1 **Spatial scale influence 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 yet,

16   it is still unclear how the spatial scale of plant associations modulates foraging choice of animal;

17   an inherently spatial process in itself. Using a meta-analysis, we investigated how spatial scale

18   modifies associational effects of neighboring plants on the susceptibility to deer-sized herbivores.

19   From 2496 articles found in main literature databases, we selected 46 studies providing a total of

20   168 differences of means in damage or survival with and without neighboring plants. We tested

21   the impact of spatial scale, estimated as the distance between the focal plant and its neighbors,

22   and the type of associational on the effect sizes reported in these studies using a meta-analysis

23   mixed model. The strength of associational effects slightly increases between 0 and 1 m and

24   decrease at scales larger than 1 m. Associational defence (i.e. decrease in susceptibility with

25   repulsive neighbors) had stronger effects than any other type of associational effects, but was not

26   more frequent. Our study is the first addressing the magnitude of change in associational effects

27   with spatial scale. Further empirical studies should test associational effects between plants at

28   multiple spatial scales simultaneously. The high remaining heterogeneity between the studies

29   suggests that untested factors modulate associational effects, such as nutritional quality of focal

30   and neighboring plants or timing of browsing. Associational effects can be exploited as a

31   management tool to alleviate the effect of herbivores (e.g. planting susceptible plants under nurse

32   species) so understanding these intratrophic relationships shaping multitrophic interactions could

33   improve the utility of the tool.

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 itself determined the nutritional

40   requirements of the herbivores (Pyke et al. 1977), and by intrinsic (e.g. nutritive quality, Pyke et

41   al. 1977), and extrinsic characteristics of the plants and of the environment (e.g. vegetation

42   assemblage, Atsatt and O'Dowd 1976). Multiple studies have demonstrated the influence of

43   vegetation assemblage on forage selection, a process named neighboring or associational effects

44   (Milchunas and Noy-Meir 2002, Barbosa et al. 2009), yet the conditions in which a specific plant

45   assemblage will increase or reduce susceptibility to herbivory are still unclear. The distance

46   between neighboring plants could explain part of the residual variability observed in

47   associational effects (Underwood et al. 2014). Associational effects can be exploited as a

48   management tool to alleviate the effect of herbivores; for example, Perea and Gil (2014)

49   recommend planting seedlings under shrubs as to reduce damage by browsers. Understanding

50   these intratrophic relationships shaping multitrophic interactions could improve the utility of the

51   tool.

52   Four different types of associational effects on plant susceptibility to herbivores have been

53   described in the literature (Table 1), mostly depending on whether the neighboring plant

54   increases herbivory on a focal plant, i.e. the plant for which herbivory is measured (Thomas 1986,

55   Hjältén et al. 1993), or decreases it (Tahvanainen and Root 1972, Atsatt and O'Dowd 1976).

56   Associational susceptibility is the increase of herbivory damage in the presence of a preferred

57   neighboring plant (Thomas 1986, Hjältén et al. 1993) while associational defence, or

58   associational resistance, is the reduction of damage in the presence of an avoided neighboring

59   plant (Tahvanainen and Root 1972, Atsatt and O'Dowd 1976, Bergvall et al. 2006). Neighbor

60   contrast susceptibility (Bergvall et al. 2006), also known as the attractant-decoy hypothesis

61   (Atsatt and O'Dowd 1976) represents also an increase in susceptibility to herbivory, but in a

62   presence of an avoided neighbor. Its mirror interaction is the neighbor contrast defence, a

63   decrease of damage in presence of a preferred neighbor (Bergvall et al. 2006, Rautio et al. 2012).

64   A meta-analysis of all associational effects by Barbosa et al. (2009) revealed that associational

65   effects are influenced by herbivore taxonomy (e.g. mammals or insects), plant taxonomic

66   relatedness and the palatability of the neighboring plant, but unexplained variation remains in the

67   associational effects of neighboring plants on the susceptibility to herbivory.

