REVIEW AND SYNTHESIS

Responses of insect herbivores and herbivory to habitat fragmentation: a hierarchical meta-analysis

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Abstract

Loss and fragmentation of natural habitats can lead to alterations of plant–animal interactions and ecosystems functioning. Insect herbivory, an important antagonistic interaction is expected to be influenced by habitat fragmentation through direct negative effects on herbivore community richness and indirect positive effects due to losses of natural enemies. Plant community changes with habitat fragmentation added to the indirect effects but with little predictable impact. Here, we evaluated habitat fragmentation effects on both herbivory and herbivore diversity, using novel hierarchical meta-analyses. Across 89 studies, we found a negative effect of habitat fragmentation on abundance and species richness of herbivores, but only a non-significant trend on herbivory. Reduced area and increased isolation of remaining fragments yielded the strongest effect on abundance and species richness, while specialist herbivores were the most vulnerable to habitat fragmentation. These fragmentation effects were more pronounced in studies with large spatial extent. The strong reduction in herbivore diversity, but not herbivory, indicates how important common generalist species can be in maintaining herbivory as a major ecosystem process.

Keywords

Body size, effect size, feeding type, fragment area, generalist herbivores, insect herbivory, isolation, spatial extent, species richness.

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INTRODUCTION

The loss and fragmentation of natural habitats caused by human activities represent the most severe threats for biodiversity (Brooks *et al.* 2002). The loss of species can lead to alterations of ecosystems functioning and stability (Tilman *et al.* 2014). There has been a growing interest in assessing habitat fragmentation effects on ecosystem processes, with special attention to mutualistic plant–animal interactions such as pollination (Aguilar *et al.* 2006) and seed dispersal (Markl *et al.* 2012) and to antagonistic interactions like predation and herbivory (Magrach *et al.* 2014; Chávez-Pesqueira *et al.* 2015). Plant–herbivore interaction is recognised as a key ecosystem process as the consumption by herbivores mediates competitive ability of plants, biomass production and energy transfer to higher trophic levels (Speight *et al.* 2008). Among herbivores, insects are the most diverse and abundant group and they can consume all types of plant organs and tissues, potentially affecting plant growth and reproduction (Crawley 1989). At community level, insect herbivores regulate plant diversity and community structure through their selective damage, impinging on competition within and among plant species (Hulme 1996). Therefore, any change in herbivore community and herbivory following habitat fragmentation

may trigger alterations in plant community structure and an array of ecosystem functions (Maguire *et al.* 2015).

Habitat fragmentation can influence insect herbivory through direct effects on herbivore community, but also through indirect effects on plant communities (bottom-up processes) and natural enemies (top-down processes) that may lead to changes in herbivory patterns (Hunter & Price 1992). A decrease in herbivory levels with reduced area of habitat fragments (e.g. Haynes & Crist 2009; Harvey & MacDougall 2015) is frequently attributed to a direct loss of herbivore species and/or reduced herbivore abundance (De La Vega *et al.* 2012; Harvey & MacDougall 2015). Increased isolation of fragments can disrupt insect movement, thereby increasing extinction probability and decreasing damage on plants in more isolated habitats (e.g. Watts & Didham 2006; Savilaakso *et al.* 2009). In addition to the direct influence, habitat fragmentation can have bottom-up effects through changes in plant community composition. As habitat fragments become smaller and more isolated, plant communities impoverish in diversity and change their structure (Ibáñez *et al.* 2014), which may lead to a decrease in associated herbivore species and thus of overall plant damage (Scherber *et al.* 2010).

Nevertheless, plant community changes induced by habitat fragmentation may also have a positive bottom-up effect,

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increasing herbivory levels. As small fragments are dominated by edge conditions (i.e. decreased soil and air humidity and increased light and temperature; Laurance *et al.* 1998; Christianini & Oliveira 2013), they are usually colonised by early successional and pioneering plant species (Tabarelli *et al.* 2012). Such plant species have typically acquisitive resource-use strategies with high growth rates, palatable broad leaves, low or no defences against herbivores and thereby, are the preferred hosts of insect herbivores (Coley *et al.* 1985). Moreover, another potential mechanism for a positive effect of habitat fragmentation on herbivory may be associated with reduction in natural enemy populations, which are often more vulnerable to fragmentation than herbivores because of their higher trophic-level position (Holt *et al.* 1999). Such top-down process involves herbivore release from natural enemy control (e.g. Thies *et al.* 2003), and can occur together with direct effects and bottom-up forces (Hunter & Price 1992).

