1 **Spatial extent of neighboring plants influences the strength of associational effects on**

2 **mammal herbivory. Insights from a meta-analysis**

3 Emilie Champagne[1], Jean-Pierre Tremblay[1,2], Steeve D. Côté[1]

4 [1]Département de biologie & Centre d'études nordiques, Université Laval, 1045 ave de la

5 Médecine, Québec, (Québec) G1V 0A6, Canada, emilie.champagne.2@ulaval.ca, jean-

6 pierre.tremblay@bio.ulaval.ca, steeve.cote@bio.ulaval.ca

7 [2] Centre d'étude de la forêt, Université Laval, Québec (Québec) G1V 0A6, Canada

8

9 Corresponding author : emilie.champagne.2@ulaval.ca

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11 **Abstract**

12 There is high variability in the level of herbivory between individual plants from the same

13 species with potential effects on population dynamics, community composition, and ecosystem

14 structure and function. This variability can be partly explained by associational effects i.e. the

15 impact of the presence of neighboring plants on the level of herbivory experienced by a focal

16 plant, but it is still unclear how the spatial scale of plant neighborhood modulates foraging choice

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

18 spatial scale modifies associational effects on the susceptibility to browsing by herbivores with

19 movement capacities similar to deer. From 2496 articles found in literature databases, we

20 selected 46 studies providing a total of 168 differences of means in damage by herbivores or

21 survival to woody plants (mostly) with and without neighboring plants. Spatial scales were

22 reported as distance between plants or as plot size. We estimated the relationships between the

23 effect sizes and spatial scale, type of associational effects and nature of the experiment using

24 meta-analysis mixed models. The strength of associational effects declined with increasing plot

25 size, regardless of the type of associational effects. Associational defences (i.e. decrease in

26 herbivory for focal plants associated with unpalatable neighbors) had stronger magnitude than

27 associational susceptibilities. The high remaining heterogeneity among studies suggests that

28 untested factors modulate associational effects, such as nutritional quality of focal and

29 neighboring plants, density of herbivores, timing of browsing, etc. Associational effects are

30 already considered in multiple restoration contexts worldwide, but a better understanding of

31 these relationships could improve their use in conservation, restoration and forest exploitation

32 when browsing is a concern. This study is the first to investigate spatial patterns of associational

33 effects across species and ecosystems, an issue that is essential to determine differential

34 herbivory damages among plants.

35   Keywords: neighboring effects, attractant-decoy hypothesis; associational resistance; plant-

36   herbivore relationships, spatial scale, meta-analysis

Introduction

Herbivory can modify the composition, structure and functions of ecosystems (Hester et al. 2006). There is high variability in the susceptibility of different plant species and individuals to herbivory. This variability is driven by forage selection, whom in itself is determined by the nutritional requirements of herbivores (Pyke et al. 1977), intrinsic (e.g. nutritive quality, Pyke et al. 1977), and extrinsic characteristics of both the plants and the environment (e.g. neighboring plants, Atsatt and O'Dowd 1976). Multiple studies have demonstrated the influence of neighboring plants on forage selection, a process named neighboring or associational effects (Milchunas and Noy-Meir 2002, Barbosa et al. 2009), yet the conditions in which a specific neighborhood will increase or reduce herbivory are not fully understood. The distance between neighboring plants could explain part of the residual variability observed in associational effects (Underwood et al. 2014). Associational effects can be exploited as a management tool to alleviate the effect of herbivores; for example, Perea and Gil (2014) recommend planting seedlings under shrubs to reduce damage to the seedlings by browsers. Other recent studies (Noumi et al. 2015, Stutz et al. 2015, Torroba-Balmori et al. 2015) explored the application and limits of associational effects for the restoration of plant species, but without considering the spatial extent of plant neighborhood, although Stutz et al. (2015) quantified vegetation variables at two spatial scales. A better understanding of associational effects could improve and generalize their use in restoration, conservation and exploitation.

Four different types of associational effects have been described in the literature (Figure 1a), depending on the difference in palatability between the focal and the neighboring plants: (1) associational susceptibility involves a neighboring plant preferred to the focal plant, leading to increased consumption of the focal (Thomas 1986, Hjältén et al. 1993); (2) neighbor contrast

60   defence describes the situation where the preferred neighbor concentrates the browsing pressure,

61   thus decreasing herbivory on the focal plant (Bergvall et al. 2006, Rautio et al. 2012); (3)

62   neighbor contrast susceptibility occurs when the less preferred or avoided neighbor leads to

63   higher herbivory level on the focal plant (Bergvall et al. 2006; attractant-decoy hypothesis, Atsatt

64   and O'Dowd 1976); (4) associational defence, or associational resistance, occurs when a less-

65   preferred plant provides a protection from herbivory to the focal plant (Tahvanainen and Root

66   1972, Atsatt and O'Dowd 1976, Bergvall et al. 2006). A meta-analysis of all four associational

67   effects by Barbosa et al. (2009) revealed that the direction and strength of effects are influenced

68   by herbivore taxonomy (e.g. mammals or insects), plant taxonomic relatedness and the

69   palatability of the neighboring plant, but unexplained variation remains. The focus of this meta-

70   analysis is the contribution of the spatial scale of the neighborhood to the unexplained variation

71   in associational effects.

72   Forage selection is an inherently spatial phenomenon and its impacts can be measured at

73   multiple spatial scales from the choice of a single bite to the establishment of a home range

74   within the distribution range of a population (Johnson 1980, Brown and Allen 1989, Bommarco

75   and Banks 2003). At the scale of the feeding site or the patch, Bergvall et al. (2006) predicted

76   higher occurrence of associational susceptibility and associational defence effects (Figure 1,

77   effects 1 and 4). The decision to use a patch should be a function of the relative attraction of

78   adjacent patches based on the palatability and abundance of plants composing them favoring

79   classic susceptibility or defence effects (Figure 1, effects 1 and 4). Within a patch, Bergvall et al.