68   Forage selection is a phenomenon inherently spatial and its impacts can be measured at multiple

69   spatial scales from the choice of a single bite to the establishment of a home range within the

70   distribution range of a species (Johnson 1980, Brown and Allen 1989, Bommarco and Banks

71   2003). At the intermediate scales of habitat and resource selection, the selection of feeding sites

72   or patches could promote associational susceptibility and defence (Bergvall et al. 2006).

73   Herbivore would select patches presenting preferred resources and consume other plants in those

74   patches (associational susceptibility) or avoid patches rich in avoided species (associational

75   defence). Smaller scales of selection, i.e. the selection of food items inside a patch, could

76   increase the occurrence of neighbor contrast susceptibility or defence, as those effects depend on

77   the contrast between plant palatability perceived by herbivores (Bergvall et al. 2006). Although

78   multiple spatial scales have been tested with invertebrate herbivores (Thomas 1986, Karban et al.

79   2006, Karban 2010), few experiments have tested the effect of hierarchical foraging on

80   associational effects. Exceptions include a study of red deer (*Cervus elaphus*) and sheep (*Ovis*

81   *aries*) showing decreased damages on *Calluna vulgaris* with increasing distance from a grass

82 patch (Hester and Baillie 1998), an associational susceptibility that disappeared at 1 to 3 m from

83 the grass patch, depending on herbivory pressure. Bergvall et al. (2006) tested the selection of

84 fallow deer (*Dama dama*) between patches and within patches of pellets with varying tannin

85 concentration. They found that palatable food was consumed more in the immediate

86 neighborhood of highly defended food (neighbor contrast susceptibility) and highly defended

87 food was less consumed in a high palatability neighborhood (neighbor contrast defence). As

88 stated by Underwood et al. (2014), empirical data and modeling of associational effects also

89 currently lack information on the role of spatial scale.

90 Here, we used a meta-analysis approach to determine whether the spatial scale modulates

91 associational effects of neighboring plants on the risk of herbivory. Because dispersal can affect

92 the potential for large scale associational effects (Grez and Gonzalez 1995), we controlled for

93 differences in dispersal capacity by restricting our study to deer-sized herbivores. Our first

94 objective is to characterize how associational effects vary in strength with spatial scale. Second,

95 we address whether the frequency of the various associational effects (associational

96 susceptibility and defence, neighbor contrast susceptibility and defence) varies with spatial scales.

97 We hypothesized that hierarchical forage selection determine the type of associational effect i.e.

98 associational susceptibility and associational defence ("classic" type) versus neighbor contrast

99 defence and susceptibility ("contrast" type), according to the conceptual framework provided by

100 Bergvall et al. (2006). We thus predicted an interaction between spatial scale and associational

101 effect type where "classic" associational effect type will be more frequent at large spatial scale,

102 and "contrast" type will be more frequent at fine scale. This study is the first to investigate global

103 spatial patterns in associational effects, an issue essential in understanding the intraspecific

104 variation in susceptibility to herbivory (Barbosa et al. 2009, Underwood et al. 2014).

105   **Methods**

106   *Literature review*

107   We obtained 2496 peer-reviewed articles using the search strategy presented in Appendix A in

108   ISI Web of Science, Biosis preview and BioOne, and through citations used in articles previously

109   found. We searched for studies involving herbivores with movement abilities similar to deer,

110   thus excluding small mammals or very large ones (e.g. elephant and giraffe). Studies reported

111   data on damage or survival on plants (hereafter called the focal plant) with and without the

112   presence of a neighboring plant (hereafter called the neighbor plant). We included studies using

113   feeding trials in controlled or natural environments, transplantation/removal of neighbors and

114   observations in natural environments.

115   We established the criteria regarding acceptance or rejection of a study prior to conducting the

116   meta-analysis using a PRISMA inspired protocol (see process in Appendix A, Moher et al. 2009).

