (Thomas 1986, Hjältén et al. 1993) while associational  
60 defence, or associational resistance, is the reduction of damage in the presence of an avoided  
61 neighboring plant (Tahvanainen and Root 1972, Atsatt and O'Dowd 1976, Bergvall et al. 2006).  
62 Neighbor contrast susceptibility (Bergvall et al. 2006), also known as the attractant-decoy  
63 hypothesis (Atsatt and O'Dowd 1976) represents an increase in susceptibility of the focal plant to  
64 herbivory in the presence of an avoided neighbor. Its mirror interaction is called the neighbor  
65 contrast defence, a decrease of damage in presence of a preferred neighbor (Bergvall et al. 2006,  
66 Rautio et al. 2012). A meta-analysis of all associational effects by Barbosa et al. (2009) revealed  
67 that associational effects are influenced by herbivore taxonomy (e.g. mammals or insects), plant  
68 taxonomic relatedness and the palatability of the neighboring plant, but unexplained variation  
69 remains in the associational effects of neighboring plants on the susceptibility to herbivory. The  
70 focus of this meta-analysis on the importance of spatial scale in affecting associational effects of  
71 neighboring plants reflects this lack of knowledge.

72 Forage selection is a phenomenon inherently spatial and its impacts can be measured at multiple  
73 spatial scales from the choice of a single bite to the establishment of a home range within the  
74 distribution range of a species (Johnson 1980, Brown and Allen 1989, Bommarco and Banks  
75 2003). At the intermediate scales of habitat and resource selection, Bergvall et al. (2006)  
76 hypothesized that the selection of feeding sites or patches could promote associational  
77 susceptibility and defence. Herbivores might select patches presenting preferred resources and  
78 whilst there they might consume other plants in those patches (associational susceptibility);  
79 and/or they might avoid patches rich in avoided species (associational defence). At smaller scales  
80 of selection, i.e. the selection of food items inside a patch, they hypothesized an increase in the  
81 occurrence of neighbor contrast susceptibility or defence, as those effects depend on the contrast

82 between plant palatability perceived by herbivores (Bergvall et al. 2006). Although multiple  
83 spatial scales have been tested with invertebrate herbivores (Thomas 1986, Karban et al. 2006,  
84 Karban 2010), few experiments have tested the effect of hierarchical foraging on associational  
85 effects. Exceptions include a study of red deer (*Cervus elaphus*) and sheep (*Ovis aries*) showing  
86 decreased damages on *Calluna vulgaris* with increasing distance from a grass patch (Hester and  
87 Baillie 1998), an associational susceptibility that disappeared at 1 to 3 m from the grass patch,  
88 depending on herbivory pressure. Bergvall et al. (2006) tested the selection of fallow deer (*Dama*  
89 *dama*) between patches and within patches of pellets with varying tannin concentration. They  
90 found that palatable food was consumed more in the immediate neighborhood of highly  
91 defended food (neighbor contrast susceptibility) and highly defended food was less consumed in  
92 a high palatability neighborhood (neighbor contrast defence). As stated by Underwood et al.  
93 (2014), empirical data and modeling of associational effects also currently lack information on  
94 the role of spatial scale.

95 Here, we used a meta-analysis approach to determine whether the spatial scale modulates  
96 associational effects of neighboring plants on the risk of herbivory. Because dispersal can affect  
97 the potential for large scale associational effects (Grez and Gonzalez 1995), we controlled for  
98 differences in dispersal capacity by restricting our study to herbivores with movement capacities  
99 similar to deer, i.e. from small deer such as *Capreolus capreolus* to the large *Alces alces* and  
100 including herbivores from other groups if similar body sizes, such as wild boar (*Sus scrofa*) and  
101 Western grey kangaroo (*Macropus fuliginosus*). Our first objective is to address whether the  
102 frequency of the various associational effects (associational susceptibility and defence, neighbor  
103 contrast susceptibility and defence) varies with spatial scales. Second, we characterize how  
104 associational effects vary in strength with spatial scale. We hypothesized that hierarchical forage

105 selection determines the most frequent type of associational effect at the different spatial scales,  
106 i.e. the “classic” type (associational susceptibility and associational defence ) or the “contrast”  
107 type (neighbor contrast defence and susceptibility), according to the conceptual framework  
108 provided by Bergvall et al. (2006). We thus predicted an interaction between spatial scale and  
109 associational effect type where “classic” type associational effects will be more frequent at larger  
110 spatial scale (home ranges and feeding sites), and “contrast” types will be more frequent at finer  
111 scale (patches). This study is the first to investigate spatial patterns across species and  
112 ecosystems in associational effects, an issue essential in understanding the intraspecific  
113 variations in susceptibility to herbivory (Barbosa et al. 2009, Underwood et al. 2014).

