

1 **Spatial extent of neighboring plants influences the strength of associational effects on**
2 **mammal herbivory. Insights from a meta-analysis**

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10

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

37 **Introduction**

38 Herbivory can modify the composition, structure and functions of ecosystems (Hester et al.
39 2006). There is high variability in the susceptibility of different plant species and individuals to
40 herbivory. This variability is driven by forage selection, whom in itself is determined by the
41 nutritional requirements of herbivores (Pyke et al. 1977), intrinsic (e.g. nutritive quality, Pyke et
42 al. 1977), and extrinsic characteristics of both the plants and the environment (e.g. neighboring
43 plants, Atsatt and O'Dowd 1976). Multiple studies have demonstrated the influence of
44 neighboring plants on forage selection, a process named neighboring or associational effects
45 (Milchunas and Noy-Meir 2002, Barbosa et al. 2009), yet the conditions in which a specific
46 neighborhood will increase or reduce herbivory are not fully understood. The distance between
47 neighboring plants could explain part of the residual variability observed in associational effects
48 (Underwood et al. 2014). Associational effects can be exploited as a management tool to
49 alleviate the effect of herbivores; for example, Perea and Gil (2014) recommend planting
50 seedlings under shrubs to reduce damage to the seedlings by browsers. Other recent studies
51 (Noumi et al. 2015, Stutz et al. 2015, Torroba-Balmori et al. 2015) explored the application and
52 limits of associational effects for the restoration of plant species, but without considering the
53 spatial extent of plant neighborhood, although Stutz et al. (2015) quantified vegetation variables
54 at two spatial scales. A better understanding of associational effects could improve and
55 generalize their use in restoration, conservation and exploitation.

56 Four different types of associational effects have been described in the literature (Figure
57 1a), depending on the difference in palatability between the focal and the neighboring plants: (1)
58 associational susceptibility involves a neighboring plant preferred to the focal plant, leading to
59 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 m² to 148 000 m² with a median
155 = 27.5 m², 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).

294 **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 energy 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 m² plots is still a large
316 effect size according to Cohen's rule of thumb (Cohen 1988). Experiments with relatively large
317 plots (196 m², Danell et al. 1991; 400 m², 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 (Olf 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 breadth 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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420

421 **References**

- 422 Aerts, R., A. Negussie, W. H. Maes, E. November, M. Hermy, and B. Muys. 2007. Restoration
423 of dry afro-montane forest using pioneer shrubs as nurse-plants for *Olea europaea* ssp
424 *cuspidata*. *Restoration Ecology* **15**:129-138.
- 425 Atsatt, P. R. and D. J. O'Dowd. 1976. Plant defense guilds. *Science* **193**:24-29.
- 426 Baraza, E., R. Zamora, and J. A. Hódar. 2006. Conditional outcomes in plant-herbivore
427 interactions: neighbours matter. *Oikos* **113**: 148-156.
- 428 Barbosa, P., J. Hines, I. Kaplan, H. Martinson, A. Szczepaniec, and Z. Szendrei. 2009.
429 Associational resistance and associational susceptibility: having right or wrong neighbors.
430 *Annual Review of Ecology Evolution and Systematics* **40**:1-20.
- 431 Bergman, M., G. R. Iason, and A. J. Hester. 2005. Feeding patterns by roe deer and rabbits on
432 pine, willow and birch in relation to spatial arrangement. *Oikos* **109**:513-520.
- 433 Bergvall, U., P. Rautio, H. Siren, J. Tuomi, and O. Leimar. 2008. The effect of spatial scale on
434 plant associational defences against mammalian herbivores. *Ecoscience* **15**:343-348.
- 435 Bergvall, U. A., P. Rautio, K. Kesti, J. Tuomi, and O. Leimar. 2006. Associational effects of
436 plant defences in relation to within- and between-patch food choice by a mammalian
437 herbivore: neighbour contrast susceptibility and defence. *Oecologia* **147**:253-260.
- 438 Bland, J. M. and D. G. Altman. 1996. Transformations, means, and confidence intervals. *BMJ*
439 **312**:1079.
- 440 Bommarco, R. and J. E. Banks. 2003. Scale as modifier in vegetation diversity experiments:
441 effects on herbivores and predators. *Oikos* **102**:440-448.