117   The criteria were the presence of a control treatment (damage/survival without neighboring

118   plant), a palatable plant in the focal-neighbor group and a difference in palatability between

119   plants. To evaluate the effect of spatial scale, each study needed to clearly state the size of the

120   plot where data were recorded or the distance between the focal and neighboring plant. We

121   rejected data on seed predation a posteriori. A single observer (EC) reviewed and selected all

122   articles and recorded each rejection criterion. To ensure the reproducibility of article selection, a

123   second observer screened a subsample of 460 articles; the first and second observer agreed on

124   456 articles (452 rejected, 4 accepted) leading to a kappa statistic (Cohen 1960) of 0.66,

125   exceeding the level of 0.60 and thus indicating that article selection was reproducible (Côté et al.

126   2013). Following this procedure (Appendix A), we kept 46 articles from the original 2496

127   (Supplement).

128   *Data extraction and effect size computation*

129   For each article, a single observer (EC) extracted information regarding the study, such as the

130   type of experiment, identity of the herbivore, plot size, etc (see Appendix B for a complete list).

131   To compare associational effects among studies, we extracted means and variance of

132   damage/survival with and without neighboring plants. We used this information to compile

133   standardized effect sizes that indicate the size of the impact of neighboring plant on susceptibility

134   to herbivory of the focal plants (see below for details). We also extracted moderator variables, i.e.

135   a source of variation among studies that can account for part of the variability in effect sizes

136   (Koricheva et al. 2013a), such as the type of associational effect ("classic" i.e. associational

137   defence and susceptibility, or "contrast", i.e. neighbor contrast defence and susceptibility, Table

138   1) and the direction of the effect. By direction, we mean increase in susceptibility with neighbor

139   presence (now referred as the susceptibility subgroup) or decrease in susceptibility with neighbor

140   presence (now referred as the defence subgroup). Some studies measured associational effects in

141   plots while others rather reported a distance between focal and neighbor plants. We combined

142   those under a single variable, the radius (r), equivalent to the distance between the focal and

143   neighbor plant. We chose this metric because many studies centered a circular plot on the focal

144   plant. Variables extracted from articles are detailed in the Appendix B. Data presented in graphs

145   were extracted using Web Plot Digitizer V2.5 (Copyright 2010-2012 Ankit Rohatgi). We

146   contacted authors for missing data, such as plot size, variance, Pearson's r or precision on the

147   herbivore species. Effect sizes that can only be calculated through that supplementary

148   information are indicated in supplementary Table 2.

149   The data extraction provided 283 distinct observations of damage/survival with and without

150   neighboring plants. Data available in the form of means with variance were computed into

151   standardized mean difference (d), a common effect size used for meta-analysis in ecology

152   (Borenstein et al. 2009, Rosenberg et al. 2013). In the few cases where data were reported as

153   percentage of all focal plants browsed, we computed log odd ratios (OR) using a 2 x 2

154   contingency table with browsed/unbrowsed columns and with/without neighbors rows

155   (Borenstein et al. 2009, Rosenberg et al. 2013). Other studies correlated damage to the

156   abundance (e.g. cover) of the neighbor species and reported Pearson's r as an effect size statistic

157   (Borenstein et al. 2009, Rosenberg et al. 2013). Depending on whether the direction of the effect

158   was susceptibility or defence, values of d and Pearson's r could be negative or positive. We

159   transformed them into absolute values as the categorical variable "direction" already report

160   whether they belong to the increased susceptibility or increased defence subgroup (Appendix B).

161   Effect sizes computed as OR and r were converted into d and added into a single analysis using

162   equations from Borenstein et al. (2009). We selected d for common effect size as most data were

163   available as a difference of means (Appendix B) and because of its simple interpretation; the

164   higher the d value, the greater is the influence of the neighboring plant on the focal plant

165   susceptibility to herbivory. Although not frequently used (but see Hamm et al. 2010, Thomson et

166   al. 2013), converting effect sizes allow the inclusion of all data answering a same broad question

167   and avoid information loss through rejection of relevant studies (Borenstein et al. 2009).