## 114 **Methods**

### 115 *Literature review*

116 We obtained 2496 peer-reviewed articles using the search strategy presented in Appendix A in  
117 ISI Web of Science, Biosis preview and BioOne, and through citations used in articles previously  
118 found in the search. We searched for studies involving herbivores with movement capacities  
119 similar to deer from the smallest to the largest deer species, thus excluding small mammals or  
120 very large ones (e.g. elephant and giraffe). The minimal and maximal sizes for herbivores were  
121 defined using the studies found. The smallest herbivore in our dataset is *Capreoleus capreoleus*  
122 and the largest is *Bison bonasus*. Studies reported data on damage or survival on plants (hereafter  
123 called the focal plant) with and without the presence of a neighboring plant (hereafter called the  
124 neighbor plant). We included studies using feeding trials in controlled or natural environments,  
125 transplantation/removal of neighbors and observations in natural environments.

126 We established the criteria regarding acceptance or rejection of a study prior to conducting the  
127 meta-analysis using a PRISMA inspired protocol (see process in Appendix A, Moher et al. 2009).

128 The criteria were the presence of a control treatment (damage/survival without neighboring  
129 plant), a palatable plant in the focal-neighbor group and a difference in palatability between  
130 plants. To evaluate the effect of spatial scale, each study needed to clearly state the size of the  
131 plot where data were recorded or the distance between the focal and neighboring plant. We  
132 rejected data on seed predation a posteriori. A single observer (EC) reviewed and selected all  
133 articles and recorded each rejection criterion. To ensure the reproducibility of article selection, a  
134 second observer screened a subsample of 460 articles; the first and second observer agreed on  
135 456 articles (452 rejected, 4 accepted) leading to a kappa statistic (Cohen 1960) of 0.66,  
136 exceeding the level of 0.60 and thus indicating that article selection was reproducible (Côté et al.  
137 2013). Following this procedure (Appendix A), we kept 46 articles from the original 2496  
138 (Supplement).

### 139 *Data extraction and effect size computation*

140 For each article, a single observer (EC) extracted information regarding the study, such as the  
141 type of experiment, identity of the herbivore, plot size, etc (see Appendix B for a complete list).  
142 To compare associational effects among studies, we extracted means and variance of  
143 damage/survival with and without neighboring plants. We used this information to compile  
144 standardized effect sizes that indicate the size of the impact of neighboring plant on susceptibility  
145 to herbivory of the focal plants (see below for details). We also extracted moderator variables, i.e.  
146 a source of variation among studies that can account for part of the variability in effect sizes  
147 (Koricheva et al. 2013a), such as the type of associational effect (“classic” i.e. associational  
148 defence and susceptibility, or “contrast”, i.e. neighbor contrast defence and susceptibility, Table  
149 1) and the direction of the effect. By direction, we mean increase in susceptibility with neighbor  
150 (preferred or avoided) presence (now referred as the susceptibility subgroup) or decrease in



151 susceptibility with neighbor presence (now referred as the defence subgroup). Some studies  
152 measured associational effects in plots while others rather reported a distance between focal and  
153 neighbor plants. We combined those under a single variable, the radius ( $r$ ), equivalent to the  
154 distance between the focal and neighbor plant. We chose this metric because many studies  
155 centered a circular plot on the focal plant. Variables extracted from articles are detailed in the  
156 Appendix B. Data presented in graphs were extracted using Web Plot Digitizer V2.5 (Copyright  
157 2010-2012 Ankit Rohatgi). We contacted authors for missing data, such as plot size, variance,  
158 Pearson's  $r$  or precision on the herbivore species. Effect sizes that can only be calculated through  
159 that supplementary information are indicated in supplementary Table 2.