80   (2006) predicted higher occurrence of neighbor contrast defence or susceptibility (Figure 1,

81   effects 2 and 3), because the choice made by the animal would then be a function of its ability to

82   detect differences in palatability of adjacent plants. Although multiple spatial scales have been

83   tested with invertebrate herbivores (Thomas 1986, Karban et al. 2006, Karban 2010), few

84   experiments have tested the effect of hierarchical foraging on associational effects. Exceptions

85   include a study of red deer (*Cervus elaphus*) and sheep (*Ovis aries*) showing decreased herbivory

86   on *Calluna vulgaris* with increasing distance from preferred grass patches (Hester and Baillie

87   1998); this associational susceptibility disappeared at 1 to 3 m from the grass patch, depending

88   on herbivory pressure. Bergvall et al. (2006) tested the selection of fallow deer (*Dama dama*)

89   between patches and within patches of pellets with varying tannin concentration. They found that

90   palatable food was consumed more in the immediate neighborhood of highly defended food

91   (neighbor contrast susceptibility) and highly defended food was consumed less in a high

92   palatability neighborhood (neighbor contrast defence). Underwood et al. (2014), also raised that

93   empirical studies and modeling of associational effects currently lack consideration for the role

94   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 level 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 roe deer (*Capreolus capreolus*) to moose (*Alces*

100   *alces)*, and including herbivores from other groups of similar body sizes, such as wild boar (*Sus*

101   *scrofa*) and Western grey kangaroo (*Macropus fuliginosus*). Our first objective was to

102   characterize how associational effects vary in strength, depending on their type (numbers 1 to 4,

103   Figure 1). Second, we described how associational effects vary in strength with the spatial scale

104   considered. We hypothesized that hierarchical forage selection determines the most frequent type

105   of associational effects within and between patches, i.e. the "classic" type (associational

106   susceptibility and associational defence) or the "contrast" type (neighbor contrast defence and

107   susceptibility), according to the conceptual framework provided by Bergvall et al. (2006). We

108   thus predicted an interaction between distance and associational effect type (Figure 1b) where

109   associational susceptibility or defence would be more frequent at larger spatial scales (home

110   ranges, patches) when herbivore select resources based on the relative abundance of resources,

111   while "neighbor contrast" would be more frequent once herbivores are feeding within a patch

112   and selecting individual plant species. This study is the first to investigate how spatial scale

113   drives associational effects across herbivore species and ecosystems, an issue essential for

114   understanding variations in the level of herbivory incurred by individuals within a population

115   (Barbosa et al. 2009, Underwood et al. 2014).

116   **Methods**

117   *Literature review*

118   We obtained 2496 peer-reviewed publications using the search strategy presented in Appendix A

119   in ISI Web of Science, Biosis preview and BioOne (in July 2013), and through citations found in

120   these publications. We searched for studies involving herbivores with movement capacities

121   similar to deer from the smallest to the largest deer species; the smallest herbivore in our dataset

122   is European roe deer and the largest is the European bison (*Bison bonasus)*. Studies reported data

123   on damage or survival of plants (hereafter called the focal plants) with and without the presence

124   of a neighboring plant (hereafter called the neighbor plant). Damage was inferred from counts of

125   browsed twigs or leaves, or biomass removal and did not include measures of growth or

126   regrowth following herbivory. We included studies using feeding trials in controlled or natural

127   environments, transplantation/removal of neighbors and observations in natural environments.

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

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

130   The criteria were the presence of a control treatment (herbivory without neighboring plant), a

131   palatable plant in the focal-neighbor group, and a difference in palatability between plants. To

132   evaluate the effect of spatial scale, each study needed to clearly state the size of the plot where

133   data were recorded or the distance between the focal and neighboring plant. We rejected data on

134   seed predation a posteriori. A single observer (EC) reviewed and selected all articles and

135   recorded each rejection criterion. To ensure the reproducibility of study selection, a second

136   observer screened a subsample of 460 publications; the first and second observers agreed on 456

137   publications (452 rejected, 4 accepted) leading to a kappa statistic (Cohen 1960) of 0.66,

138   exceeding the level of 0.60 and thus indicating that publication selection was reproducible (Côté

139   et al. 2013). Following this procedure (Appendix A), we kept 46 publications from the original

140   2496 (Supplement).

141   *Data extraction and effect size computation*

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

143   nature of the experiment, identity of the herbivore, plot size, etc. (see Appendix B for a complete

144   list). To compare associational effects among studies, we extracted means and variance of

145   damage and/or survival with and without neighboring plants. We used this information to

146   compile standardized effect sizes that indicate the size of the impact of a neighboring plant on

147   herbivory on the focal plants (see below for details). We also extracted independent variables,

148   such as the type of associational effect ("classic" or "contrast", Figure 1) and the direction of the

149   effect. By direction, we mean the effect on the level of herbivory on the focal plant (Figure 1),

150   which is increase in herbivory (now referred as the susceptibility subgroup) or decrease in

151   herbivory (now referred as the defence subgroup). Some studies measured associational effects

152   in plots while others reported a linear distance between focal and neighbor plants. We decided

153   not to combine the plot-based and distance-based studies because of the variation in the spatial

154   range they covered (plot-based studies: range varying from 0.01 m^2 to 148 000 m^2 with a median

155   = 27.5 m^2, distance-based studies: range from 0 to 2 m, median = 0.02 m). Focal plants located

156   underneath their neighbor without further indication were given a distance value of 0. Variables

157   extracted from articles are detailed in the Appendix B. Data presented in graphs were extracted

158   using Web Plot Digitizer V2.5 (Copyright 2010-2012 Ankit Rohatgi). We contacted authors for

159   missing data, such as plot size, variance, Pearson's r or identity of the herbivore species (See

160   supplementary Table 2).

