

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 (Magrath *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 breadth and dispersal capability (Tscharnke *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 (Tscharnke *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 (Tscharnke & 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 (Magrath *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; Magrath *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 below) 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.

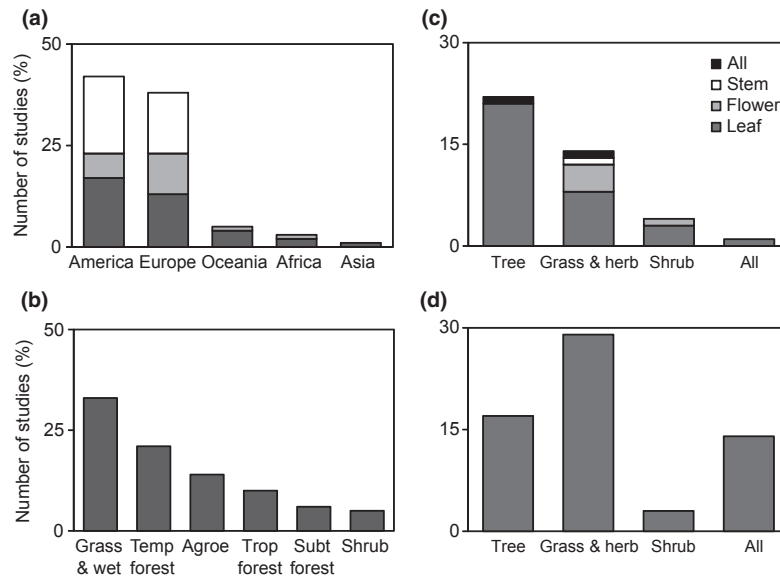


Figure 1 On the left, number of studies conducted in each continent (a) and type of ecosystem: grasslands and wetlands ('Grass & wet'), temperate forest ('Temp forest'), agroecosystems ('Agroe'), tropical forest ('Trop forest'), subtropical forest ('Subt forest') and shrubland ('Shrub') (b). In (a) dark 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.

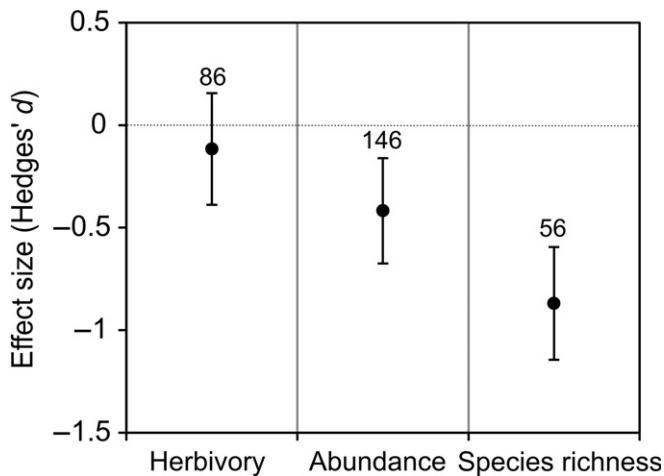


Figure 2 Habitat fragmentation effects on herbivory, herbivore abundance and species richness. Mean effect size \pm 95% CIs. Numbers indicate sample size.

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.	<i>Q</i>	<i>P</i>
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
Abundance	Residual	65	268.32	< 0.001
	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
Species richness	Spatial extent	1	1.67	0.195
	Residual	144	381.95	< 0.001
	Fragmentation variable	2	6.22	0.044
Species level	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

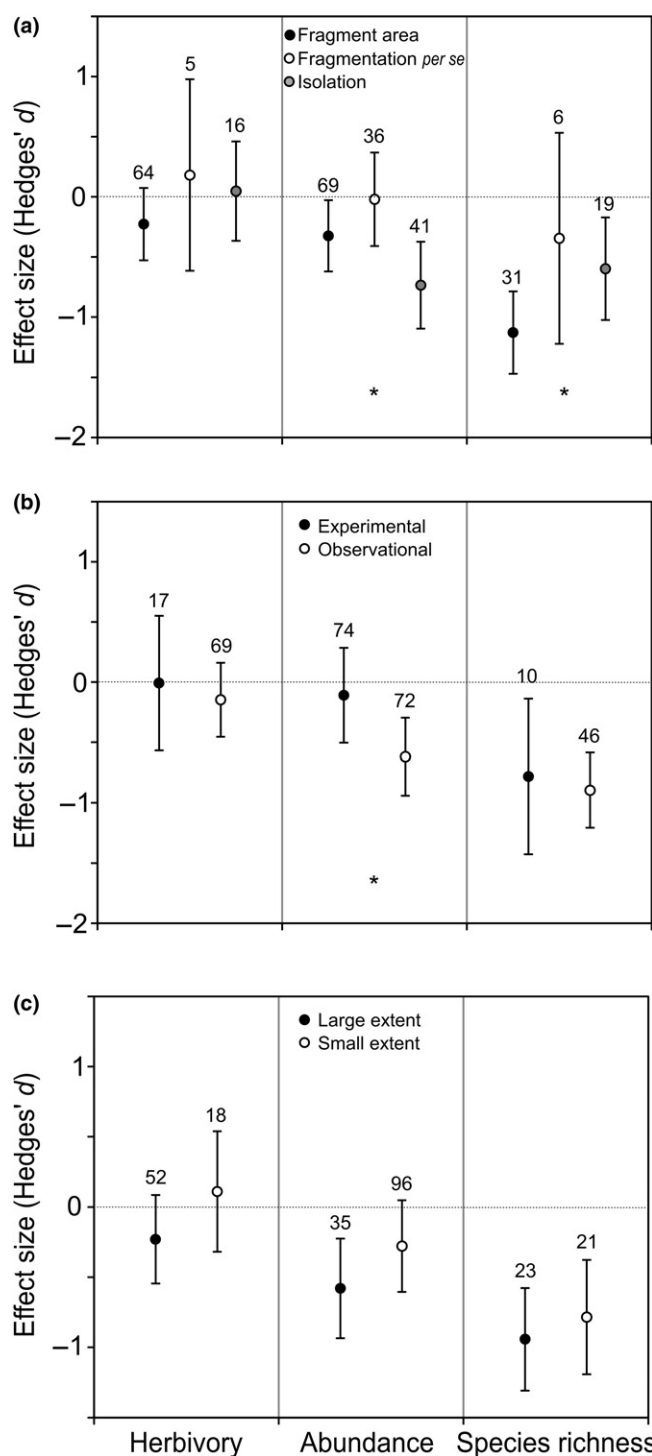


Figure 3 Effects of habitat fragmentation on herbivory, herbivore abundance and species richness depending on type of fragmentation variable (a), type of study (b) and spatial extent (c). Mean effect size ± 95% CI. Numbers indicate sample size. Asterisk denotes a significant difference among categories (**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.

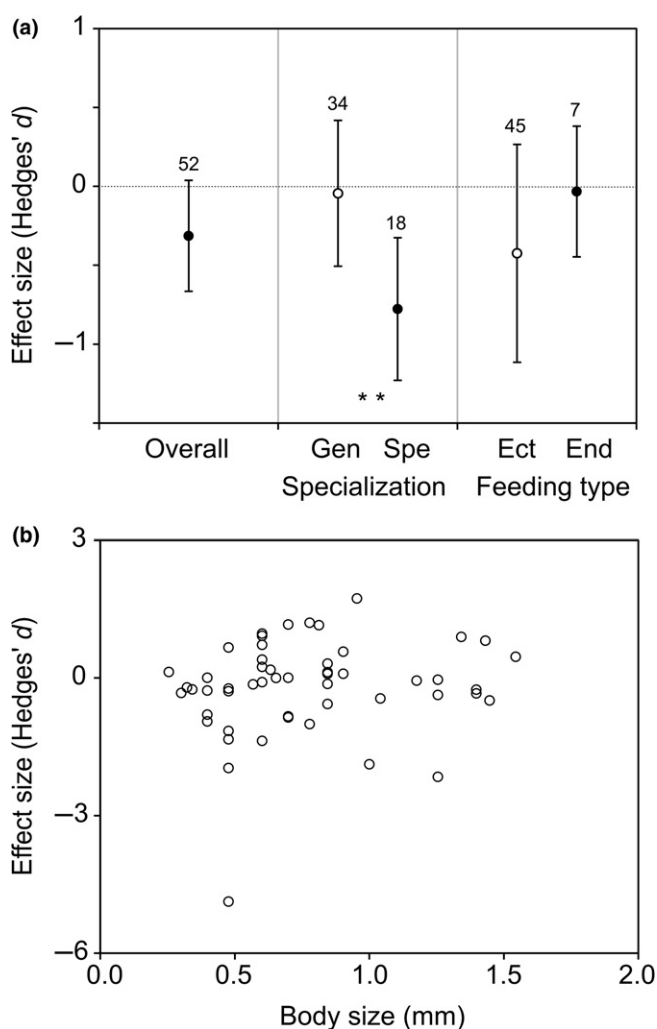


Figure 4 Effects of habitat fragmentation on insect herbivores depending on species characteristics. (a) Mean effect size \pm 95% CIs according to host specialisation (Gen: generalist, Spe: specialist) and feeding type (Ect: ectophagous, End: endophagous). Numbers indicate sample size. Asterisk denotes 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 (Tschardt *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 (Metcalf *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.

