Review

Synthesizing habitat fragmentation effects on plant–antagonist interactions in a phylogenetic context

Mariana Chávez-Pesqueira [a],[*],[1], Diego Carmona [b],[1], Pilar Suárez-Montes [a], Juan Núñez-Farfán [a], Ramiro Aguilar [c]

[a] Laboratorio de Genética Ecológica y Evolución, Departamento de Ecología Evolutiva, Instituto de Ecología, Universidad Nacional Autónoma de México, 70-275, 04510 Distrito Federal, Mexico
[b] Department of Biology, University of Toronto Mississauga, Mississauga, ON L5L 1C6, Canada
[c] Instituto Multidisciplinario de Biología Vegetal, Universidad Nacional de Córdoba, CONICET, CC 495, CP5000 Córdoba, Argentina

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ABSTRACT

Plant–antagonist interactions shape the structure, composition and dynamics of plant communities and ecosystems. Due to their key importance, much research has been advocated to evaluate anthropogenic habitat loss and fragmentation effects on plant–antagonist interactions but no clear response patterns have arisen. Even recent quantitative reviews have failed to provide consistent generalizations. Here we conduct the first phylogenetically independent meta-analysis along with a traditional meta-analytical approach. We examined whether characteristics of the interaction, the fragmented landscape, and methodological approaches modulate the magnitude of effects. Traditional meta-analysis showed that plants within habitat fragments suffer on average less damage from antagonists. However, when incorporating the phylogenetic relationships among plants, the overall effect and the particular effects of moderators became non-significant. Interestingly, we found a strong and consistent trend between both meta-analytical approaches in the overall effect of habitat fragmentation on folivory elicited by insects. This implies the first genuine fragmentation effect that transcends the phylogeny of plants and is not undermined by statistical problems of pseudoreplication. Decreased insect folivory will favor certain plant species, especially those with acquisitive resource use traits such as pioneer and exotic invasive, thereby affecting plant community composition in fragmented habitats. Here, we highlight the importance of incorporating the phylogeny in meta-analytical contexts. Our results imply that current studies worldwide represent a phylogenetically-conserved sample of fragmentation effects on plant-antagonist interactions. Thus, more studies on distantly phylogenetically-related plants are needed to have a broader, more representative, sample of responses across angiosperms.

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* Corresponding author.
   E-mail addresses: mchpesqueira@gmail.com (M. Chávez-Pesqueira), diego.carmona@utoronto.ca (D. Carmona), mapoland7@gmail.com (P. Suárez-Montes), farfan@unam.mx
(J. Núñez-Farfán), raguilar@imbiv.unc.edu.ar (R. Aguilar).
   [1] Co-first authorship.

1. Introduction

Antagonistic plant–animal interactions, the most common and ancient interactions in nature (Scott, 1983; Labandeira, 1998), involve the direct and indirect damages of plants by animals (or viruses and pathogens) for food or housing (Southwood, 1973; García and Chacoff, 2007). Antagonistic interactions include principally folivores (leaf consumers), florivores (flower consumers), and seed predators (seed consumers), and some frugivores (fruit consumers that damage seeds), which collectively are called herbivores. The interaction between plants and their natural enemies influences the dynamics and structure of ecosystems and vice versa. Emerging causal effects from the individual level to the population-level processes can potentially affect forest regeneration and maintenance of plant diversity (Faveri et al., 2008). For instance, plant demography can be altered if the impact of herbivory changes due to plant ontogenetic stage or to the type of tissue that is consumed (Crawley, 1997; Simonetti et al., 2006). This may also impact the community level if herbivores modify seedling recruitment altering the number or composition of plant species in the seed rain and seed bank (Hoffmesiter et al., 2005; Del Val, 2012). Also, being a fundamental part of the food webs, antagonists are of relevant importance on the ecosystems' energy flow, both in the effects of superior trophic levels, as well as in the reincorporation process of nutrients (McNaughton et al. 1997). Therefore, plant-antagonist interactions represent primary conservation targets because of their pivotal role in plant regeneration processes, plant community structure, ecosystem functioning, and biodiversity evolution (García and Chacoff, 2007). Interestingly, such antagonistic interactions are also affected by modifications at community and ecosystem levels in a feedback fashion.

The current rates of defaunation and habitat fragmentation are dramatically affecting the interactions between plants and their natural enemies (Galetti et al., 2003; Galetti and Dirzo, 2013; Dirzo et al., 2014). The transformation of continuous habitats into mosaics of isolated forest fragments exposes organisms surviving in the fragments to a modified surrounding environment, where decreasing population size and connectivity often disrupts biotic interactions (Murcia, 1995; Tscharntke and Brandl, 2004). Only 10% of recent publications referring to ecology of fragmented habitats evaluate interactions and focus mostly on mutualistic interactions, such as pollination and seed dispersal (Ghazoul, 2005; Aguilar et al., 2006, 2009; Markl et al., 2012). Much less attention is given to antagonistic interactions. Existent literature from the last decades show no clear response patterns on whether damage by antagonists decrease, increase or remain unaltered in fragmented landscapes. Some studies support the hypothesis of lower levels of damage in fragments, (Bersciano et al., 1999; Benítez-Malvido, 2001; Arnold and Asquith, 2002; Ledergerber et al., 2002; Vásquez et al., 2007; Simonetti et al., 2007; Faveri et al., 2008; Ruiz-Guerra et al., 2010), while others suggest increased damage in fragmented habitats (Kruess and Tscharntke, 1994; Lienert et al., 2002; Elzinga et al., 2005; Stoll et al., 2006; Christie and Hochuli, 2005; Galetti et al., 2015). Moreover, the amount and quality of food resources for antagonists may also change with habitat fragmentation negatively affecting plant productivity and leaf chemistry (Yamasaki and Kikuzawa, 2003).

Interestingly, three recent reviews have addressed the effects of habitat fragmentation on plant-animal interactions, including the antagonistic relations between plants and herbivores using different scopes, and they have also shown contrasting outcomes (De Carvalho Guimaraes et al., 2014; Magrach et al., 2014; Martinson and Fagan, 2014). While Martinson and Fagan (2014) found lower herbivory in habitat fragments than in continuous habitats, De Carvalho Guimaraes et al. (2014) found the inverse pattern: plants in habitat edges suffered more damage than plants inside habitats. Finally, Magrach et al. (2014) suggested that antagonistic interactions are more robust to habitat fragmentation since they did not find any effect of habitat fragmentation. Such disparity of general response patterns in the three reviews is quite surprising. Systematic quantitative reviews such as meta-analysis are powerful objective statistical tools that allow estimating an overall effect size of a common factor by combining the results of independent studies addressing similar research questions (Gurevitch and Hedges, 2001). Such contradictory overall effects among reviews may be ascribed to different approaches of effect size calculations, criteria of study inclusion, as well as the scopes and databases used by the different reviewers. Despite the reasons, these important attempts to summarize the existent empirical evidence have failed to find a consistent clear response pattern of habitat fragmentation effects on plant-antagonistic interactions.

Moreover, none of these three reviews accounted for phylogenetic non-independence in their overall effect size estimations. Meta-analytic data in ecology and evolutionary biology can seriously violate statistical assumptions of independence, especially when effect sizes are calculated from individual species, as is the case in these reviews. Common shared ancestry of taxonomically related species introduces a correlated error structure that needs to be accounted for in order to avoid misleading conclusions in meta-analyses (Lajeunesse, 2009; Chamberlain et al., 2012). Additionally, phylogenetically independent meta-analyses can also allow us to unravel the relative importance of evolutionary phylogenetic relationships over the ecological effects of habitat fragmentation.