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

162   neighboring plants. Data reported as means with variance were transformed into standardized

163   mean difference (*d*), a common effect size used for meta-analysis in ecology (Borenstein et al.

164   2009, Rosenberg et al. 2013). In the few cases where data were reported as percentage of all

165   focal plants browsed, we computed log odd ratios (OR) using a 2 x 2 contingency table with

166   browsed/unbrowsed columns and with/without neighbors rows (Borenstein et al. 2009,

167   Rosenberg et al. 2013). Other studies correlated damage to the abundance (e.g. cover) of the

168   neighbor species and reported Pearson's r as an effect size statistic (Borenstein et al. 2009,

169   Rosenberg et al. 2013). Depending on whether the direction of the effect was susceptibility or

170   defence, values of *d* and Pearson's r could be negative or positive. We transformed them into

171   absolute values as the categorical variable "direction" already reports whether they belong to the

172   increased susceptibility or increased defence subgroups (Appendix B). Effect sizes computed as

173   OR and r were converted into *d* and added into a single analysis using equations from Borenstein

174 et al. (2009). We selected *d* for common effect size as most data were available as a difference of

175 means (Appendix B) and because of its simple interpretation; the higher the *d* value, the greater

176 is the influence of the neighboring plant on the focal plant herbivory level. Although not

177 frequently used (but see Hamm et al. 2010, Thomson et al. 2013), converting effect sizes allows

178 the inclusion of all data answering the same broad question and avoids information loss through

179 rejection of relevant studies (Borenstein et al. 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 (distance between neighbors or

183 plot size), similar to Barbosa et al. (2009), which meant keeping more than one effect size per

184 study in some cases. When the same combination occurred in the same study, we combined

185 those redundant effect sizes following Borenstein et al. (2009) (Appendix A and Supplement for

186 details). Following those steps, we obtained a total of 168 effect sizes from 44 studies.

187 *Statistical analyses*

188 We tested the impact of independent variables on the standardized difference of mean (*d*) in

189 three meta-analysis mixed models using the function *rma* of the metafor package (Viechtbauer

190 2010) in R 3.1.2 (R Core Team 2013). For our first objective, we used the complete dataset to

191 test the variation in effect size depending on the direction of the association (susceptibility,

192 defence; figure 1a), type of association ("classic": associational defence/associational

193 susceptibility, "contrast": neighbor contrast defence/neighbor contrast susceptibility; figure 1a)

194 and interaction between direction and type of association. We also included the nature of the

195 experiment (feeding trial, observation study, transplantation or removal experiments) since effect

196 sizes from controlled experiments such as feeding trials could be stronger than results of

197   observational studies where foraging by herbivores would be influenced by uncontrolled factors.

198   The conversion of OR and r in *d* could have generated a bias in the values of the effect sizes; we

199   tested this supposition in a simple model with effect size class (d, r or OR) as an independent

200   variable. Since effect size class did not influence the value of *d* (*d*-class compared to OR-class: z

201   = -0.2, p = 0.8; compared to r-class: z = -0.5, p = 0.6), we did not include it in our final model.

202   For our second objective, we tested the effect of spatial scale on associational effect strength for

203   plot-based and distance-based studies separately. We log-transformed plot size to control for its

204   large dispersion (Bland and Altman 1996). For both models, together with the variables

205   describing the linear and quadratic parameters for the spatial scale (log plot size or linear

206   distance), we included the type of association and their interactions to test for predictions of

207   higher frequency of "classic" interaction at a finer scales and higher frequency of "contrast"

208   interaction at a larger scales (Figure 1b). Both models also included the nature of the experiment

209   as an independent variable to control for differences in effect sizes from different experiments.

210   The function *rma* weights effect sizes using the inverse-variance method for mixed models

211   following this equation (Viechtbauer 2010):

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

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

213   variance, calculated from the effect sizes. The percentage of heterogeneity in the effect sizes

214   explained by independent variables was estimated by how much the addition of variables

215   reduced the estimate of residual heterogeneity (Viechtbauer 2010). We further evaluated the

216   heterogeneity of all effect sizes inside each level of independent variables by calculating the

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

218   (Borenstein et al. 2009); a 0 value of I^2 indicates no between-study variation, while a high value

219   indicates untested independent variables.

220   We tested the sensibility of our model to outliers (Viechtbauer and Cheung 2010) using the

221   function *influence* of the metafor package (Viechtbauer 2010). We tested for publication bias

222   using funnel plots with Egger's regression test (Sterne et al. 2001, Jennions et al. 2013) and the

223   trim and fill method (Duval 2005, Jennions et al. 2013), using the *regtest* and *trimfill* functions of

224   the metafor package for R 3.1.2 (R Core Team 2013) with standard error as the predictor

225   (Viechtbauer 2010). Additionally, we performed a cumulative meta-analysis and tested year of

226   publication as an independent variable to ensure the absence of a temporal trend in the effect

227   sizes (Koricheva et al. 2013). All statistical analyses were performed using $\alpha = 0.05$ and results

228   are presented as means with 95% confidence intervals.