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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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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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Supporting Information

Figure S1 PRISMA flow diagram representing the flow of information through the decision process (i.e. the number of studies identified, rejected, and accepted)

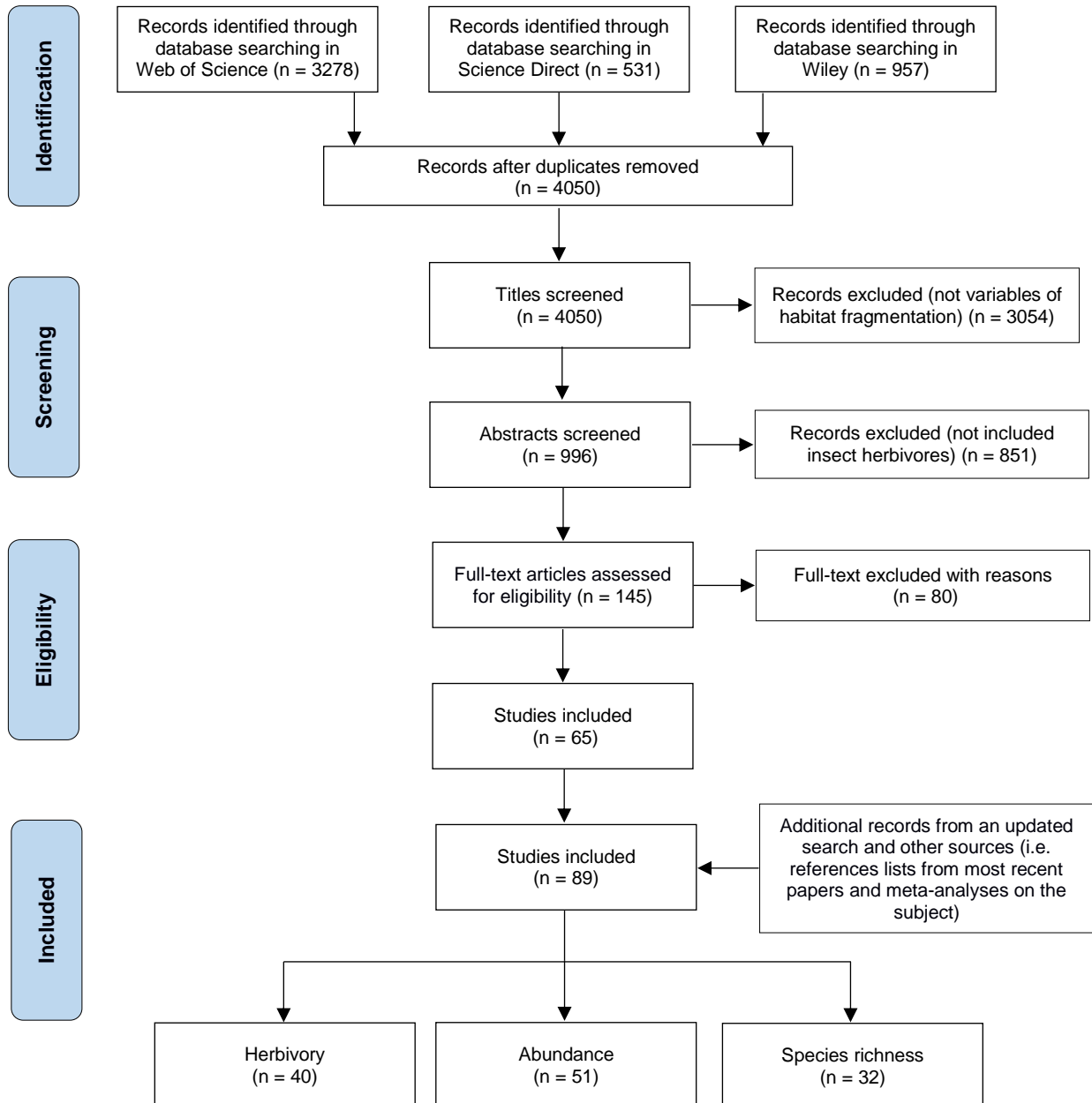


Table S1 Categorization of studies into large and small spatial extent of fragmentation variable. Minimum, maximum and mean values (\pm standard error) for area and isolation of fragments

Spatial extent	Fragmentation variable*	Minimum	Maximum	Mean \pm standard error	Difference between extreme values	
Large	Area (41 studies)	Small fragments (ha)	0.1	1.7	4.3 \pm 1.7	1.7 - 9999
		Large fragments (ha)	65	10000	1007.9 \pm 339.0	
	Isolation (22 studies)	Isolated (m)	330	3590	1292.1 \pm 273.1	322 - 3589
		Connected (m)	0	500	79.9 \pm 33.9	
Small	Area (27 studies)	Small fragments (ha)	2.5 e ⁻⁵	4.5 e ⁻⁴	4 e ⁻³ \pm 3 e ⁻³	3 e ⁻⁴ - 0.5
		Large fragments (ha)	0.05	0.50	9.1 e ⁻² \pm 4 e ⁻²	
	Isolation (13 studies)	Isolated (m)	5	250	127.9 \pm 26.0	0 - 250
		Connected (m)	0	20	2.8 \pm 1.9	

* All studies evaluating fragmentation *per se* were considered as small extent of fragmentation variable since fragmented and not fragmented area were always < 0.1 ha

† Mean values of isolated and connected do not include studies that estimated isolation as connectivity index

Table S2 References and effect sizes extracted from articles analysing effect of habitat fragmentation on insect herbivory. Vd = variance of Hedges' *d*.

Study	Insect herbivores	Plant species	Fragmentation variable	Spatial extent	Study type	Hedges' <i>d</i>	Vd
Altamirano <i>et al.</i> 2016	Gallers	<i>Geoffroea decorticans</i>	Area	Large	Observational	-2.521	0.956
Altamirano <i>et al.</i> 2016	Gallers	<i>Lycium cestroides</i>	Area	Large	Observational	-0.144	0.428
Altamirano <i>et al.</i> 2016	Gallers	<i>Celtis erhembergiana</i>	Area	Large	Observational	0.218	0.431
Altamirano <i>et al.</i> 2016	Gallers	<i>Celtis erhembergiana</i>	Area	Large	Observational	0.457	0.444
Arnold & Asquit 2002	Lepidopterans	<i>Protium tenuifolium</i>	Area	Large	Observational	-0.211	0.018
Arnold & Asquit 2002	Lepidopterans	<i>Ouratea lucens</i>	Area	Large	Observational	-0.169	0.008
Arnold & Asquit 2002	Lepidopterans	<i>Protium panamense</i>	Area	Large	Observational	-0.078	0.008
Arnold & Asquit 2002	Lepidopterans	<i>Heisteria concinna</i>	Area	Large	Observational	-0.193	0.005
Bach & Kelly 2004	<i>Zelleria spp</i>	<i>Alepis flavida</i>	Isolation	Small	Observational	1.098	0.334
Bañuelos & Kollmann 2011	<i>Phytomyza ilicis</i>	<i>Ilex aquifolium</i>	Area	Small	Observational	0.687	0.447
Benítez-Malvido <i>et al.</i> 1999	Insect community	<i>Chrysophyllum pomiferum</i>	Area	Large	Experimental	-0.073	0.096
Benítez-Malvido <i>et al.</i> 1999	Insect community	<i>Micropholis venulosa</i>	Area	Large	Experimental	0.764	0.103
Benítez-Malvido <i>et al.</i> 1999	Insect community	<i>Pouteria caimito</i>	Area	Large	Experimental	-0.229	0.096
Botzat <i>et al.</i> 2013*	Insect community	Seedling community	Area	Large	Observational	-0.071	0.284
Botzat <i>et al.</i> 2013	Insect community	Seedling community	Area	Large	Observational	-0.337	0.288
Botzat <i>et al.</i> 2013	Insect community	Seedling community	Area	Large	Observational	-0.864	0.315
Botzat <i>et al.</i> 2013	Insect community	Sapling community	Area	Large	Observational	-0.064	0.284
Botzat <i>et al.</i> 2013	Insect community	Sapling community	Area	Large	Observational	-0.031	0.284
Botzat <i>et al.</i> 2013	Insect community	Sapling community	Area	Large	Observational	0.420	0.291
Braschler <i>et al.</i> 2003	Aphids	Herb community	Fragmentation <i>per se</i>	Small	Experimental	0.762	0.065
Christie & Hochuli 2005	Chewers	<i>Angophora costata</i>	Area	Large	Observational	2.411	0.617
De la Vega <i>et al.</i> 2012	Insect community	<i>Aristotelia chilensis</i>	Area	Large	Observational	-0.531	0.190
Elzinga <i>et al.</i> 2005	<i>Hadena bicruris</i>	<i>Silene latifolia</i>	Isolation	Large	Observational	0.082	0.134
Elzinga <i>et al.</i> 2005	<i>Hadena bicruris</i>	<i>Silene latifolia</i>	Area	Small	Observational	0.773	0.145
Evans <i>et al.</i> 2012*	Grasshoppers	<i>Solanum americanum</i>	Isolation	Small	Experimental	0.312	0.226
Evans <i>et al.</i> 2012	Grasshoppers	<i>Solanum americanum</i>	Isolation	Small	Experimental	1.612	0.304
Faeth & Simberloff 1981	Leafminers	<i>Quercus hemisphaerica</i>	Isolation	Small	Observational	-0.120	0.183
Fáveri <i>et al.</i> 2008	Insect community	<i>Protium hebetatum</i>	Area	Large	Observational	-0.372	0.423
Fáveri <i>et al.</i> 2008	Insect community	<i>Henriettella caudata</i>	Area	Large	Observational	-3.616	1.220
Fáveri <i>et al.</i> 2008	Insect community	Sapling community	Area	Large	Observational	-2.033	0.708
Harvey & MacDougall 2015	Insect community	<i>Quercus ellipsoidalis</i>	Area	Small	Experimental	-0.747	0.182
Harvey & MacDougall 2015	Insect community	<i>Quercus ellipsoidalis</i>	Isolation	Large	Experimental	-0.628	0.175
Haynes & Crist 2009	Leafhoppers	<i>Trifolium pratense</i>	Fragmentation <i>per se</i>	Small	Experimental	-0.998	0.440
Haynes & Crist 2009	Leafhoppers	<i>Trifolium pratense</i>	Area	Small	Experimental	-1.167	0.463
Klapwijk & Lewis 2012	<i>Phytomyza ilicis</i>	<i>Ilex aquifolium</i>	Area	Small	Observational	0.364	0.395
Lakeman-Fraser & Ewers 2014 [†]	<i>Cleora scriptaria</i>	<i>Macropiper excelsum</i>	Area	Large	Observational	0.558	0.477
Lakeman-Fraser & Ewers 2014	<i>Cleora scriptaria</i>	<i>Macropiper excelsum</i>	Area	Large	Observational	0.255	0.441
Lakeman-Fraser & Ewers 2014	<i>Cleora scriptaria</i>	<i>Macropiper excelsum</i>	Area	Large	Observational	0.028	0.432
Lakeman-Fraser & Ewers 2014	<i>Cleora scriptaria</i>	<i>Macropiper excelsum</i>	Area	Large	Observational	-0.586	0.481
Lakeman-Fraser & Ewers 2014	<i>Cleora scriptaria</i>	<i>Macropiper excelsum</i>	Area	Large	Observational	-0.748	0.512
Ledergerber <i>et al.</i> 2002	Grasshoppers	<i>Trifolium repens</i>	Fragmentation <i>per se</i>	Small	Experimental	-0.623	0.163
Ledergerber <i>et al.</i> 2002	Grasshoppers	<i>Trifolium repens</i>	Area	Small	Experimental	-0.375	0.158
Leong & Bailey 2000 [‡]	<i>Frankliniella minuta</i>	<i>Blennosperma bakeri</i>	Isolation	Small	Observational	-1.202	0.468
Leong & Bailey 2000	<i>Frankliniella minuta</i>	<i>Blennosperma bakeri</i>	Area	Small	Experimental	-0.821	0.482
Leong & Bailey 2000	<i>Frankliniella minuta</i>	<i>Blennosperma bakeri</i>	Area	Small	Observational	1.076	0.523
Lienert & Fischer 2003	Insect community	<i>Primula farinosa</i>	Area	Large	Observational	1.444	0.371
Lienert & Fischer 2003	Insect community	<i>Primula farinosa</i>	Isolation	Large	Observational	0.367	0.143
Lienert <i>et al.</i> 2002	Grasshoppers	<i>Swertia perennis</i>	Area	Large	Observational	1.029	0.328
Lienert <i>et al.</i> 2002	Grasshoppers	<i>Swertia perennis</i>	Isolation	Large	Observational	1.348	0.359
Maguire <i>et al.</i> 2014	Chewers and suckers	<i>Hacer saccharum</i>	Area & Isolation	Large	Observational	0.000	0.426
Maguire <i>et al.</i> 2016	Insect community	<i>Acer saccharum</i>	Area	Large	Observational	-0.035	0.033
Maguire <i>et al.</i> 2016	Insect community	<i>Acer saccharum</i>	Isolation	Large	Observational	0.609	0.034