Methodological factors may be important sources of variation in herbivory patterns. Components of habitat fragmentation that are evaluated, the spatial scale and type of sampling may mediate the responses of insect herbivory to habitat fragmentation. For example, studies at larger scales generally include a greater spatial extent involving greater difference between fragmented and control conditions thus being able to detect stronger fragmentation effects (Martinson & Fagan 2014). Responses of herbivore species may also depend on life-history traits such as trophic position, diet breath and dispersal capability (Tscharntke *et al.* 2002). For instance, generalist herbivores, as compared to specialists, may be less susceptible to changes in plant species composition due to habitat fragmentation, as they can switch host plants at any time (Tscharntke *et al.* 2002). Similarly, larger insect herbivore species with higher mobility can potentially move across inhospitable matrices, and thus may be present in small and isolated habitat fragments, whereas small insect herbivores may not (Tscharntke & Brandl 2004). On the contrary, endophagous insects that feed inside the plant (e.g. borers and leaf miners) may be more affected due to their narrow host range (Schoonhoven *et al.* 2008) and restricted movement in early stages of their life cycle (Connor & Taverner 1997).

All the processes and factors mentioned above can operate simultaneously and in opposite directions, which may explain the mixed responses of insect herbivores and herbivory to habitat loss and fragmentation, found in the literature. Thus, finding a global response pattern may be difficult to attain. Indeed, recent quantitative syntheses of fragmentation effects on plant herbivory reported no effect (Magrach *et al.* 2014), positive (De Carvalho Guimarães *et al.* 2014) or negative effects of habitat fragmentation on herbivory (Martinson & Fagan 2014; Chávez-Pesqueira *et al.* 2015). The most recent one found a strong negative effect of habitat fragmentation on insect herbivory, even after controlling for the phylogenetic relationship of plant species in their meta-analysis (Chávez-Pesqueira *et al.* 2015). While these studies have reviewed evidence about insect damage on plants in a habitat fragmentation context, none of them has simultaneously taken into account herbivore richness and abundance patterns. While De Carvalho Guimarães *et al.* (2014) did assess both herbivory and herbivore richness and abundance, they only considered

edge effect as main factor, which represents only one aspect of habitat fragmentation (Didham 2010).

Here, we conduct the first hierarchical meta-analysis to evaluate habitat fragmentation effects on insect herbivore community and herbivory. Hierarchical meta-analysis, which has so far been considered in only a few recent ecological syntheses (Ibáñez *et al.* 2014; Tuck *et al.* 2014), takes into account the nested structure of data due to non-independence of several outcomes coming from the same study. Hierarchical analysis allowed us to incorporate all important information from each study, thus increasing statistical power while controlling potential non-independence of correlated error structure associated with data coming from the same study (Mengersen *et al.* 2013). Also, here we significantly expanded and updated the dataset compared with previous meta-analyses, and because we focused our synthesis on both herbivory and herbivore diversity together for the first time, we were able to ask new questions: (1) Does habitat fragmentation affect herbivore abundance and species richness, and overall herbivory to a similar degree? (2) Do the effects of habitat fragmentation depend on the methodological approaches (i.e. type of fragmentation variable, observational vs. experimental and spatial extent of fragmentation) used by the studies? (3) Do fragmentation effects depend on the life-history and ecological attributes of insect herbivores (i.e. host specialisation, feeding type and body size)?

METHODS

Literature search and compilation of dataset

We conducted a literature search using keyword combinations in three online databases: ISI Web of Knowledge, Science Direct and Wiley Online Library (articles published between June 1981 and October 2016). We used the following keyword combination that related habitat fragmentation to insect herbivory and herbivore richness and abundance: (fragment* OR 'habitat loss' OR isolation OR connectivity) AND (herbivor* OR folivor* OR defoliat* OR phytophag* OR beetle* OR 'leaf miner*' OR leafminer* OR chew* OR suck* OR borer* OR grasshopper* OR leafhopper*). This combination permitted to cover publications studying the three response variables evaluated here (insect herbivory, abundance and species richness). Publications included in recent related meta-analyses of habitat fragmentation (i.e. De Carvalho Guimarães *et al.* 2014; Magrach *et al.* 2014; Martinson & Fagan 2014) also complemented the list of studies.

A publication was included in our analysis only if it reported the effects of habitat fragmentation on the following response variables: herbivory, herbivore abundance and/or species richness (Fig. S1). Insect herbivory was reported either as damage at a single point in time (generally cumulative herbivory, i.e. damage accumulated over the growing season) or as a rate (either over leaf lifespan or at several points in time), and it included consumption on different plant tissues such as leaves, stems or flowers. Leaf herbivory included damage on leaves at different stages of leaf lifespan. Species richness was measured as the number of herbivore species in most cases, although Shannon index (Zschokke *et al.* 2000) and herbivore