229   **Results**

230   The selected studies reported results related to over 51 focal plant species; 15 were reported in

231   more than one article and only one out of 15 was not a woody plant (*Medicago sativa*). Most

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

233   focal species in 11 and six articles, respectively. Over 70 different neighbor plant species were

234   found; *Betula pendula* was present in five articles, but most neighbor species were reported in

235   only one study. Twelve studies reported domestic sheep (*Ovis aries*) as the main herbivore. *Alces*

236   *alces* and *Capreolus capreolus* were mentioned in eight studies and *Cervus elaphus* in seven

237   studies. The extracted data were equally distributed between decreased and increased herbivory

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

239   susceptibility, n = 104) were more frequent than "contrast" types (neighbor contrast defence and

240   neighbor contrast susceptibility, n = 47). Most effect sizes resulted from feeding trials (n = 71),

241   where various assemblages were proposed to herbivores, but 54 came from observational studies

242   and 38 from transplantation experiments. Removal experiments were rarely used (n = 5).

243   Additional summary data can be found in Appendix B.

244   The first model using the complete dataset explained 23% of the heterogeneity between effect

245   sizes (omnibus test for independent variables: $Q_{df = 8} = 50.0$, p < 0.0001) and the pseudo-R^2 for

246   the model reached 23.0%. There was, however, a high residual heterogeneity in the model (test

247   for residual heterogeneity: $Q_{df = 159} = 1047.0$, p <0.0001). Effect sizes for defence associational

248   effects (associational defence and neighbor contrast defence) had a greater magnitude than

249   susceptibility associational effects (associational susceptibility and neighbor contrast

250   susceptibility; Figure 2). Classic associational effects also had a greater value than contrast

251   associational effects (Figure 2). Except for the contrast level of associational effects, all I^2 were

252   above 70%, indicating the presence of untested variables (Figure 2). Transplantation experiments

253   presented the strongest and more variable values of d, while feeding trials found consistently

254   small associational effects (Figure 2); values for observational studies were intermediate (Figure

255   2) .

256   The model of the effect of plot size on associational effects explained 68% of the heterogeneity

257   (omnibus test for independent variables $Q_{df = 9} = 28.5$, p = 0.0008, pseudo-R^2 = 19.6 %) but also

258   presented high remaining heterogeneity ($Q_{df = 86} = 312.9$, p <0.0001). As the log-plot size

259   increased, there was a linear decrease in the strength of associational effects (Figure 3a, estimate

260   = -0.13 [-0.22, -0.05]). There was no interaction between the type of associational effect and plot

261   size (z = -0.22, p = 0.8). The model of the relationships between associational effect size and

262   distance between the focal and neighboring plant explained a low amount of heterogeneity (3%;

263   pseudo-R^2 = 19.1 %; omnibus test for independent variables $Q_{df = 6} = 20.5$, p = 0.002) and

264 consequently had a high amount of remaining heterogeneity ($Q_{df = 65} = 674.0$, p <0.0001). There

265 was no effect of the distance between neighbors on the strength of associational effects (linear

266 estimate: z = -0.1, p = 0.2; quadratic estimate: z = -0.1, p = 0.9), nor of the interaction between

267 distance and type of associational effect (z = 0.4, p = 0.7). Visual examination of the data

268 revealed a sharp decline in effect size after 0.1 m (Figure 3b).

269 The sensitivity analysis for outliers uncovered nine effect sizes that could potentially change the

270 results in the associational effect type model, seven in the spatial scale model with plot-based

271 studies and three in the spatial scale model with distance-based studies. We analyzed each of the

272 models without each of their outliers sequentially. In the associational effect type model, the

273 removal of the data from a transplantation study (ID 156-157, Supplement) makes the nature of

274 the experiment different (observational studies significantly higher from the others) while

275 removing ID 64 (Häsler and Senn 2012) generates an interaction between type and direction of

276 effect size. The effect size from that study was computed from two particularly high R^2 values

277 (0.96 and 0.61), combined as they represented a single combination of plants, distance and

278 herbivores. Removing the only observation presenting a very large spatial scale (size = 148 000

279 m^2, DeGabriel et al. 2011) did not modify the relationship with plot size in the spatial scale

280 model. Because there was no reason to exclude any of those effect sizes based on the study

281 characteristics, we kept the outliers in the final model (Viechtbauer and Cheung 2010). We also

282 found some evidence of potential publication bias in funnel plots for the entire dataset and used

283 the trim and fill method to test the robustness of the overall mean effect size (Appendix C). The

284 trim and fill method identifies and correct the asymmetry by imputing smaller effect sizes around

285 an estimated true center (Viechtbauer 2010). For the entire dataset, the trim and fill method

286 generated more values of associational susceptibilities, suggesting either a publication bias in the

287   analyses or a naturally higher frequency of associational defences (Appendix C). In addition, our

288   analyses revealed potential publication bias among the effect sizes calculated as difference of the

289   means (effect size of class *d*) and in observational studies (Appendix C). Even with input values,

290   the *d*-class subgroup mean is similar to the r and OR-class subgroups and thus should not modify

291   our conclusions. The trim and fill method suggests more associational susceptibilities in the

292   observational studies subgroup, but this asymmetry could also result from the higher natural

293   occurrence of associational defences. We found no evidence of a temporal trend (Appendix C).

Discussion

295   Using a meta-analysis based on 46 studies and 168 data points on associational effects of

296   neighboring plants on the level of herbivory, we found a decrease in associational effect strength

297   with spatial scale. In contradiction with our hypothesis, the decrease was independent of the type

298   of associational effect (i.e. "classic" or "contrast" type). We also found that associational

299   defences had stronger effects than associational susceptibilities. There is a common agreement

300   that hierarchical forage selection has been overlooked in associational effect studies (Barbosa et

301   al. 2009, Hambäck et al. 2014, Underwood et al. 2014). Our study is the first pointing out the

302   magnitude of change in associational effects with spatial scale.