The effects of habitat fragmentation on antagonistic interactions can be influenced by sources of variability related to the interaction and/or to external landscape features. Yet, these factors have not been thoroughly analyzed for multiple species. For instance, responses to habitat fragmentation may differ depending on the type of interaction and degree of specialization, where more specialized plant–antagonist interactions may be more susceptible to be lost in fragmented habitats compared to more generalist interactions. On the other hand, the identity of the interacting partner may also show differential response. For example, if we only consider the mobility of natural enemies we could expect that the higher mobility of birds and mammals may render less susceptibility to fragmentation effects compared to insects, which have comparatively lower mobility. Also, certain types of antagonist interactions may be more susceptible than others. If seed predation is mostly performed by birds and mammals (as in the tropics), then it may be less negatively affected by habitat loss compared to folivory, which is mainly accomplished by insects. Moreover, external landscape features of the fragmented habitats can also influence the magnitude of fragmentation effects on plant–antagonist interactions. The matrix surrounding the fragments may affect plant's susceptibility to antagonist animals by conditioning their dispersion and mobility capacity throughout the landscape (Driscoll et al., 2013; Mendes et al., 2015). Also, the time elapsed since the onset of fragmentation can determine when biotic interactions would show a change promoted by habitat fragmentation. Because local extinction of species can occur with a considerable delay after the event of habitat loss (i.e., undergo extinction debts; sensu Tilman et al., 1994), recently fragmented habitats may not show significant changes in biotic interactions relative to continuous, undisturbed original habitats. Finally, methodological approaches of published research may also influence the sensibility to find habitat fragmentation effects; experimental studies that deliberately create fragmented environments or place individuals within certain arrangements may have different ability to detect effects compared to observational studies. Despite the fact that experimental approaches are a key tool for disentangling causation, they may have a cost in terms of loosing external validity when facing complex and dynamic processes such as habitat fragmentation (Sagarin and Pauchard, 2009). In fact, the multiple approaches and definitions used by experimental studies may be introducing an important amount of artificial variance that dilutes important effects when studying habitat fragmentation. For instance, experimental approaches could mask the effect of factors such as number of generations since fragmentation, the spatial arrangement of fragments, and the degree of isolation of habitat fragments, among others.

In the present study we conduct phylogenetically independent and traditional meta-analyses to assess the overall magnitude and direction of habitat fragmentation effects on plant–antagonist interactions. We also examine whether certain characteristics of the plant–antagonist interaction (type of interaction, degree of specialization, and identity of antagonist), the approach used by authors (experimental vs. observational studies), and features of the fragmented habitats (type of habitat, time elapsed in fragmentation condition and matrix type surrounding fragments), modulate the magnitude of effects on antagonistic interactions.

2. Material and methods

We conducted extensive surveys in electronic bibliographic data bases (Scopus and Google Scholar) and searched for studies evaluating habitat fragmentation effects on the interaction of plant species and their antagonists. To attain this we used the following keyword combination for searching the literature: fragment* AND (herbivor* OR folivor* OR frugivor* OR florivor* OR "seed predat*" OR parasit* OR pathogen* OR antagonist*). Therefore, the antagonistic interactions included here were: folivory, frugivory, florivory, seed predation, parasitism, and damage by pathogens. For a study to be included in our analysis, quantitative data of plant damage inflicted by the antagonist had to be reported. In the case of frugivory, we only included studies that explicitly indicated that seeds were predated along with the fruit; thereby excluding all studies where frugivory was involved in effective seed dispersal. Because of this, for the analyses we merged the studies of seed predation and frugivory as one category (seed predation). Due to the large amount of approaches to the study of habitat fragmentation, we included studies that compared plant damage in (1) continuous habitat vs. habitat fragments, (2) plant populations with different degrees of isolation, and (3) plants evaluated in the interior and edges of habitats. Despite the approaches used by authors, all studies included here were explicitly aimed at measuring habitat fragmentation effects. For studies that included multiple species, we incorporated each of the species as independent studies to avoid subjective decisions and losing information provided by each species (Gurevitch and Hedges, 1999). For studies with repeated measures in time, we consistently chose the last measure to avoid pseudoreplication effects from a single study when effects are obtained more than once for the same species (Gurevitch and Hedges, 2001). Many studies included comparisons of continuous habitat with several habitat fragments of different sizes; in these cases we selected the medium size fragment to have a conservative estimation. When comparisons of continuous habitat were made against two fragments we chose the smallest one. Furthermore, we went through the metadata used by the three recent reviews (De Carvalho Guimaraes et al., 2014; Magrach et al., 2014; Martinson and Fagan, 2014), to check for studies that did not appear in our initial search but that matched our selection criteria for inclusion. We were able to incorporate and use 41 effect sizes from these reviews. All non-fragmentation studies from these databases were not included here.

Based on the information given in articles, we classified the plant species according to the identity of the antagonist partner (birds, fungus, insects, mammals and mixed), and the degree of specialization of the antagonist interaction (generalist vs. specialist). Furthermore, we obtained information about the fragmentation context of every study such as the type of natural habitat (tropical forest, temperate forest, desert/xeric shrubland, grassland and wet meadow (sensu Olsen et al., 2001), the type of matrix around fragments (pastures, cultivated land, forestry plantations, urban areas, water (in the case of wet meadows) or mixed) and time since fragmentation, which included three broad categories reflecting the most frequent time periods of fragmented habitats assessed by authors (≤ 30 years, 31–60 years and ≥60 years). We also recorded the methodological approach used by the studies as to whether the evaluation was experimental or observational. If some

information was not given in the article, we either contacted the authors or looked it up in other articles (e.g., characteristics of species or study sites). All this context-dependent information was used to detect attributes in the studies that could influence the magnitude of habitat fragmentation effects on antagonist interactions.

2.1. Data analysis

We performed all meta-analyses using Hedges' unbiased standardized mean differences (Hedges' d) as the effect size estimator. Hedges' d expresses the difference in plant damage inflicted by antagonists between fragmented and continuous habitats. To calculate Hedges' d for each species, we obtained the mean values, sample sizes and standard deviations of damage values for each of the two landscape conditions. We used Datathief III software (http://datathief.org/) to obtain the data from graphs. If some of the data were not provided, we either contacted the authors or excluded it. In a few studies using correlational approaches (e.g., plant damage by antagonists along gradients of habitat isolation) we used Pearson correlation coefficients and sample sizes to calculate Hedges' d through arithmetical transformations (Borenstein et al., 2009). Because variation in effect sizes can be due not only to sampling error but also due to a true random component (Raudenbush, 1994; Gurevitch and Hedges, 1999) we used random-effects models for all the analyses.