Maldonado-López <i>et al.</i> 2015	Folivorous	<i>Quercus castanea</i>	Area	Large	Observational	1.440	0.325
Maldonado-López <i>et al.</i> 2015	Leafminers	<i>Quercus castanea</i>	Area	Large	Observational	-0.740	0.323
Malo & Parra-Tabla 2001	Ants	<i>Myrmecophikz tibirinis</i>	Area	Large	Observational	0.918	0.496
Marino & Cornell 1992	<i>Phytomyza ilicicola</i>	<i>Ilex opaca</i>	Area	Small	Experimental	-0.593	0.456
Marino & Cornell 1992	<i>Phytomyza ilicicola</i>	<i>Ilex opaca</i>	Isolation	Small	Experimental	0.288	0.433
McEuen & Curran 2006	Insect community	<i>Lindera benzoin</i>	Isolation	Large	Observational	0.577	0.368
Peter <i>et al.</i> 2014	Chewers	Plant community		Isolation	Large	0.108	0.364
Rossetti <i>et al.</i> 2014	Leafminers	<i>Croton lachnostachyus</i>	Area	Large	Observational	-0.875	0.490
Rossetti <i>et al.</i> 2014	Chewers	<i>Croton lachnostachyus</i>	Area	Large	Observational	-2.426	0.917
Rossetti <i>et al.</i> 2014	Suckers	<i>Croton lachnostachyus</i>	Area	Large	Observational	-0.991	0.508
Ruiz-Guerra <i>et al.</i> 2010	Chewers	Plant community	Area	Large	Observational	-0.679	0.029
Ruiz-Guerra <i>et al.</i> 2010	Chewers	<i>Pseudolmedia oxyphyllaria</i>	Area	Large	Observational	-0.160	0.065
Ruiz-Guerra <i>et al.</i> 2010	Chewers	<i>Rhedia edulis</i>	Area	Large	Observational	-0.592	0.067
Ruiz-Guerra <i>et al.</i> 2010	Chewers	<i>Siparuna andina</i>	Area	Large	Observational	0.585	0.067
Ruiz-Guerra <i>et al.</i> 2010	Chewers	<i>Faramea occidentalis</i>	Area	Large	Observational	-0.519	0.067
Ruiz-Guerra <i>et al.</i> 2010	Chewers	<i>Cymbopetalum baillonii</i>	Area	Large	Observational	-0.674	0.068
Ruiz-Guerra <i>et al.</i> 2010	Chewers	<i>Myriocarpa longipes</i>	Area	Large	Observational	-0.379	0.066
Ruiz-Guerra <i>et al.</i> 2010	Chewers	<i>Hampea nutricia</i>	Area	Large	Observational	-0.352	0.066
Ruiz-Guerra <i>et al.</i> 2010	Chewers	<i>Acalypha diversifolia</i>	Area	Large	Observational	0.338	0.065
Samnegard <i>et al.</i> 2014	<i>Leucoplema dohertyi</i>	<i>Coffea arabica</i>	Area	Large	Observational	-0.014	0.219
Samnegard <i>et al.</i> 2014	<i>Leucoptera coffeina</i>	<i>Coffea arabica</i>	Area	Large	Observational	-0.348	0.222
Samnegard <i>et al.</i> 2014	<i>Cryphiomystis aletreuta</i>	<i>Coffea arabica</i>	Area	Large	Observational	-0.158	0.219
Savilaakso <i>et al.</i> 2009	Caterpillars	<i>Neoboutonia macrocalyx</i>	Isolation	Large	Observational	-0.957	0.206
Savilaakso <i>et al.</i> 2009	Caterpillars	<i>Neoboutonia macrocalyx</i>	Area	Large	Observational	-2.130	0.296
Schüepp <i>et al.</i> 2014	Chewers	<i>Prunus avium</i>	Isolation	Small	Observational	0.338	0.097
Simonetti <i>et al.</i> 2007	Insect community	<i>Cryptocarya alba</i>	Area	Large	Observational	-3.457	0.197
Simonetti <i>et al.</i> 2007	Insect community	<i>Persea lingue</i>	Area	Large	Observational	-1.743	0.107
Söber <i>et al.</i> 2009	<i>Cionus nigratarsis</i>	<i>Verbascum nigrum</i>	Area	Small	Observational	-1.744	0.444
Souza <i>et al.</i> 2013	Chewers	Plant community	Area	Large	Observational	-0.224	0.328
Stoll <i>et al.</i> 2006 [§]	Grasshoppers	<i>Betonica officinalis</i>	Fragmentation <i>per se</i>	Small	Experimental	1.302	0.484
Stoll <i>et al.</i> 2006	Grasshoppers	<i>Betonica officinalis</i>	Fragmentation <i>per se</i>	Small	Experimental	1.620	0.542
Valdivia 2011	Chewers	<i>Bomarea salsilla</i>	Area	Large	Observational	-0.742	0.042
Valladares <i>et al.</i> 2006	Leafminers	Plant community	Area	Large	Observational	-0.842	0.361
Watts & Didham 2006	<i>Batrachedra</i> sp	<i>Sporadanthus ferrugineus</i>	Isolation	Large	Observational	-0.979	0.374

* Publications that evaluated effects of fragment area, isolation or fragmentation *per se* on herbivory in different matrix types

† Lakeman-Fraser & Ewers (2014) reported effects of habitat fragmentation on herbivory in five latitudes

‡ Leong & Bailey (2000) reported effects of fragment area on herbivory in artificial and natural patches of *Blennosperma bakeri*

§ Stoll *et al.* (2006) reported effects of fragmentation *per se* on herbivory in more than one site

Table S3 References and effect sizes extracted from articles analysing effect of habitat fragmentation on herbivore abundance. Vd = variance of Hedges' *d*.