family richness (González *et al.* 2014) were also reported in two publications. We included studies assessing response variables as a function of (1) fragment area either used in categorical or continuous designs and plant population sizes (i.e. studies that used natural patchy distribution of plants to investigate fragmentation effects), (2) isolation of fragments either used in categorical or continuous designs and (3) fragmentation *per se* that included experimental studies comparing fragmented vs. continuous conditions while maintaining the same habitat amount (e.g. Ledergerber *et al.* 2002). When two spatial variables of fragmentation were evaluated in the same study, we handled them as separate observations. In studies investigating different matrix types around fragments, we considered each one of them as separate observations to avoid subjective decisions and losing information. Studies evaluated abundance and herbivory at community level (abundance or damage by several or many insect species) or at species level (abundance or damage by a single species). When the same publication reported the outcomes for several herbivores species separately, each species was considered a separate observation (Aguilar *et al.* 2006). In addition, several articles investigated habitat fragmentation effects more than once. Herbivore damage in general accumulates over the year, and thus we selected always the latest herbivory measurement, coinciding with the highest value reported (Watts & Didham 2006; De La Vega *et al.* 2012). However, as insect abundance and species richness experienced fluctuations within a year (e.g. De la Vega & Grez 2008; Ruiz-Guerra *et al.* 2012), whenever a study reported abundance or species richness in multiple times (e.g. months, years), we considered all reported measurements and performed a fixed-effect model meta-analysis to summarise the effect sizes from the same study into one effect size, which was subsequently included in the overall meta-analysis.

Based on the information given in publications, we classified the studies according to the type of fragmentation variable (fragment area, isolation, fragmentation *per se*), the type of methodological approach (observational vs. experimental) and the spatial extent of fragmentation (small vs. large). Observational studies included publications evaluating fragmented systems driven by human activity with crop, forest plantation or urbanisation as the surrounding matrix. Experimental studies included publications conducting experiments that produced contrasting habitats (fragmented vs. continuous; large vs. small fragments) to investigate fragmentation effects. With respect to spatial extent of fragmentation, studies were categorised into small extent when the difference between the treatment (small fragments) and control (large fragments or continuous forests) was < 0.5 ha or the isolation distance was ≤ 250 m. Large spatial extent studies had larger differences in the size of the smallest and largest fragment area or larger isolation distance (details can be seen in Table S1). Studies that estimated isolation through connectivity index or percentage of natural habitat surrounded fragments were classified as small extent when they calculated index in a radius ≤ 100 m, otherwise they were considered large extent. All studies evaluating fragmentation *per se* were considered small extent as they examined fragmented vs. not fragmented sites in plots < 0.1 ha.

Publications that focused on herbivore abundance at the species level were used to classify according to host specialisation (specialist and generalist), feeding type (ectophagous and endophagous) and body size of adult individuals (total body length in mm). This information was provided by the original publication or obtained from online databases. Ectophagous were herbivores eating external parts of the plant such as chewers and suckers, whereas endophagous included herbivore species that consume internal plant tissues such as borers, galls and leaf miners (Schoonhoven *et al.* 2008). We classified herbivores in two groups regarding their diet breadth: specialists included herbivores feeding on one or a few closely related plant taxa and generalist feeding on several plant species within one botanical family, or on species belonging to more than one plant family. This classification was based on diet breadth for the studied life stage of herbivores, e.g. caterpillars in case of butterflies. Body size was estimated as the mean body length registered for each species in adult stage, with only two exceptions, where body length of larvae was considered due to the absence of data on adult body size.

Meta-analysis

We used Hedges' d as an estimate of the unbiased standardised mean difference (i.e. the effect size) that has the advantage of being unbiased by small sample size (Gurevitch *et al.* 2001). To calculate Hedges' d, we obtained (from text, tables or graphs) the mean values, sample sizes and some variability measure of herbivory, abundance and species richness in each of the two contrasting landscape conditions (control: continuous, large or non-isolated habitats vs. treatment: fragmented, small or isolated habitats). Negative Hedges' d effect sizes imply lower mean values of herbivory, herbivore abundance or species richness in small, isolated and fragmented conditions, and vice versa. When fragment area or isolation was evaluated as a continuous variable in a primary study, we used the lowest and highest values of the independent variable to be comparable with studies selecting categorical contrasts in a factorial design.

We performed hierarchical mixed effects meta-analyses, which allow the specification of nesting groups. Mixed effects models were used with fixed (see moderators bellow) and random effects to account for differences across studies assuming they do not share a common mean effect but that there is random variation among studies, in addition to within-study sampling variation (Borenstein *et al.* 2009). The models also took into account the hierarchical dependence in our data due to cases where multiple observations (i.e. effect sizes) were obtained from the same study. Having several effect sizes from the same publication violates the assumption that effect sizes are independent (Tuck *et al.* 2014). A publication-level random effect as a nesting factor was included to incorporate this dependency of multiple outcomes within study observations (Stevens & Taylor 2009).