168   When confronted with multiple effect sizes from one study, we extracted them all, unless a

169   global mean was available (e.g. Russell and Fowler 2004). In the final analysis, we kept only one

170   combination of neighboring plants, herbivore and spatial scale, similar to Barbosa et al. (2009),

171   which meant keeping more than one effect size per study in some cases. When the same

172   combination occurred in the same study, we combined those redundant effect sizes following

173   Borenstein et al. (2009) (Appendix A and Supplement for details). Following those steps, we

174   obtained a total of 168 effect sizes from 44 studies.

175   *Statistical analyses*

176   We tested the impact of moderators (i.e. independent variables) on the standardized difference of

177   mean (*d*) in a meta-analysis mixed model using the function *rma* of the metafor package

178   (Viechtbauer 2010) in R 3.1.2 (R Core Team 2013). The moderators were spatial scale (linear

179   and quadratic effects), direction of the association (susceptibility, defence), type of association

180   ("classic": associational defence/associational susceptibility, "contrast": neighbor contrast

181   defence/neighbor contrast susceptibility), interaction between direction and type of association

182   and between type of association and spatial scale. To test the impact of the conversion of OR and

183   Pearson's r into *d*, we included the effect size class (*d*, r or OR) in as a moderator. The proxy of

184   spatial scale, the radius, was log-transformed to correct for its large dispersion (Bland and

185   Altman 1996). The function *rma* weights effect sizes using the inverse-variance method for

186   mixed models following this equation (Viechtbauer 2010):

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

187   where V_i is an estimate of the within-study variance and T^2 an estimate of between-studies

188   variance, calculated from the effect sizes. The percent of heterogeneity between the effect sizes

189   explained by a moderator was estimated by how much the addition of moderators reduced the

190   estimate of residual amount of heterogeneity (Viechtbauer 2010). We further evaluated the

191   heterogeneity of all effect sizes inside each moderator groups (Figure 1) by calculating the value

192   of I^2, the proportion of observed variance reflecting real differences among effect sizes

193   (Borenstein et al. 2009); a small value of I^2 indicates that all variance is spurious, while a high

194 value indicates untested moderators. We tested the sensibility of our model to outliers

195 (Viechtbauer and Cheung 2010) using the function *influence* of the metafor package

196 (Viechtbauer 2010). We tested for publication bias using funnel plots with Egger's regression

197 test (Sterne et al. 2001, Jennions et al. 2013) and the trim and fill method (Duval 2005, Jennions

198 et al. 2013), using the *regtest* and *trimfill* functions of the metafor package for R 3.1.2 (R Core

199 Team 2013) with standard error as the predictor (Viechtbauer 2010). Additionally, we performed

200 a cumulative meta-analysis and tested year of publication as a moderator to ensure the absence of

201 a temporal trend in the effect sizes (Koricheva et al. 2013b). All statistical analyses were

202 performed using $\alpha = 0.05$ and results are presented as means with 95% confidence intervals.

203 **Results**

204 The selected studies reported results related to over 51 focal species; 15 were reported in more

205 than one article and only one out of 15 was not a woody plant (*Medicago sativa*). While most

206 woody plants were reported in two to three studies, *Pinus sylvestris* and *Picea abies* were the

207 focal species in 11 and six articles, respectively. Over 70 different neighbor plants were found;

208 *Betula pendula* was present in five articles but most neighbor species were reported in only one

209 study. Twelve studies reported domestic sheep (*Ovis aries*) as herbivore, alone or among others.