Study	Insect herbivores	Plant species	Fragmentation variable	Spatial extent	Study type	Hedges' <i>d</i>	Vd
Athen & Tschamtké 1999	<i>Lipara pullitarsis</i>	<i>Phragmites australis</i>	Area	Small	Observational	-0.862	0.277
Athen & Tschamtké 1999	<i>Giraudiella inclusa</i>	<i>Phragmites australis</i>	Area	Small	Observational	-1.371	0.317
Banks 1998	<i>Phyllotreta cruciferae</i>	<i>Brassica oleracea</i>	Fragmentation <i>per se</i>	Small	Experimental	-1.155	0.537
Banks 1998	<i>Brevicoryne brassicae</i>	<i>Brassica oleracea</i>	Area	Small	Experimental	-0.946	0.080
Benitez-Malvido <i>et al.</i> 2016	Insect community	<i>Heliconia aurantiaca</i>	Area	Large	Observational	-2.240	0.049
Bergerot <i>et al.</i> 2010	<i>Pieris brassicae</i>	Brassicaceae	Isolation	Large	Observational	-0.258	0.286
Botzat <i>et al.</i> 2013*	Coleopterans and hemipterans	Sapling and seedling community	Area	Large	Observational	-0.021	0.284
Botzat <i>et al.</i> 2013	Coleopterans and hemipterans	Sapling and seedling community	Area	Large	Observational	0.604	0.299
Botzat <i>et al.</i> 2013	Coleopterans and hemipterans	Sapling and seedling community	Area	Large	Observational	0.896	0.317
Braschler <i>et al.</i> 2003	Aphids	Herb community	Area	Small	Experimental	-0.715	0.166
Braschler <i>et al.</i> 2003	Aphids	Herb community	Fragmentation <i>per se</i>	Small	Experimental	-0.084	0.106
Braschler <i>et al.</i> 2009	Caeliferan community	Plant community	Fragmentation <i>per se</i>	Small	Experimental	0.566	0.261
Braschler <i>et al.</i> 2009	Ensifera community	Plant community	Fragmentation <i>per se</i>	Small	Experimental	2.107	0.409
Brückmann <i>et al.</i> 2011	<i>Polyommatus coridon</i>	<i>Hippocrepis comosa</i>	Area	Large	Observational	0.510	0.394
Brückmann <i>et al.</i> 2011	<i>Polyommatus coridon</i>	<i>Hippocrepis comosa</i>	Isolation	Large	Observational	-1.557	0.529
Bukovinszky <i>et al.</i> 2005*	<i>Brevicoryne brassicae</i>	<i>Brassica oleracea</i>	Area	Small	Experimental	-0.949	0.274
Bukovinszky <i>et al.</i> 2005	<i>Brevicoryne brassicae</i>	<i>Brassica oleracea</i>	Area	Small	Experimental	0.161	0.220
Bukovinszky <i>et al.</i> 2005	<i>Pieris rapae</i>	<i>Brassica oleracea</i>	Area	Small	Experimental	0.621	0.224
Bukovinszky <i>et al.</i> 2005	<i>Pieris rapae</i>	<i>Brassica oleracea</i>	Area	Small	Experimental	0.250	0.259
Bukovinszky <i>et al.</i> 2005	<i>Plutella xylostella</i>	<i>Brassica oleracea</i>	Area	Small	Experimental	-1.775	0.375
Bukovinszky <i>et al.</i> 2005	<i>Plutella xylostella</i>	<i>Brassica oleracea</i>	Area	Small	Experimental	-0.447	0.320
Cronin 2003	<i>Prokelisia crocea</i>	<i>Spartina pectinate</i>	Area	Small	Observational	-4.875	1.274
De la Vega & Grez 2008	Chrysomelids	<i>Aristotelia chilensis</i>	Area	Large	Observational	-0.116	0.094
De la Vega & Grez 2008	Curculionids	<i>Aristotelia chilensis</i>	Area	Large	Observational	0.100	0.093
De la Vega & Grez 2008	Elaterids	<i>Aristotelia chilensis</i>	Area	Large	Observational	0.380	0.101
De la Vega & Grez 2008	Scarabaeids	<i>Aristotelia chilensis</i>	Area	Large	Observational	0.024	0.094
De la Vega & Grez 2008	Tenebrionids	<i>Aristotelia chilensis</i>	Area	Large	Observational	0.022	0.110
De la Vega & Grez 2008	Lepidopterans	<i>Aristotelia chilensis</i>	Area	Large	Observational	0.028	0.093
De la Vega & Grez 2008	Rhaphidophorids	<i>Aristotelia chilensis</i>	Area	Large	Observational	-0.013	0.093
De la Vega & Grez 2008	Tettigonids	<i>Aristotelia chilensis</i>	Area	Large	Observational	-0.208	0.094
De la Vega <i>et al.</i> 2012	Insect community	<i>Aristotelia chilensis</i>	Area	Large	Observational	-0.272	0.253
Dempster <i>et al.</i> 1995	<i>Chaetorellia jaceae</i>	<i>Centaurea nigra</i>	Area	Small	Observational	-0.839	0.313
Derriak <i>et al.</i> 2002	Hemipterans	<i>Olearia bullata</i>	Isolation	Large	Observational	-0.418	0.228
Dubbert <i>et al.</i> 1998	<i>Eriopeltis</i> sp	<i>Calamagrostis epigeios</i>	Isolation	Small	Observational	-1.111	0.564
Evans <i>et al.</i> 2012*	Grasshoppers	<i>Solanum americanum</i>	Isolation	Small	Experimental	0.742	0.240
Evans <i>et al.</i> 2012	Grasshoppers	<i>Solanum americanum</i>	Isolation	Small	Experimental	-0.445	0.229
Golden & Crist 1999	<i>Empoasca flavescens</i>	Plant community	Fragmentation <i>per se</i>	Small	Experimental	-0.139	0.329
Golden & Crist 1999	<i>Cicadella hieroglyphica</i>	Plant community	Fragmentation <i>per se</i>	Small	Experimental	-0.571	0.367
Golden & Crist 1999	<i>Oecanthus nigricornis</i>	Plant community	Fragmentation <i>per se</i>	Small	Experimental	-0.040	0.326
Golden & Crist 1999	<i>Philaenus spumarius</i>	Plant community	Fragmentation <i>per se</i>	Small	Experimental	0.090	0.327
Golden & Crist 1999	<i>Ophraella cribrata</i>	Plant community	Fragmentation <i>per se</i>	Small	Experimental	0.313	0.338
Golden & Crist 1999	<i>Thamnotettix nigrifrons</i>	Plant community	Fragmentation <i>per se</i>	Small	Experimental	0.571	0.367
Golden & Crist 1999	<i>Chaetocnema confinis</i>	Plant community	Fragmentation <i>per se</i>	Small	Experimental	0.129	0.328
Golden & Crist 1999	<i>Mordellistena nigricans</i>	Plant community	Fragmentation <i>per se</i>	Small	Experimental	0.175	0.330
Grez 1997*	<i>Brevicoryne brassicae</i>	<i>Brassica oleracea</i>	Fragmentation <i>per se</i>	Small	Experimental	0.248	0.185
Grez 1997	<i>Brevicoryne brassicae</i>	<i>Brassica oleracea</i>	Fragmentation <i>per se</i>	Small	Experimental	-0.241	0.184
Grez <i>et al.</i> 2008	<i>Aphis craccivora</i>	<i>Medicago sativa</i>	Fragmentation <i>per se</i>	Small	Experimental	-0.285	0.330
Grez <i>et al.</i> 2008	<i>Aphis craccivora</i>	<i>Medicago sativa</i>	Area	Small	Experimental	-0.370	0.333
Grez <i>et al.</i> 2008	<i>Therioaphis trifolii</i>	<i>Medicago sativa</i>	Fragmentation <i>per se</i>	Small	Experimental	0.111	0.326
Grez <i>et al.</i> 2008	<i>Therioaphis trifolii</i>	<i>Medicago sativa</i>	Area	Small	Experimental	-0.536	0.340
Hambäck <i>et al.</i> 2010	<i>Delia radicum</i>	<i>Brassica oleracea</i>	Area	Small	Experimental	1.732	0.565
Hambäck <i>et al.</i> 2010	<i>Plutella xylostella</i>	<i>Brassica oleracea</i>	Area	Small	Experimental	1.204	0.517

Harvey & MacDougall 2014	Orthopterans	Plant community	Isolation	Large	Experimental	-2.120	0.326
Harvey & MacDougall 2014	Hemipterans	Plant community	Isolation	Large	Experimental	-2.199	0.335
Haynes & Crist 2009*	<i>Empoasca fabae</i>	<i>Trifolium pratense</i>	Area	Small	Experimental	-0.291	0.473
Haynes & Crist 2009	<i>Empoasca fabae</i>	<i>Trifolium pratense</i>	Area	Small	Experimental	-0.545	0.452
Haynes & Crist 2009	<i>Empoasca fabae</i>	<i>Trifolium pratense</i>	Fragmentation per se	Small	Experimental	-0.240	0.473
Haynes & Crist 2009	<i>Empoasca fabae</i>	<i>Trifolium pratense</i>	Fragmentation per se	Small	Experimental	0.129	0.441
Haynes & Crist 2009	<i>Agallia constricta</i>	<i>Trifolium pratense</i>	Area	Small	Experimental	0.497	0.444
Haynes & Crist 2009	<i>Agallia constricta</i>	<i>Trifolium pratense</i>	Area	Small	Experimental	2.110	0.578
Haynes & Crist 2009	<i>Agallia constricta</i>	<i>Trifolium pratense</i>	Fragmentation per se	Small	Experimental	0.887	0.470
Haynes & Crist 2009	<i>Agallia constricta</i>	<i>Trifolium pratense</i>	Fragmentation per se	Small	Experimental	0.635	0.468
Haynes & Crist 2009	<i>Halticus bractatus</i>	<i>Trifolium pratense</i>	Area	Small	Experimental	-0.347	0.443
Haynes & Crist 2009	<i>Halticus bractatus</i>	<i>Trifolium pratense</i>	Area	Small	Experimental	-0.714	0.453
Haynes & Crist 2009	<i>Halticus bractatus</i>	<i>Trifolium pratense</i>	Fragmentation per se	Small	Experimental	0.164	0.439
Haynes & Crist 2009	<i>Halticus bractatus</i>	<i>Trifolium pratense</i>	Fragmentation per se	Small	Experimental	-0.135	0.436
Haynes & Crist 2009	<i>Lygus lineolaris</i>	<i>Trifolium pratense</i>	Area	Small	Experimental	-0.172	0.444
Haynes & Crist 2009	<i>Lygus lineolaris</i>	<i>Trifolium pratense</i>	Area	Small	Experimental	-0.298	0.456
Haynes & Crist 2009	<i>Lygus lineolaris</i>	<i>Trifolium pratense</i>	Fragmentation per se	Small	Experimental	-0.147	0.466
Haynes & Crist 2009	<i>Lygus lineolaris</i>	<i>Trifolium pratense</i>	Fragmentation per se	Small	Experimental	0.096	0.449
Haynes & Crist 2009	<i>Therioaphis trifolii</i>	<i>Trifolium pratense</i>	Area	Small	Experimental	0.406	0.388
Haynes & Crist 2009	<i>Therioaphis trifolii</i>	<i>Trifolium pratense</i>	Area	Small	Experimental	0.644	0.404
Haynes & Crist 2009	<i>Therioaphis trifolii</i>	<i>Trifolium pratense</i>	Fragmentation per se	Small	Experimental	0.089	0.378
Haynes & Crist 2009	<i>Therioaphis trifolii</i>	<i>Trifolium pratense</i>	Fragmentation per se	Small	Experimental	-0.087	0.378
Haynes et al. 2007*	<i>Melanoplus femurrubrum</i>	<i>Trifolium pratense</i>	Area	Small	Experimental	-1.634	0.544
Haynes et al. 2007	<i>Melanoplus femurrubrum</i>	<i>Trifolium pratense</i>	Fragmentation per se	Small	Experimental	-0.217	0.381
Haynes et al. 2007	<i>Melanoplus femurrubrum</i>	<i>Trifolium pratense</i>	Area	Small	Experimental	-0.641	0.403
Haynes et al. 2007	<i>Melanoplus femurrubrum</i>	<i>Trifolium pratense</i>	Fragmentation per se	Small	Experimental	0.164	0.379
Herrmann et al. 2012	Curculionids	<i>Malus domestica</i>	Isolation	Small	Experimental	-0.393	0.133
Herrmann et al. 2012	Curculionids	<i>Prunus avium</i>	Isolation	Small	Experimental	-0.694	0.195
Hines et al. 2005	<i>Destria bisignata</i>	<i>Spartina patens</i>	Area	Small	Observational	0.239	0.381
Hines et al. 2005	<i>Amplicephalus simplex</i>	<i>Spartina patens</i>	Area	Small	Observational	1.164	0.462
Hines et al. 2005	<i>Tumidagena minuta</i>	<i>Spartina patens</i>	Area	Small	Observational	-1.341	0.490
Hines et al. 2005	<i>Aphelonema simplex</i>	<i>Spartina patens</i>	Area	Small	Observational	-1.962	0.618
Hines et al. 2005	<i>Delphacodes detecta</i>	<i>Spartina patens</i>	Area	Small	Observational	0.719	0.410
Kéry et al. 2001	<i>Maculinea rebeli</i>	<i>Gentiana cruciata</i>	Area	Large	Observational	-2.155	0.558
Kormann et al. 2015	Butterflies	Plant community	Isolation	Large	Observational	0.092	0.224
Kormann et al. 2015	Grasshoppers	Plant community	Isolation	Large	Observational	-0.672	0.237
Kormann et al. 2015	True bugs	Plant community	Isolation	Large	Observational	-0.314	0.226
Kruess & Tschardtke 1994	Stemboriers	<i>Trifolium pratense</i>	Isolation	Large	Experimental	-2.018	0.530
Lakeman-Fraser & Ewers 2014 [†]	<i>Cleora scriptaria</i>	<i>Macropiper excelsum</i>	Area	Large	Observational	0.572	0.479
Lakeman-Fraser & Ewers 2014	<i>Cleora scriptaria</i>	<i>Macropiper excelsum</i>	Area	Large	Observational	0.249	0.441
Lakeman-Fraser & Ewers 2014	<i>Cleora scriptaria</i>	<i>Macropiper excelsum</i>	Area	Large	Observational	0.044	0.433
Lakeman-Fraser & Ewers 2014	<i>Cleora scriptaria</i>	<i>Macropiper excelsum</i>	Area	Large	Observational	-0.579	0.480
Lakeman-Fraser & Ewers 2014	<i>Cleora scriptaria</i>	<i>Macropiper excelsum</i>	Area	Large	Observational	-0.710	0.504
Ledergerber et al. 2002 [‡]	Grasshoppers	<i>Trifolium repens</i>	Fragmentation per se	Small	Experimental	-0.108	0.155
Ledergerber et al. 2002	Grasshoppers	<i>Trifolium repens</i>	Fragmentation per se	Small	Experimental	0.266	0.097
Ledergerber et al. 2002	Grasshoppers	<i>Trifolium repens</i>	Fragmentation per se	Small	Experimental	0.069	0.118
Marino & Cornell 1992	<i>Phytomyza illicicola</i>	<i>Ilex opaca</i>	Area	Small	Experimental	0.371	0.438
Marino & Cornell 1992	<i>Phytomyza illicicola</i>	<i>Ilex opaca</i>	Isolation	Small	Experimental	-0.052	0.326
Müller & Gossner 2007	Coleopterans	<i>Quercus petraea</i>	Isolation	Small	Observational	-1.870	0.718
Müller & Gossner 2007	Heteropterans	<i>Quercus petraea</i>	Isolation	Small	Observational	-2.101	0.794
Núño et al. 2009	Grasshoppers	Plant community	Area	Large	Observational	-0.513	0.448
Östman et al. 2007	Homopterans	Plant community	Area	Large	Observational	0.000	0.378
Östman et al. 2007	Homopterans	Plant community	Isolation	Small	Observational	-0.666	0.310
Östman et al. 2007	Orthopterans	Plant community	Area	Large	Observational	-0.049	0.378
Östman et al. 2007	Orthopterans	Plant community	Isolation	Small	Observational	-0.139	0.292
Östman et al. 2009	Leafhoppers	Plant community	Isolation	Large	Observational	-2.880	0.373