We used the R package metafor (Viechtbauer, 2010) to run traditional meta-analyses. Fragmentation effect was considered significant if the 95% biased-corrected bootstrap confidence interval (CI) of the effect size (d) did not overlap zero (Rosenberg et al., 2000). Positive values of the effect size (d) imply that habitat fragmentation increases plant damage (i.e., higher plant damage in habitat fragments) whereas negative d values imply that habitat fragmentation decreases plant damage. In order to test the explanatory power of moderator variables we used between groups Chi-squared test $Q_{between}$ (Hedges and Olkin, 1985). Significant $Q_{between}$ indicates that a particular categorical moderator variable (e.g., type of antagonist partner, habitat type, time since fragmentation, etc.) explains part of the heterogeneity among effect sizes. Finally, the possibility of publication bias was evaluated graphically using a funnel plot and statistically calculating a rank correlation test for the asymmetry in the funnel plot. Both examine the relationship between effect sizes and sample sizes across studies. If publication bias exists then studies with small or null effect sizes are missing and the funnel shape is asymmetric and correlation tests are significant. We also calculated a weighted fail-safe number, which indicates whether results are robust regardless of any publication bias (Rosenberg, 2005). The weighted fail-safe number value indicates the number of non-significant, unpublished or missing studies that would need to be added to a meta-analysis in order to nullify the overall effect sizes (Rosenthal, 1979). If the calculated fail-safe number is greater than $5n + 10$, where n is the number of studies, then publication bias may be safely ignored (Rosenberg, 2005).

When considering several effect sizes from different plant species the statistical assumption of independent samples can be violated due to the correlated error structure associated to the intrinsic evolutionary relationship among species, thus potentially affecting general conclusions about response patterns in quantitative reviews (Lajeunesse, 2009; Chamberlain et al., 2012). The inclusion of phylogenetic information within meta-analysis allows for correct phylogenetically independent estimations of overall effects. To run a phylogenetically independent meta-analysis we constructed a phylogenetic tree of all the plant species included in our review with S.PhyloMaker function implemented in R (provided in supplementary data; Qian and Jin, 2015). The hypothesized tree sets the phylogenetic relationships among all the species considered in this review using the Zanne et al. (2014) megatree based on an updated and expanded version called PhytoPhylo (Qian and Jin, 2015). The internal branch-length was estimated according to this megatree (Fig. 1A). S.PhyloMaker generates three different outputs
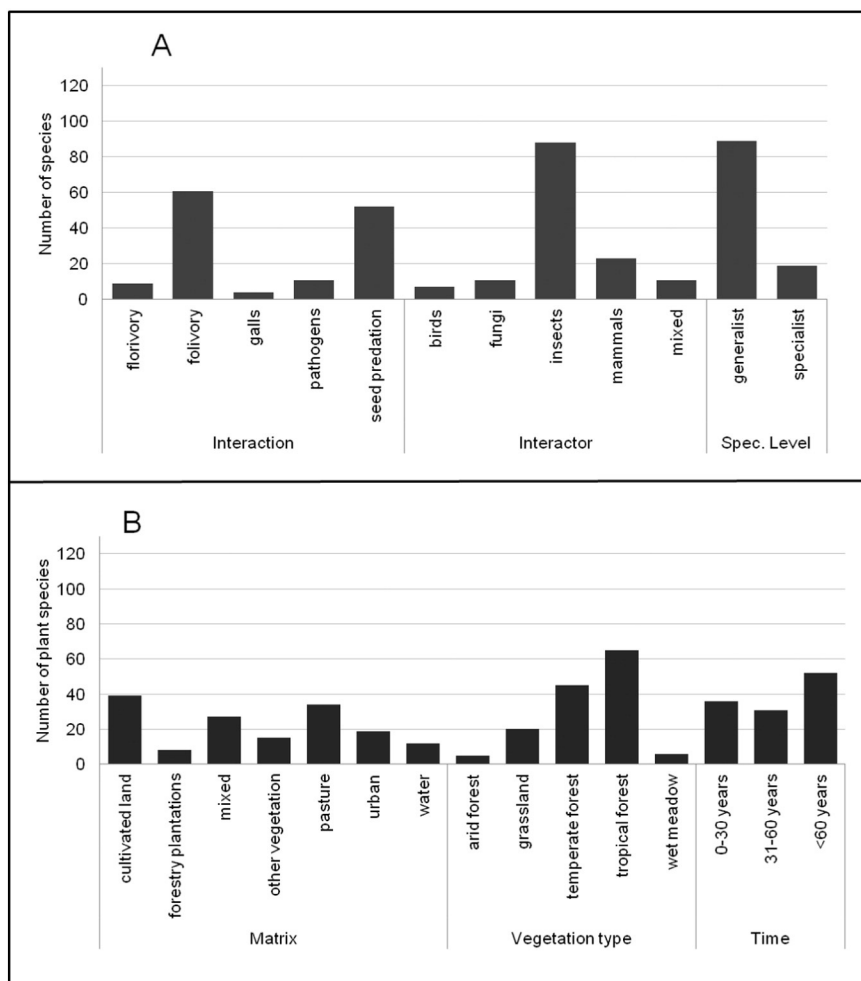
Fig. 1. Number of plant species analyzed within each moderator variable included in the review. (A) Type of the antagonistic interaction, and (B) landscape features of the fragmented habitat.

based on three different approaches (scenarios) used to add taxa to a phylogeny (Newick file A1). The tree generated under the third scenario was saved and used for further analyses. This scenario adds taxa as polytomies within their parental taxa and assigns branch lengths using BLADJ as Phylomatic does (Webb and Donoghue, 2005; Webb et al., 2008; Qian and Jin, 2015). Three of four polytomies were solved based on published papers (Swenson and Anderberg, 2005 (Sapotaceae); Gunn, 2004; Roncal et al., 2008; Baker et al., 2011 (Arecaeae); Manos et al., 1999 (Fagaceae)). This procedure satisfies the assumptions of the relationship between the phylogenetic correlations and the time since divergence (Lajeunesse, 2009) and also makes effect sizes comparable with the traditional meta-analysis. Lajeunesse's (2009) method was performed with PHYLOMETA that uses a weighted GLS approach to account for phylogenetic correlations among species. In the case where multiple effect sizes were available for the same species (this happened for 18 species), we pooled them prior to performing the phylogenetically independent meta-analysis. To do this, the overall effect size for each repeated species was estimated using a traditional meta-analysis with a fixed-effect model (Lajeunesse et al., 2013). We built a global phylogenetic tree with the entire sample of species for overall fragmentation effect estimations. When analyzing each predictor or moderator variable, we constructed a subset phylogenetic tree for each moderator (e.g., type of antagonist interaction, identity of antagonist, etc.), which contained only the species present in that particular comparison and retains all the branch length information found in the original hypothesized tree. Finally, we

estimated Blomberg's K (Blomberg et al., 2003), which measures the strength of the phylogenetic signal in phylogenetic trees, in order to understand the potential contrasting results between traditional and phylogenetically independent meta-analyses (Chamberlain et al., 2012). In the context of a meta-analysis, K values approaching zero imply that closely related species do not share similar effect sizes, whereas values of K near or larger than one suggest that closely related species do share similar effect sizes (i.e., effect sizes are conserved). This parameter was obtained using the R package "phytools" and the function phylosig (Revell, 2012).

3. Results

The literature search comprised the period 1999–2013 of published studies related to habitat fragmentation and antagonistic interactions. A careful screening was performed to determine their suitability for inclusion in our synthesis. We ended up with 77 published papers and two PhD theses that evaluated the effects of habitat fragmentation on different plant-antagonist interactions. These studies yielded 141 data points from 96 plant species from 54 plant families (Table A1). In Fig. 1 we summarize the number of plant species within some of the categories examined. In general, tropical forest, as habitat type, and insects, as antagonist partners where the most represented within our review dataset.

