

Insect and plant traits drive local and landscape effects on herbivory in grassland fragments

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Abstract. Herbivory is one of the most important antagonistic insect–plant interactions and can be influenced by factors at local and landscape scales. Landscape fragmentation may reduce herbivory directly (i.e., decreasing abundance and species richness of herbivores), but also indirectly increase herbivory (i.e., releasing herbivores from top-down control). At a local scale, reduced plant diversity may enhance herbivory through lessened associated resistance, while resource availability (i.e., higher vegetation height and cover) may promote herbivory. Few studies have simultaneously considered the influence of local and landscape variables on insect herbivory. We evaluate effects of landscape (fragment size, connectivity, and arable land percentage) and local factors (plant cover and height and plant species richness) on insect herbivory in fragmented calcareous grasslands. Further, we ask whether these effects depend on feeding traits of herbivores (chewers vs. suckers) and habitat specialization of plants (specialists vs. generalists). Results show that herbivory was best explained by models including variables at both local and landscape scales. However, local factors were more important than landscape variables. Herbivory was in all cases positively related to height of herbs (i.e., taller and more heterogeneous food resources), whereas the effect of plant species richness varied with feeding traits of herbivores. Herbivory by chewers, which are commonly more generalist feeders, was negatively affected by plant species richness, supporting the idea of associated plant resistance. In contrast, herbivory by suckers, which tend to be more specialized, increased with plant richness. Although there was little influence of landscape scale, herbivory on specialist plants was significantly higher in smaller grasslands probably as a consequence of herbivore release from natural enemies. Functional redundancy among herbivore species would allow to maintain overall herbivory in fragmented calcareous grasslands. This study highlights the need to consider different herbivore and plant traits for a better understanding of herbivory responses to local and landscape factors.

Key words: calcareous grasslands; feeding type; habitat fragmentation; habitat specialization; insect herbivory; plant richness; vegetation structure.

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INTRODUCTION

Insect herbivory is one of the most important antagonistic interactions between plants and animals, since it affects plant performance and thereby vegetation structure and plant community composition (Crawley 1989). Insect herbivory is also involved in nutrient cycling and represents a driving force in plant evolution (Linhart 1991, Metcalfe et al. 2013). Hence, identification of factors regulating herbivory has received considerable attention. A number of studies have examined the variation in herbivory between and within plant individuals as a function of physical and chemical traits (Kozlov and Zvereva 2018). At a larger scale, evidence shows that habitat fragmentation can alter insect herbivory via a variety of direct and indirect mechanisms (Chávez-Pesqueira et al. 2015, Rossetti et al. 2017).

Habitat fragmentation can influence insect herbivory via direct negative effects on species richness and abundance of herbivores (Wirth et al. 2008). Lower abundance and species richness of herbivores in smaller fragments can lead to decreased herbivory (e.g., Fáveri et al. 2008, Nufio et al. 2011). These species and herbivory declines can be exacerbated by fragment isolation that usually increases in fragmented landscapes and hamper herbivore movement among habitats (Rösch et al. 2013, Brudvig et al. 2015, Maguire et al. 2015). In addition, amount and configuration of natural habitats in the landscape are increasingly considered as factors affecting dispersal ability and persistence of species (Haddad et al. 2017). For example, impoverished communities of several insect groups in fragmented grasslands have been observed in simplified landscapes with high cover of arable land compared to complex landscapes (Kormann et al. 2015). The same pattern would be expected for insect herbivory in landscapes dominated by arable land, although this needs to be examined since most of the studies so far have focused on other ecosystem processes like predation and parasitism (Chaplin-Kramer et al. 2011).

Positive and neutral effects of landscape fragmentation on insect herbivory have also been observed (e.g., Levey et al. 2016, Morante-Filho et al. 2016). These results can be attributed to functional redundancy in the herbivore

community with less vulnerable species maintaining herbivory at the same level as in unfragmented habitats (Yachi and Loreau 1999). Landscape fragmentation could increase insect herbivory through indirect effects, as natural enemies like predators and parasitoids are often more sensitive to fragmentation than herbivores because of their higher trophic level (Tschamntke and Kruess 1999, Thies et al. 2003, Holt 2010). Therefore, herbivore abundance and herbivory may increase in small and isolated fragments if they are released from natural enemies or the top-down regulation is relaxed (Schüepp et al. 2014, Genua et al. 2017).

Insect herbivory can also be regulated by factors operating at local scale such as plant diversity and vegetation structure within habitats (Kozlov and Zvereva 2018). In particular, the relationship between plant species richness and damage by herbivores remains controversial (reviewed by Moreira et al. 2016). According to the resource specialization hypothesis, increased plant diversity involves a greater diversity of resources for a greater number of herbivore species favoring an increase in herbivory levels (Haddad et al. 2009, Moreira et al. 2016). However, the associational resistance hypothesis states that increased plant diversity may disrupt or dilute the visual and chemical cues that herbivores use to locate and select their host (Barbosa et al. 2009, Castagnyrol et al. 2014). In this sense, the presence of non-host plants may negatively influence host finding and colonization, and consequently, decrease damage by herbivores.