- 442 Borenstein, M., L. V. Hedges, J. P. T. Higgins, and H. R. Rothstein. 2009. Introduction to meta-
443 analysis. John Wiley & Sons, Ltd., Chichester, UK.
- 444 Brown, B. J. and T. F. H. Allen. 1989. The importance of scale in evaluating herbivory impacts.
445 *Oikos* **54**:189-194.
- 446 Castagneyrol, B., M. Regolini, and H. Jactel. 2014. Tree species composition rather than
447 diversity triggers associational resistance to the pine processionary moth. *Basic and*
448 *Applied Ecology* **15**: 516-523.
- 449 Callaway, R. M. and L. R. Walker. 1997. Competition and facilitation: a synthetic approach to
450 interactions in plant communities. *Ecology* **78**: 1958-1965.
- 451 Cohen, J. 1960. A coefficient of agreement for nominal scale. *Educational and psychological*
452 *measurement* **20**:37-46.
- 453 Cohen, J. 1988. *Statistical power analysis for the behavioral sciences*. 2nd edition. Lawrence
454 Erlbaum Associates, Inc., Hillsdale, USA.
- 455 Côté, I. M., P. S. Curtis, H. R. Rothstein, and G. B. Stewart. 2013. Gathering data: searching
456 literature and selection criteria. Pages 37-51 *in* J. Koricheva, J. Gurevitch, and K.
457 Mengersen, editors. *Handbook of meta-analysis in ecology and evolution*. Princeton
458 University Press, Princeton, USA.
- 459 Courant, S. and D. Fortin. 2010. Foraging decisions of bison for rapid energy gains can explain
460 the relative risk to neighboring plants in complex swards. *Ecology* **91**:1841-1849.
- 461 Danell, K., L. Edenius, and P. Lundberg. 1991. Herbivory and tree stand composition: moose
462 patch use in winter. *Ecology* **72**: 1350-1357.

- 463 DeGabriel, J. L., S. D. Albon, D. A. Fielding, D. J. Riach, S. Westaway, and R. J. Irvine. 2011.
464 The presence of sheep leads to increases in plant diversity and reductions in the impact of
465 deer on heather. *Journal of Applied Ecology* **48**:1269-1277.
- 466 Duval, S. 2005. The trim and fill method. Pages 127-144 *in* H. R. Rothstein, A. J. Sutton, and M.
467 Borenstein, editors. *Publication bias in meta-analysis*. John Wiley & Sons, Ltd,
468 Chichester, UK.
- 469 Emerson, S. E., J. S. Brown, C. J. Whelan, and K. A. Schmidt. 2012. Scale-dependent
470 neighborhood effects: shared doom and associational refuge. *Oecologia* **168**:659-670.
- 471 Graff, P., M. R. Aguiar, and E. J. Chaneton. 2007. Shifts in positive and negative plant
472 interactions along a grazing intensity gradient. *Ecology* **88**:188-199.
- 473 Grez, A. A. and R. H. Gonzalez. 1995. Resource concentration hypothesis: effect of host-plant
474 patch size on density of herbivorous insects. *Oecologia* **103**:471-474.
- 475 Hambäck, P. A., B. D. Inouye, P. Andersson, and N. Underwood. 2014. Effects of plant
476 neighborhoods on plant-herbivore interactions: resource dilution and associational effects.
477 *Ecology* **95**:1370-1383.
- 478 Hamm, M. P., L. Hartling, A. Milne, L. Tjosvold, B. Vandermeer, D. Thomson, S. Curtis, and T.
479 P. Klassen. 2010. A descriptive analysis of a representative sample of pediatric
480 randomized controlled trials published in 2007. *BMC Pediatrics* **10**:96.
- 481 Häslér, H. and J. Senn. 2012. Ungulate browsing on European silver fir *Abies alba*: the role of
482 occasions, food shortage and diet preferences. *Wildlife Biology* **18**:67-74.
- 483 Haukioja, E. and J. Koricheva. 2000. Tolerance to herbivory in woody vs. herbaceous plants.
484 *Evolutionary Ecology* **14**:551-562.