303   The descriptors of spatial scale, i.e. presence of neighbors in a plot or distance between focal and

304   neighbor, highly influenced the relation between scale and associational effects. Distance

305   between plants is a one-dimensional measure, mostly used when studying the relationships

306   between two individual plants (e.g. nurse plant studies or in feeding trials). This is reflected by

307   the small range of distances in our dataset. When considering those simple interactions,

308   associational effects declined quickly with increased distance between the plants. Typical

309   mechanisms of associational effects, like reduction of apparency of the focal plant or induction

310   of chemical defence (Barbosa et al. 2009), could only be expected when neighboring plants are

311   close to one another. On the other side, multiple focal and neighboring plants can be present in a

312   plot, complexifying the interactions, thus possibly explaining the slower decline of associational

313   effects with increasing scale. Resource selection and enerfy maximization by herbivores could

314   also explain large scale associational effects (Courant and Fortin 2010). Even if the strength of

315   associational effects decreases with plot area, a predicted d of 0.82 for 10 m^2 plots is still a large

316   effect size according to Cohen's rule of thumb (Cohen 1988). Experiments with relatively large

317   plots (196 m^2, Danell et al. 1991; 400 m^2, Milligan and Koricheva 2013 and Vehviläinen and

318   Koricheva 2006) also presented large d according to Cohen (1988). The information reported in

319   the publications prevented us from testing the effect of the relative density between focal and

320   neighboring plants, but this would probably explain part of the variation in associational effects

321   in larger plots. Few studies investigated associational effects at large distance or in very large

322   plots. Moore et al. (2015) recently demonstrated associational susceptibility and neighbor

323   contrast defence for *Calluna vulgaris* within 1000 m of grass patches in the Scottish heathlands.

324   We did not find support for the predictions that "classic" effects should influence patch choice

325   by herbivores while "contrast" effects should affect within patch selection (Bergvall et al 2006).

326   Because few associational effects reported were measured in large patches, the model could have

327   been unable to detect an interaction between type of association and distance. Every type of

328   effects could also be seen at all scales because of the additive effects of herbivore selection at

329   multiple scales (Miller et al. 2006). The associational effect seen at a specific scale could result

330   from the addition of associational effects at other scales; fine scale associational susceptibilities

331   or defences could be triggered by large-scale distribution of neighboring plants. This could be

332   particularly important in studies performed in natural environments. Aside from Bergvall et al.

333   (2006) and their following work (Bergvall et al. 2008, Rautio et al. 2008, Rautio et al. 2012), few

334   authors have studied how spatial scaling relates to associational effects through the foraging

335   behavior of large herbivores (but see Courant and Fortin 2010, Wang et al. 2010, Stutz et al.

336   2015). For small mammals, Emerson et al. (2012) tested associational effects at three spatial

337   scales (between patches > between feeding stations > within feeding stations) with squirrels

338   (*Sciurus* spp.), and found that both neighbor contrast susceptibility and associational defence

339   occur among patches and among feeding stations. At a larger scale, they found only associational

340   defence; high palatability seeds were less susceptible to be consumed in low palatability patches.

341   The study of associational effects could be greatly improved by more experimentation with

342   varying patch size and distance between neighbors, which could test the extent of associational

343   susceptibilities and defences such as the study by Oom and Hester (1999).

344   Associational defences had stronger effects than associational susceptibilities, thereby suggesting

345   stronger effects of facilitation. Facilitation between plants is known to be common in stressful

346   environments, such as those with high herbivory pressure (Callaway and Walker 1997). High

347   herbivory pressure, however, can also reduce the impact of associational defences, as herbivores

348   could become less selective when competition between individuals increases (Baraza et al. 2006).

349   Some studies have demonstrated a relation between herbivory pressure and associational effects

350   (Aerts et al. 2007, Graff et al. 2007, Smit et al. 2007), but the heterogeneity in reporting

351   herbivore pressure prevented us to test this factor. "Classic" type of associational effects also

352   presented stronger effects than "contrast" type. Although Atsatt and O'Dowd (1976) introduced

353   the attractant-decoy hypothesis 40 years ago, interest in contrast associational effects is more

354   recent (see Bergvall et al. 2006) and they might be understudied; only 47 of our effect sizes

355   concerned "contrast" interactions.

356   The strength of associational effects were also dependent on the nature of the experimental

357   design. We expected observational studies to have low and variable associational effects, since

358   the environment is uncontrolled and thus more variable. Surprisingly, feeding trials reported the

359   lowest associational effect sizes, and transplantation experiments in natural environments

360   reported effects of the highest magnitude. The simplicity of the feeding trials could explain the

361   low values and low variance of those associational effects. As demonstrated by Wang et al.

362   (2010), complex neighborhood can provide associational defence, either by a passive reduction

363   of selectivity or by generating mistakes in foraging choices. They reported that the palatable

364   grass *Medicago sativa* was less consumed by sheep in complex heterogenous environment

365   including three plant species compared to homogenous environment (Wang et al. 2010).

366   Herbivores integrate information at multiple spatial and temporal scales in natural environments

367   to make foraging decisions (Miller et al. 2006) thereby generating associational effects.