Vegetation structure could be as important as plant diversity in determining the herbivore community and damage on plants at a local scale (Marques et al. 2000, Brose 2003). Size and height of plants may be related to structural complexity of the vegetation, which has been shown, in general, to benefit both diversity and abundance of insect herbivores (e.g., Körösi et al. 2012, Schlinkert et al. 2016), although the opposite pattern was also registered (Woodcock and Pywell 2009). Furthermore, large plants are more apparent and emit volatiles through bigger surface area, so they are more likely to be located by herbivores (Feeny 1976, Bruce et al. 2005). Indeed, more damage by herbivores has been frequently reported in taller plants compared to smaller ones (Cornelissen et al. 2008, Schlinkert et al.

2016). Several studies have examined the influence of local diversity and structure of vegetation on herbivore communities and herbivory (Cornelissen et al. 2008, Moreira et al. 2016), but only two have considered both local and landscape variables simultaneously (Schnitzler et al. 2011, Peter et al. 2014). These studies reported that local abundance of host plants but not habitat fragmentation affected herbivory (Schnitzler et al. 2011), while no influence of forest fragmentation or tree diversity (local scale) was found on herbivory (Peter et al. 2014).

The relative influence of local variables and landscape fragmentation on herbivory may vary depending on herbivore and plant traits, although these variables have not been considered in previous studies. Sucking insects usually have narrower diet breadth than chewers (Novotny et al. 2010; but see Forister et al. 2015) and therefore could be more affected by habitat fragmentation (Rossetti et al. 2017), and their damage may be drastically reduced in isolated and small fragments. With respect to plant traits, habitat specialization could modify local and landscape effects on herbivory. Habitat generalist plants represent a more widespread and continuous resource than specialist plants, which are restricted to specific habitats (e.g., calcareous grasslands; Rösch et al. 2013). According to the host plant geographical distribution hypothesis, widespread plants could have richer local communities of herbivores since these are subsets of the regional species pool (Cornell and Lawton 1992, Marques et al. 2000). Therefore, damage on generalist plants could be less affected by landscape fragmentation than herbivory on specialist ones. In the present study, we examine herbivory responses to local and landscape scales in calcareous grasslands in Germany. These semi-natural ecosystems are characterized by an exceptionally high diversity of plants and animals (Ellenberg and Leuschner 2010). Large areas of calcareous grasslands have been lost and fragmented, mainly as a consequence of agricultural intensification (Riecken et al. 1994). Here, we aimed to answer the following questions: (1) How is insect herbivory influenced by habitat fragmentation (size and connectivity of fragments and arable land percentage) and local variables (height of herbs, plant cover, and herb species richness)? (2) Do the landscape and local

effects depend on insect (feeding type) and/or plant (habitat specialization) traits? We expect a higher influence of landscape variables on leaf damage on specialist plants and on sucking herbivory since the most abundant species of suckers have narrower diet breadths than the most abundant species of chewers in these calcareous grasslands (Kormann et al. 2015). As far as we know, this is the first study examining local- and landscape-scale effects acting in concert considering feeding type of herbivores and plant traits in fragmented habitats.

METHODS

Study area

The study area was located in the vicinity of the city of Göttingen in southern Lower Saxony in Central Germany. We selected 26 fragments of calcareous grassland, a semi-natural habitat type (51.5° N, 9.9° E) belonging to the plant association *Mesobrometum erecti* Koch 1926 (Fig. 1A, B; Ellenberg and Leuschner 2010). In the study area, these grasslands are frequently located on steep slopes and are managed by mowing or grazing with sheep, goats, cattle, or horses (Rösch et al. 2013). We performed samplings always before grasslands were mown and selected fragments with more than ten plant species that are typical for calcareous grasslands in order to maintain habitat-type characteristics as similar as possible and to assure that the fragments exhibited the characteristics of calcareous grasslands (Krauss et al. 2003).

Landscape and local variables

By analyzing digital maps with the geographical information system ArcGIS 10.0 (ESRI Geoinformatik GmbH, Hannover, Germany), we calculated for each of the 26 fragments three landscape variables: size of calcareous grassland, arable land percentage, and habitat connectivity. Grassland size ranged from 0.1 to 8.8 ha, and percentage of arable land was estimated within a radius 500 m around each fragment and ranged from 27% to 68%. Habitat connectivity was measured as a connectivity index described by Hanski et al. (2000):