- 485 Hester, A. J. and G. J. Baillie. 1998. Spatial and temporal patterns of heather use by sheep and
486 red deer within natural heather/grass mosaics. *Journal of Applied Ecology* **35**:772-784.
- 487 Hester, A. J., M. Bergman, G. R. Iason, and J. Moen. 2006. Impacts of large herbivore on plant
488 community structure and dynamics. Pages 97-141 *in* K. Danell, R. Bergström, P. Duncan,
489 and J. Pastor, editors. *Large herbivore ecology, ecosystem dynamics and conservation*.
490 Cambridge University Press, Cambridge, UK.
- 491 Hjältén, J., K. Danell, and P. Lundberg. 1993. Herbivore avoidance by association: vole and hare
492 utilization of woody plants. *Oikos* **68**:125-131.
- 493 Jennions, M. D., C. J. Lortie, M. S. Rosenberg, and H. R. Rothstein. 2013. Publication and
494 related biases. Pages 207-236 *in* J. Koricheva, J. Gurevitch, and K. Mengersen, editors.
495 *Handbook of meta-analysis in ecology and evolution*. Princeton University Press,
496 Princeton, USA.
- 497 Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating
498 resource preference. *Ecology* **61**:65-71.
- 499 Karban, R. 2010. Neighbors affect resistance to herbivory – a new mechanism. *New Phytologist*
500 **186**:564-566.
- 501 Karban, R., K. Shiojiri, M. Huntzinger, and A. C. McCall. 2006. Damage-induced resistance in
502 sagebrush: volatiles are key to intra-and interplant communication. *Ecology* **87**:922-930.
- 503 Koricheva, J., M. D. Jennions, and J. Lau. 2013. Temporal trends in effect sizes: causes,
504 detection and implications. Pages 236-254 *in* J. Koricheva, J. Gurevitch, and K.
505 Mengersen, editors. *Handbook of meta-analysis in ecology and evolution*. Princeton
506 University Press, Princeton, USA.

- 507 Milchunas, D. and I. Noy-Meir. 2002. Grazing refuges, external avoidance of herbivory and
508 plant diversity. *Oikos* **99**:113-130.
- 509 Miller, A. M., C. McArthur and P. J. Smethurst. 2006. Characteristics of tree seedlings and
510 neighbouring vegetation have an additive influence on browsing by generalist herbivores.
511 *Forest Ecology and Management* **228**: 197-205.
- 512 Milligan, H. T. and J. Koricheva. 2013. Effects of tree species richness and composition on
513 moose winter browsing damage and foraging selectivity: an experimental study. *Journal*
514 *of Animal Ecology* **82**:739-748.
- 515 Moher, D., A. Liberati, J. Tetzlaff, D. G. Altman, and The Prisma Group. 2009. Preferred
516 reporting items for systematic reviews and meta-analyses: the PRISMA statement. *PLoS*
517 *Med* **6**:e1000097.
- 518 Moore, E. K., A. J. Britton, G. Iason, J. Pemberton, and R. J. Pakeman. 2015. Landscape-scale
519 vegetation patterns influence small-scale grazing impacts. *Biological Conservation* **192**:
520 218-225.
- 521 Noumi, Z., M. Chaieb, R. Michalet, and B. Touzard. 2015. Limitations to the use of facilitation
522 as a restoration tool in arid grazed savanna: a case study. *Applied Vegetation Science*.
- 523 Olf, H., F. W. M. Vera, J. Bokdam, E. S. Bakker, J. M. Gleichman, K. de Maeyer, and R. Smit.
524 1999. Shifting mosaics in grazed woodlands driven by the alternation of plant facilitation
525 and competition. *Plant Biology* **1**:127-137.
- 526 Perea, R. and L. Gil. 2014. Tree regeneration under high levels of wild ungulates: the use of
527 chemically vs. physically-defended shrubs. *Forest Ecology and Management* **312**:47-54.