Heterogeneity of effect sizes was assessed with Q statistics, which are weighted sums of squares tested against a χ^2 distribution (Hedges & Olkin 1985). Specifically, we examined the P values of $Q_{between}$ statistics that describe the variation in

effect sizes that can be attributed to differences among categories of each predictor variable (e.g. type of study, host specialisation, etc.). Effect sizes were considered significantly different from zero if their 95% confidence intervals (CI) did not include zero (Borenstein *et al.* 2009). We performed three separate mixed effects meta-analyses with the type of fragmentation approach (fragment area, isolation, fragmentation *per se*), type of study (observational vs. experimental) and spatial extent of fragmentation (small vs. large) as main factors to investigate whether they moderate the magnitude of habitat fragmentation effects on herbivore richness, herbivore abundance and herbivory. Herbivory included several types of measurements involving damage on different plant organs and stages of life cycle, and such variability in these measurements may blur herbivory responses to habitat fragmentation (Andrew *et al.* 2012). Thus, three meta-analyses were performed with type of measurement (cumulative herbivory vs. rate of herbivory), plant organ damaged (leaves vs. flowers) and stage of leaf lifespan (random collection, new, mature and all leaves) as moderators to examine whether herbivory response to habitat fragmentation depends on the way that herbivory was measured.

With the subset of studies evaluating herbivore abundance in fragmented habitats at the species level, we were able to assess whether habitat fragmentation effects depend on particular herbivore traits. We gathered 52 observations classified according to the above-described traits. We conducted separate meta-analyses with host specialisation (specialist vs. generalist), feeding type (endophagous vs. ectophagous) and body size (continuous variable) of each species as moderators. Body size was log10-transformed to increase linearity. For herbivore species with more than one outcome per study (e.g. Bukovinszky *et al.* 2005; Haynes & Crist 2009), we conducted a fixed-effect model meta-analysis allowing us to summarise all these outcomes into one effect size, thus ending up with one observation per herbivore species per each publication. All the analyses were conducted in R using the *metafor* package (Viechtbauer 2010; R Core Team 2015).

We explored the possibility of publication bias graphically (funnel plots), numerically (Rosenthal's fail safe number) and statistically (rank correlation and trim and fill procedures) (Rothstein *et al.* 2005). Rosenthal's fail safe number calculates the number of non-significant, unpublished studies that need to be added to a meta-analysis to change its overall results from significant to non-significant. A fail safe number is often considered robust if it is $> 5n + 10$, where n is the original number of studies (Rosenthal 1991). Kendall's rank correlation test examines the relationship between the standardised effect size and sample size across the studies (Begg 1994). Significant P values may indicate publication bias whereby studies with small sample size are only published if they show large effect sizes. The 'trim and fill' method is used as a sensitivity analysis and recalculates the estimated mean effect size by trimming the smaller studies from the positive side and filling it mirrored on the negative side of funnel plot thereby removing funnel asymmetry. This technique provides an estimate of how the overall effect size would change if we were able to incorporate all missing studies (Jennions & Møller 2002).

RESULTS

We identified 89 publications evaluating fragmentation effects on insect herbivore community and their damage on plants (for PRISMA flow diagram see Fig. S1). These studies yielded 86 observations for herbivory, 146 for herbivore abundance and 56 for herbivore species richness (details of studies with effect sizes in Tables S2, S3, S4). Almost half of the publications were carried out in only three countries indicating a strong geographic bias: USA, Switzerland and Germany (Fig. S2 and Fig. 1a). The whole dataset covered a wide range of habitats, although the most frequent systems studied were fragmented temperate grasslands and temperate forests (Fig. S2 and Fig. 1b). There were some biases in the selection criteria of researchers in the studied subjects. Trees were the life form of plants most examined for herbivory variable while grasses and herbs for abundance and species richness, and most of the publications reported damage on leaves as a measure of herbivory (Fig. 1c and d).

Herbivore abundance and species richness, but not herbivory, were significantly negatively affected by habitat fragmentation (Fig. 2). For herbivore abundance and species richness, habitat fragmentation effects depended on the fragmentation variable examined (Table 1, Fig. 3a). Abundance of herbivores significantly decreased with increased spatial patch isolation (Fig. 3a), whereas species richness significantly decreased with isolation and reduction in fragment area, the latter factor having the strongest negative effect on herbivore richness (Fig. 3a). None of the spatial moderators of habitat fragmentation significantly affected herbivory. Studies assessing habitat fragmentation through observational approaches found stronger negative effects than experimental studies, with a significant difference between both approaches only for herbivore abundance (Table 1, Fig. 3b). Studies of habitat fragmentation covering large spatial extent had stronger negative effects than studies conducted across small spatial extents. While no statistical difference was observed between them, large extent studies showed statistically significant negative fragmentation effects for herbivore abundance and species richness, whereas small extent studies only found negative effects for species richness (Table 1, Fig. 3c). Finally, habitat fragmentation effects did not depend on methodologies used to estimate insect damage as none of the moderators had any significant effect (type of measurement, plant organ damaged and stages of leaf lifespan) (Table 1, Fig. S3).