$$CI_i = \sum_{j \neq i} \exp(-\alpha d_{ij}) A_j^\beta$$

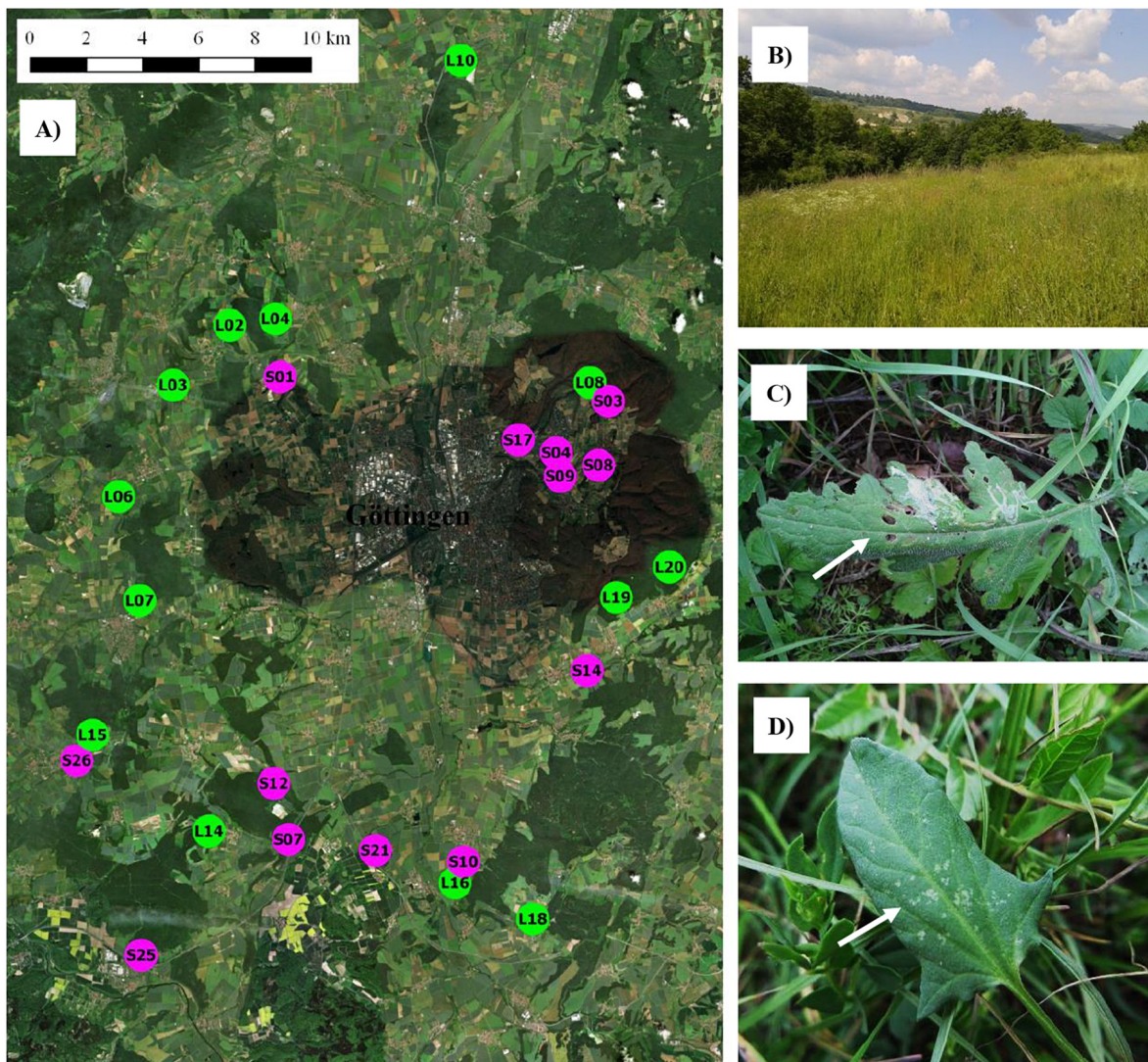


Fig. 1. Location of study sites around the city of Göttingen (A), large grasslands are marked with “L,” small grasslands with “S,” both with a subsequent site number. One of the calcareous grasslands selected for this study (B) and different types of damage by insect herbivores in these grasslands. Chewing damage on leaves of *Scabiosa columbaria* (C), and sucking damage on leaves of *Convolvulus arvensis* (D).

A_j is the area of the neighboring fragment j (in m^2), and d_{ij} is the edge to edge distance (in meters) from the focal fragment i to the neighboring fragment j . α is a species-specific parameter describing a species’ dispersal ability, and β is a parameter that describes the scaling of immigration. The values of the connectivity index ranged between 20 and 849, with large values indicating high levels of connectivity (see Rösch et al. 2013 for more details about calculation of connectivity

index). We measured local factors in twelve plots (50×50 cm) per fragment located at least 5 m from the fragment edge to minimize edge effects. Plots were placed along four lines (10–14 m long) separated among them approximately by 4–6 m; hence, the same area was sampled in all grasslands (Appendix S1: Fig. S1). On each plot, we measured species richness of dicotyledonous herbs (henceforth, referred to as “herb species,” range: 2–21 species), height of the highest herb

(range: 4–60 cm), and percentage of plant cover (range: 50–100%). On all plots, the same person (MRR) estimated visually percentage of plant cover.

Insect herbivory

We estimated leaf damage by chewing and sucking insects in all dicotyledonous herbaceous plants (up to ten leaves per plant) within each of the twelve plots per fragment during June and July 2014. We restricted our measurements to dicotyledonous herbs since they generally have higher leaf herbivory levels than monocotyledonous species (Dominy et al. 2008, Grubb et al. 2008). Whenever possible, only the oldest leaves were considered to standardize leaf age.

