

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

2 **Insights from a meta-analysis**

3

4 Emilie Champagne¹, Jean-Pierre Tremblay^{1,2}, Steeve D. Côté¹

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

6 Médecine, Québec, (Québec) G1V 0A6, Canada, emilie.champagne.2@ulaval.ca, [7 \[pierre.tremblay@bio.ulaval.ca\]\(mailto:pierre.tremblay@bio.ulaval.ca\), \[steeve.cote@bio.ulaval.ca\]\(mailto:steeve.cote@bio.ulaval.ca\)](mailto:jean-</p></div><div data-bbox=)

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

9

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

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).

247 **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 m²
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 (Olf 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 ($r \sim 10$ 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. Häslér 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 afro-montane

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 breadth and densities of neighboring and focal plants, as those variables could
349 explain the high residual heterogeneity of associational effects.

350 **Acknowledgements**

351 This project is part of the Natural Sciences and Engineering Research Council of Canada
352 (NSERC) Chair in integrated resource management of Anticosti Island

353 (<http://www.chaireanticosti.ulaval.ca/>). E.C. received scholarships from NSERC. We thank M.
354 Courchesne for help with article selection steps, and A. Hester, V. Saucier, P. Morissette and M.
355 Bonin for reviewing an earlier version of this manuscript. H. Crépeau from the Service de
356 consultation statistique at Université Laval provided statistical guidance.

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]

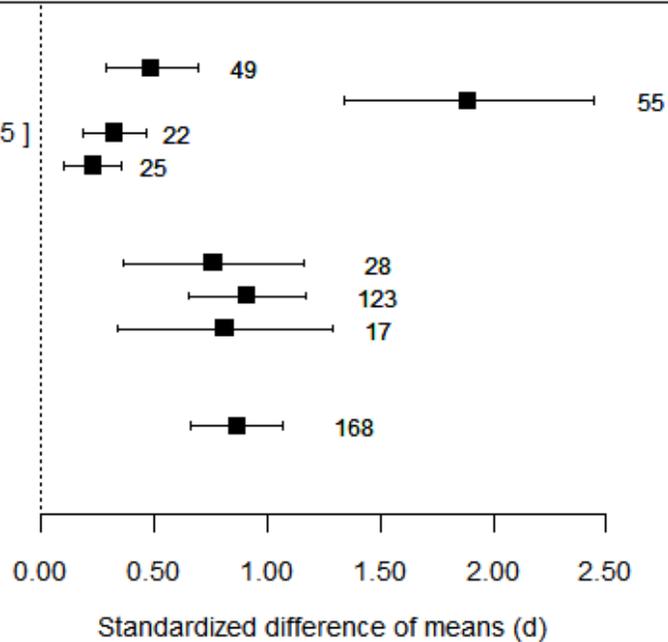
Effect size class

r, 94 [91, 97]

d, 94 [93, 96]

OR, 92 [79, 96]