210 *Alces alces* and *Capreolus capreolus* were mentioned in eight studies and *Cervus elaphus* in

211 seven studies. The extracted data were equally divided between decreased and increased

212 susceptibility with neighboring plant, but "classical" types (associational defence and

213 associational susceptibility, n = 104) were more frequent than "contrast" types (neighbor contrast

214 defence and neighbor contrast susceptibility, n = 47). Additional summary data can be found in

215 Appendix B.

216 The tested moderators explained 27% of the heterogeneity between effect sizes (omnibus test for

217 moderators: $Q_{df = 10} = 50.5$, p < 0.0001). There is, however, a high residual heterogeneity in the

218 model (test for residual heterogeneity: $Q_{df = 157} = 1081.9$, p <0.0001). Associational susceptibility,

219 neighbor contrast defence and neighbor contrast susceptibility had similar *d* values, but

220 associational defence effects were higher (Figure 1). The strength of associational effects

221 increased by 15 % from 0 to 1 m and decreased by 22 % and 56% from a radius of 1 m to a

222 radius of 10 m and 100 m, respectively (Figure 2; intercept = 1.9 [1.5, 2.3], z = 8.4, p = < 0.0001;

223 linear estimate = -0.1 [-0.3, 0.02], z = -1.7, p = 0.08; quadratic estimate = -0.02 [-0.05, -0.002], z

224 = -2.1, p = 0.03). There was no interaction between the type of associational effects and spatial

225 scale (z = - 0.2, p = 0.8). The conversion of metrics used to express the effect size did not explain

226 the variation between effect sizes (*d* vs OR-type: z = 1.1, p = 0.3; *d* vs r-type: z = 0.9, p = 0.3,

227 Figure 1). Except for the "contrast" associational effects, all I^2 were above 88%, indicating the

228 presence of untested moderators.

229 The sensitivity analysis for outliers uncovered four effect sizes that could potentially change the

230 results (ID 33, 64, 156 and 157, Supplement). One of those was the only analysis presenting a

231 very large spatial scale (radius = 217.05 m, DeGabriel et al. 2011). We first analyzed the data

232 without this effect size, which slightly decreased the p-value of the linear parameter of the slope

233 to 0.06, and slightly changed the parameter of the slope (from -0.12 [-0.30, 0.02] to -0.15 [-0.30,

234 0.01]). Second, we analyzed the data without each of the other outliers and only one (ID 64)

235 could modify our conclusion, increasing the p-value of the linear and quadratic parameter of the

236 slope to 0.20 and to 0.08, respectively. The effect size from that study was computed from two

237 particularly high R^2 values (0.96 and 0.61), combined as they represent a single combination of

238 plant, spatial scale and herbivores. Because there was no reason to exclude any of those effect

239   sizes based on the study characteristics, we kept the outliers in the final model (Viechtbauer and

240   Cheung 2010) but we caution that the value of the relation between scale and associational effect

241   strength depends on these extreme data points. We also found some evidence of potential

242   publication bias, again suggesting caution in the interpretation of the value of the summary effect

243   size (Appendix C). In addition, our analyses revealed potential bias among the *d*-class effect

244   sizes, but the trim-and-fill method indicates that our conclusion concerning the lack of difference

245   between classes of effect size is robust (Appendix C). We found no evidence of a temporal trend

246   (Appendix C).

Discussion

248   Using a meta-analysis based on 46 studies and 168 data points on the impact of neighboring

249   plants on the susceptibility to herbivory, we found a slightly increasing associational effect

250   strength between spatial scales of 0 to 1m, followed by a decrease in associational effect strength

251   at larger scales. In contradiction with our hypothesis, this decrease did not interact with the type

252   of associational effect (i.e. "classic" or "contrast" type). There is a common agreement that

253   spatial scale and herbivore hierarchical forage selection has been overlooked in associational

254   effect studies (Barbosa et al. 2009, Hambäck et al. 2014, Underwood et al. 2014). Our study is

255   the first pointing out the magnitude of change in associational effects with spatial scale and the

256   first suggesting a threshold after which associational effects decreases. Even if strength decreases

257   with scale, there is still large effects of neighboring species on the risk of browsing at large

258   spatial scales; our model predicted a *d* of 1.74 at a range of 10 meters between the focal and

259   neighboring plant, a considerable effect size according to Cohen's rule of thumb (Cohen 1988).