Total herbivory, chewing herbivory, and sucking herbivory were estimated as percentage of damaged leaves to the total leaves [damaged leaves/(damaged + undamaged) × 100] per plant species. Chewing herbivory was additionally estimated as leaf area consumed by chewers since loss of photosynthetic tissue is the major impact on the plants (Zhang et al. 2016, Kozlov and Zvereva 2018). Leaf area loss by chewers was estimated by using six damage categories (0 = 0%; 1 = 1–5%; 2 = 6–12%; 3 = 13–25%, 4 = 26–50%, 5 = 51–100%; Benitez-Malvido et al. 1999), which were used to calculate a percentage of leaf area damaged per plant as: $\sum(C_i \times n_i)/N$, where C_i corresponds to the percentage midpoint of each category, n_i is the number of leaves in the i_{th} category of damage, and N is the total number of leaves. This method allows assessing herbivory non-destructively in the field with precision and accuracy (Johnson et al. 2016). Chewing herbivory was detected as missing parts of the lamina, for example, holes or incomplete leaf margins (Fig. 1C), and was likely to be caused by species from the orders Lepidoptera (e.g., larvae from genera *Argynnis*, *Pieris*, *Polyommatus*, *Zygaena*), Orthoptera (e.g., species from genera *Chorthippus*, *Metrioptera*; Kormann et al. 2015), and Coleoptera (adults and larvae). Sap-sucking damage was identified as pale punctures or scrapes on the leaf surfaces (Fig. 1D), and the main insects causing this type of damage belong to the order Hemiptera, that is, true bugs (e.g., genera *Acalypta*, *Halticus*, *Ortholomus*, *Megalonotus*) and leafhoppers (e.g., genera *Adarrus*, *Arocephalus*, *Turrutus*, *Ribautodelphax*; Kormann et al. 2015).

Herbivory was separately evaluated according to habitat specialization of plants. Two groups of plant species were defined according to von Drachenfels (1994): habitat specialist and generalist plants. This classification was also used in studies in the same study region by Krauss et al. (2004) and Rösch et al. (2013). Calcareous grassland specialists include those plant species mainly restricted to calcareous grasslands, while the generalist species comprise plants with no habitat preferences or preferences for other habitats (Krauss et al. 2004). The classification in calcareous grassland specialist and generalists is clearly reflected in the Ellenberg values; that is, calcareous grassland specialist species have significantly lower nitrogen ($t = 7.6184$, $df = 47.065$, $P = <0.001$) and moisture values ($t = 5.4417$, $df = 64.62$, $P = <0.001$) than the species classified as generalists (see Appendix S1: Fig. S2).

Data analysis

We analyzed the influence of the landscape and local scales on herbivory using linear mixed-effects models (LME, nlme package; Pinheiro et al. 2015) with the following explanatory variables: height of herbs, species richness, plant cover, fragment size, arable land percentage, and connectivity index. Plant cover was arcsine-square-root-transformed and connectivity index and fragment size log₁₀-transformed to linearize relationships. The explanatory variables were uncorrelated, and no collinearity was detected (Smith et al. 2009; Appendix S1: Table S1; function vif from the R package car; Fox and Weisberg 2011). Site was incorporated as random effect to consider the spatial dependence among plots within the same fragment. Response variables were total herbivory, chewing herbivory, sucking herbivory, and herbivory on specialist and generalist plants. We selected leaf area lost as chewing herbivory for the analysis since both herbivory variables were correlated ($r = 0.7$, $P < 0.001$) and leaf area loss is the most common and accurate measure of this type of damage. Herbivory was averaged per plant species and then per plot. Chewing herbivory and sucking herbivory were arcsine-square-root-transformed to achieve normality of the residuals, and we used the cvarIdent variance function to account for heteroscedasticity allowing different variances for each site (Pinheiro and Bates 2000).

We examined the relative effects of local- and landscape-scale variables on herbivory using a multimodel inference approach (Burnham and Anderson 2002). We started off with full models for each response variable containing all predictors and two-way interactions between the landscape variables. Then, we compared all candidate models using Akaike Information Criterion, adjusted for small sample sizes (AICc, Burnham and Anderson 2002), and we selected and averaged best models those with $\Delta AIC < 2$ (MuMIn package, Barton 2016). Finally, we calculated the relative importance of each variable by summing the AICc weights of the models in which each variable appears; the larger this value, the more important is the variable when considering the entire set of models (Burnham and Anderson 2002).

Herbivory on the six most common herbaceous plant species (three specialist and three generalist plants, which were present in more than 20 fragments) was analyzed separately in order to examine whether the community pattern of herbivory reflects individual responses of the most common plants or the global pattern is the net result of idiosyncratic and highly variable responses. The initial model included all local and landscape predictors and interactions among the last ones as explanatory variables and total

herbivory (averaged per fragment) as response variable. Model selection was performed using a multimodel inference approach as described above. All analyses were performed in R, version 3.4.0 (R Development Core Team 2017). To visualize the relative importance of the explanatory variables, we plotted the significant predictors of herbivory with the visreg package in R (Breheny and Burchett 2013).