160 The data extraction provided 283 distinct observations of damage/survival with and without  
161 neighboring plants. Data available in the form of means with variance were computed into  
162 standardized mean difference ( $d$ ), a common effect size used for meta-analysis in ecology  
163 (Borenstein et al. 2009, Rosenberg et al. 2013). In the few cases where data were reported as  
164 percentage of all focal plants browsed, we computed log odd ratios (OR) using a 2 x 2  
165 contingency table with browsed/unbrowsed columns and with/without neighbors rows  
166 (Borenstein et al. 2009, Rosenberg et al. 2013). Other studies correlated damage to the  
167 abundance (e.g. cover) of the neighbor species and reported Pearson's  $r$  as an effect size statistic  
168 (Borenstein et al. 2009, Rosenberg et al. 2013). Depending on whether the direction of the effect  
169 was susceptibility or defence, values of  $d$  and Pearson's  $r$  could be negative or positive. We  
170 transformed them into absolute values as the categorical variable "direction" already reports  
171 whether they belong to the increased susceptibility or increased defence subgroup (Appendix B).  
172 Effect sizes computed as OR and  $r$  were converted into  $d$  and added into a single analysis using  
173 equations from Borenstein et al. (2009). We selected  $d$  for common effect size as most data were

174 available as a difference of means (Appendix B) and because of its simple interpretation; the  
175 higher the  $d$  value, the greater is the influence of the neighboring plant on the focal plant  
176 susceptibility to herbivory. Although not frequently used (but see Hamm et al. 2010, Thomson et  
177 al. 2013), converting effect sizes allows the inclusion of all data answering the same broad  
178 question and avoids information loss through rejection of relevant studies (Borenstein et al.  
179 2009).

180 When confronted with multiple effect sizes from one study, we extracted them all, unless a  
181 global mean was available (e.g. Russell and Fowler 2004). In the final analysis, we kept only one  
182 combination of neighboring plants, herbivore and spatial scale, similar to Barbosa et al. (2009),  
183 which meant keeping more than one effect size per study in some cases. When the same  
184 combination occurred in the same study, we combined those redundant effect sizes following  
185 Borenstein et al. (2009) (Appendix A and Supplement for details). Following those steps, we  
186 obtained a total of 168 effect sizes from 44 studies.

### 187 *Statistical analyses*

188 We tested the impact of moderators (i.e. independent variables) on the standardized difference of  
189 mean ( $d$ ) in a meta-analysis mixed model using the function *rma* of the metafor package  
190 (Viechtbauer 2010) in R 3.1.2 (R Core Team 2013). The moderators were spatial scale (linear  
191 and quadratic effects), direction of the association (susceptibility, defence), type of association  
192 (“classic”: associational defence/associational susceptibility, “contrast”: neighbor contrast  
193 defence/neighbor contrast susceptibility), interaction between direction and type of association  
194 and between type of association and spatial scale. To test the impact of the conversion of OR and  
195 Pearson’s  $r$  into  $d$ , we included the effect size class ( $d$ ,  $r$  or OR) in as a moderator. The proxy of  
196 spatial scale, the radius, was log-transformed to correct for its large dispersion (Bland and

197 Altman 1996). The function *rma* weights effect sizes using the inverse-variance method for  
198 mixed models following this equation (Viechtbauer 2010):