368   In their meta-analysis, Barbosa et al. (2009) stated that associational defence was the most

369   frequent associational effect under mammalian herbivory. Our results indicate, however, that

370   associations with a plant providing defence (n = 81) are not more frequent than associations with

371   a plant increasing consumption (n = 87). The asymmetry found in effect sizes could be an

372   indication that associational defences are more frequent as the distribution of effect sizes is

373   skewed towards them, but could also result from publication bias. Our dataset is dominated by

374   woody plants already including a large variation in functional traits, still consideration for a

375   wider range of functional types could help disentangle which of increased defence or

376   susceptibility in presence of neighbors is more prevalent for herbivores with movement abilities

377   similar to deer. Woody plants could be more apparent to herbivores than herbaceous plants

378   because of their larger size and longer life span (Haukioja and Koricheva 2000) and those

379   differences could be reflected in associational effects. Most studies of associational effects

380   involving herbaceous species that we reviewed measured parameters such as growth, height or

381   survival of individuals that did not always allow distinction of the effects of herbivory from

382   interactions such as competition or facilitation.

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

384   work focused on herbivores with movement abilities similar to deer and the results cannot be

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

386   Small herbivores are relatively more selective than larger ones and can discriminate between

387   plants and plant parts at finer spatial scales so we should not expect associational effects of the

388   same magnitude (Olff et al. 1999). For example, in one study roe deer (*Capreolus capreolus*)

389   selected forages at both patch and plant levels, while rabbits (*Oryctolagus cuniculus*) selected

390   plants only at the species level and were not influenced by the spatial arrangement of plants

391   (Bergman et al. 2005). Second, the large heterogeneity found in effect sizes (Figure 2) indicates

392   that many untested variables influenced the magnitude of associational effects and their

393   interactions with scale. For example, we did not take into account the season; in seasonal

394   environments, selectivity could be lower in winter because of the lack of resources, or higher

395   given energy constraints, respectively reducing or increasing the strength of associational effects.

396   Many of the studies included in our meta-analysis presented survival or damage for an entire

397   year and we combined the data from multiple seasons or years, which partly explain the

398   remaining heterogeneity. Our goal was to explore general patterns, but we contend that multiple

399   factors can influence associational effects, such as relative abundance or density of focal or

400   neighbor plants (Emerson et al. 2012, Hambäck et al. 2014, Underwood et al. 2014), richness of

401   food patches (Milligan and Koricheva 2013), diversity (Castagneyrol et al. 2014), herbivore

402   density (Aerts et al. 2007, Graff et al. 2007, Smit et al. 2007), etc. Finally, our sensitivity

403   analyses for outliers and recombined effect sizes showed a consistent negative effect of plot size

404   on the value of effect sizes.

405   Our study updates and extends previous work, providing new insights that should fuel further

406   research, on the spatial range of associational effects, the spread of contrast type interactions and

407   the prevalence of associational defence and susceptibility in large herbivores. We suggest a more

408   systematic reporting of contextual data, such as herbivore densities, herbivores diet breath and

409   densities of neighboring and focal plants, as those variables could explain the high residual

410   heterogeneity of associational effects.

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411

420

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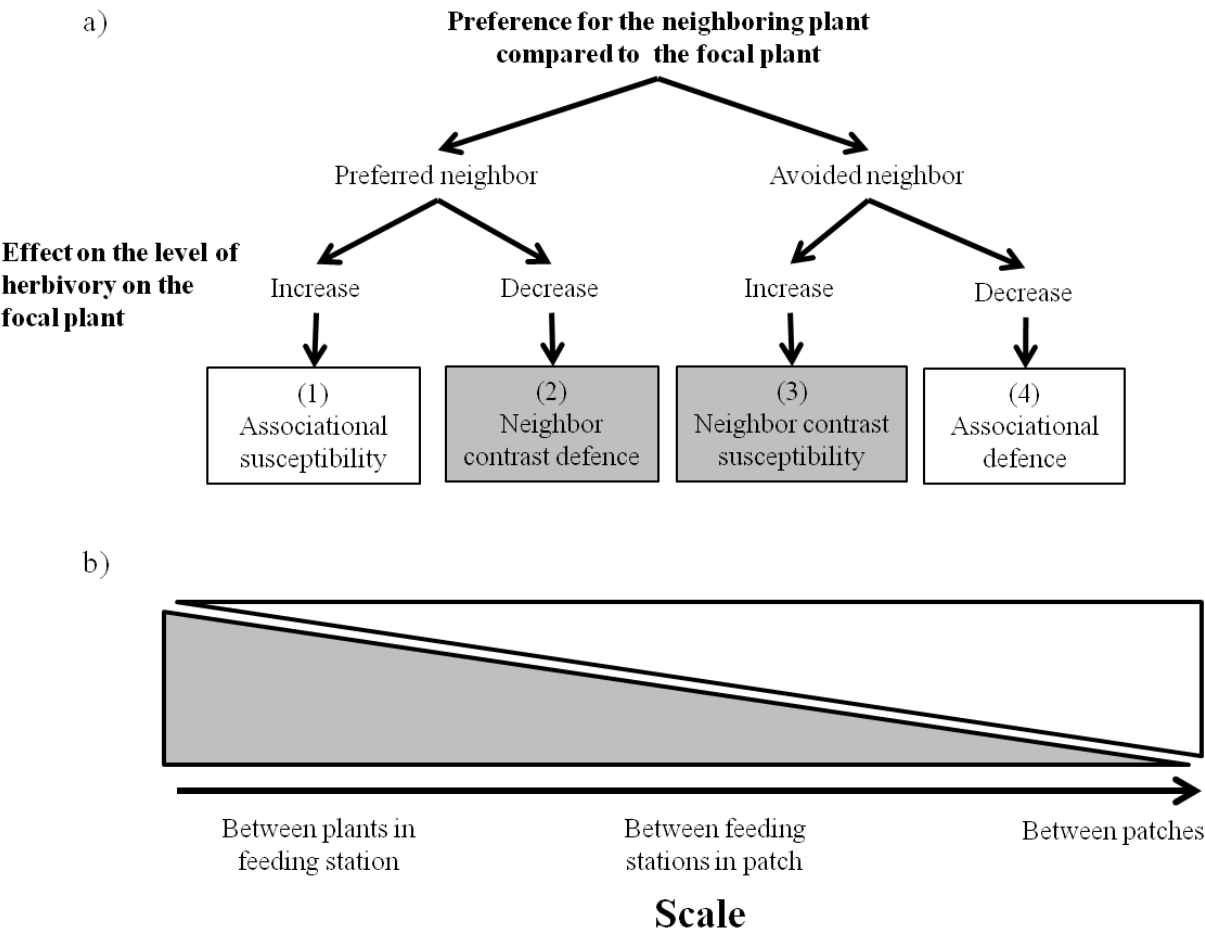
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575   **Figure legends**