260   Moreover, our proxy of spatial scale is expressed as a one dimension measure, but plant

261   assemblage is a three dimensional measure and associational effects will thus impact larger areas

262   than our analysis suggests. Few studies investigated associational effects at large scales; aside

263   from the landscape level of DeGabriel et al. (2011) study (ID 33, Supplement), that was not

264   intended to test associational effects, the largest scales of analysis can be found in the experiment

265   of Vehviläinen and Koricheva (2006) and Milligan and Koricheva (2013) where plots of 400 m^2

266   were used (ID 78-115, Supplement).

267   According to Bergvall et al. (2006), "classical" effects influence patch choice by herbivore while

268   "contrast" effects are expected to affect fine scale patch selection. We did not find support for

269   this hypothesis as "classic" and "contrast" associational effects did not vary in strength with

270   spatial scale. Because few associational effects were measured at large spatial scale, the model

271   could have been unable to detect an interaction between type of association and scale. Aside

272   from Bergvall et al. (2006) and their following work (Bergvall et al. 2008, Rautio et al. 2008,

273   Rautio et al. 2012), few authors have studied how spatial scaling relates to associational effects

274   through the foraging behavior of large herbivores (but see Wang et al. 2010). For small

275   mammals, Emerson et al. (2012) tested associational effects at three spatial scales (among

276   stations > among patches > within patches) with squirrels (*Sciurus* spp.), and found that both

277   neighbor contrast susceptibility and associational defence occur among stations and among

278   patches. At a larger scale, they found only associational defence; high palatability seeds were

279   less susceptible in low palatability stations. The study of associational effects could be greatly

280   improved by more experimentation with varying spatial scales, which could test the extent of

281   associational susceptibilities and defences.

282   Associational effects vary in strength depending on whether they increase or decrease

283   susceptibility to browsing and whether the neighboring plant is preferred or avoided by the

284   herbivores. In their meta-analysis, Barbosa et al. (2009) stated that associational defence was

285   more frequent for mammalian herbivores. In opposition, our results indicate that associations

286   with a plant providing defense are not more frequent than associations with a plant increasing

287   susceptibility to consumption. Associational susceptibility, neighbor contrast susceptibility and

288   neighbor contrast defence had lower effect sizes than associational defence, but were as

289   prevalent in the literature as defence associational effects. Because there was a high prevalence

290   of woody plants in our dataset, a wider range of plant species could help disentangle which of

291   increased defence or susceptibility in presence of neighbors is more prevalent for herbivores with

292   movement abilities similar to deer. Woody plants could be more apparent to herbivores than

293   herbaceous plants because of their larger size and longer life span (Haukioja and Koricheva 2000)

294   and those differences could be reflected in associational effects. Most studies of associational

295   effects involving herbaceous species that we reviewed measured the effects using parameters

296   such as growth, height or survival and those parameters cannot distinguished herbivory effects

297   from direct interactions such as competition or facilitation.

298   As with many meta-analyses, there are restrictions to the generalization of our results. First, our

299   work was focused on herbivores with movement abilities similar to deer and the results cannot

300   be exported to smaller mammals or invertebrates, as their foraging behavior is much different.