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



357

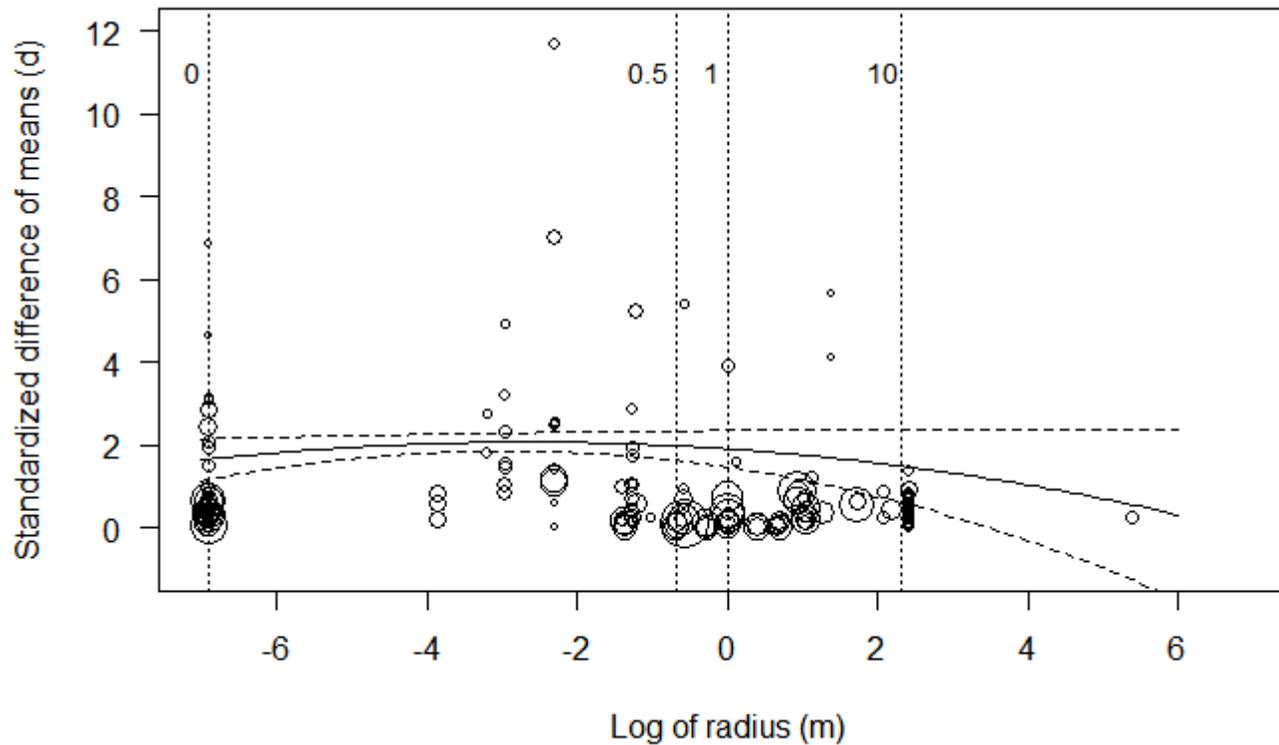
358 Figure 1. Summary of difference in damage/survival with and without a neighboring plant (d , standardized difference of means)

359 separated by the moderator levels tested, with 95% CI and I^2 , the percentage of total variability due to heterogeneity among d 's. A

360 higher d indicates a higher associational effect of the neighboring plant on the focal plant susceptibility to herbivory. Numbers to the

361 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

362 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

References

- Aerts, R., A. Negussie, W. H. Maes, E. November, M. Hermy, and B. Muys. 2007. Restoration of dry afro-montane forest using pioneer shrubs as nurse-plants for *Olea europaea* ssp *cuspidata*. *Restoration Ecology* **15**:129-138.
- Atsatt, P. R. and D. J. O'Dowd. 1976. Plant defense guilds. *Science* **193**:24-29.
- Barbosa, P., J. Hines, I. Kaplan, H. Martinson, A. Szczepaniec, and Z. Szendrei. 2009. Associational resistance and associational susceptibility: having right or wrong neighbors. *Annual Review of Ecology Evolution and Systematics* **40**:1-20.
- Bergman, M., G. R. Iason, and A. J. Hester. 2005. Feeding patterns by roe deer and rabbits on pine, willow and birch in relation to spatial arrangement. *Oikos* **109**:513-520.
- Bergvall, U., P. Rautio, H. Siren, J. Tuomi, and O. Leimar. 2008. The effect of spatial scale on plant associational defences against mammalian herbivores. *Ecoscience* **15**:343-348.
- Bergvall, U. A., P. Rautio, K. Kesti, J. Tuomi, and O. Leimar. 2006. Associational effects of plant defences in relation to within- and between-patch food choice by a mammalian herbivore: neighbour contrast susceptibility and defence. *Oecologia* **147**:253-260.
- Bland, J. M. and D. G. Altman. 1996. Transformations, means, and confidence intervals. *BMJ* **312**:1079.
- Bommarco, R. and J. E. Banks. 2003. Scale as modifier in vegetation diversity experiments: effects on herbivores and predators. *Oikos* **102**:440-448.

- Borenstein, M., L. V. Hedges, J. P. T. Higgins, and H. R. Rothstein. 2009. Introduction to meta-analysis. John Wiley & Sons, Ltd., Chichester, UK.
- Brown, B. J. and T. F. H. Allen. 1989. The importance of scale in evaluating herbivory impacts. *Oikos* **54**:189-194.
- Cohen, J. 1960. A coefficient of agreement for nominal scale. *Educational and psychological measurement* **20**:37-46.
- Cohen, J. 1988. *Statistical power analysis for the behavioral sciences*. 2nd edition. Lawrence Erlbaum Associates, Inc., Hillsdale, USA.
- Côté, I. M., P. S. Curtis, H. R. Rothstein, and G. B. Stewart. 2013. Gathering data: searching literature and selection criteria. Pages 37-51 in J. Koricheva, J. Gurevitch, and K. Mengersen, editors. *Handbook of meta-analysis in ecology and evolution*. Princeton University Press, Princeton, USA.
- Côté, S. D., T. P. Rooney, J.-P. Tremblay, C. Dussault, and D. M. Waller. 2004. Ecological impacts of deer overabundance. *Annual Review of Ecology Evolution and Systematics* **35**:113-147.
- Courant, S. and D. Fortin. 2010. Foraging decisions of bison for rapid energy gains can explain the relative risk to neighboring plants in complex swards. *Ecology* **91**:1841-1849.
- DeGabriel, J. L., S. D. Albon, D. A. Fielding, D. J. Riach, S. Westaway, and R. J. Irvine. 2011. The presence of sheep leads to increases in plant diversity and reductions in the impact of deer on heather. *Journal of Applied Ecology* **48**:1269-1277.