We found no evidence for publication bias in our data. The funnel plot of effect size vs. sample size showed no skewness suggesting no

bias in reporting results from the studies included in this review (Fig. A2). This result was supported by the non significant rank correlation test for funnel plot asymmetry (Kendall's Tau $= -0.484$, $P = 0.401$), as well as by the calculated weighted fail-safe number (2598), which resulted greater than the expected without publication bias ($5n + 10 = 715$).

The overall weighted mean effect size of habitat fragmentation on the interactions of plants with antagonists across all studies was negative and significantly different from zero when evaluated with the traditional meta-analysis ($d_+ = -0.3557$, df $= 140$, $P = 0.0012$, CI 95% -0.5705 to -0.1409) indicating that on average, plants in habitat fragments suffer significantly less attacks from antagonists compared to plants in continuous habitats. Nevertheless, this effect became nonsignificant when the phylogenetically independent meta-analysis was performed ($d^P = 0.160$, df $= 95$, $P = 0.5180$, CI 95% -0.325 to 0.645) (Fig. 2). Decreased sample size in the phylogenetically independent meta-analysis (N $= 96$) (Table A2) might reduce power to test for significant overall effect. To test this possibility we performed a traditional meta-analysis with the same 96 observations used in the phylogenetically independent meta-analysis. This analysis detected the same qualitative result than performing the traditional meta-analysis with 141 observations ($d_+ = -0.280$, df $= 96$, $P = 0.0362$, -0.5424 to -0.0181) indicating that nullification of the overall effect was not due to a reduction on the statistical power. The same caution was taken
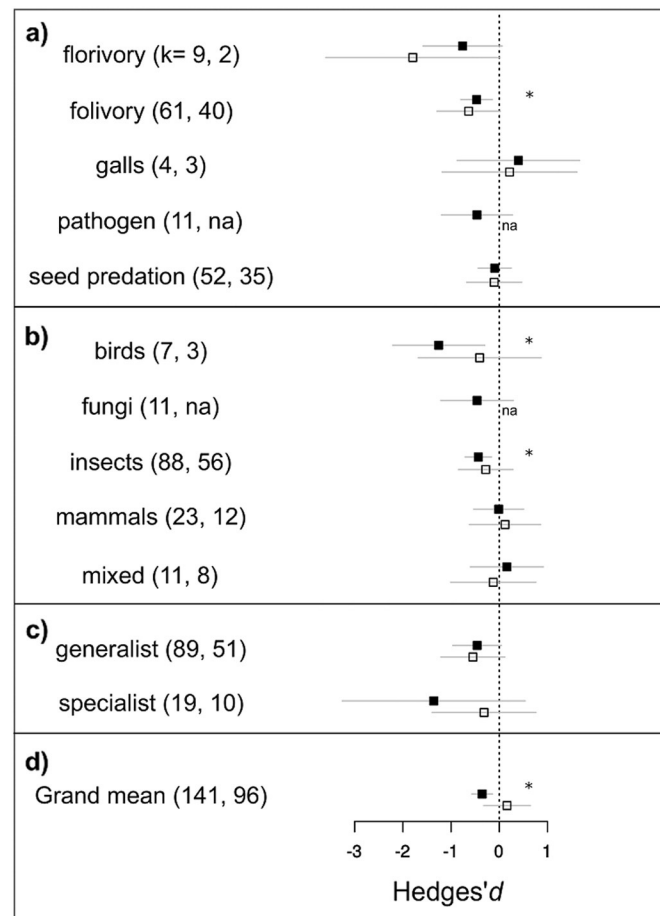
Fig. 2. Weighted mean effect sizes for the plant species and 95% bias-corrected CI of habitat fragmentation on plant–antagonist interactions by the type of interaction (a), type of antagonist (b), specialization of the interaction (c), and for all species (i.e. the grand mean; d). Black squares represent the results for the traditional meta-analysis; white squares represent the results for the phylogenetically-independent meta-analysis. The vertical line represents Hedge's $d = 0$. Values within a parenthesis indicates the sample sizes (k) for traditional and phylogenetically-independent meta-analysis.* denotes a significant effect.

when exploring subsequent analysis including different categories (Table A3). The contrasting outcomes between the traditional and the phylogenetically independent meta-analyses were generally consistent as we examined the different moderators. Moderators with sample size smaller than 10 are not reported in our results nor discussed, but are reported in tables.

Among the type of antagonistic interactions, folivory was the only interaction with a significantly negative habitat fragmentation effect ($d = -0.471^{significant = *}$), but as observed for the overall effect, this was only detected in the traditional meta-analysis. None of the other types of antagonist interactions showed significant fragmentation effects in both meta-analyses (i.e., effect sizes overlapping zero Hedges' d value; Table 1, Fig. 2). Similarly, within the type of antagonist, only insects ($d = -0.434^*$) showed significant negative fragmentation effects (Table 1, Fig. 2), which also became non-significant in the phylogenetically independent meta-analysis. No difference was observed between generalist and specialist antagonist interactions (Table 1, Fig. 2) in neither of the two types of meta-analyses.

When exploring features of the fragmented landscape we found that studies assessing fragmentation effects with cultivated lands as surrounding matrices showed significantly stronger negative effects, implying lower damage by antagonists in fragmented habitats than in continuous habitats ($d = -0.524^*$; Table 1; Fig. 3). In terms of habitat type, significantly lower levels of damage were found in habitat fragments of temperate and tropical forests ($d = -0.399^*$ and $d = -0.397^*$, respectively) (Table 1; Fig. 3). When assessing the time since fragmentation we found that plants from fragmented habitats of more than 60 years showed less attacks compared to continuous habitats ($d = -0.432^*$) (Table 1; Fig. 3). As observed before, all these effects become non significant when incorporating the phylogeny in effect size calculations. The only exception was the effect observed in tropical forests, which remained significant in the phylogenetically independent meta-analysis.

With regards to the methodological approaches used in fragmentation studies assessing antagonistic interactions, only observational approaches showed a negative and significant mean effect size ($d = -0.499^*$) whereas experimental studies showed no significant effects. Again, effect size of observational studies became non-significant when controlling for phylogenetic relationships among plant species.

All the estimated phylogenetic signals ($K_{Blomberg}$, Blomberg et al., 2003), either for the phylogenetic tree constructed with the entire set of species ($K_{Blomberg} = 0.182$, $P = 0.815$) as well as for each tree built for each moderator variable (range 0.186–0.281; see Table 1), were all relatively low and always non-significant, implying that effect sizes are not conserved across the phylogeny.