301   Small, relatively more selective mammalian herbivores, can discriminate between plants at finer

302   spatial scales and we should not find evidence for associational defence or neighbor contrast

303   defence with them (Olff et al. 1999). For example, roe deer (*Capreolus capreolus*) selected

304   forages at both patch and species levels, while rabbits (*Oryctolagus cuniculus*) selected plants

305   only at the species level and were not influenced by the spatial arrangement of plants (Bergman

306   et al. 2005). Second, the large heterogeneity found in effect sizes (Figure 2) indicates that many

307   untested moderators influenced the magnitude of associational effects and their interactions with

308   scale. For example, we did not take into account the season; in seasonal environments selectivity

309   could be lower in winter because of the lack of resources, thereby reducing the strength of

310   associational effects. Many of the selected studies present survival or damage for an entire year

311   and we combined the data from multiple seasons or years, which partly explain the remaining

312   heterogeneity. Our goal was to explore general patterns, but we contend that multiple factors can

313   influence associational effects, such as density of focal or neighbor plants (Emerson et al. 2012,

314   Hambäck et al. 2014, Underwood et al. 2014), richness of food patches (Milligan and Koricheva

315   2013) or herbivore density (Aerts et al. 2007, Graff et al. 2007, Smit et al. 2007). Finally, we

316   caution against the interpretation of the slope of the decline in associational effects with

317   increasing spatial scale since we observed a large gap between studies reporting associational

318   relationships at the patch scale (r~10 m) and one study reporting results at a much larger scale

319   (r=217 m; DeGabriel et al. (2011). Most data point around the patch scale are combined data

320   from two papers presenting results from the same study with multiple combination of plant

321   associations (Vehviläinen and Koricheva 2006 and Milligan and Koricheva 2013). In addition,

322   the presence of an outlier (i.e. Häsler and Senn 2012) that can affect the slope of this relation

323   suggests caution in the interpretation of these results.

324   Associational effects could be used as a tool for managers in plant conservation. Considering that

325   deer populations are generally increasing worldwide (Côté et al. 2004) and that complete deer-

326   exclusion techniques such as fences are expensive to build and maintain (Lavsund 1987,

327   Mackenzie and Keith 2009), applied research on associational effects could provide alternative

328   conservation methods based on associational effects. For example, Aerts et al. (2007)

329   recommend planting *Olea europaea* under preestablished pioneer shrubs that protect seedlings

330   from domestic goat browsing (associational defence) in order to restore the dry afromontane

331   forest in Northern Ethiopia. Research on associational effects would also benefit from a

332   combination with optimal resource selection and habitat selection approaches, as foraging rules

333   of energy maximization can largely explain associational effects (Courant and Fortin 2010,

334   Emerson et al. 2012). Information about the quantity and quality of resources could possibly

335   explain a large part of the residual heterogeneity found in our meta-analysis, and allow

336   predictions about when and between which plants associational effects should occur.

337   In conclusion, our study revealed that associational effects vary with the spatial scale, a pattern

338   likely explained by the influence of scale in herbivores' resource selection. The strength of

339   associational effects are stable or slightly increases at very small scale and decreases when the

340   neighbor is more than 1 m away. Further studies on associational effects should take into account

341   this effect of spatial scale and, if possible, study the phenomenon at multiple scales

342   simultaneously. Associational effects have been largely studied, but linking them to management

343   and conservation could contribute to reduce problems in systems with overabundant herbivores,

344   for example. Our study updates and extends previous work, providing new insights that should

345   fuel further research, on the spatial range of associational effects, the spread of contrast type

346   interactions and the prevalence of associational defence and susceptibility in large herbivores.

347   We suggest a more systematic reporting of contextual data, such as herbivore densities,

348   herbivore diet breath and densities of neighboring and focal plants, as those variables could

349   explain the high residual heterogeneity of associational effects.