Östman <i>et al.</i> 2009	Leafhoppers	Plant community	Area	Small	Observational	-1.706	0.669
Ozanne <i>et al.</i> 2000	Insect community	<i>Pinus sylvestris</i>	Area	Large	Observational	-0.220	0.430
Peter <i>et al.</i> 2014	Chewers	Plant community	Isolation	Large	Observational	-0.072	0.363
Rösch <i>et al.</i> 2013	Leafhoppers	Plant community	Area	Large	Observational	-0.274	0.136
Rösch <i>et al.</i> 2013	Leafhoppers	Plant community	Area	Large	Observational	0.134	0.135
Rösch <i>et al.</i> 2013	Leafhoppers	Plant community	Isolation	Large	Observational	-0.518	0.260
Ruiz-Guerra <i>et al.</i> 2012	Insect community	Sapling community	Area	Large	Observational	1.217	0.550
Ruiz-Guerra <i>et al.</i> 2012	Lepidopterans	Sapling community	Area	Large	Observational	-0.192	0.474
Ryall & Fahrig 2005	<i>Ips pini</i>	<i>Pinus resinosa</i>	Isolation	Large	Observational	1.148	0.392
Sanchez & Parmenter 2002	<i>Semiothisa colorata</i>	<i>Larrea tridentata</i>	Isolation	Large	Observational	0.837	0.170
Sanchez & Parmenter 2002	<i>Pachybrachis xantholucens</i>	<i>Larrea tridentata</i>	Isolation	Large	Observational	-0.292	0.157
Sanchez & Parmenter 2002	<i>Psylliodes</i> sp	<i>Larrea tridentata</i>	Isolation	Large	Observational	0.000	0.155
Sanchez & Parmenter 2002	<i>Asphondylia auripila</i>	<i>Larrea tridentata</i>	Isolation	Large	Observational	0.965	0.174
Sanchez & Parmenter 2002	<i>Phytocoris nigrinus</i>	<i>Larrea tridentata</i>	Isolation	Large	Observational	0.124	0.155
Sanchez & Parmenter 2002	<i>Phytocoris vanduzeei</i>	<i>Larrea tridentata</i>	Isolation	Large	Observational	0.090	0.155
Sanchez & Parmenter 2002	<i>Thyanta custator</i>	<i>Larrea tridentata</i>	Isolation	Large	Observational	-0.446	0.159
Sanchez & Parmenter 2002	<i>Hysteropterum unum</i>	<i>Larrea tridentata</i>	Isolation	Large	Observational	-0.798	0.168
Sanchez & Parmenter 2002	<i>Multaris cornutus</i>	<i>Larrea tridentata</i>	Isolation	Large	Observational	-0.094	0.155
Sanchez & Parmenter 2002	<i>Multaris</i> sp	<i>Larrea tridentata</i>	Isolation	Large	Observational	0.399	0.158
Sanchez & Parmenter 2002	<i>Heteropsylla texana</i>	<i>Larrea tridentata</i>	Isolation	Large	Observational	0.664	0.164
Sanchez & Parmenter 2002	<i>Boottettix argentatus</i>	<i>Larrea tridentata</i>	Isolation	Large	Observational	-0.339	0.157
Savilaakso <i>et al.</i> 2009	Caterpillars	<i>Neoboutonia macrocalyx</i>	Area	Large	Observational	-1.482	0.238
Savilaakso <i>et al.</i> 2009	Caterpillars	<i>Neoboutonia macrocalyx</i>	Isolation	Large	Observational	-1.695	0.255
Schüepf <i>et al.</i> 2014	Insect community	<i>Prunus avium</i>	Isolation	Small	Observational	0.494	0.357
Stireman <i>et al.</i> 2014	Chewers	Plant community	Area	Large	Observational	-0.733	0.353
Stoll <i>et al.</i> 2006 [†]	Grasshoppers	<i>Betonica officinalis</i>	Fragmentation <i>per se</i>	Small	Experimental	0.895	0.428
Stoll <i>et al.</i> 2006	Grasshoppers	<i>Betonica officinalis</i>	Fragmentation <i>per se</i>	Small	Experimental	-0.028	0.378
Stoll <i>et al.</i> 2006	Grasshoppers	<i>Betonica officinalis</i>	Fragmentation <i>per se</i>	Small	Experimental	0.855	0.423
Stoll <i>et al.</i> 2006	Grasshoppers	<i>Betonica officinalis</i>	Area	Small	Experimental	0.628	0.402
Turrini & Knop 2015	Bugs	<i>Betula pendula</i>	Isolation	Small	Observational	-0.698	0.113
Turrini & Knop 2015	Beetles	<i>Betula pendula</i>	Isolation	Small	Observational	0.248	0.107
Turrini & Knop 2015	Leafhoppers	<i>Betula pendula</i>	Isolation	Small	Observational	-0.039	0.106
Watts & Didham 2006	<i>Batrachedra</i> sp	<i>Sporadanthus ferrugineus</i>	Isolation	Large	Observational	-1.883	0.330
Zabel & Tschamtkke 1998	Insect community	<i>Urtica dioica</i>	Area	Small	Observational	-1.096	0.261
Zschokke <i>et al.</i> 2000	<i>Chorthippus biguttulus</i>	Plant community	Area	Small	Experimental	1.131	0.466
Zschokke <i>et al.</i> 2000	<i>Chorthippus biguttulus</i>	Plant community	Fragmentation <i>per se</i>	Small	Experimental	0.655	0.462
Zschokke <i>et al.</i> 2000	<i>Stenobothrus lineatus</i>	Plant community	Area	Small	Experimental	0.989	0.508
Zschokke <i>et al.</i> 2000	<i>Stenobothrus lineatus</i>	Plant community	Fragmentation <i>per se</i>	Small	Experimental	0.652	0.462

* Publications that evaluated effects of fragment area, isolation or fragmentation *per se* on herbivore abundance in different matrix types

† Lakeman-Fraser & Ewers (2014) reported effects of habitat fragmentation on herbivore abundance in five latitudes

‡ Publications that reported effects of fragmentation *per se* on herbivore abundance in more than one site

Table S4 References and effect sizes extracted from articles analysing effect of habitat fragmentation on species richness of insect herbivores. Vd = variance of Hedges' *d*.