We found 21 studies investigating insect herbivores at the species level, comprising a total of 49 unique herbivore species (Table S5). Habitat fragmentation had a non-significant negative effect on herbivore abundance at species level (mean $d = -0.31$, 95% CI = $-0.69/0.06$) (Table 1). Abundance of specialist herbivores was significantly negatively affected by habitat fragmentation, but generalist herbivores abundance was not (Table 1, Fig. 4). The type of herbivore feeding habits (ectophagous and endophagous) and body size did not moderate habitat fragmentation effects on herbivores (Table 1, Fig. 4). Finally, we performed sensitivity analyses of these species-level results by removing one outlier effect size ($d = -4.87$), and refitting the above meta-analysis models.
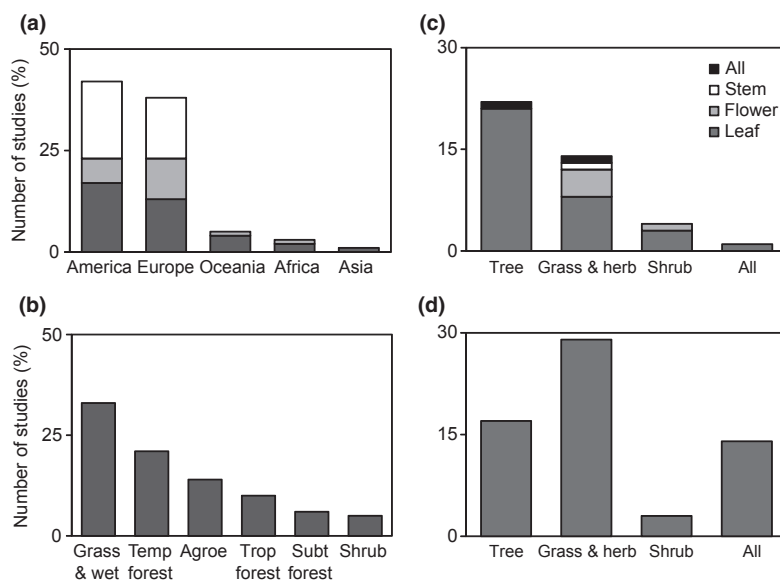
Figure 1 On the left, number of studies conducted in each continent (a) and type of ecosystem: grasslands and wetlands ('Grass & wet'), temperate forest ('Temp forest'), agroecosystems ('Agroe'), tropical forest ('Trop forest'), subtropical forest ('Subt forest') and shrubland ('Shrub') (b). In (a) dark grey represents the country with the highest number of studies per region (United States in America, Switzerland in Europe, New Zealand in Oceania, Uganda in Africa and Korea in Asia), light grey indicates the country with the second highest number of studies (Chile in America, Germany in Europe, Australia in Oceania and Uganda in Africa) and white indicates the rest of the countries. On the right, number of studies evaluating herbivory (c), abundance and species richness on different life forms of plants (d). In (c) each colour indicates plant organ damaged by herbivores.
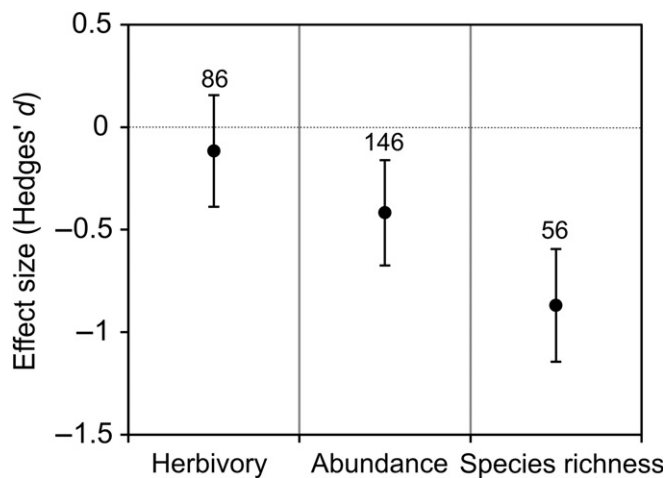
Figure 2 Habitat fragmentation effects on herbivory, herbivore abundance and species richness. Mean effect size ± 95% CIs. Numbers indicate sample size.

There was a small increase in the overall effect size (mean $d = -0.21$, 95% CI = $-0.52/0.10$), but responses of herbivore abundance to habitat fragmentation remained the same as previously (Table S6, Fig. S4).

Publication bias

None of the funnel plots of effect size vs. sample size showed skewness (Fig. S5), indicating no initial evidence of publication bias in our dataset. The calculated fail safe numbers were 505 for herbivory, 1019 for abundance, 2013 for species richness and 46 for abundance at species level (Table S7). These fail safe numbers indicate that results found are robust regardless of publication bias with the exceptions of meta-analyses on abundance at species level, which were smaller than expected without publication bias. Kendall's rank correlation tests did not show significant relationships between effect sizes and sample sizes, except for meta-analyses on species richness. Lately, trim-and-fill procedures indicate that missing studies would not qualitatively change the results.