Duval, S. 2005. The trim and fill method. Pages 127-144 *in* H. R. Rothstein, A. J. Sutton, and M. Borenstein, editors. Publication bias in meta-analysis. John Wiley & Sons, Ltd, Chischester, UK.

Emerson, S. E., J. S. Brown, C. J. Whelan, and K. A. Schmidt. 2012. Scale-dependent neighborhood effects: shared doom and associational refuge. *Oecologia* **168**:659-670.

Graff, P., M. R. Aguiar, and E. J. Chaneton. 2007. Shifts in positive and negative plant interactions along a grazing intensity gradient. *Ecology* **88**:188-199.

Grez, A. A. and R. H. Gonzalez. 1995. Resource concentration hypothesis: effect of host-plant patch size on density of herbivorous insects. *Oecologia* **103**:471-474.

Hambäck, P. A., B. D. Inouye, P. Andersson, and N. Underwood. 2014. Effects of plant neighborhoods on plant-herbivore interactions: resource dilution and associational effects. *Ecology* **95**:1370-1383.

Hamm, M. P., L. Hartling, A. Milne, L. Tjosvold, B. Vandermeer, D. Thomson, S. Curtis, and T. P. Klassen. 2010. A descriptive analysis of a representative sample of pediatric randomized controlled trials published in 2007. *BMC Pediatrics* **10**:96.

Häsler, H. and J. Senn. 2012. Ungulate browsing on European silver fir *Abies alba*: the role of occasions, food shortage and diet preferences. *Wildlife Biology* **18**:67-74.

Haukioja, E. and J. Koricheva. 2000. Tolerance to herbivory in woody vs. herbaceous plants. *Evolutionary Ecology* **14**:551-562.

Hester, A. J. and G. J. Baillie. 1998. Spatial and temporal patterns of heather use by sheep and red deer within natural heather/grass mosaics. *Journal of Applied Ecology* **35**:772-784.

Hester, A. J., M. Bergman, G. R. Iason, and J. Moen. 2006. Impacts of large herbivore on plant community structure and dynamics. Pages 97-141 *in* K. Danell, R. Bergström, P. Duncan, and J. Pastor, editors. Large herbivore ecology, ecosystem dynamics and conservation. Cambridge University Press, Cambridge, UK.

Hjältén, J., K. Danell, and P. Lundberg. 1993. Herbivore avoidance by association: vole and hare utilization of woody plants. *Oikos* **68**:125-131.

Jennions, M. D., C. J. Lortie, M. S. Rosenberg, and H. R. Rothstein. 2013. Publication and related biases. Pages 207-236 *in* J. Koricheva, J. Gurevitch, and K. Mengersen, editors. Handbook of meta-analysis in ecology and evolution. Princeton University Press, Princeton, USA.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* **61**:65-71.

Karban, R. 2010. Neighbors affect resistance to herbivory – a new mechanism. *New Phytologist* **186**:564-566.

Karban, R., K. Shiojiri, M. Huntzinger, and A. C. McCall. 2006. Damage-induced resistance in sagebrush: volatiles are key to intra-and interplant communication. *Ecology* **87**:922-930.

Koricheva, J., J. Gurevitch, and K. Mengersen. 2013a. Handbook of meta-analysis in ecology and evolution. Princeton University Press, Princeton, USA.

Koricheva, J., M. D. Jennions, and J. Lau. 2013b. Temporal trends in effect sizes: causes, detection and implications. Pages 236-254 in J. Koricheva, J. Gurevitch, and K. Mengersen, editors. Handbook of meta-analysis in ecology and evolution. Princeton University Press, Princeton, USA.

Lavsund, S. 1987. Moose relationships to forestry in Finland, Norway and Sweden. Sweden Wildlife Research **1 (Suppl.):**229-244.