- 528 Pyke, G. H., H. R. Pulliam, and E. L. Charnov. 1977. Optimal foraging: a selective review of
529 theory and tests. *Quarterly Review of Biology* **52**:137-154.
- 530 R Core Team, editor. 2013. R: A Language and Environment for Statistical Computing, Vienna,
531 Austria.
- 532 Rautio, P., U. A. Bergvall, J. Tuomi, K. Kesti, and O. Leimar. 2012. Food selection by
533 herbivores and neighbourhood effects in the evolution of plant defences. *Annales*
534 *Zoologici Fennici* **49**:45-57.
- 535 Rautio, P., K. Kesti, U. A. Bergvall, J. Tuomi, and O. Leimar. 2008. Spatial scales of foraging in
536 fallow deer: implications for associational effects in plant defences. *Acta Oecologica*
537 **34**:12-20.
- 538 Rosenberg, M. S., H. R. Rothstein, and J. Gurevitch. 2013. Effect sizes: conventional choices
539 and calculation. Pages 61-71 in J. Koricheva, J. Gurevitch, and K. Mengersen, editors.
540 Handbook of meta-analysis in ecology and evolution. Princeton University Press,
541 Princeton, USA.
- 542 Russell, F. L. and N. L. Fowler. 2004. Effects of white-tailed deer on the population dynamics of
543 acorns, seedlings and small saplings of *Quercus buckleyi*. *Plant Ecology* **173**:59-72.
- 544 Smit, C., C. Vandenberghe, J. den Ouden, and H. Müller-Schärer. 2007. Nurse plants, tree
545 saplings and grazing pressure: changes in facilitation along a biotic environmental
546 gradient. *Oecologia* **152**:265-273.
- 547 Sterne, J. A. C., M. Egger, and G. D. Smith. 2001. Systematic reviews in health care -
548 Investigating and dealing with publication and other biases in meta-analysis. *British*
549 *Medical Journal* **323**:101-105.

- 550 Stutz, R. S., P. B. Banks, N. Dexter, and C. McArthur. 2015. Associational refuge in practice:
551 can existing vegetation facilitate woodland restoration? *Oikos* **124**:571-580.
- 552 Tahvanainen, J. O. and R. B. Root. 1972. The influence of vegetational diversity on the
553 population ecology of a specialized herbivore, *Phyllotreta cruciferae* (Coleoptera:
554 Chrysomelidae). *Oecologia* **10**:321-346.
- 555 Thomas, C. D. 1986. Butterfly larvae reduce host plant survival in vicinity of alternative host
556 species. *Oecologia* **70**:113-117.
- 557 Thomson, H., S. Thomas, E. Sellstrom, and M. Petticrew. 2013. Housing improvements for
558 health and associated socio-economic outcomes. The Cochrane Collaboration.
- 559 Torroba-Balmori, P., P. Zaldívar, J. G. Alday, B. Fernández-Santos, and C. Martínez-Ruiz. 2015.
560 Recovering *Quercus* species on reclaimed coal wastes using native shrubs as restoration
561 nurse plants. *Ecological Engineering* **77**:146-153.
- 562 Underwood, N., B. D. Inouye, and P. A. Hambäck. 2014. A conceptual framework for
563 associational effects: when do neighbors matter and how would we know? *The Quarterly*
564 *Review of Biology* **89**:1-19.
- 565 Vehviläinen, H. and J. Koricheva. 2006. Moose and vole browsing patterns in experimentally
566 assembled pure and mixed forest stands. *Ecography* **29**:497-506.
- 567 Viechtbauer, W. 2010. Conducting meta-analyses in R with the metafor package. *Journal of*
568 *statistical software* **36**:1-48.
- 569 Viechtbauer, W. and M. W. L. Cheung. 2010. Outlier and influence diagnostics for meta-analysis.
570 *Research Synthesis Methods* **1**:112-125.