RESULTS

We recorded insect herbivory on leaves of 76 plant species (Appendix S1: Table S2). Total herbivory as percentage of damaged leaves per plot averaged 45.99% (± 0.91 , standard error), and considering different feeding types, we registered 36.61% (± 0.85) leaves damaged by chewers and 13.75% (± 0.88) damaged by suckers. In addition, the leaf area lost by chewers averaged 2.11% (± 0.08) per plot. Total herbivory was best explained by models including two local variables (height and cover of plants) as well as connectivity and fragment size at the landscape scale (Table 1). The local variables were the most important variables (importance = 1) and had a significant effect on total herbivory. Height of herbs and plant cover positively influenced herbivory (Fig. 2A, B, Table 1). The models that

Table 1. Summary table of linear mixed model results for total herbivory, chewing herbivory, and sucking herbivory after multimodel averaging of best candidate models showing relative importance (I) of each variable and estimated effect on the response variable \pm standard error (SE).

Response variable	Scale	Explanatory variable†	I (%)‡	Multimodel estimate \pm SE§	Z value§	P value§
Total	Local	Height of herbs	1	0.197 \pm 0.081	2.420	0.015
		Plant cover	1	21.375 \pm 5.088	4.183	<0.001
	Landscape	Connectivity	0.32	4.707 \pm 3.639	1.228	0.219
		Fragment size	0.20	-2.200 \pm 2.552	0.819	0.413
Chewing herbivory	Local	Height of herbs	1	0.001 \pm 0.000	3.623	<0.001
		Species richness	1	-0.002 \pm 0.000	3.321	<0.001
	Landscape	Arable land	0.59	0.002 \pm 0.003	0.895	0.371
		Connectivity	0.63	0.051 \pm 0.059	0.848	0.396
		Fragment size	0.61	-0.029 \pm 0.036	0.799	0.424
		Arable land \times Connectivity	0.25	-0.002 \pm 0.001	1.808	0.070
	Connectivity \times Fragment size	0.19	0.026 \pm 0.017	1.450	0.147	
Sucking herbivory	Local	Height of herbs	1	0.002 \pm 0.001	2.371	0.017
		Species richness	0.66	0.007 \pm 0.003	2.189	0.029
		Plant cover	0.43	0.084 \pm 0.054	1.552	0.121

Note: Bold values indicate significant effect at $P \leq 0.05$.

† Explanatory variables included in the best models.

‡ Relative importance of each variable is the summed of AICc weights of the models in which each variable appears.

§ Estimates, Z and P values after multimodel averaging of the top-model set ($\Delta AIC < 2$).