3.1. The case of insects

Insects were by far the most represented antagonist group (Fig. 1) and they showed a strong negative mean effect size in the traditional meta-analysis (Table 2; Fig. 4). Because of the large sample size of the insect group, we run further analyses using the same moderators and methods described above. As previously observed, many significant effects of habitat fragmentation found in the traditional meta-analyses were lost when we performed the phylogenetically independent meta-analyses. This was the case for damage by generalist antagonist interactions that was lower in habitat fragments in the traditional meta-analysis ($d = -0.685^*$) but was not consistent between meta-analyses ($d^P = -0.594$). Similarly, significant decreased damage by insects in tropical forest fragments was not consistent in both meta-analyses ($d = -0.463^*$, $d^P = -0.226$), nor in the temperate forests ($d = -0.534^*$, $d^P = -0.620$), which showed a non-significant effect in the phylogenetically independent meta-analysis (Table 2). Furthermore, habitat fragments immersed in cultivated land matrices showed negative effects only in the traditional meta-analysis (Table 2). However, and very interestingly, we found that plants in fragmented habitats

Table 1

Traditional and phylogenetically independent meta-analyses of habitat fragmentation effects on plant-antagonist interactions. Q_b test evaluating between-group differences are reported by each moderator evaluated. Sample sizes (K), the weighted mean effect sizes (Hedges' d_+) and 95% confidence intervals shown. Superscript ^{P} refers to phylogenetically independent meta-analyses. $K_{Blomberg}$ are shown for each partial phylogeny built with the species included in each moderator contrast. Numbers in bold indicate significant values.

Grouping categories	Traditional meta-analysis				Phylogenetically-independent meta-analysis			
	K	d_+	LCI	UCI	K^P	$d_+{}^P$	LCI	UCI
Interaction	$Q_b = 5.146$, d.f. = 4, $P = 0.2726$				$Q_b^P = \mathbf{7.24}$, **d.f. = 1, $P = 0.0071$**			
					$K_{Blomberg} = 0.197, P = 0.798$			
Florivory	9	−0.764	−1.596	0.067	2	−1.794	−3.596	0.007
Folivory	61	**−0.472**	**−0.801**	**−0.142**	40	−0.656	−1.313	0.002
Galls	4	0.395	−0.888	1.679	3	0.212	−1.183	1.607
Pathogens	11	−0.463	−1.207	0.282	NA	NA	NA	NA
Seed predation	52	0.029	−0.421	0.262	35	−0.091	−0.658	0.477
Antagonist	$Q_b = 7.258$, d.f. = 4, $P = 0.1228$				$Q_b^P = 2.12$, d.f. = 1, $P = 0.1458$			
					$K_{Blomberg} = 0.194, P = 0.786$			
Birds	7	**−1.256**	**−2.212**	**−0.301**	3	−0.408	−1.682	0.867
Fungi	11	−0.462	−1.214	0.290	NA	NA	NA	NA
Insects	88	**−0.434**	**−0.707**	**−0.161**	56	−0.282	−0.848	0.284
Mammals	23	−0.012	−0.531	0.507	12	0.120	−0.620	0.859
Mixed	11	0.156	−0.600	0.913	8	−0.126	−1.010	0.758
Level of specialization	$Q_b = 0.8066$, d.f. = 1, $P = 0.3691$				$Q_b^P = 0.0$, d.f. = 1, $P = 0.9616$			
					$K_{Blomberg} = 0.281, P = 0.409$			
Generalist	89	−0.460	−0.965	0.044	50	−0.547	−1.212	0.117
Specialist	19	−1.361	−3.259	0.538	10	−0.316	−1.393	0.760
Matrix	$Q_b = 2.843$, d.f. = 6, $P = 0.8282$				$Q_b^P = \mathbf{7.94}$, **d.f. = 1, $P = 0.0048$**			
					$K_{Blomberg} = 0.187, P = 0.772$			
Cultivated land	33	**−0.524**	**−0.976**	**−0.071**	20	−0.467	−1.254	0.321
Forestry plantation	8	**−0.864**	**−1.735**	**−0.006**	5	**−1.508**	**−2.677**	**−0.339**
Mixed	27	−0.347	−0.838	0.143	14	−0.203	−1.056	0.651
Other types of vegetation	15	−0.224	−0.883	0.434	9	0.078	−0.825	0.981
Pasture	34	−0.248	−0.709	0.212	25	−0.220	−1.040	0.599
Urban	10	0.012	−0.851	0.826	5	0.025	−1.428	1.479
Water	12	−0.036	−1.124	0.400	11	−0.528	−1.449	0.392
Habitat type	$Q_b = 5.463$, d.f. = 4, $P = 0.2429$				$Q_b^P = \mathbf{5.11}$, **d.f. = 1, $P = 0.0238$**			
					$K_{Blomberg} = 0.193, P = 0.739$			
Desert/xeric shrubland	5	−0.956	−2.105	0.193	4	−0.215	−1.651	1.221
Grassland	20	0.146	−0.402	0.694	14	0.443	−0.451	1.338
Temperate forest	45	**−0.399**	**−0.774**	**−0.024**	27	−0.471	−1.196	0.257
Tropical forest	65	**−0.397**	**−0.715**	**−0.079**	45	−0.386	−1.082	0.309
Wet meadow	6	−0.932	−2.021	0.155	4	−1.185	−2.777	0.408
Time since fragmentation	$Q_b = 0.071$, d.f. = 2, $P = 0.9653$				$Q_b^P = 0.871$, d.f. = 1, $P = 0.351$			
					$K_{Blomberg} = 0.266, P = 0.156$			
<30 years	36	−0.364	−0.806	0.076	21	0.348	−1.211	0.516
30–60 years	31	−0.367	−0.841	0.106	20	−0.682	−1.467	0.103
>60 years	52	**−0.432**	**−0.797**	**−0.066**	33	−0.204	−0.872	0.464
Approach	$Q_b = 1.461$, d.f. = 1, $P = 0.2268$				$Q_b = 1.56$, d.f. = 1, $P = 0.212$			
					$K_{Blomberg} = 0.186, P = 0.822$			
Experimental	74	−0.234	−0.525	0.058	49	0.226	−0.773	0.321
Observational	**67**	**−0.499**	**−0.817**	**−0.182**	42	−0.278	−0.940	0.383

presented significantly less damage due to insect folivory compared to continuous habitats, and this result was consistent in the phylogenetically independent meta-analysis ($d = -0.621^*$; $d^P = -0.838^*$). Also interesting, when evaluating the effects of habitat fragmentation depending on the time elapsed since it occurred, we detected a contrasting result: the traditional meta-analysis indicates a negative mean effect sizes in plants from fragmented habitats of >30 years old ($d = -0.839$ and $d = -0.511$; i.e. less attacks in fragments than in continuous habitats) while phylogenetically independent meta-analysis detected the same trend but only in fragmented habitats of 30–60 years old ($d^P = -1.011^*$) (Table 2; Fig. 4). Phylogenetic trees built with data of only insects showed in general larger phylogenetic signals (i.e., larger values for Blomberg's K).