$$\frac{1}{(V_i + T^2)}$$

199 where  $V_i$  is an estimate of the within-study variance and  $T^2$  an estimate of between-studies  
200 variance, calculated from the effect sizes. The percent of heterogeneity between the effect sizes  
201 explained by a moderator was estimated by how much the addition of moderators reduced the  
202 estimate of residual amount of heterogeneity (Viechtbauer 2010). We further evaluated the  
203 heterogeneity of all effect sizes inside each moderator group (Figure 1) by calculating the value  
204 of  $I^2$ , the proportion of observed variance reflecting real differences among effect sizes  
205 (Borenstein et al. 2009); a small value of  $I^2$  indicates that all variance is spurious, while a high  
206 value indicates untested moderators. We tested the sensibility of our model to outliers  
207 (Viechtbauer and Cheung 2010) using the function *influence* of the metafor package  
208 (Viechtbauer 2010). We tested for publication bias using funnel plots with Egger's regression  
209 test (Sterne et al. 2001, Jennions et al. 2013) and the trim and fill method (Duval 2005, Jennions  
210 et al. 2013), using the *regtest* and *trimfill* functions of the metafor package for R 3.1.2 (R Core  
211 Team 2013) with standard error as the predictor (Viechtbauer 2010). Additionally, we performed  
212 a cumulative meta-analysis and tested year of publication as a moderator to ensure the absence of  
213 a temporal trend in the effect sizes (Koricheva et al. 2013b). All statistical analyses were  
214 performed using  $\alpha = 0.05$  and results are presented as means with 95% confidence intervals.

## 215 **Results**

216 The selected studies reported results related to over 51 focal species; 15 were reported in more  
217 than one article and only one out of 15 was not a woody plant (*Medicago sativa*). While most

218 woody plants were reported in two to three studies, *Pinus sylvestris* and *Picea abies* were the  
219 focal species in 11 and six articles, respectively. Over 70 different neighbor plants were found;  
220 *Betula pendula* was present in five articles but most neighbor species were reported in only one  
221 study. Twelve studies reported domestic sheep (*Ovis aries*) as herbivores, alone or among others.  
222 *Alces alces* and *Capreolus capreolus* were mentioned in eight studies and *Cervus elaphus* in  
223 seven studies. The extracted data were equally divided between decreased and increased  
224 susceptibility with neighboring plant, but “classical” types (associational defence and  
225 associational susceptibility,  $n = 104$ ) were more frequent than “contrast” types (neighbor contrast  
226 defence and neighbor contrast susceptibility,  $n = 47$ ). Additional summary data can be found in  
227 Appendix B.

228 The tested moderators explained 27% of the heterogeneity between effect sizes (omnibus test for  
229 moderators:  $Q_{df=10} = 50.5$ ,  $p < 0.0001$ ). There is, however, a high residual heterogeneity in the  
230 model (test for residual heterogeneity:  $Q_{df=157} = 1081.9$ ,  $p < 0.0001$ ). Associational susceptibility,  
231 neighbor contrast defence and neighbor contrast susceptibility had similar  $d$  values based on their  
232 estimates and 95% confidence interval, but associational defence effects were higher (Figure 1).  
233 The strength of associational effects increased by 15 % from 0 to 1 m and decreased by 22 % and  
234 56% from a radius of 1 m to a radius of 10 m and 100 m, respectively (Figure 2; intercept = 1.9  
235 [1.5, 2.3],  $z = 8.4$ ,  $p = < 0.0001$ ; linear estimate = (-0.1 [-0.3, 0.02],  $z = -1.7$ ,  $p = 0.08$ ; quadratic  
236 estimate = -0.02 [-0.05, -0.002],  $z = -2.1$ ,  $p = 0.03$ ). There was no interaction between the type of  
237 associational effects and spatial scale ( $z = -0.2$ ,  $p = 0.8$ ). The conversion of metrics used to  
238 express the effect size did not explain the variation between effect sizes ( $d$  vs OR-type:  $z = 1.4$ ,  $p$   
239 = 0.2;  $d$  vs r-type:  $z = 0.8$ ,  $p = 0.4$ , Figure 1). Except for the “contrast” associational effects, all  $I^2$   
240 were above 88%, indicating the presence of untested moderators.