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

574

575 **Figure legends**

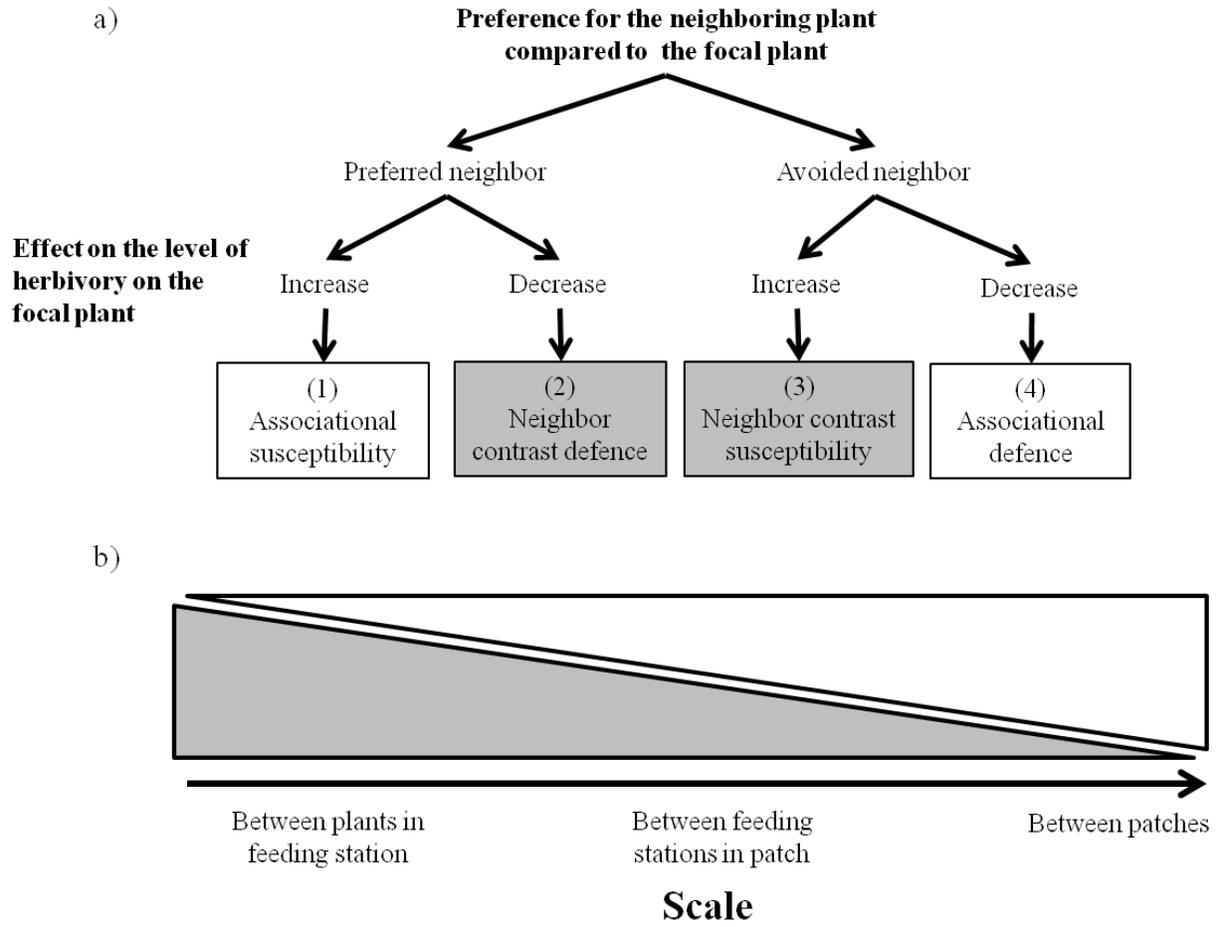
576 Figure 1. a) Flowchart of the type of associational effects affecting the level of herbivory on the
577 focal plant based on the preference of the herbivore for the neighboring plants versus the focal
578 plant (first level of the flowchart) and on the direction of the association (second level). “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.