4. Discussion

Detrimental effects of antagonists on plants represent a central ecological interaction that affects plant fitness, shaping the structure, composition and dynamics of plant communities and ecosystems (Scott, 1983; Crawley, 1997). Due to its key importance, much research has been advocated over the past decades to evaluate how current anthropogenic habitat loss and fragmentation affects plant-antagonist interactions (e.g. Benítez-Malvido et al., 1999; Groppe et al., 2001; Arnold and Asquith, 2002; Farwig et al., 2008; Herrerias-Diego et al., 2008; González-Varo, 2010; Ruiz-Guerra et al., 2010; De Crop et al., 2012; among others). Individual studies have mainly focused on evaluating fragmentation effects on single plant species or single plant–antagonist interactions, showing varied and contrasting response patterns. Due to such species-specific responses, the sample of species and interactions studied so far can condition the generality of literature syntheses. Within the studied antagonist interactions found in this review, we observed some biases in the selection criteria of researchers (i.e., research bias), where folivory and seed predation in tropical and temperate habitats were the interactions most frequently evaluated. Likewise, insects have been the most studied antagonist group, and most studies evaluated generalist interactions. The particular overrepresentation of generalist insects, however, may be reflecting their normal prevalence in plant–animal interactions in nature (e.g., Waser et al., 1996). In spite of such natural dominance, there are still many other groups of antagonists (pathogens such as fungi and virus, galls, mammals and birds) currently underrepresented in habitat fragmentation research, and they may show a higher degree of plant resource specialization. Such gap of understudied plant–santagonist interactions needs to be filled in future studies for a thorough and robust diagnosis of
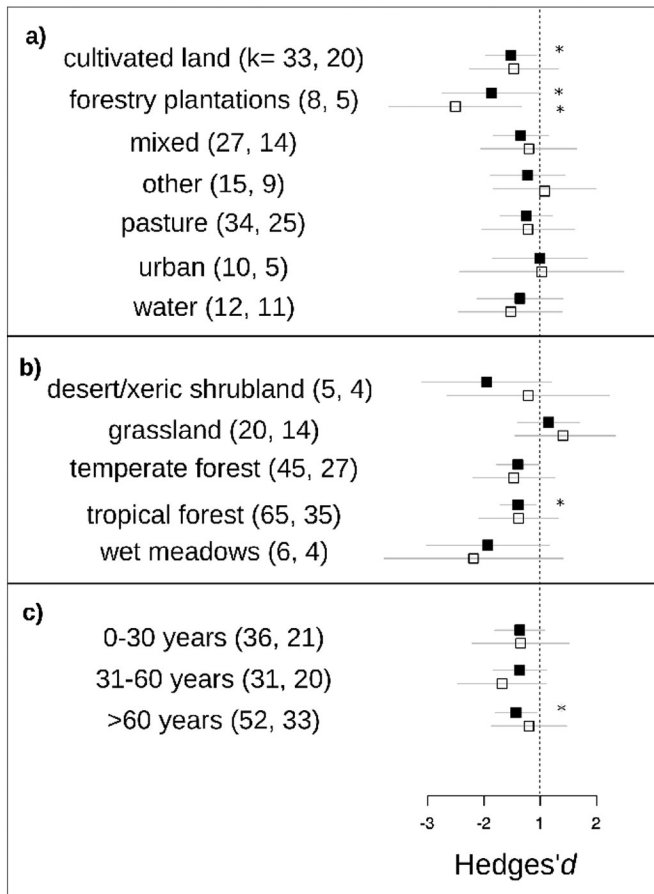
Fig. 3. Weighted mean effect for the plant species sizes and 95% bias-corrected CI of habitat fragmentation over the interactions of plants with their antagonists and categorized by type of matrix (a), natural habitat (b), time since fragmentation (c). Black squares represent the results for the traditional meta-analysis; white squares represent the results for the phylogenetically-independent meta-analysis. The vertical line represents Hedge's $d = 0$. Values within a parenthesis indicates the sample sizes (k) for traditional and phylogenetically-independent meta-analysis.* denotes a significant effect.

fragmentation effects. Moreover, we suggest to explore plant families poorly studied and to include abundance data of plants and their interactuants. This will help, for example, to understand the effect of habitat fragmentation over antagonists' populations and explain the decrease of plant damage in habitat fragments. Also, including fitness evaluations of attacked plants will help recognize to what extent antagonists compromise the persistence of plant populations in fragmented habitats.

While it is not expected to attain any generalization from single species studies, it is especially intriguing that the three quantitative reviews recently conducted (De Carvalho Guimaraes et al., 2014; Magrach et al., 2014; Martinson and Fagan, 2014) do not provide consistent global response patterns of fragmentation effects on plant–antagonist interactions. Here, we conducted the first phylogenetically independent meta-analysis of habitat fragmentation effects on plant–antagonist interactions, which also included metadata from these three recent reviews. Our results offer supported conclusions that must be considered to gain a new perspective of global responses of plants by antagonists in fragmented habitats, which may help understand the contrasting findings in previous systematic reviews.

4.1. Traditional meta-analysis

The results of the traditional meta-analysis for 141 data points from 96 plant species from 54 families showed an overall negative effect of fragmentation on the interaction of plants and their natural enemies,

indicating that plants within habitat fragments suffer on average less damage from antagonists than in continuous habitats. This response pattern was particularly clear and strong for the interaction of folivory (44% of the studies), with insects as the main antagonists (80% of folivory studies), concurring with the results obtained by the traditional meta-analysis of Martinson and Fagan (2014). Habitat loss and fragmentation can disrupt plant-animal interactions as a result of the structural changes occurring at the landscape level (decreased area of habitat remnants and increased isolation among them; e.g., Didham et al., 1996; Fahrig, 2003). Such changes and the presence of inhospitable anthropogenic matrices among habitat remnants impose physical barriers for interacting animal partners. Insect fauna in particular has shown to be highly susceptible to habitat fragmentation effects, which has been ascribed to their limited dispersal ability and shorter generation times compared to vertebrates, declining in abundance and species richness (Didham et al., 1996; Ewers and Didham, 2006; Martinson and Fagan, 2014). The results found here agree with this expectation, as insects were the only group of antagonists that showed a negative and significant fragmentation effect, decreasing insect plant damage in habitat fragments. On the contrary, the absence of fragmentation effects on birds and mammals may be due to their higher mobility between fragments (Andren, 1994; Bayne and Hobson, 1998; Pardini et al., 2005), being less susceptible to habitat fragmentation than insects. In fact, seed predation was not significantly affected by habitat fragmentation, and such result may be linked to the higher number of studies where seed predators were mainly birds and mammals; thus counteracting or diluting the negative effect of insect seed predators. As expected, higher specialization in plant–antagonist interactions showed a stronger negative magnitude of fragmentation effects than generalist interactions, but this difference was not statistically significant. Such result may be due to the low sample size of specialists, which generates large confidence intervals for this group and thus low power for testing the null hypothesis.

Some of the landscape features assessed here showed significant influences in shaping the magnitude of fragmentation effects within the traditional meta-analysis. Regarding the matrix type, we found that plants in habitat fragments surrounded by cultivated land had significant lower levels of damage than in continuous habitats, therefore representing barriers for some natural enemies of plants. The use of chemical products such as insecticides, herbicides, and pesticides in cultivated land matrices may have an additional negative impact, especially on insect populations (e.g., Winfree et al., 2009). Also, studies conducted in tropical and temperate habitats showed a significant decrease of antagonist attacks in plants inhabiting fragments whereas the rest of habitat types showed non-significant effects. However, such results are most likely the consequence of higher statistical power of these two habitat types, which comprised 78% of the studies. Finally, we found that plants surviving in fragmented habitats of more than 60 years showed a significant decrease from antagonist attacks compared to more recently fragmented landscapes. This result agrees with the theoretical expectation that the time elapsed in fragmentation conditions can determine whether extinction debts are paid or not (Tilman et al., 1994). Our results imply that older fragmented systems have already paid extinction debts of antagonists; therefore showing decreased abundance and diversity of natural enemies of plants. Considering the time scale of habitat fragmentation effects is important to understand the response of plants' interactions with their natural enemies in fragmented habitats (Aguilar et al., 2008; Rivera-Ortiz et al., 2014).