241 The sensitivity analysis for outliers uncovered four effect sizes that could potentially change the  
242 results (ID 33, 64, 156 and 157, Supplement). One of those was the only analysis presenting a  
243 very large spatial scale (radius = 217.05 m, DeGabriel et al. 2011). We first analyzed the data  
244 without this effect size, which slightly decreased the p-value of the linear parameter of the slope  
245 to 0.06, and slightly changed the parameter of the slope (from -0.12 [-0.30, 0.02] to -0.15 [-0.30,  
246 0.01]). Second, we analyzed the data without each of the other outliers and only one (ID 64)  
247 could modify our conclusion, increasing the p-value of the linear and quadratic parameter of the  
248 slope to 0.20 and to 0.08, respectively. The effect size from that study was computed from two  
249 particularly high  $R^2$  values (0.96 and 0.61), combined as they represent a single combination of  
250 plant, spatial scale and herbivores. Because there was no reason to exclude any of those effect  
251 sizes based on the study characteristics, we kept the outliers in the final model (Viechtbauer and  
252 Cheung 2010) but we caution that the value of the relationship between scale and associational  
253 effect strength depends on these extreme data points. We also found some evidence of potential  
254 publication bias, again suggesting caution in the interpretation of the value of the summary effect  
255 size (Appendix C). In addition, our analyses revealed potential bias among the *d*-class effect  
256 sizes, but the trim-and-fill method indicates that our conclusion concerning the lack of difference  
257 between classes of effect size is robust (Appendix C). We found no evidence of a temporal trend  
258 (Appendix C).

## 259 **Discussion**

260 Using a meta-analysis based on 46 studies and 168 data points on the impact of neighboring  
261 plants on the susceptibility to herbivory, we found a slightly increasing associational effect  
262 strength between spatial scales of 0 to 1m, followed by a decrease in associational effect strength  
263 at larger scales. In contradiction with our hypothesis, this decrease did not interact with the type

264 of associational effect (i.e. “classic” or “contrast” type). There is a common agreement that  
265 spatial scale and herbivore hierarchical forage selection has been overlooked in associational  
266 effect studies (Barbosa et al. 2009, Hambäck et al. 2014, Underwood et al. 2014). Our study is  
267 the first pointing out the magnitude of change in associational effects with spatial scale and the  
268 first suggesting a threshold after which associational effects decreases. Even if strength decreases  
269 with scale, there are still large effects of neighboring species on the risk of browsing at large  
270 spatial scales; our model predicted a  $d$  of 1.74 at a range of 10 meters between the focal and  
271 neighboring plant, a considerable effect size according to Cohen’s rule of thumb (Cohen 1988).  
272 Moreover, our proxy of spatial scale is expressed as a one dimensional measure, but plant  
273 assemblage is a three dimensional measure and associational effects will thus impact larger areas  
274 than our analysis suggests. Few studies investigated associational effects at large scales; aside  
275 from the landscape level of DeGabriel et al. (2011) study (ID 33, Supplement), that was not  
276 intended to test associational effects, the largest scales of analysis can be found in the experiment  
277 of Vehviläinen and Koricheva (2006) and Milligan and Koricheva (2013) where plots of 400 m<sup>2</sup>  
278 were used (ID 78-115, Supplement).

279 According to Bergvall et al. (2006), “classical” effects influence patch choice by herbivores  
280 while “contrast” effects are expected to affect fine scale patch selection. We did not find support  
281 for this hypothesis as “classic” and “contrast” associational effects did not vary in strength with  
282 spatial scale. But because few associational effects were measured at large spatial scales, the  
283 model could have been unable to detect an interaction between type of association and scale.  
284 Aside from Bergvall et al. (2006) and their following work (Bergvall et al. 2008, Rautio et al.  
285 2008, Rautio et al. 2012), few authors have studied how spatial scaling relates to associational  
286 effects through the foraging behavior of large herbivores (but see Wang et al. 2010, Stutz et al.

287 2015). For small mammals, Emerson et al. (2012) tested associational effects at three spatial  
288 scales (among stations > among patches > within patches) with squirrels (*Sciurus* spp.), and  
289 found that both neighbor contrast susceptibility and associational defence occur among stations  
290 and among patches. At a larger scale, they found only associational defence; high palatability  
291 seeds were less susceptible in low palatability stations. The study of associational effects could  
292 be greatly improved by more experimentation with varying spatial scales, which could test the  
293 extent of associational susceptibilities and defences.