DISCUSSION

Numerous studies, including meta-analyses, have reported habitat fragmentation effects on insect herbivory, with mixed results and no general patterns (e.g. De Carvalho Guimarães *et al.* 2014; Magrach *et al.* 2014). In this work, we expanded those analyses to summarise not only the overall effects of habitat fragmentation on insect herbivory but also on insect herbivore communities. Our study is the most up to date and deals with the hierarchical structure of multiple within-publication effect sizes allowing us to include all important information. Interestingly, we found reductions in herbivore species richness and abundance in fragmented habitats but they did not translate into effects on herbivory levels. The type of fragmentation variable used and host specialisation of herbivores were the most influential in determining herbivore responses to habitat fragmentation.

Species richness of insect herbivores is strongly reduced in small habitat fragments, as observed also for other groups of insects (Bommarco *et al.* 2010; Hill *et al.* 2011). Herbivore abundance, however, appears to be more negatively affected by isolation, probably due to dispersal limitation (Ricketts

Table 1 Summary table showing tests of moderators and heterogeneities from each meta-analysis

Response variable	Moderators	d.f.	Q	P
Herbivory	Fragmentation variable*	2	2.26	0.322
	Residual	82	286.32	< 0.001
	Study type†	1	0.18	0.664
	Residual	84	312.15	< 0.001
	Spatial extent‡	1	1.76	0.184
	Residual	84	306.19	< 0.001
	Type of measurement§	1	0.08	0.769
	Residual	84	316.69	< 0.001
	Plant organ damaged	1	0.19	0.659
	Residual	79	304.57	< 0.001
	Leaf stage	3	0.203	0.977
	Residual	65	268.32	< 0.001
Abundance	**Fragmentation variable**	**2**	**7.98**	**0.018**
	Residual	143	367.35	< 0.001
	Study type	**1**	**3.84**	**0.049**
	Residual	144	379.80	< 0.001
	Spatial extent	1	1.67	0.195
	Residual	144	381.95	< 0.001
Species richness	**Fragmentation variable**	**2**	**6.22**	**0.044**
	Residual	53	154.15	< 0.001
	Study type	1	0.09	0.755
	Residual	54	160.29	< 0.001
	Spatial extent	1	0.34	0.559
	Residual	54	160.56	< 0.001
Species level	**Host specialisation**	**1**	**8.14**	**0.004**
	Residual	50	111.06	< 0.001
	Feeding type	1	1.17	0.278
	Residual	50	115.08	< 0.001
	Body size	1	0.70	0.402
	Residual	50	113.89	< 0.001

Significant influence of moderators is indicated in bold (when 95% CI does not include zero).

*Fragmentation variable involved components of habitat fragmentation: fragment area, isolation and fragmentation *per se*.

†Study type involved type of methodological approach: observational vs. experimental.

‡Spatial extent involved small (where the difference between small fragments and large or continuous forests was < 0.5 ha or the isolation distance was ≤ 250 m) and large extent (studies with larger differences between the size of the smallest and largest fragment area or larger isolation distance).

§Type of measurement involved insect damage estimated as cumulative herbivory vs. rate of herbivory.