4.2. Phylogenetically independent meta-analysis

Incorporating the phylogenetic relationships in meta-analyses initially addresses the non-independence of effect sizes from species with shared evolutionary history, thus solving a clear violation of statistical assumptions (Adams, 2008; Lajeunesse, 2009). Here, when we incorporated the phylogenetic relationships among the plant species

Table 2
Traditional and phylogenetically independent meta-analyses of habitat fragmentation effects on only plant–insect interactions. Q_b test evaluating between-group differences are reported by each moderator evaluated. Sample sizes (K), the weighted mean effect sizes (Hedges' d_+) and 95% confidence intervals are shown. Superscript ^{p} refers to phylogenetically independent meta-analysis. $K_{Blomberg}$ are shown for each partial phylogeny built with the species included in each moderator contrast. Numbers in bold indicate significant values.

| Grouping categories	Traditional meta-analysis				Phylogenetically-independent meta-analysis			
	K	d_+	LCI	UCI	K^P	$d_+{}^P$	LCI	UCI
Interaction	$Q_b = 6.841$, d.f. $= 3$, $P = 0.0771$				$Q_b^P = 7.83$, **d.f. $= 1$, $P = 0.0051$**			
					$K_{Blomberg} = 0.281$, $P = 0.825$			
Florivory	8	−0.812	−1.659	0.035	2	−1.791	−3.733	0.150
Folivory	52	**−0.621**	**−0.964**	**−0.277**	32	**−0.849**	**−1.603**	**−0.094**
Galls	4	0.402	−0.826	1.630	3	0.225	−1.291	1.740
Pathogen	NA	NA	NA	NA	NA	NA	NA	NA
Seed predation	220.018	−0.478	0.514	14	0.000	−0.776	0.776	
Level of specialization	$Q_b = 0.4705$, d.f. $= 1$, $P = 0.4928$				$Q_b^P = 0.13$, d.f. $= 1$, $P = 0.7186$			
					$K_{Blomberg} = 0.461$, $P = 0.320$			
Generalist	47	**−0.685**	**−1.205**	**−0.166**	22	−0.594	−1.512	0.325
Specialist	16	−1.333	−3.112	0.445	8	−0.685	−2.011	0.642
Matrix	$Q_b = 6.911$, d.f. $= 6$, $P = 0.3219$				$Q_b^P = 13.5$, **d.f. $= 1$, $P = 0.0002$**			
					$K_{Blomberg} = 0.232$, $P = 0.740$			
Cultivated land	18	**−0.628**	**−1.197**	**−0.058**	11	−0.596	−1.544	0.352
Forestry plantation	4	**−1.508**	**−2.643**	**−0.374**	3	−2.123	−3.551	−0.694
Mixed	23	−0.335	−0.828	0.157	12	−0.229	−1.154	0.696
Other type of vegetation	11	−0.058	−0.772	0.655	8	−0.016	−1.025	0.992
Pasture	19	−0.326	−0.927	0.274	11	−0.820	−1.945	0.305
Urban	7	−0.192	−1.150	0.764	3	0.771	−1.114	2.656
Water	4	−1.266	−2.623	0.090	4	−1.346	−2.898	0.206
Habitat type	$Q_b = 1.7092$, d.f. $= 4$, $P = 0.7898$				$Q_b^P = 0.25$, d.f. $= 1$, $P = 0.6145$			
					$K_{Blomberg} = 0.224$, $P = 0.766$			
Desert/xeric shrubland	4	−0.296	−1.507	0.913	4	−0.229	−1.799	1.341
Grassland	14	−0.098	−0.732	0.536	9	−0.089	−1.223	1.045
Temperate forest	27	**−0.534**	**−1.005**	**−0.064**	16	−0.620	−1.508	0.268
Tropical forest	38	**−0.463**	**−0.872**	**−0.055**	23	−0.226	−1.145	0.692
Wet meadow	5	−0.801	−1.962	0.359	3	−0.892	−2.865	1.082
Time since fragmentation	$Q_b = 2.328$, d.f. $= 2$, $P = 0.3122$				$Q_b^P = 1.19$, d.f. $= 1$, $P = 0.2758$			
					$K_{Blomberg} = 0.511$, $P = 0.012$			
<30 years	27	−0.246	−0.731	0.236	15	−0.545	−1.523	0.433
30–60 years	17	**−0.839**	**−1.427**	**−0.251**	10	**−1.011**	**−2.020**	**−0.003**
>60 years	27	**−0.511**	**−1.000**	**−0.022**	16	−0.132	−1.038	0.773
Approach	$Q_b = 1.178$, d.f. $= 1$, $P = 0.2776$				$Q_b^P = 0.06$, d.f. $= 1$, $P = 0.8040$			
					$K_{Blomberg} = 0.234$, $P = 0.749$			
Experimental	36	−0.263	−0.662	0.135	18	−0.272	−1.021	0.478
Observational	**52**	**−0.554**	**−0.895**	**−0.213**	36	−0.401	−1.06	0.303

included in this review, the overall fragmentation effect as well as the particular effects of each moderator variable became non-significant. Such nullifying influence of phylogeny on meta-analytical global effects has been recently put in a broad context by Chamberlain et al. (2012), who re-analyzed 30 published ecological meta-analyses after incorporating the correlated error structure of phylogenetic relationships among species. They found that accounting for phylogeny reduced overall effect size significance in 40% of the random-effects models meta-analyses. More specifically, decreases in pooled effect sizes after incorporating phylogenetic information were associated with larger phylogenies and those with stronger phylogenetic signal (Chamberlain et al., 2012). Thus, phylogeny can act as an explanatory variable and its relative influence in meta-analytical syntheses will depend on the particular assemblage of the species included in the review, which should be closely linked to the sample of species globally studied so far, after a thorough literature search.

In accordance, when effect sizes are not conserved within the phylogeny (i.e., there is weak or null phylogenetic signal) any phylogenetic correction may have a trivial effect on meta-analytical results, as effect sizes would be fundamentally independent across the phylogeny (Chamberlain et al., 2012). The phylogeny built with 96 unique species from 54 plant families included in our review showed a low and non-significant phylogenetic signal ($K_{Blomberg} = 0.182$, $P = 0.815$; Blomberg et al., 2003), but still the overall effects were nullified when running the phylogenetically independent meta-analysis. Such result may be plausible as Blomberg's K measures only trait variation that deviates from Brownian motion (Blomberg et al., 2003). Trait conservatism (here, effect size), however, does not necessary imply Brownian

evolutionary dynamics. Thus, the phylogenetic signal in our synthesis appears to be present across the dataset, despite low Blomberg's K, where effect sizes are conserved within the phylogeny and therefore do not represent a random sample of fragmentation effects on plant–antagonist interactions across angiosperms (Chamberlain et al., 2012). In this regard, we may argue that the subset of plant species studied by researcher around the world represent a phylogenetically-conserved sample of fragmentation effects on plant-antagonist interactions. When analyzed together in a phylogenetic context, the plant species studied so far do not significantly change their antagonist interaction dynamics in fragmented habitats. Our results imply that more studies assessing fragmentation effects on distantly phylogenetically-related plant species are needed to have a broader, more representative, sample of responses across angiosperms. Such effort will ensure assessing whether habitat fragmentation has ecological significant effects on plant-antagonist interactions or not.