Mackenzie, B. D. E. and D. A. Keith. 2009. Adaptive management in practice: conservation of a threatened plant population. Ecological Management & Restoration **10:**S129-S135.

Milchunas, D. and I. Noy-Meir. 2002. Grazing refuges, external avoidance of herbivory and plant diversity. Oikos **99:**113-130.

Milligan, H. T. and J. Koricheva. 2013. Effects of tree species richness and composition on moose winter browsing damage and foraging selectivity: an experimental study. Journal of Animal Ecology **82:**739-748.

Moher, D., A. Liberati, J. Tetzlaff, D. G. Altman, and The Prisma Group. 2009. Preferred reporting items for systematic reviews and meta-analyses: the PRISMA statement. PLoS Med **6:**e1000097.

Olf, H., F. W. M. Vera, J. Bokdam, E. S. Bakker, J. M. Gleichman, K. de Maeyer, and R. Smit. 1999. Shifting mosaics in grazed woodlands driven by the alternation of plant facilitation and competition. Plant Biology **1:**127-137.

- Perea, R. and L. Gil. 2014. Tree regeneration under high levels of wild ungulates: the use of chemically vs. physically-defended shrubs. *Forest Ecology and Management* **312**:47-54.
- Pyke, G. H., H. R. Pulliam, and E. L. Charnov. 1977. Optimal foraging: a selective review of theory and tests. *Quarterly Review of Biology* **52**:137-154.
- R Core Team, editor. 2013. *R: A Language and Environment for Statistical Computing*, Vienna, Austria.
- Rautio, P., U. A. Bergvall, J. Tuomi, K. Kesti, and O. Leimar. 2012. Food selection by herbivores and neighbourhood effects in the evolution of plant defences. *Annales Zoologici Fennici* **49**:45-57.
- Rautio, P., K. Kesti, U. A. Bergvall, J. Tuomi, and O. Leimar. 2008. Spatial scales of foraging in fallow deer: implications for associational effects in plant defences. *Acta Oecologica* **34**:12-20.
- Rosenberg, M. S., H. R. Rothstein, and J. Gurevitch. 2013. Effect sizes: conventional choices and calculation. Pages 61-71 in J. Koricheva, J. Gurevitch, and K. Mengersen, editors. *Handbook of meta-analysis in ecology and evolution*. Princeton University Press, Princeton, USA.
- Russell, F. L. and N. L. Fowler. 2004. Effects of white-tailed deer on the population dynamics of acorns, seedlings and small saplings of *Quercus buckleyi*. *Plant Ecology* **173**:59-72.

Smit, C., C. Vandenberghe, J. den Ouden, and H. Müller-Schärer. 2007. Nurse plants, tree saplings and grazing pressure: changes in facilitation along a biotic environmental gradient. *Oecologia* **152**:265-273.

Sterne, J. A. C., M. Egger, and G. D. Smith. 2001. Systematic reviews in health care - Investigating and dealing with publication and other biases in meta-analysis. *British Medical Journal* **323**:101-105.

Tahvanainen, J. O. and R. B. Root. 1972. The influence of vegetational diversity on the population ecology of a specialized herbivore, *Phyllotreta cruciferae* (Coleoptera: Chrysomelidae). *Oecologia* **10**:321-346.

Thomas, C. D. 1986. Butterfly larvae reduce host plant survival in vicinity of alternative host species. *Oecologia* **70**:113-117.

Thomson, H., S. Thomas, E. Sellstrom, and M. Petticrew. 2013. Housing improvements for health and associated socio-economic outcomes. The Cochrane Collaboration.

Underwood, N., B. D. Inouye, and P. A. Hambäck. 2014. A conceptual framework for associational effects: when do neighbors matter and how would we know? *The Quarterly Review of Biology* **89**:1-19.

Vehviläinen, H. and J. Koricheva. 2006. Moose and vole browsing patterns in experimentally assembled pure and mixed forest stands. *Ecography* **29**:497-506.

Viechtbauer, W. 2010. Conducting meta-analyses in R with the metafor package. *Journal of statistical software* **36**:1-48.

Viechtbauer, W. and M. W. L. Cheung. 2010. Outlier and influence diagnostics for meta-analysis. *Research Synthesis Methods* **1**:112-125.

Wang, L., D. Wang, Y. Bai, Y. Huang, M. Fan, J. Liu, and Y. Li. 2010. Spatially complex neighboring relationships among grassland plant species as an effective mechanism of defense against herbivory. *Oecologia* **164**:193-200.