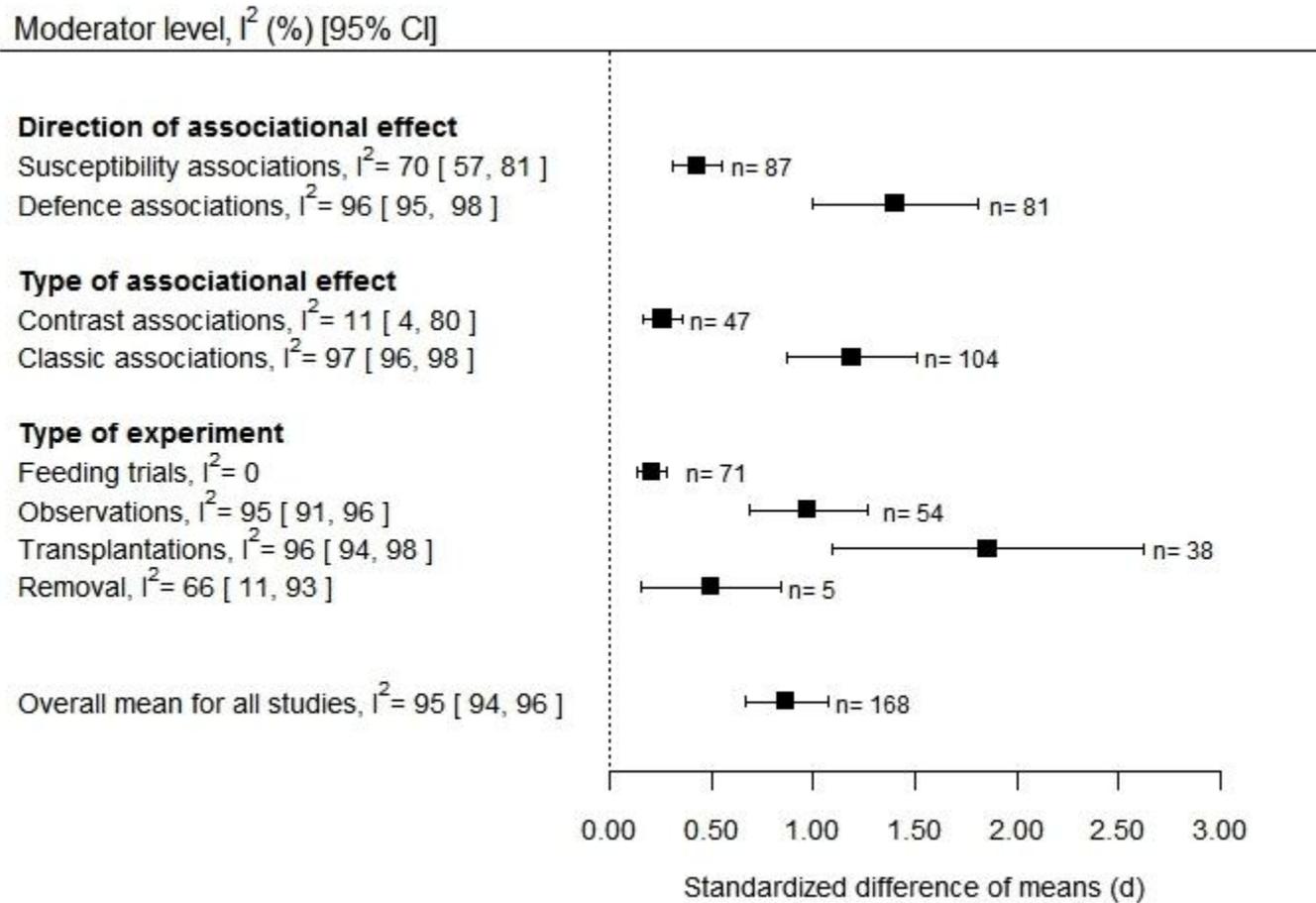
599 Figure 1.