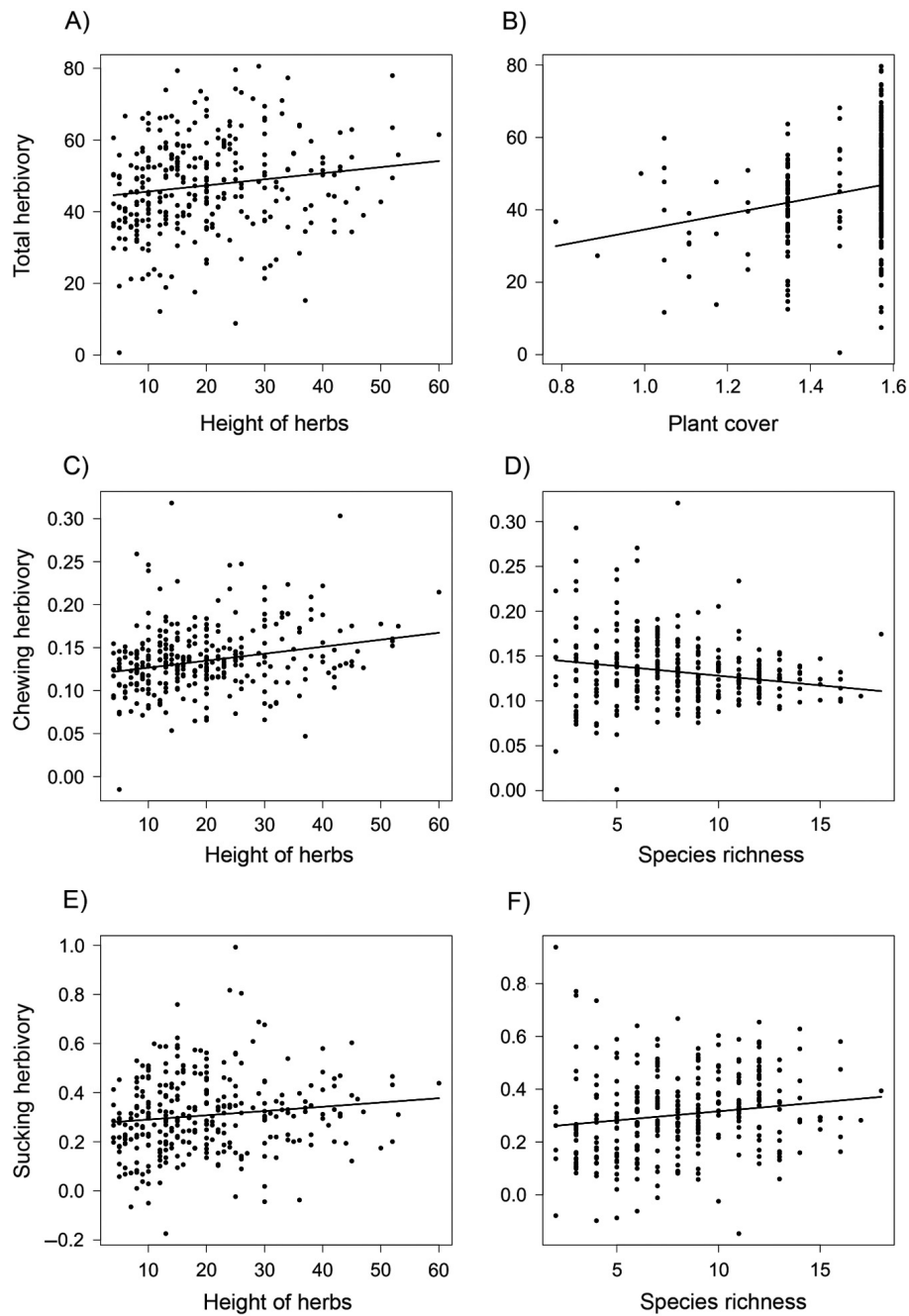


Fig. 2. Insect herbivory in relationship to the significant predictors included in the best models. Total herbivory as a function of height of herbs and plant cover (A, B), and chewing and sucking herbivory in function of height of herbs (C, E) and species richness (D, F). Total herbivory and sucking herbivory represent percentage of damaged leaves, and herbivory by chewers represents leaf area lost estimated through herbivory index. Species richness is the number of dicotyledonous herb species in 0.25 m². Chewing damage and sucking damage were arcsine-square-root-transformed to achieve normality. Plant cover was arcsine-square-root-transformed to linearize relationships. Points are the partial residuals for each explanatory variable accounting for the effects of all other factors in the model, which are calculated using the package visreg.

best explained herbivory by chewers included all landscape variables, two interactions (arable land × connectivity and fragment size × connectivity), and height and species richness of herbs at the local scale. These local variables had the highest relative importance (importance = 1) in determining herbivory by chewers (Table 1), which was significantly increased with increasing height of herbs, whereas decreased as herb species richness increased (Fig. 2C, D). Sucking herbivory was best explained by the three local variables only (Table 1). Height of herbs and species richness had higher relative importance (importance > 0.5) than plant cover (importance = 0.43; Table 1) with height of herbs and species richness showing a positive and significant relation to sucking herbivory (Fig. 2E, F).

Percentage of damaged leaves was, on average, similar in grassland specialist (44.40 ± 1.15%) and generalist plants (47.53 ± 1.24%; Appendix S1: Table S3). The best models explaining total herbivory on both groups of herbs included all local variables and connectivity and fragment size at the landscape scale (Table 2). Two local variables and fragment size at landscape scale were the most important variables (importance = 1) and had significant effects on herbivory on specialist plants (Table 2). This leaf damage was higher with increasing plant height and cover and with decreasing fragment size

(Fig. 3A–C). The local scale was more important (importance ≥ 0.50) than connectivity and fragment size (importance ≤ 0.25) for herbivory on generalist plants (Table 2). Height of herbs and plant cover had a positive and significant influence on this type of herbivory (Fig. 3D, E).

Herbivory was separately analyzed for the most common grassland specialist (*Sanguisorba minor*, *Viola hirta*, *Scabiosa columbaria*) and generalist (*Centaurea jacea*, *Plantago lanceolata*, and *Lotus corniculatus*) plant species and the herbivory on each species showed different responses to local and landscape variables (Table 3). Among local effects, height of herbs was included in the final models of four plant species with highest importance (importance = 1) and significant influence on herbivory on *Sanguisorba minor* and *Lotus corniculatus*. Plant cover was included in the best models explaining herbivory on three plant species, but its importance was always lower than height of herbs (importance < 0.25), and it had a significant and negative influence on herbivory on *Lotus corniculatus* exclusively. Species richness was included in the best models explaining herbivory on only *Scabiosa columbaria* with low importance as predictor variable (importance = 0.23). Among landscape variables, they were included in most of the best models but with different effects on herbivory. Connectivity was included in the best models as predictor of herbivory on five plant species (importance ≥ 0.2),

Table 2. Summary table of linear mixed model results for herbivory on specialists and generalist herbs of calcareous grasslands after multimodel averaging of best candidate models showing relative importance (I) of each variable and estimated effect on the response variable ± standard error (SE).

Response variable	Scale	Explanatory Variable†	I (%)‡	Multimodel estimate ± SE §	Z value§	P value§
Herbivory on specialist herbs	Local	Height of herbs	1	0.246 ± 0.107	2.293	0.022
		Plant cover	1	25.867 ± 6.423	4.010	<0.001
	Landscape	Species richness	0.19	−0.275 ± 0.322	0.851	0.394
		Connectivity	0.32	4.902 ± 3.755	1.237	0.216
Herbivory on generalist herbs	Local	Fragment size	1	−6.087 ± 2.654	2.177	0.029
		Height of herbs	1	0.351 ± 0.129	2.708	0.007
		Plant cover	0.88	18.745 ± 8.335	2.239	0.025
	Landscape	Species richness	0.50	0.712 ± 0.413	1.718	0.086
		Connectivity	0.25	5.869 ± 5.549	1.006	0.314
		Fragment size	0.13	3.798 ± 3.638	0.991	0.321

Note: Bold values indicate significant effect at $P \leq 0.05$.

† Explanatory variables included in the best models.