294 Associational effects vary in strength depending on whether they increase or decrease  
295 susceptibility to browsing and whether the neighboring plant is preferred or avoided by the  
296 herbivores. In their meta-analysis, Barbosa et al. (2009) stated that associational defence was  
297 more frequent for mammalian herbivores. In opposition, our results indicate that associations  
298 with a plant providing defense are not more frequent than associations with a plant increasing  
299 susceptibility to consumption. Associational susceptibility, neighbor contrast susceptibility and  
300 neighbor contrast defence had lower effect sizes than associational defence, but were as  
301 prevalent in the literature as defence associational effects. Because there was a high prevalence  
302 of woody plants in our dataset, a wider range of plant species could help disentangle which of  
303 increased defence or susceptibility in presence of neighbors is more prevalent for herbivores with  
304 movement abilities similar to deer. Woody plants could be more apparent to herbivores than  
305 herbaceous plants because of their larger size and longer life span (Haukioja and Koricheva 2000)  
306 and those differences could be reflected in associational effects. Most studies of associational  
307 effects involving herbaceous species that we reviewed measured the effects using parameters  
308 such as growth, height or survival and those parameters cannot distinguish herbivory effects  
309 from direct interactions such as competition or facilitation.

310 As with many meta-analyses, there are restrictions to the generalization of our results. First, our  
311 work was focused on herbivores with movement abilities similar to deer and the results cannot  
312 be exported to smaller mammals or invertebrates, as their foraging behavior is much different.  
313 Small, relatively more selective mammalian herbivores, can discriminate between plants at finer  
314 spatial scales and we should not find evidence for associational defence or neighbor contrast  
315 defence with them (Olf et al. 1999). For example, in one study roe deer (*Capreolus capreolus*)  
316 selected forages at both patch and species levels, while rabbits (*Oryctolagus cuniculus*) selected  
317 plants only at the species level and were not influenced by the spatial arrangement of plants  
318 (Bergman et al. 2005). Second, the large heterogeneity found in effect sizes (Figure 2) indicates  
319 that many untested moderators influenced the magnitude of associational effects and their  
320 interactions with scale. For example, we did not take into account the season; in seasonal  
321 environments selectivity could be lower in winter because of the lack of resources, thereby  
322 reducing the strength of associational effects. Many of the selected studies present survival or  
323 damage for an entire year and we combined the data from multiple seasons or years, which partly  
324 explain the remaining heterogeneity. Our goal was to explore general patterns, but we contend  
325 that multiple factors can influence associational effects, such as density of focal or neighbor  
326 plants (Emerson et al. 2012, Hambäck et al. 2014, Underwood et al. 2014), richness of food  
327 patches (Milligan and Koricheva 2013) or herbivore density (Aerts et al. 2007, Graff et al. 2007,  
328 Smit et al. 2007). Finally, we caution against the interpretation of the slope of the decline in  
329 associational effects with increasing spatial scale since we observed a large gap between studies  
330 reporting associational relationships at the patch scale ( $r \sim 10$  m) and one study reporting results at  
331 a much larger scale ( $r = 217$  m; DeGabriel et al. (2011)). Most data points around the patch scale  
332 are combined data from two papers presenting results from the same study with multiple



333 combinations of plant associations (Vehviläinen and Koricheva 2006 and Milligan and  
334 Koricheva 2013). In addition, the presence of an outlier (i.e. Häsler and Senn 2012) that can  
335 affect the slope of this relationship suggests caution in the interpretation of these results.

336 Associational effects could be used as a tool for managers in plant conservation. Considering that  
337 deer populations are generally increasing worldwide (Côté et al. 2004) and that complete deer-  
338 exclusion techniques such as fences are expensive to build and maintain (Lavsund 1987,  
339 Mackenzie and Keith 2009), the use of naturally occurring associational effects could reduce the  
340 susceptibility to herbivores of land conservation targets. For example, Aerts et al. (2007)  
341 recommend planting *Olea europaea* under pre-established pioneer shrubs that protect seedlings  
342 from domestic goat browsing (associational defence) in order to restore the dry afro-montane  
343 forest in Northern Ethiopia. Research on associational effects would also benefit from a  
344 combination with optimal resource selection and habitat selection approaches, as foraging rules  
345 of energy maximization can largely explain associational effects (Courant and Fortin 2010,  
346 Emerson et al. 2012). Information about the quantity and quality of resources could possibly  
347 explain a large part of the residual heterogeneity found in our meta-analysis, and might allow  
348 predictions about when and between which plants associational effects should occur.