Study	Insect herbivores	Plant species	Fragmentation variable	Spatial extent	Study type	Hedges' <i>d</i>	Vd
Athen & Tscharrntke 1999	Borers	<i>Phragmites australis</i>	Area	Small	Observational	-1.952	0.386
Cagnolo <i>et al.</i> 2009*	Leafminers	Plant community	Area	Large	Observational	-1.414	0.426
Cagnolo <i>et al.</i> 2009	Leafminers	Plant community	Area	Large	Observational	-1.350	0.417
Bommarco <i>et al.</i> 2014	Butterflies	Plant community	Isolation	Large	Observational	-1.264	0.204
Choi & An 2011	Moths	Plant community	Area	Large	Observational	-1.067	0.331
De la Vega & Grez 2008	Folivorous	<i>Aristotelia chilensis</i>	Area	Large	Observational	-0.070	0.250
Derraik <i>et al.</i> 2002	Hemipterans	<i>Olearia bullata</i>	Area	Small	Observational	-0.763	0.271
Dubbert <i>et al.</i> 1998	Insect community	<i>Calamagrostis epigeios</i>	Isolation	Small	Observational	0.566	0.169
Dubbert <i>et al.</i> 1998	Insect community	<i>Calamagrostis epigeios</i>	Area	Small	Observational	-0.448	0.164
Faeth & Simberloff 1981	Leafminers	<i>Quercus falcata</i>	Isolation	Small	Observational	1.141	0.489
Faeth & Simberloff 1981	Leafminers	<i>Quercus hemisphaerica</i>	Isolation	Small	Observational	-0.807	0.408
Faeth & Simberloff 1981	Leafminers	<i>Quercus nigra</i>	Isolation	Small	Observational	-1.346	0.553
Golden & Crist 1999	Chewers	Plant community	Fragmentation <i>per se</i>	Small	Experimental	-0.997	0.470
Golden & Crist 1999	Suckers	Plant community	Fragmentation <i>per se</i>	Small	Experimental	-0.001	0.585
González <i>et al.</i> 2014	Insect community	Three plant species	Area	Large	Observational	-1.411	0.592
Hines <i>et al.</i> 2005	Sap-feeders	<i>Spartina patens</i>	Area	Small	Observational	-0.581	0.258
Juliao <i>et al.</i> 2004	Gallers	Plant community	Area	Large	Observational	-1.495	0.438
Knop <i>et al.</i> 2010	Orthopterans	Plant community	Isolation	Small	Observational	-0.940	0.226
Kruess & Tscharrntke 2000	Four insect species	<i>Vicia sepium</i>	Isolation	Large	Observational	-2.858	0.888
Kormann <i>et al.</i> 2015	Butterflies	Plant community	Isolation	Large	Observational	-0.460	0.230
Kormann <i>et al.</i> 2015	Grasshoppers	Plant community	Isolation	Large	Observational	-0.446	0.230
Kormann <i>et al.</i> 2015	True bugs	Plant community	Isolation	Large	Observational	-0.087	0.224
Kruess & Tscharrntke 2000	Four insect species	<i>Vicia sepium</i>	Area	Large	Observational	-3.249	1.038
Nufio <i>et al.</i> 2011	Grasshoppers (Melanoplinae)	Plant community	Area	Large	Observational	-1.656	0.655
Nufio <i>et al.</i> 2011	Grasshoppers (Oedipodinae)	Plant community	Area	Large	Observational	-2.990	1.172
Nufio <i>et al.</i> 2011	Grasshoppers (Gomphocerinae)	Plant community	Area	Large	Observational	-2.227	0.840
Östman <i>et al.</i> 2007	Orthopterans	Plant community	Area	Large	Observational	-0.734	0.411
Östman <i>et al.</i> 2007	Homopterans	Plant community	Area	Large	Observational	-0.584	0.399
Östman <i>et al.</i> 2007	Orthopterans	Plant community	Isolation	Small	Observational	-0.065	0.292
Östman <i>et al.</i> 2007	Homopterans	Plant community	Isolation	Small	Observational	-0.930	0.328
Ozanne <i>et al.</i> 2000	Homopterans	<i>Pinus sylvestris</i>	Area	Large	Observational	-2.155	0.813
Peintinger <i>et al.</i> 2003	Grasshoppers	Plant community	Area	Large	Observational	-1.157	0.393
Peter <i>et al.</i> 2014	Chewers	Plant community	Isolation	Large	Observational	-0.018	0.363
Rösch <i>et al.</i> 2013*	Leafhoppers	Plant community	Area	Large	Observational	0.305	0.136
Rösch <i>et al.</i> 2013	Leafhoppers	Plant community	Area	Large	Observational	-0.274	0.130
Rösch <i>et al.</i> 2013	Leafhoppers	Plant community	Isolation	Large	Observational	-0.377	0.255
Sanchez & Parmenter 2002	Insect community	<i>Larrea tridentata</i>	Area	Small	Observational	-1.769	0.275
Sanchez & Parmenter 2002	Insect community	<i>Larrea tridentata</i>	Isolation	Large	Observational	-1.846	0.426
Savilaakso <i>et al.</i> 2009	Caterpillars	<i>Neoboutonia macrocalyx</i>	Area	Large	Observational	-3.242	0.446
Savilaakso <i>et al.</i> 2009	Caterpillars	<i>Neoboutonia macrocalyx</i>	Isolation	Large	Observational	-0.015	0.183
Sebek <i>et al.</i> 2015	Butterflies	Plant community	Isolation	Small	Experimental	-0.549	0.056
Sebek <i>et al.</i> 2015	Moths	Plant community	Isolation	Small	Experimental	-0.216	0.065
Stireman <i>et al.</i> 2014	Chewers	Plant community	Area	Large	Observational	-1.307	0.412
Stoll <i>et al.</i> 2006 [†]	Grasshoppers	<i>Betonica officinalis</i>	Fragmentation <i>per se</i>	Small	Experimental	-0.993	0.439
Stoll <i>et al.</i> 2006	Grasshoppers	<i>Betonica officinalis</i>	Fragmentation <i>per se</i>	Small	Experimental	-0.528	0.395
Stoll <i>et al.</i> 2006	Grasshoppers	<i>Betonica officinalis</i>	Fragmentation <i>per se</i>	Small	Experimental	-0.790	0.417
Torma <i>et al.</i> 2014	True bugs	Plant community	Isolation	Large	Observational	-1.235	0.347
Van Noordwijk <i>et al.</i> 2015*	Carabid beetles	Plant community	Area	Large	Observational	-0.334	0.205
Van Noordwijk <i>et al.</i> 2015	Carabid beetles	Plant community	Area	Large	Observational	1.295	0.176
Van Noordwijk <i>et al.</i> 2015	Carabid beetles	Plant community	Area	Large	Observational	0.828	0.170
Wettstein & Schmid 1999	Grasshoppers	Plant community	Area	Large	Observational	-2.190	0.826

Wettstein & Schmid 1999	Grasshoppers	Plant community	Area	Large	Observational	-0.047	0.426
With & Pavuk 2011	Insect community	<i>Trifolium pratense</i>	Area	Small	Experimental	-1.931	0.080
With & Pavuk 2011	Insect community	<i>Trifolium pratense</i>	Fragmentation <i>per se</i>	Small	Experimental	-0.103	0.326
Zabel & Tscharrntke 1998	Insect community	<i>Urtica dioica</i>	Area	Small	Observational	-1.475	0.291
Zschokke <i>et al.</i> 2000	Grasshoppers	Plant community	Area	Small	Experimental	-1.014	0.176

* Publications that reported effects of habitat fragmentation on more than one group of herbivorous according to host or habitat specialization

† Publications that reported effects of fragmentation *per se* on species richness of herbivores in more than one site

Table S5 References and effect sizes extracted from articles analysing effect of habitat fragmentation on herbivore abundance at species level. Vd = variance of Hedges' *d*.

Herbivore species	Plant species	Host specialization	Feeding type	Body size (mm) [†]	Hedges' <i>d</i>	Vd	Source
<i>Agallia constricta</i>	<i>Trifolium pratense</i>	Generalist	Ectophagous	4	0.918	0.242	http://bugguide.net/node/view/1099243/bgimage
<i>Amplicephalus simplex</i>	<i>Spartina patens</i>	Generalist	Ectophagous	5	1.164	0.463	http://bugguide.net/node/view/717417
<i>Aphelonema simplex</i>	<i>Spartina patens</i>	Generalist	Ectophagous	3	-1.963	0.619	http://bugguide.net/node/view/357893/bgpage
<i>Aphis craccivora</i>	<i>Medicago sativa</i>	Generalist	Ectophagous	2.3	-0.327	0.407	http://influentialpoints.com/Gallery/Aphis_aphids.htm
<i>Asphondylia auripila</i>	<i>Larrea tridentata</i>	Specialist	Endophagous	4	0.965	0.175	http://www.scielo.br/pdf/rbent/v53n2/v53n2a02.pdf
<i>Batrachedra sp</i>	<i>Sporadanthus ferrugineus</i>	Specialist	Endophagous	10	-1.883	0.330	Perring, T.M., El-Shafie, H.A.F. & Wakil, W. (2015). Carob moth, lesser date moth, and raisin moth. In: <i>Sustainable pest management in date palm: current status and emerging challenges</i> (eds. Wakil, W., Faleiro, J.R. & Miller, T.A.). Springer, Switzerland, pp. 137.
<i>Boottetix argentatus</i>	<i>Larrea tridentata</i>	Specialist	Ectophagous	25	-0.339	0.158	http://bugguide.net/node/view/1110174/bgimage
<i>Brevicoryne brassicae</i> *	<i>Brassica oleracea</i>	Generalist	Ectophagous	2.5	-0.275	0.172	http://entnemdept.ufl.edu/creatures/veg/aphid/cabbage_aphid.htm
<i>Brevicoryne brassicae</i>	<i>Brassica oleracea</i>	Generalist	Ectophagous	2.5	0.004	0.304	http://entnemdept.ufl.edu/creatures/veg/aphid/cabbage_aphid.htm
<i>Brevicoryne brassicae</i>	<i>Brassica oleracea</i>	Generalist	Ectophagous	2.5	-0.947	0.08	http://entnemdept.ufl.edu/creatures/veg/aphid/cabbage_aphid.htm
<i>Chaetocnema confinis</i>	Plant community	Generalist	Ectophagous	1.8	0.130	0.329	Jolivet, P. (2004). Sweetpotato flea beetle, <i>Chaetocnema confinis</i> (Coleoptera: Chrysomelidae: Alticinae). In: <i>Encyclopedia of entomology</i> . Springer Netherlands, pp. 2156-2158.
<i>Chaetorellia jaceae</i>	<i>Centaurea nigra</i>	Specialist	Endophagous	5	-0.840	0.313	http://aramel.free.fr/INSECTES15-6'.shtml
<i>Chorthippus biguttulus</i>	Plant community	Generalist	Ectophagous	22	0.892	0.481	http://www.commanster.eu/commanster/Insects/Grasshoppers/SpGrasshoppers/Chorthippus.biguttulus.htm
<i>Cicadella hieroglyphica</i>	Plant community	Generalist	Ectophagous	7	-0.571	0.367	http://tpwd.texas.gov/publications/pwdpubs/media/pwd_bk_p4000_0043.pdf
<i>Cleora scriptaria</i>	<i>Macropiper excelsum</i>	Generalist	Ectophagous	15	-0.059	0.209	http://naturalista.conabio.gob.mx/observations/2661050
<i>Delia radicum</i>	<i>Brassica olearacea</i>	Generalist	Ectophagous	9	1.732	0.566	http://actazool.nhms.hu/49/2/darvas.pdf
<i>Delphacodes detecta</i>	<i>Spartina patens</i>	Generalist	Ectophagous	4	0.719	0.410	http://bugguide.net/node/view/1177078
<i>Destria bisignata</i>	<i>Spartina patens</i>	Generalist	Ectophagous	4	0.240	0.382	http://bugguide.net/node/view/613383
<i>Empoasca fabae</i>	<i>Trifolium pratense</i>	Generalist	Ectophagous	3	-0.231	0.230	http://www.omafra.gov.on.ca/english/crops/facts/whleaf.htm#potato
<i>Empoasca flavescens</i>	Plant community	Generalist	Ectophagous	3.7	-0.139	0.329	http://bugguide.net/node/view/865173
<i>Giraudiella inclusa</i>	<i>Phragmites australis</i>	Specialist	Endophagous	4	-1.371	0.318	http://www.cabi.org/phragmites/gira_inc.html
<i>Halticus bractatus</i>	<i>Trifolium pratense</i>	Generalist	Ectophagous	2.2	-0.251	0.222	http://entnemdept.ufl.edu/creatures/veg/leaf/fleahopper.htm
<i>Heteropsylla texana</i>	<i>Larrea tridentata</i>	Generalist	Ectophagous	3	0.664	0.165	http://bugguide.net/node/view/1079261#2038513
<i>Hysteropterum unum</i>	<i>Larrea tridentata</i>	Specialist	Ectophagous	2.5	-0.799	0.169	http://bugguide.net/node/view/165734/bgimage
<i>Ips pini</i>	<i>Pinus resinosa</i>	Generalist	Endophagous	6.5	1.148	0.392	http://entnemdept.ufl.edu/creatures/trees/beetles/ips_beetles.htm