With the aim of comparing our results with previous reviews, we attempted to introduce the phylogenetic information and re-analyze the previous traditional meta-analyses (Magrach et al., 2014; Martinson and Fagan, 2014; De Carvalho Guimaraes et al., 2014) but they all failed to provide and report the correct data to do so. Martinson and Fagan (2014) were the only ones providing a complete list of plant species studied in their review but surprisingly (similar to Magrach et al., 2014) they only presented effect size values of each species but did not report their variances, precluding the possibility of repeating straightforward their meta-analyses. Thus we do not know for certain how phylogenetic information would affect their overall conclusions. Moreover, their database also includes some plant species
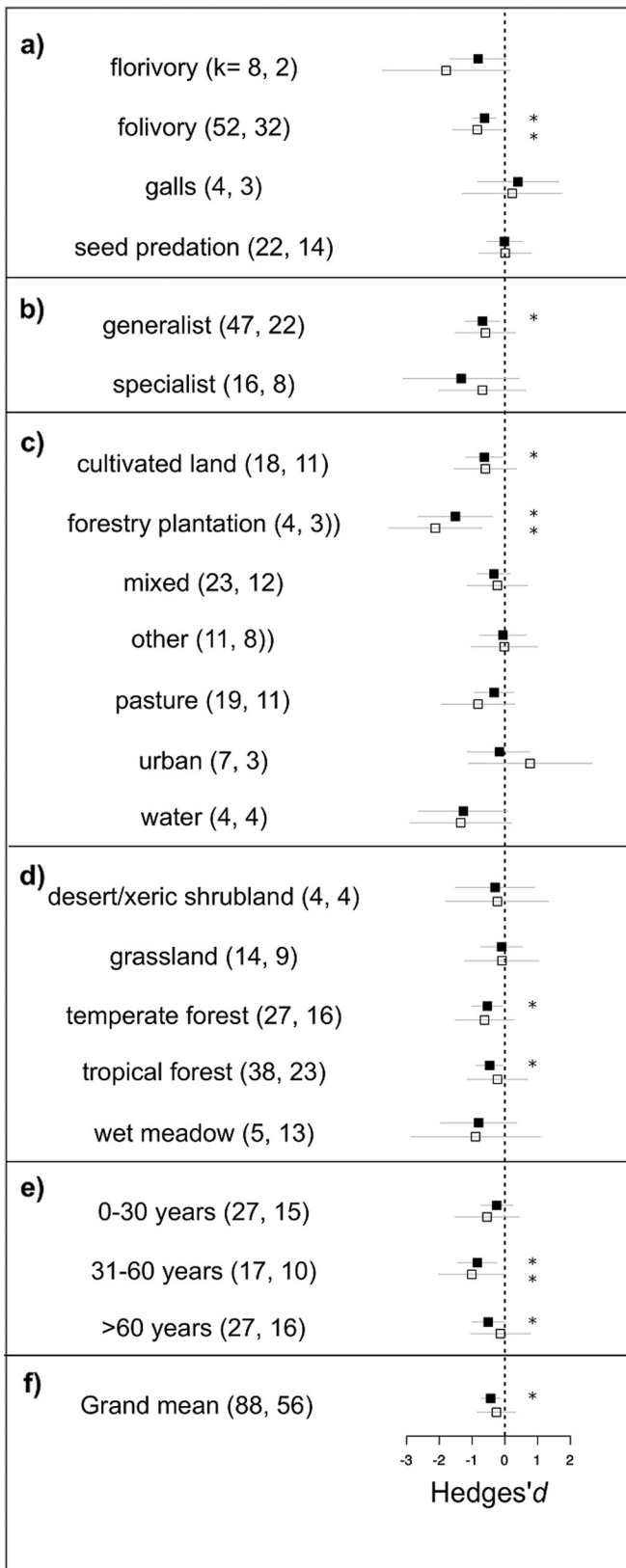
Fig. 4. Weighted mean effect sizes for the plant species and 95% bias-corrected CI of habitat fragmentation over the interactions of plants with only insect as antagonists categorized by type of interaction (a), time since fragmentation (b), and for all species (c). Black squares represent the results for the traditional meta-analysis; white squares represent the results for the phylogenetically-independent meta-analysis. The vertical line represents Hedge's d = 0. Values within a parenthesis indicates the sample sizes (k) for traditional and phylogenetically-independent meta-analysis.* denotes a significant effect.

assemblages (community level) as well as many studies assessing naturally fragmented spatial structure rather than anthropogenic habitat fragmentation. Thus, their contrasting outcomes may be the result of (i) singular assemblages of species included in their review due to different inclusion criteria, (ii) not focusing strictly on anthropogenic habitat fragmentation, and/or (iii) not controlling for phylogenetic information.

4.3. The case of insects

When assessing only the group of insects, there was a strong and consistent trend for the folivory interaction. Folivory by insects is a well-studied antagonist interaction and of recognized importance on plant fitness, community structure and ecosystems processes (Southwood, 1973; Crawley, 1997; Del Val, 2012). This interaction showed decreased damage in habitat fragments and this effect was consistent with both meta-analytical approaches. This result is important as it implies for the first time a genuine fragmentation effect that transcends the phylogenetic background of plant species sampled and that is not undermined by statistical problems of pseudoreplication.

Significant, phylogenetic-independent negative overall fragmentation effects on insect folivory imply that plant populations surviving in fragmented habitats are subjected to less insect damage. Decreased insect folivory will favor certain plant species, especially those with acquisitive resource use traits such as pioneer and exotic invasive, thereby affecting plant community composition in fragmented habitats. In the long run, forest remnants may undergo plant taxonomic and functional homogenization as a result of decreased insect folivory. Interestingly, previous quantitative reviews assessing fragmentation effects on bee pollinators (Winfree et al., 2009) and on plant pollination and reproduction (Aguilar et al., 2006) have shown significant negative global effects. By integrating these syntheses outcomes we may envision a compensative fragmentation effects whereby overall reductions in richness and abundance of pollinator and herbivore insects negatively affects sexual plant reproduction but positively reduces plant mortality and performance by less insect herbivores. The integrated, simultaneous research of mutualist and antagonist interactions within the same plant species will help disentangle the net fragmentation effects on long term plant population viability (Aguilar et al., 2009), with key implications for plant community structure, ecosystem functioning, and biodiversity evolution in current ubiquitous fragmented landscapes.

4.4. Final considerations

Our review highlights the importance of not just simply incorporating the phylogenetic relationships among sampled species, which resolves the problem of non-independence of effect sizes, but also of analyzing the phylogenetic signal of each phylogeny, as they can affect overall conclusions (Chamberlain et al., 2012). Any attempt to generalize across a broad range of taxa without evaluating the phylogenetic information can seriously undermine the validity of conclusions drawn from such reviews. Moreover, meta-analyses intended to synthesize on plant-animal interactions in particular, should also attempt to generate phylogenies from both the plant and the animal sides of the interactions. Unfortunately, studies currently tend to focus on one side of the interaction, and thus do not provide sufficient taxonomic information on the interacting counterpart. In this regard, incipient studies focusing on interaction web analyses should help to begin informing on both sides of the interacting web structure, allowing building and analyzing simultaneously plant and animal phylogenies in meta-analytical contexts.

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