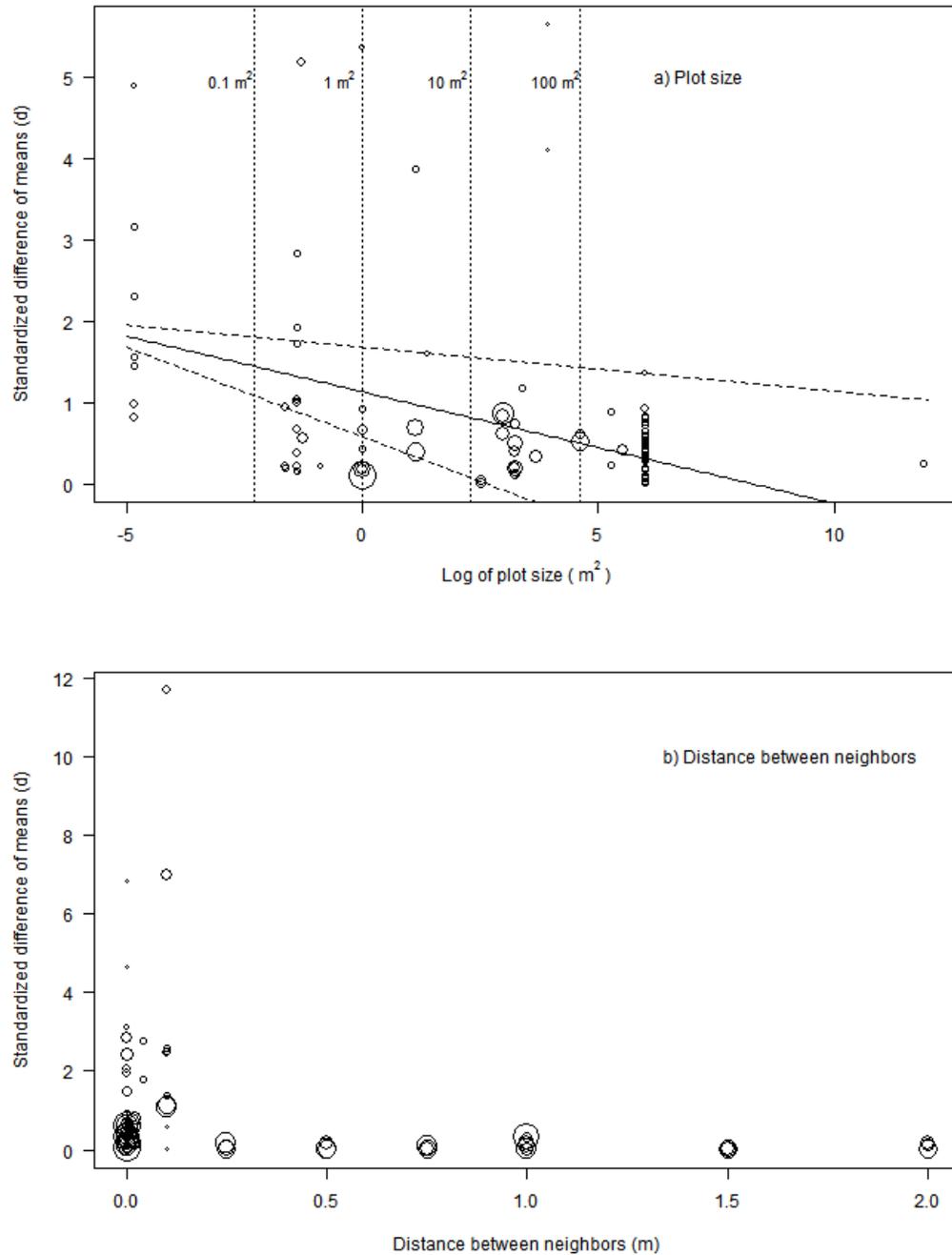
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602 Figure 2.



604 Figure 3.



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