349 In conclusion, our study revealed that associational effects vary with the spatial scale, a pattern  
350 likely explained by the influence of scale in herbivore resource selection. The strength of  
351 associational effects is stable or slightly increases at very small scales and decreases when the  
352 neighbor is more than 1 m away. Further studies on associational effects should take into account  
353 this effect of spatial scale and, if possible, study the phenomenon at multiple scales  
354 simultaneously. Associational effects *per se* have been quite well studied, but linking them to  
355 management and conservation could contribute to reducing problems in systems with

356 overabundant herbivores, for example by generating guidelines for seedling planting in  
357 restoration contexts. Stutz et al. (2015) suggested the strategic placement of seedlings in  
358 vegetation that induce associational defence and Torroba-Balmori et al. (2015) proposed the use  
359 of nurse plants to reduce acorn predation for the reintroduction of *Quercus* species in  
360 Mediterranean mined areas. As is suggested in our analysis, associational defence could  
361 effectively reduce herbivory and thus increase survival and growth of plants. Our study updates  
362 and extends previous work, providing new insights that should fuel further research, on the  
363 spatial range of associational effects, the spread of contrast type interactions and the prevalence  
364 of associational defence and susceptibility in large herbivores. We suggest a more systematic  
365 reporting of contextual data, such as herbivore densities, herbivore diet breadth and densities of  
366 neighboring and focal plants, as those variables could explain the high residual heterogeneity of  
367 associational effects.

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376

377 Table 1. Associational effects affecting susceptibility to herbivory based on the preference of the  
378 herbivore for the neighboring plant versus the focal plant and on the direction of the  
379 associational effect.

		Direction of associational effect	
		<b>Increase of susceptibility</b>	<b>Reduction of susceptibility</b>
Preference for the neighboring plant compared to the focal	<b>Preferred</b>	Associational susceptibility	Neighbor contrast defence
	<b>Avoided</b>	Neighbor contrast susceptibility	Associational defence

380

381 **Figure legends**

382 Figure 1. Summary of difference in damage/survival with and without a neighboring plant ( $d$ ,  
383 standardized difference of means) separated by the moderator levels tested, with 95% CI and  $I^2$ ,  
384 the percentage of total variability due to heterogeneity among  $d$ 's. A higher  $d$  indicates a higher  
385 associational effect of the neighboring plant on the focal plant's susceptibility to herbivory.  
386 Numbers to the right of the data points are the number of effect sizes in each summary effect.  
387 We used a meta-analysis mixed model to test the impact of moderators on the standardized  
388 difference of means.

389 Figure 2. Decrease in the difference in damage/survival with and without a neighboring plant  
390 (standardized difference of means) according to spatial scale (natural logarithm of radius of plot  
391 size + 0.001). The size of each point indicates the weight of each effect size in the meta-analysis  
392 mixed effect model, calculated with the inverse-variance method. Vertical lines and numbers  
393 above correspond to untransformed values of radius (m). Regression line results from a meta-  
394 analysis mixed model and dotted lines represent predicted values with 95% CI.

395

396 Figure 1.

Moderator level,  $I^2$  (%) [95% CI]

**Associational effect**

Associational susceptibility, 88 [ 81, 93 ]

Associational defence, 96 [ 95, 98 ]

Neighbor contrast susceptibility, 20 [ 61, 95 ]

Neighbor contrast defence 0 [ 0, 0 ]