2001; Haynes & Cronin 2004). Besides the direct effects of habitat fragmentation, the negative impact on the herbivore community could be also due to a bottom-up force via reductions in plant species diversity or changes in plant community composition (Ibáñez *et al.* 2014). Herbivory, in contrast, was not significantly reduced in fragmented habitats, even when different measures, plant organs and leaf stages were discriminated. These results mean that the ecosystem function is maintained by mostly generalist species that remain in fragmented habitats. Such resilience in functioning may be explained by two hypotheses: (1) the functional role of once abundant species is substituted by other previously less abundant species (Yachi & Loreau 1999); or (2) herbivory is driven by a few common and dominant species that are not affected by habitat fragmentation. The great
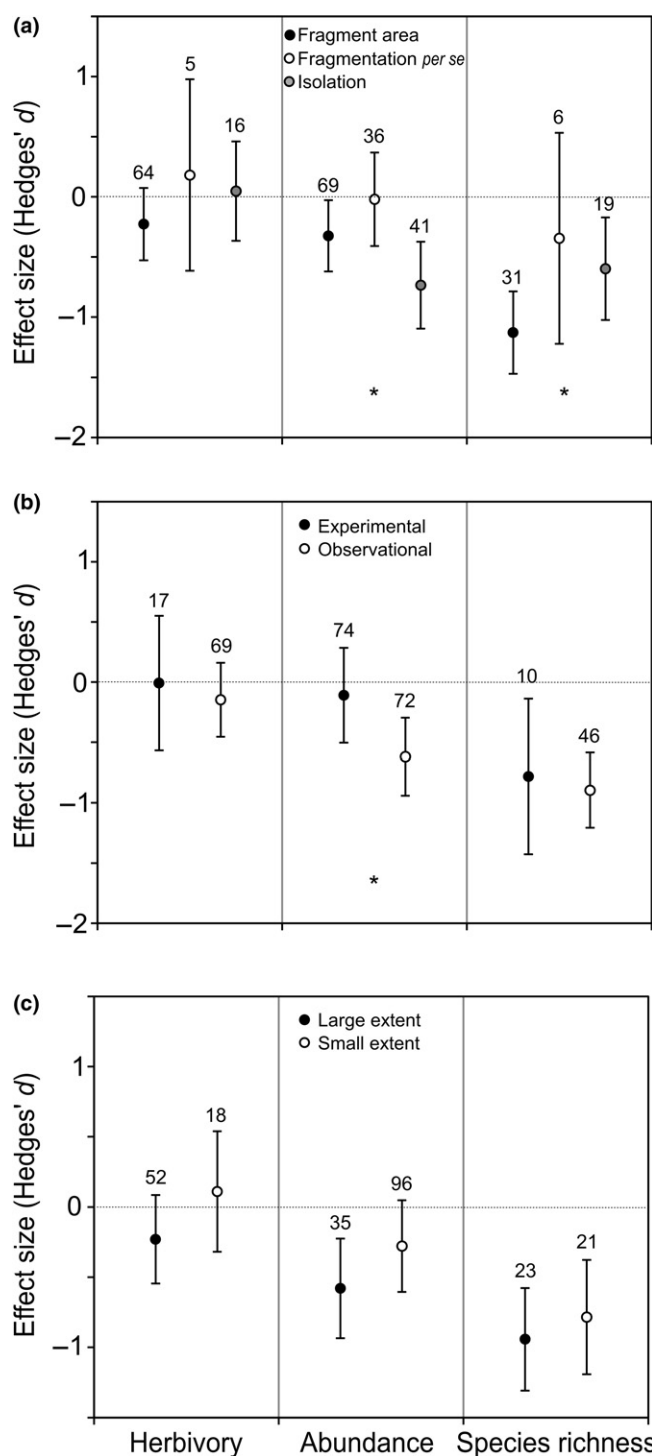
Figure 3 Effects of habitat fragmentation on herbivory, herbivore abundance and species richness depending on type of fragmentation variable (a), type of study (b) and spatial extent (c). Mean effect size ± 95% CI. Numbers indicate sample size. Asterisk denotes a significant difference among categories (*P < 0.05). In (c) small extent category involves studies in which the difference between the treatment (small fragments) and control (large fragments or continuous forests) was < 0.5 ha or the isolation distance was ≤ 250 m. Large extent category included studies with larger differences between the size of the smallest and largest fragment area or larger isolation distance.
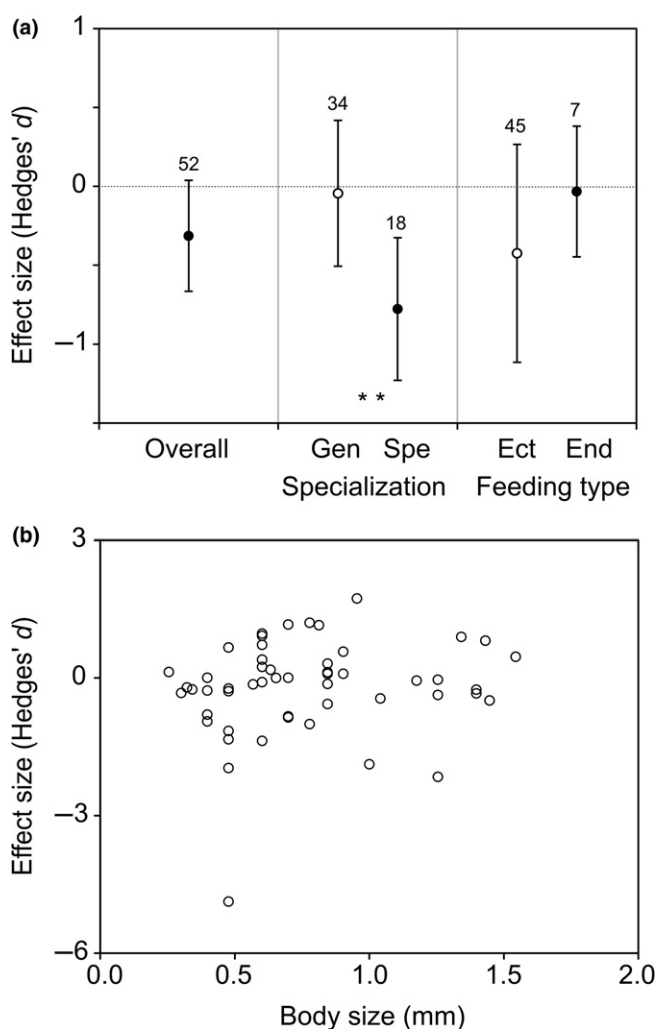
Figure 4 Effects of habitat fragmentation on insect herbivores depending on species characteristics. (a) Mean effect size ± 95% CIs according to host specialisation (Gen: generalist, Spe: specialist) and feeding type (Ect: ectophagous, End: endophagous). Numbers indicate sample size. Asterisk denotes a significant difference among categories (**$P < 0.01$). (b) The relationship between fragmentation effect size and herbivore body size (i.e. log10-transformed body length of each herbivore species). Slope of meta-regression: 0.11.