<i>Lipara pullitarsis</i>	<i>Phragmites australis</i>	Specialist	Endophagous	5	-0.862	0.277	http://www.cabi.org/Phragmites/lipa_pul.html
<i>Lygus lineolaris</i>	<i>Trifolium pratense</i>	Generalist	Ectophagous	7	-0.129	0.227	http://prairiesoilsandcrops.ca/articles/volume-4-6-screen.pdf
<i>Maculinea rebeli</i>	<i>Gentiana cruciata</i>	Specialist	Ectophagous	18	-2.156	0.559	http://www.inaturalist.org/taxa/490169-Phengaris-rebeli
<i>Melanoplus femurrubrum</i>	<i>Trifolium pratense</i>	Generalist	Ectophagous	28	-0.493	0.323	http://keys.lucidcentral.org/keys/grasshopper/nonkey/html/FactSheets/redleg.htm
<i>Mordellistena nigricans</i>	Plant community	Generalist	Ectophagous	4.3	0.175	0.330	http://fossilworks.org/?a=taxonInfo&taxon_no=317485
<i>Multareis cornutus</i>	<i>Larrea tridentata</i>	Specialist	Ectophagous	4	-0.094	0.156	http://bugguide.net/node/view/908426
<i>Multareis sp</i>	<i>Larrea tridentata</i>	Specialist	Ectophagous	4	0.399	0.159	http://bugguide.net/node/view/908426
<i>Oecanthus nigricornis</i>	Plant community	Generalist	Ectophagous	18	-0.040	0.327	http://entnemdept.ufl.edu/walker/buzz/589a.htm
<i>Ophraella cribrata</i>	Plant community	Generalist	Ectophagous	7	0.314	0.339	http://bugguide.net/node/view/839906/bgimage
<i>Pachybrachis xantholucens</i>	<i>Larrea tridentata</i>	Specialist	Ectophagous	3	-0.292	0.157	http://bugguide.net/node/view/1194020/bgimage
<i>Philaenus spumarius</i>	Plant community	Generalist	Ectophagous	8	0.091	0.328	http://bugguide.net/node/view/147705
<i>Phyllotreta cruciferae</i>	<i>Brassica oleracea</i>	Generalist	Ectophagous	3	-1.155	0.538	http://agresearch.montana.edu/wtarc/producerinfo/entomology-insect-ecology/CanolaFleaBeetles/NDSUFactSheet.pdf
<i>Phytocoris nigrinus</i>	<i>Larrea tridentata</i>	Specialist	Ectophagous	7	0.124	0.156	http://bugguide.net/node/view/1225433/bgimage
<i>Phytocoris vanduzee</i>	<i>Larrea tridentata</i>	Specialist	Ectophagous	7	0.091	0.156	http://bugguide.net/node/view/1225433/bgimage
<i>Phytomyza ilicicola</i>	<i>Ilex opaca</i>	Specialist	Endophagous	5	0.005	0.318	http://bugguide.net/node/view/1168791/bgimage
<i>Pieris brassicae</i>	Brassicaceae	Generalist	Ectophagous	25	-0.258	0.287	Bhubaneshwari, M., Kananbala, A., Joymati, L., Ronikumar L. & Binarani A. (2012). Morphometric measurement of cabbage butterfly <i>Pieris brassicae</i> linn (lepidoptera: pieridae) in the agroecosystem of Manipur. <i>International Journal of Basic and Applied Medical Sciences</i> , 3, 31-33 http://bugguide.net/node/view/3259
<i>Pieris rapae</i>	<i>Brassica oleracea</i>	Generalist	Ectophagous	35	0.462	0.170	http://bugguide.net/node/view/3259
<i>Plutella xylostella</i> *	<i>Brassica oleracea</i>	Generalist	Ectophagous	6	1.204	0.517	http://entnemdept.ufl.edu/creatures/veg/leaf/diamondback_moth.htm
<i>Plutella xylostella</i>	<i>Brassica oleracea</i>	Generalist	Ectophagous	6	-1.007	0.244	http://entnemdept.ufl.edu/creatures/veg/leaf/diamondback_moth.htm
<i>Polyommatus coridon</i>	<i>Hippocrepis comosa</i>	Specialist	Ectophagous	18	-0.371	0.475	http://www.phegea.org/Dagvlinders/BinkMONOLYC/Bink_Monograph_Pcoridon.htm
<i>Prokelisia crocea</i>	<i>Spartina pectinate</i>	Specialist	Ectophagous	3	-4.875	1.274	http://bugguide.net/node/view/443700/bgpage
<i>Psylliodes sp</i>	<i>Larrea tridentata</i>	Specialist	Ectophagous	4.5	0.000	0.155	http://www.agroatlas.ru/en/content/pests/Psylliodes_chrysocephalus/
<i>Stenobothrus lineatus</i>	Plant community	Generalist	Ectophagous	27	0.813	0.491	http://www.orthoptera.ch/arten/item/stenobothrus-lineatus-lineatus
<i>Thamnotettix nigrifrons</i>	Plant community	Generalist	Ectophagous	8	0.571	0.367	http://bugguide.net/node/view/656243/bgpage
<i>Therioaphis trifolii</i>	<i>Medicago sativa</i>	Generalist	Ectophagous	2.1	-0.205	0.408	http://www.agri.huji.ac.il/mepests/pest/Therioaphis_trifolii/
<i>Thyanta custator</i>	<i>Larrea tridentata</i>	Generalist	Ectophagous	11	-0.447	0.16	http://bugguide.net/node/view/15344
<i>Tumidagena minuta</i>	<i>Spartina patens</i>	Specialist	Ectophagous	3	-1.341	0.491	http://bugguide.net/node/view/212781/bgimage

* Herbivore species registered in more than one study that were considered as independent effect sizes

† Source indicates the online page, article or book from where information was extracted. If body length of the one particular species was not available, it was represented by the body length of the another species of the same genus

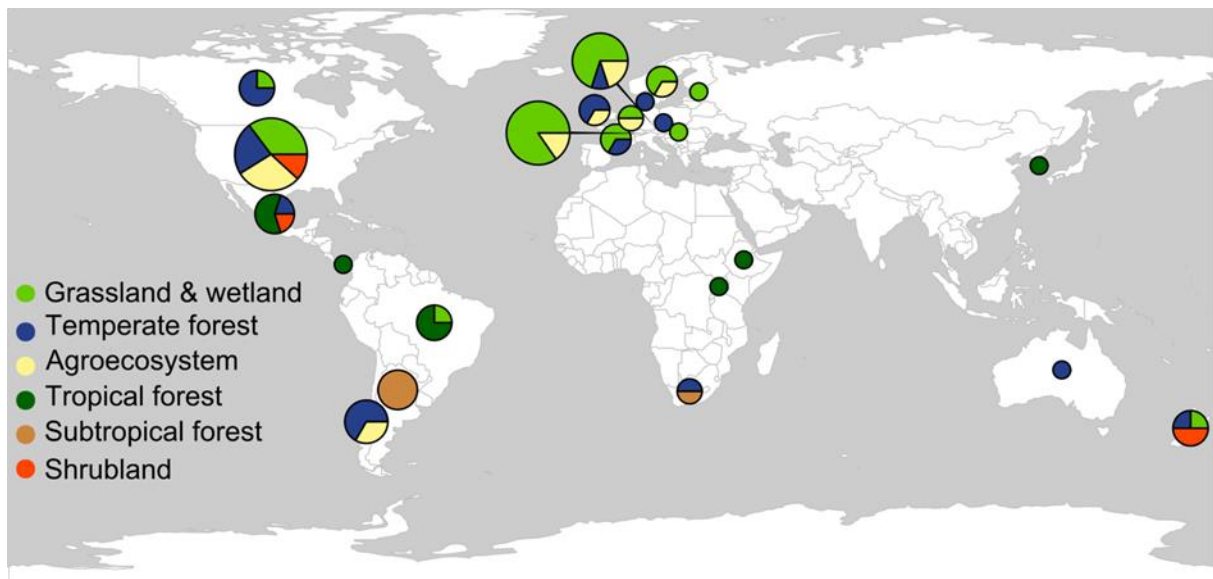


Figure S2 Location of studies evaluating habitat fragmentation effects on insect herbivore community. Size of the circles is proportional to number of studies in each country. Different colours represent studied systems

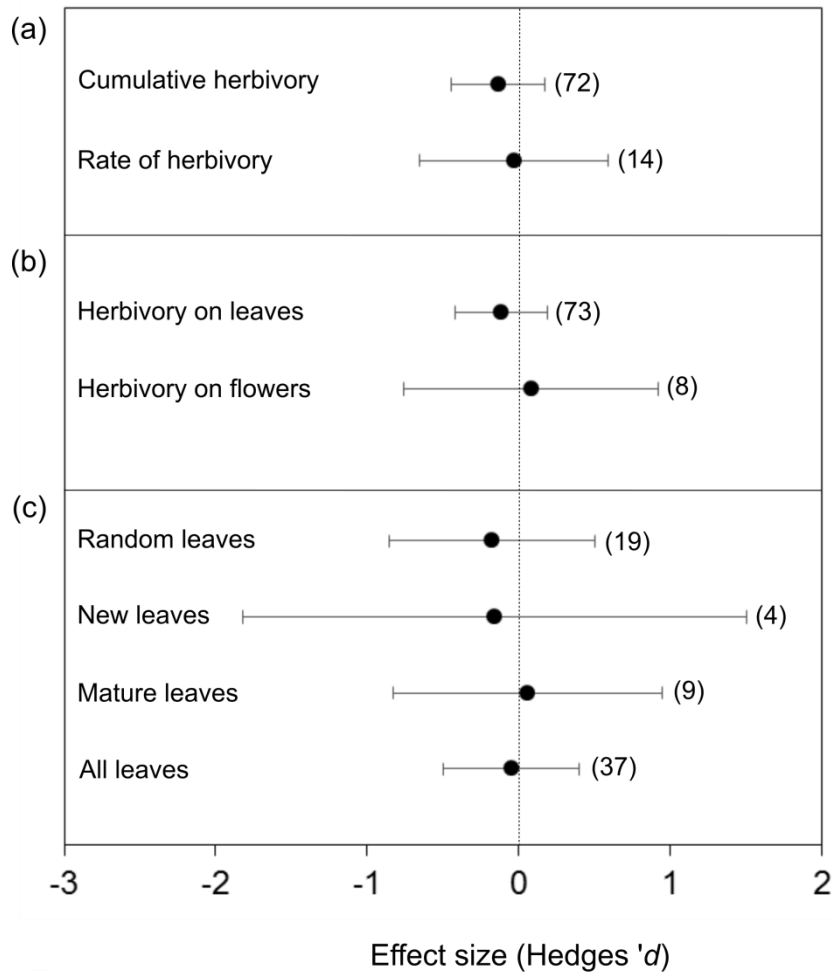


Figure S3 Effects of habitat fragmentation on insect herbivory depending on methodologies to measure damage on plants. Mean effect size \pm 95% CIs of cumulative herbivory (measured at one point) vs. rate of herbivory (percentage of damage per unit of time) (a), damage on different plant organs (b) and stages of leaf lifespan (c). Numbers indicate sample size