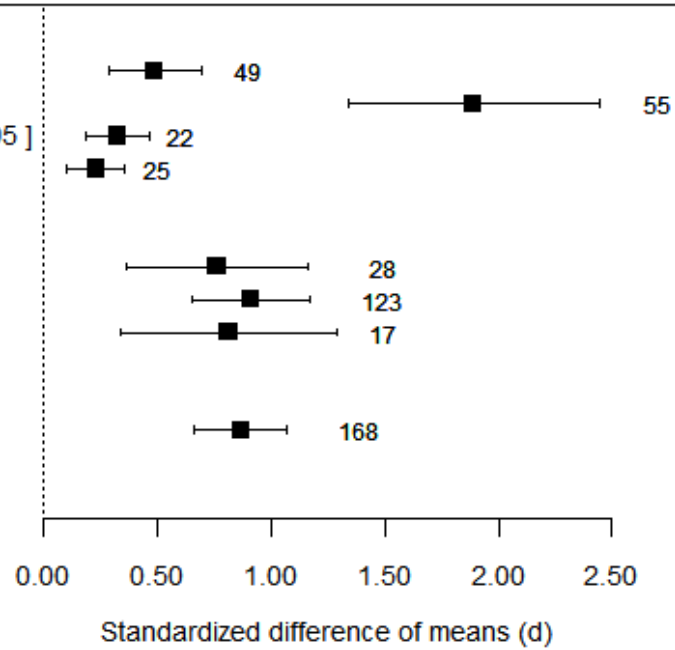
**Effect size class**

r, 94 [ 91, 97 ]

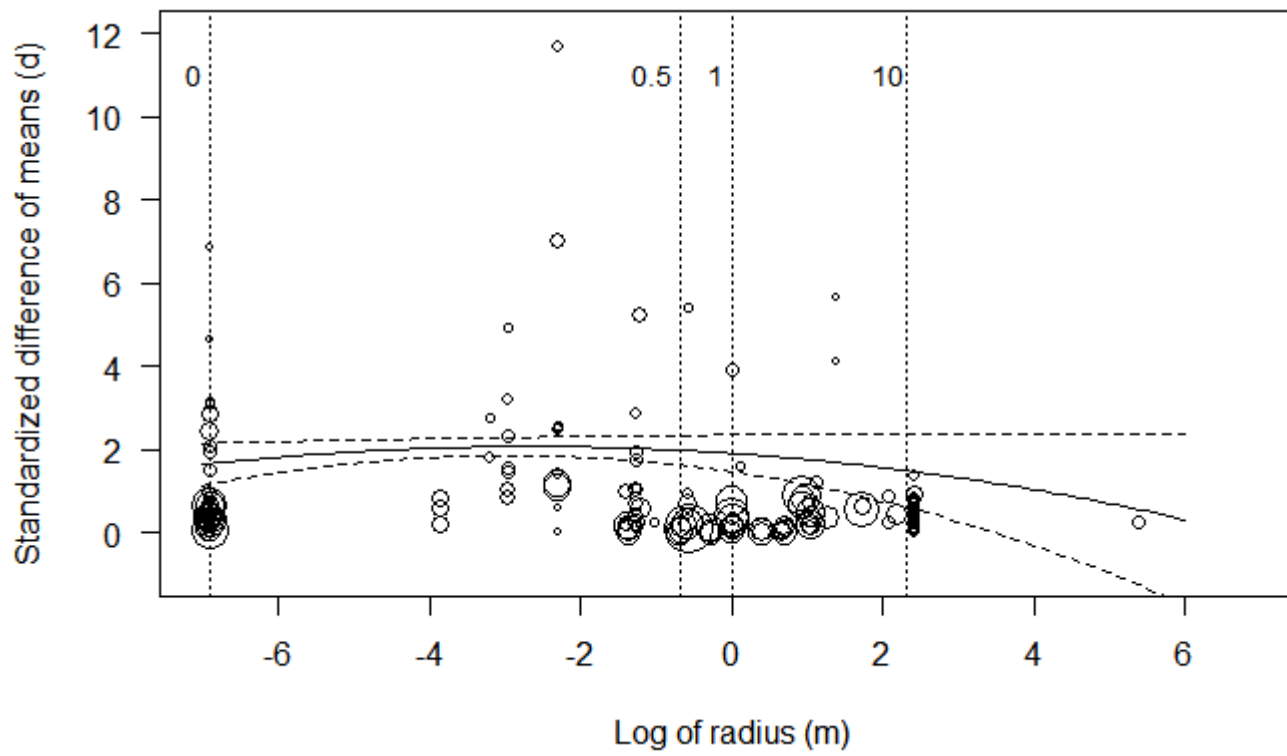
d, 94 [ 93, 96 ]

OR, 92 [ 79, 96 ]

Overall mean for all studies, 95 [ 94, 96 ]



398 Figure 2.



399

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