‡ Relative importance of each variable is the summed of AICc weights of the models in which each variable appears.

§ Estimates, Z and P values after multimodel averaging of the top-model set ($\Delta AIC < 2$).

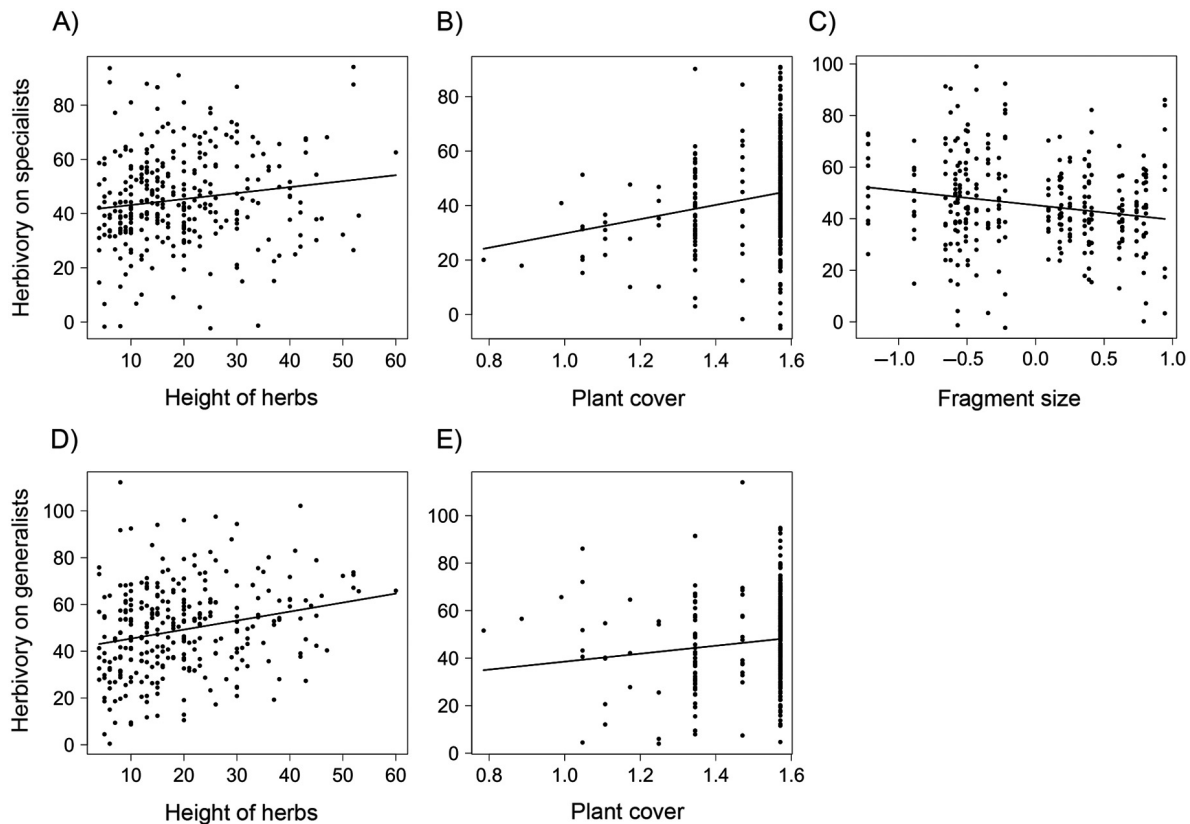


Fig. 3. Insect herbivory in relationship to the significant predictors included in the best models. Total herbivory on habitat specialist plants as a function of height of herbs (A), plant cover (B), and fragment size (C). Total herbivory on habitat generalist plants as a function of height of herbs (D) and plant cover (E). Herbivory represents percentage of damaged leaves. Species richness is the number of dicotyledonous herb species in 0.25 m². Plant cover and fragment size were arcsine-square-root-transformed and log₁₀-transformed to linearize relationships. Points are the partial residuals for each explanatory variable accounting for the effects of all other factors in the model, which are calculated using the package visreg.

and it had significant and positive influence on herbivory on *Scabiosa columbaria*. Fragment size was also included in the best models of five species (importance > 0.2), and it was a significant predictor of herbivory on *L. corniculatus* with positive influence on it. The interaction between fragment size and connectivity was in the models explaining damage on two plants and significant influence on herbivory on *L. corniculatus*. Arable land was included in the best models explaining damage on *L. corniculatus* and *C. jacea* (importance ≥ 0.65) but only was a significant predictor with negative influence for the last species. The interaction between arable land and fragment size was included as predictor of herbivory on these

two species and only significant for herbivory on *L. corniculatus*.

DISCUSSION

Our results indicate that spatial variation in insect herbivory in fragmented grasslands is mainly explained by factors at the local level, whereas habitat fragmentation does not appear to be a major driver of herbivory patterns. In addition, local and landscape influences on herbivory varied with feeding traits of herbivores and habitat specialization of plants. Although herbivory was generally low, values were within the range registered by other studies in grasslands (e.g., Scherber et al. 2006) and were in

Table 3. Summary table of linear mixed-effects model results for herbivory on the six most common plant species after multimodel averaging of best candidate models showing relative importance (I) of each variable and estimated effect on the response variable ± standard error (SE).

