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Spatial scale influences the associational effects of neighbor plants on mammal herbivory. Insights from a meta-analysis

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Abstract

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

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

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Introduction

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

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

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

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

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

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

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

Methods

Literature review

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

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

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

Data extraction and effect size computation

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

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

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

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

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

Statistical analyses

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

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

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

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

Results

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

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

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

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

Discussion

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

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

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

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

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

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

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

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

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

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

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Table 1. Associational effects affecting susceptibility to herbivory based on the preference of the herbivore for the neighboring plant versus the focal plant and on the 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

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Figure legends

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

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

Figure 1.

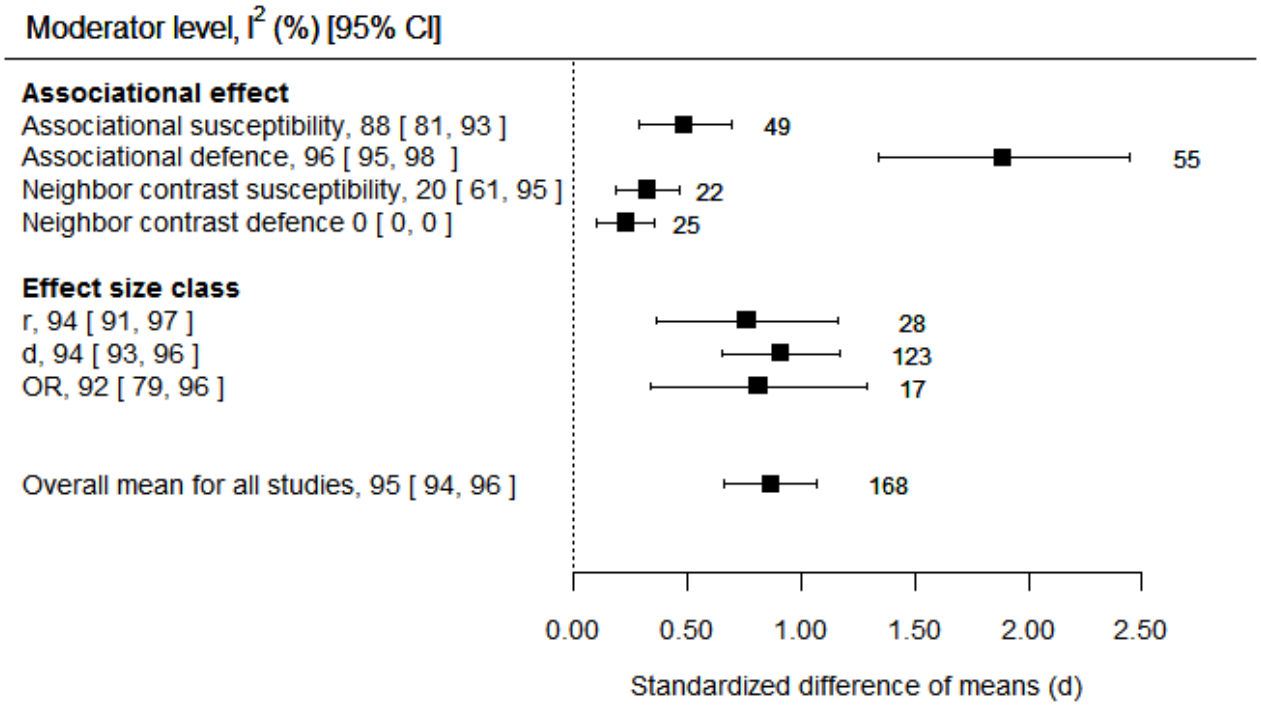
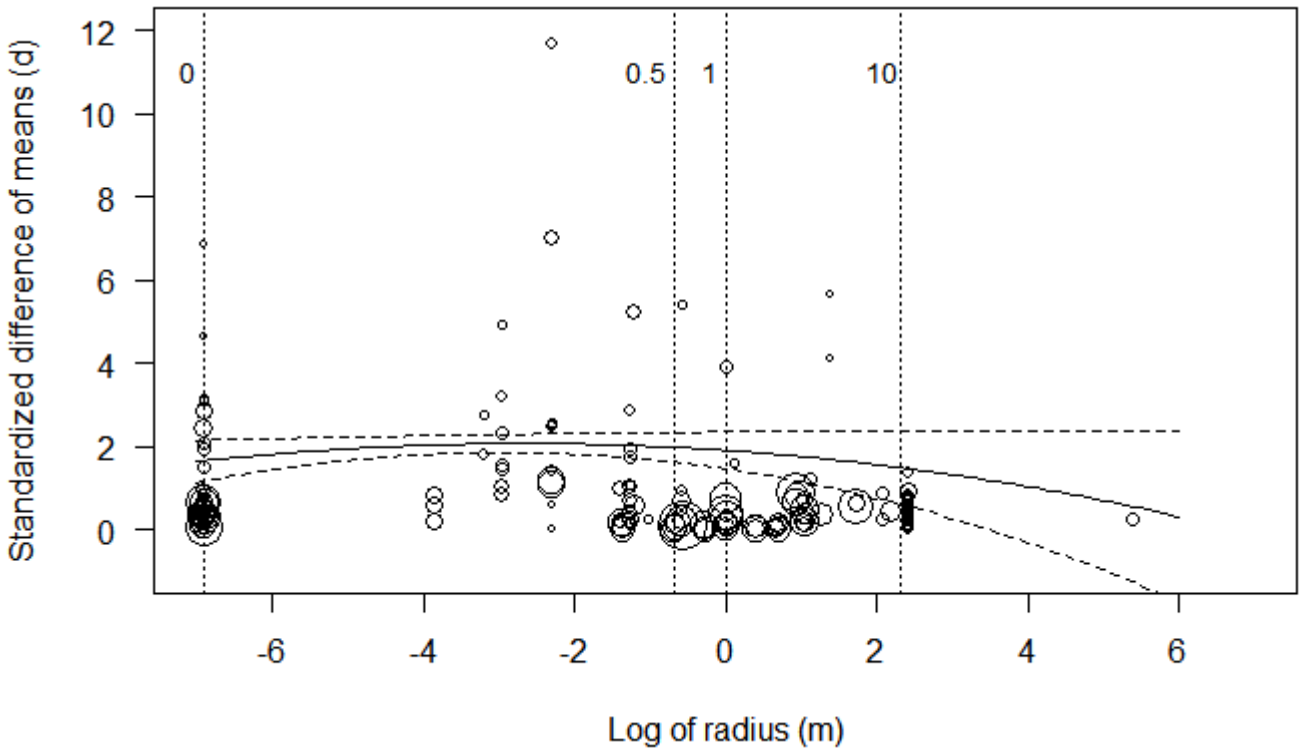

Moderator level, I2 (%) [95% CI]
Associational effect
Associational susceptibility, 88 [81, 93]
Associational defence, 96 [95, 98]
Neighbor contrast susceptibility, 20 [61, 95]
Neighbor contrast defence 0 [0, 0]
Effect size class
r, 94 [91, 97]
d, 94 [93, 96]
OR, 92 [79, 96]
Overall mean for all studies, 95 [94, 96]
49
55
22
25
28
123
17
168
0.00
0.50
1.00
1.50
2.00
2.50
Standardized difference of means (d)

Figure 2.


Standardized difference of means (d)
12
10
8
6
4
2
0
0
0.5
1
10
-6
-4
-2
0
2
4
6
Log of radius (m)

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559