576   Figure 1. a) Flowchart of the type of associational effects affecting the level of herbivory on the

577   focal plant based on the preference of the herbivore for the neighboring plants versus the focal

578   plant (first level of the flowchart) and on the direction of the association (second level). "Classic"

579   types of effects (associational susceptibility and defence) are in white boxes while "contrast"

580   types (neighbor contrast susceptibility and defence) are in grey boxes. b) Predictions about how

581   the "classic" (white) and "contrast" (grey) associational effects should vary in strength with

582   spatial scale according to Bergvall et al. (2006) framework. Scales suggested on the x-axes are

583   suggestions not representing exactly where the type of associational effects are expected to occur.

584   Figure 2. Summary of difference in damage/survival with and without a neighboring plant (d,

585   standardized difference of means) separated by the independent variable levels tested, with 95%

586   CI and I^2, the percentage of total variability due to heterogeneity among d's. A higher d indicates

587   a higher associational effect of the neighboring plant on the focal plant's herbivory level.

588   Numbers to the right of the data points are the number of effect sizes in each summary effect.

589   We used a meta-analysis mixed model to test the impact of variables on the standardized

590   difference of means.

591   Figure 3. Relationship between associational effects and two different indicators of spatial scale:

592   a) decrease in the difference in damage/survival with and without a neighboring plant

593   (standardized difference of means) according to plot size (m^2); b) associational effect limited to

594   the first 10 cm between the focal plant and its neighbors. For each figure, the size of each point

595   indicates the weight of each effect size in the meta-analysis mixed effect model, calculated with

596   the inverse-variance method. Vertical lines and numbers above correspond to untransformed

597   values of plot size (m^2). Regression line results from a meta-analysis mixed model and dotted
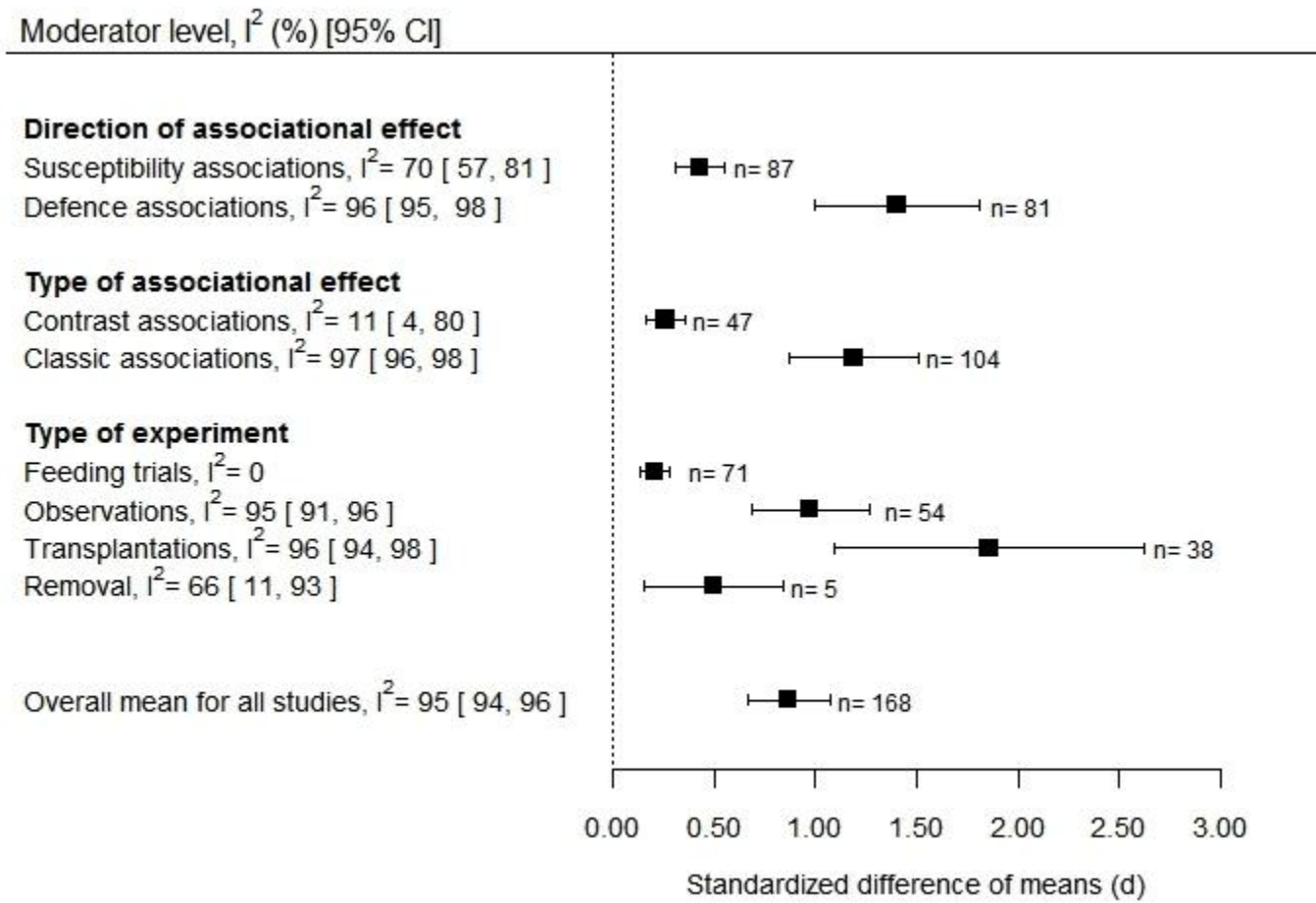
598   lines represent predicted values with 95% CI.