Table S6 Summary table showing tests of moderators and heterogeneities from sensitivity analysis examining habitat fragmentation influence on herbivore abundance at species level without the lowest effect size. Significant influence of moderators is indicated in bold (when 95% CI does not include zero)

Response variable	Moderators	df	Q	P
Species level	Host specialisation	1	6.29	0.012
	Residual	49	94.75	< 0.001
	Feeding type	1	0.07	0.789
	Residual	49	97.34	< 0.001
	Body size	1	2.45	0.117
	Residual	49	97.32	< 0.001

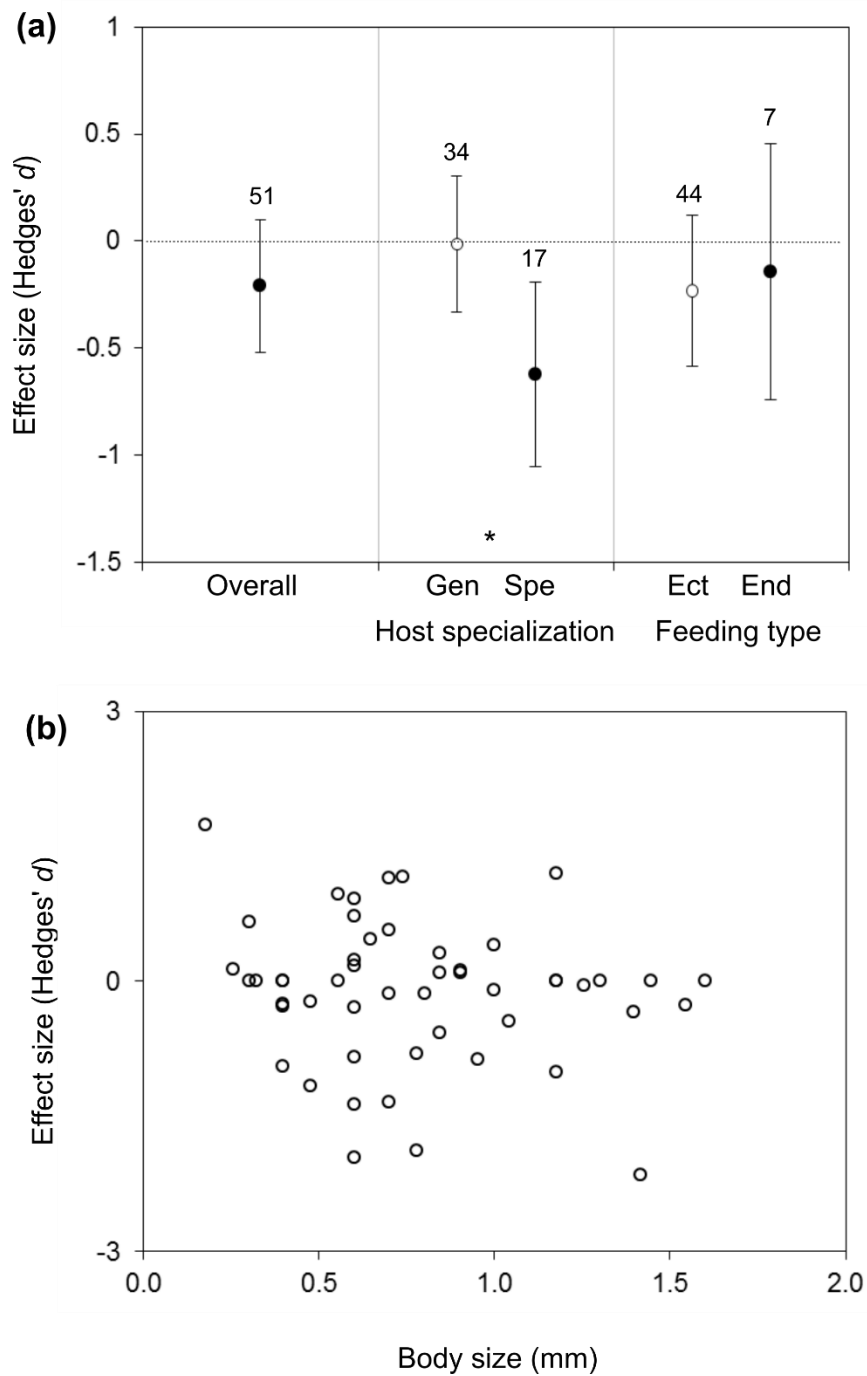


Figure S4 Effects of habitat fragmentation on insect herbivores depending on characteristics of species. Results of sensitivity analysis to the lowest effect size (a) Mean effect size \pm 95% CIs according to host specialization (Gen: generalist, Spe: specialist) and feeding type (Ect: ectophagous, End: endophagous). Numbers indicate sample size. Asterisk denotes a significant difference among categories ($*P < 0.05$). (b) The relationship between fragmentation effect size and herbivore body size (i.e. log 10-transformed body length of each herbivore species)

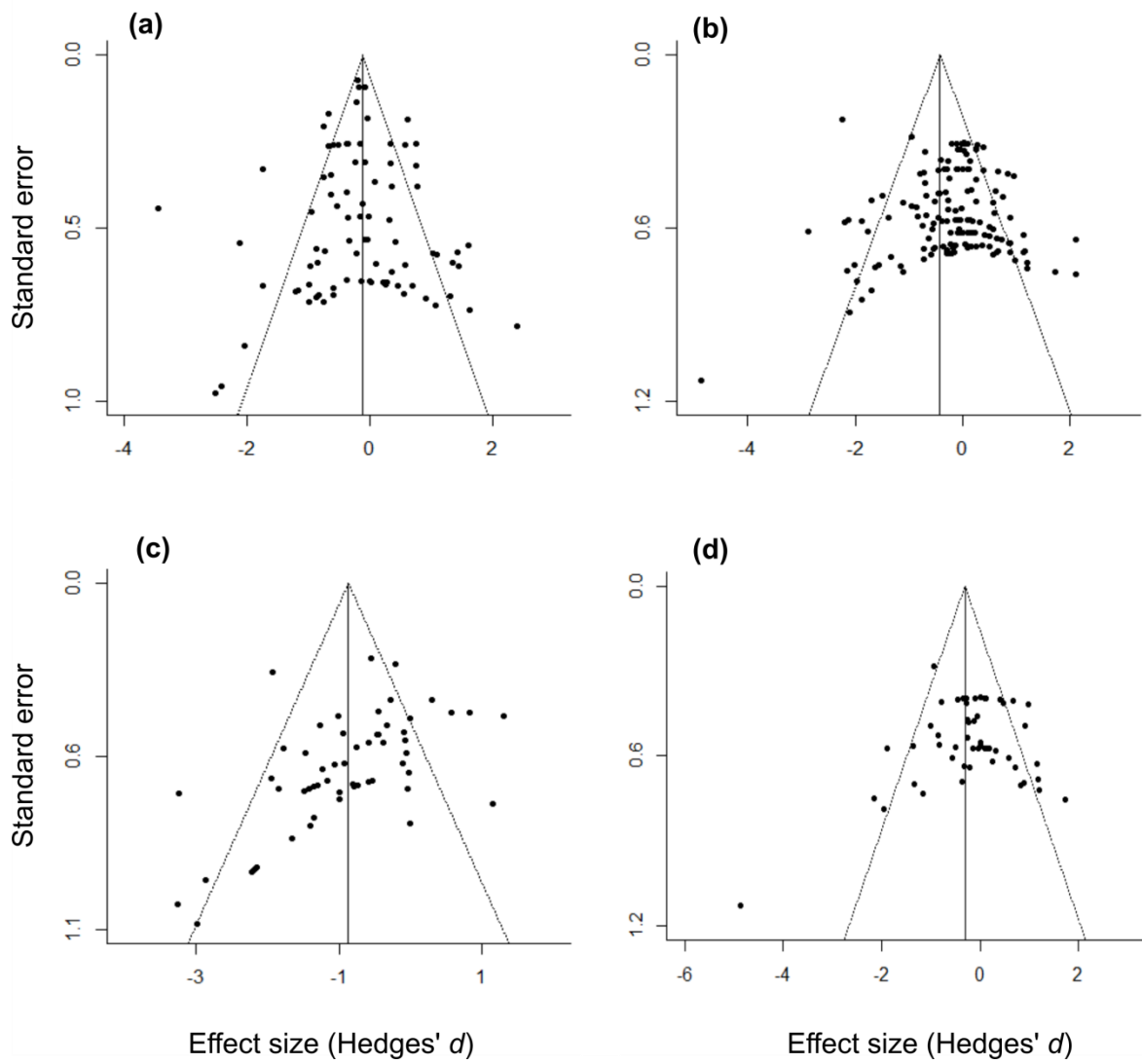


Figure S5 Funnel plots showing the relationship between effect size and standard error of herbivory (a) abundance (b) species richness (c) and the subset of data with abundance at species level (d)

Table S7 Sample size (number of observations) and results of testing publication bias and hierarchical models for each response variable. Publication bias was tested through fail safe number, Kendall's rank correlation test and trim and fill models

Outcome	<i>n</i>	Fail safe number	Rank correlation	Trim and fill model* Effect size and 95% CIs	Original model Effect size and 95% CIs
Herbivory	86	505	$z = 0.018$ $P = 0.985$	-0.273 (-0.472/-0.074)	-0.116 (-0.388/0.156)
Abundance	146	1019	$z = -1.654$ $P = 0.098$	-0.379 (-0.519/-0.238)	-0.418 (-0.674/-0.161)
Species richness	56	2310	$z = 2.239$ $P = 0.025$	-0.409 (-0.681/-0.139)	-0.998 (-1.291/-0.705)
Abundance at species level†	52	46	$z = 1.368$ $P = 0.171$	-0.279 (-0.505/-0.054)	-0.314 (-0.688/0.061)

* Trim and Fill model does not run for hierarchical models in metafor package of R (rma.mv), they were based on random model without hierarchical structure (rma)

† Subset of studies evaluating abundance at species level in order to investigate species traits as moderators of habitat fragmentation effects

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