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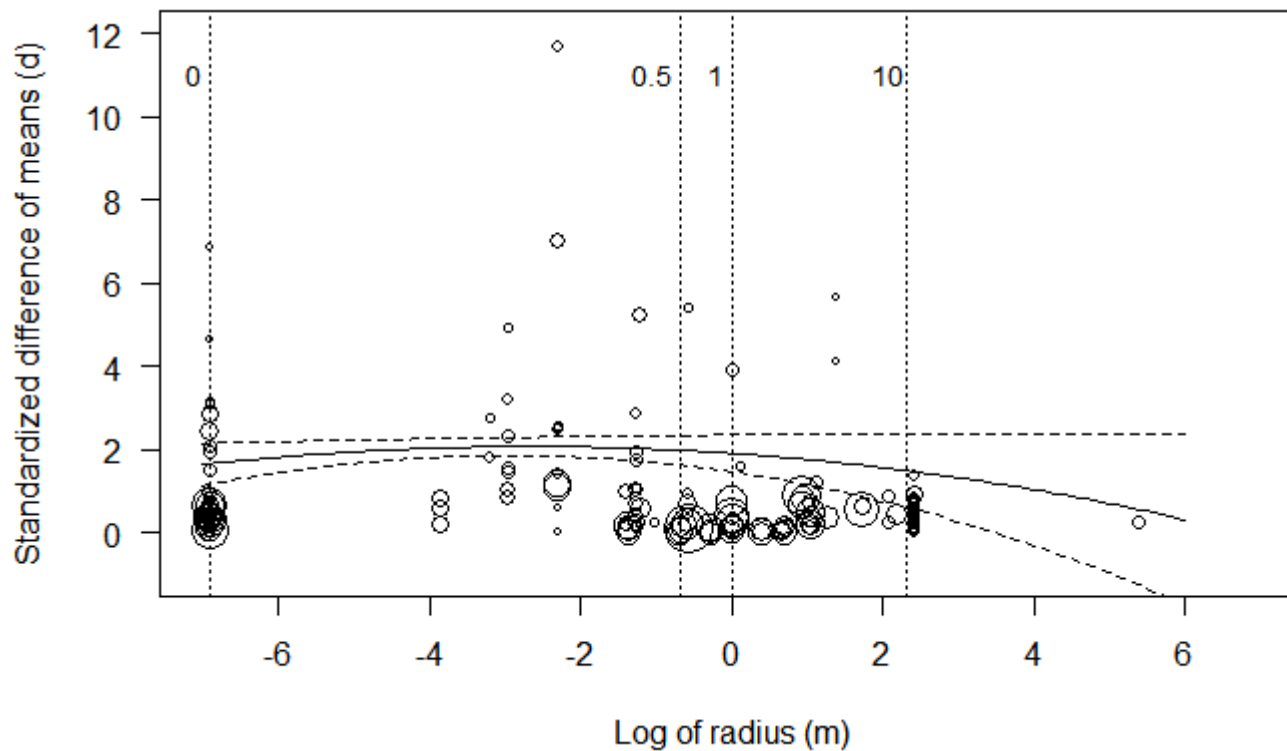
Figure 1. Summary of difference in damage/survival with and without a neighboring plant (*d*, standardized difference of means) separated by the moderator levels tested, with 95% CI and I^2, the percentage of total variability due to heterogeneity among *d*'s. A higher *d* indicates a higher associational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

363

364   Figure 2. Decrease in the difference in damage/survival with and without a neighboring plant (standardized difference of means)

365   according to spatial scale (natural logarithm of radius of plot size + 0.001). The size of each point indicates the weight of each effect

366   size in the meta-analysis mixed effect model, calculated with the inverse-variance method. Vertical lines and numbers above

367   correspond to untransformed values of radius (m). Regression line results from a meta-analysis mixed model and dotted lines

368   represent predicted values with 95% CI.

369   Table 1. Associational effects affecting susceptibility to herbivory based on the

370   preference of the herbivore for the neighboring plant versus the focal plant and on the

371   direction of the associational effect.

Direction of associational effect

		Increase of susceptibility	Reduction of susceptibility
Preference for the neighboring plant compared to the focal	**Preferred**	Associational susceptibility	Neighbor contrast defence
	Avoided	Neighbor contrast susceptibility	Associational defence

372

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