599   Figure 1.

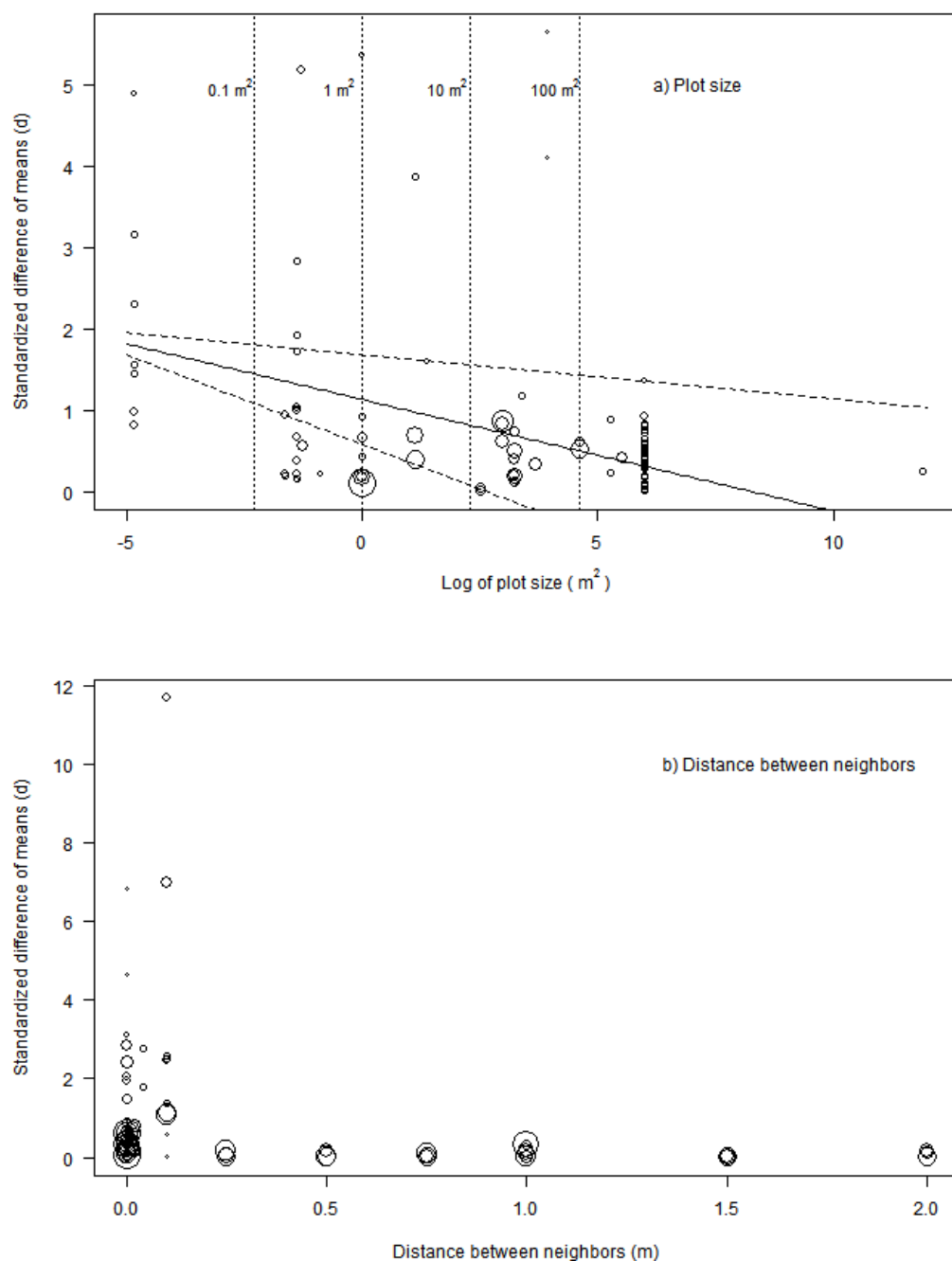600

601

602   Figure 2.

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

Direction of associational effect
Susceptibility associations, I^2= 70 [57, 81]   n= 87
Defence associations, I^2= 96 [95, 98]   n= 81

Type of associational effect
Contrast associations, I^2= 11 [4, 80]   n= 47
Classic associations, I^2= 97 [96, 98]   n= 104

Type of experiment
Feeding trials, I^2= 0   n= 71
Observations, I^2= 95 [91, 96]   n= 54
Transplantations, I^2= 96 [94, 98]   n= 38
Removal, I^2= 66 [11, 93]   n= 5

Overall mean for all studies, I^2= 95 [94, 96]   n= 168

0.00   0.50   1.00   1.50   2.00   2.50   3.00

Standardized difference of means (d)

603

604   Figure 3.

605

606