role of generalists is supported by two recent studies on pollination success indicating that the effect of species richness on an ecosystem function is less important than the abundance variation in a few dominant species (Kleijn *et al.* 2015; Winfree *et al.* 2015). Our results complement and support this finding on bee pollination with insect herbivory, as specialists, but not generalists, were affected by habitat fragmentation. Although overall herbivory was not influenced by fragmentation, changes in herbivore pressure on individual plant species can alter plant community structure through changes in plant species recruitment (Rao 2001) and primary productivity (Gera *et al.* 2013).

The type of study and spatial extent of fragmentation did not show a clear pattern. While studies performing experiments can control many potentially confounding factors, they

did not register stronger fragmentation effects than observational studies, presumably because experimental studies were performed within a smaller spatial extent than observational studies. Indeed, although non-significant, studies of habitat fragmentation with greater spatial extent tended to show stronger effects on herbivore responses than studies with smaller spatial extent, where difference between the smallest and largest fragments was < 0.5 ha or isolation distance was ≤ 250 m. In contrast, large spatial extent studies had greater differences in the size of the smallest and largest fragment area or longer isolation distance and thus are more likely to show stronger effects. The optimal spatial extent within which to measure fragmentation effects is related to the species involved in the response variable (Miguet *et al.* 2016). Insect herbivores are a highly diverse group covering a wide range of feeding strategies and movement capabilities determining differences on how species perceive the spatial scale of their habitat (Van Nouhuys 2005). Studies covering a small spatial extent may be appropriate to study herbivores that spend their whole life on a single plant or move only a few metres, as is the case of wingless aphid species (Ben-Ari *et al.* 2015). Multi-scale studies involving a large spatial extent of fragmentation are more likely to detect fragmentation effects on herbivore communities and herbivory processes.

The ecological traits of species can also influence the strength of habitat fragmentation effects on insect communities (Tscharntke *et al.* 2002). As expected, we found that abundance of specialists showed decreases, whereas generalist herbivores were not affected. Specialist herbivores face higher chances of not finding their specific plant hosts in fragmented habitat. We also expected stronger habitat fragmentation effects for small herbivores based on the assumption that small species may be less mobile and more sensitive to habitat fragmentation than large ones (Hagen *et al.* 2012). Nevertheless, body size of herbivores did not moderate habitat fragmentation effects in agreement with previous studies that have shown low power of this ecological trait as explanatory variable of insect sensitivity to habitat fragmentation (Bommarco *et al.* 2010; Martinson & Raupp 2013). They suggested that low dispersal rate may be associated with lower mortality as dispersal outside fragments may increase mortality (Bommarco *et al.* 2010), and small species might need less energy and resources and have smaller home ranges than large species (Greenleaf *et al.* 2007). Endophagous herbivorous insects were not more affected by habitat fragmentation than ectophagous species, which might be related to the fact that their feeding habit inside plant tissue protects them against extreme microclimatic conditions in small fragments dominated by edge effects (Connor & Taverner 1997). This group was, however, quite under-represented (7 observations) in our dataset compared with ectophagous insects (45 observations), which could be a reason for the lack of fragmentation effects, and emphasises the need of more studies on other insects like borers, leaf miners and gallers.

In conclusion, the capability for resilience in herbivory appeared to be exerted by generalist herbivores, the group that we found to be not vulnerable to habitat fragmentation. Generalist herbivores have the potential to exploit many host plants (Fontúrbel & Murúa 2014), and thus may contribute to

a large restructuration of the interaction networks of plant and animal species remaining in fragmented habitats. Changes in herbivore species composition towards an increased prevalence of common generalist species as a consequence of habitat fragmentation can exert significant different herbivore pressures on individual plant species. Such changes may involve significant long-term impacts on plant community structure and composition through changes in plant species recruitment (Rao 2001), affecting primary productivity (Gera *et al.* 2013) and soil nutrient cycling dynamics (Metcalfe *et al.* 2013). There is still a lack of knowledge about the impact of herbivory changes due to habitat fragmentation on other trophic levels and ecosystem processes. The incorporation of more spatial components such as matrix and edge effects and measurements of herbivory on different plant organs and tissues can improve the understanding of plant–herbivore interactions in fragmented habitats. In short, the responses of herbivore communities and herbivory to habitat fragmentation depend on the spatial variable of fragmentation and species traits with potential to trigger changes on plant community and other important ecosystem processes.

AUTHORSHIP

MRR and PB designed the research; MRR conducted literature search and analyses and wrote the first draft of the manuscript. PB and RA assisted with the meta-analysis. RA contributed to initial versions of manuscript. TT provided intellectual guidance and all authors contributed substantially to revisions.

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