Plant species	Habitat†	Explanatory variable‡	I (%)§	Multimodel estimate ± SE¶	Z value¶	P value¶
<i>Scabiosa columbaria</i>	S	<i>Species richness</i>	0.23	-1.386 ± 0.953	1.357	0.175
		Connectivity	1	45.863 ± 10.904	3.937	<0.001
		Fragment size	0.44	19.998 ± 49.717	0.389	0.697
<i>Sanguisorba minor</i>	S	Connectivity × Fragment size	0.18	-33.101 ± 21.765	1.413	0.158
		Height of herbs	1	0.026 ± 0.006	3.972	<0.001
		Connectivity	0.54	-0.201 ± 0.114	1.653	0.098
<i>Viola hirta</i>	S	<i>Height of herbs</i>	0.19	0.013 ± 0.010	1.266	0.205
		<i>Plant cover</i>	0.17	0.923 ± 0.841	1.031	0.302
		Fragment size	0.54	-0.238 ± 0.132	1.705	0.088
<i>Centaurea jacea</i>	G	<i>Height of herbs</i>	0.13	0.009 ± 0.006	1.278	0.201
		<i>Plant cover</i>	0.13	-0.713 ± 0.583	1.141	0.254
		Arable land (%)	1	-0.013 ± 0.005	2.474	0.013
		Connectivity	0.54	0.223 ± 0.117	1.792	0.073
		Fragment size	0.23	0.226 ± 0.442	0.497	0.619
<i>Lotus corniculatus</i>	G	Arable land × Fragment size	0.11	-0.014 ± 0.008	1.711	0.087
		Height of herbs	1	1.233 ± 0.279	4.093	<0.001
		<i>Plant cover</i>	0.21	-63.943 ± 30.414	1.933	0.053
		Arable land	0.65	0.378 ± 0.200	1.745	0.081
		Connectivity	0.70	16.003 ± 8.279	1.851	0.064
<i>Plantago lanceolata</i>	G	Fragment size	1	74.565 ± 35.432	2.027	0.043
		Arable land × Fragment size	0.65	-1.029 ± 0.344	2.758	0.006
		Connectivity × Fragment size	0.35	-39.319 ± 15.902	2.320	0.020
<i>Plantago lanceolata</i>	G	Connectivity	0.20	-8.473 ± 9.237	0.862	0.389
		Fragment size	0.31	6.758 ± 5.195	1.222	0.222

Note: Bold values indicate significant effect at $P \leq 0.05$.

† Plant species were classified into specialist (S) and generalists (G) according to habitat specialization of calcareous grasslands.

‡ Explanatory variables included in the best models. Variables at local scale appear in italics.

§ Relative importance of each variable is the summed of AICc weights of the models in which each variable appears.

¶ Estimates, Z and P values after multimodel averaging of the top-model set ($\Delta AIC < 2$).

agreement with the patterns observed in recent reviews of insect herbivory (Zhang et al. 2016, Kozlov and Zvereva 2018). It has been observed that even low levels of leaf area removed can trigger alterations in plant physiology and nutritional quality (Kerchev et al. 2012, Visakorpi et al. 2018) and in turn affect plant population dynamics (Stein et al. 2010, Allan and Crawley 2011).

Among local factors, height of herbs was the most consistently influential factor in determining herbivory. According to the plant apparency hypothesis, tall plants are more visible and may thus be more attractive for herbivores than short ones leading to increased herbivory (Feeny 1976, but see Endara and Coley 2011). Furthermore, taller herbs often provide more host resources and greater structural complexity offering higher variety of niches to insect herbivores (Lawton

1983). Indeed, strong evidence indicates that vegetation structure has a key role in enhancing abundance and species richness of different groups of insects (Brose 2003, Körösi et al. 2012, Schlinkert et al. 2016). Related to this, we found that plant cover had positive and significant effects on total herbivory and damage on specialist and generalist plants. Taken together, resource quantity and vegetation structure appear to be key factors for herbivore communities and herbivory in calcareous grasslands, where small plants such as grasses and herbs dominate the plant community (Ellenberg and Leuschner 2010).

Herb species richness was also an influential local factor, but with opposite effects depending on type of herbivory. Previous empirical and theoretical evidence confirmed that plant diversity effects on herbivores are controversial (reviewed

by Moreira et al. 2016). In our case, chewing herbivory decreased with increasing species number of herbs supporting the associational resistance hypothesis (Barbosa et al. 2009), whereas herbivory by suckers was positively related to plant species richness in agreement with the resource specialization hypothesis (Haddad et al. 2009, Woodcock and Pywell 2009, Loranger et al. 2014). Although we did not identify the herbivore species consuming the leaves, sucking herbivores are considered to have narrower diet breadths (Novotny et al. 2010; but see Forister et al. 2015), and they might have benefited from increased plant richness. Higher plant diversity could offer a greater diversity of resources that favor an accumulation of herbivores specializing on different plant species, consequently increasing herbivory at the community level (Haddad et al. 2009, Moreira et al. 2016).

At the landscape scale, connectivity and fragment size were included in nine of the eleven models performed. However, fragmentation variables had, in general, a weaker effect than local variables and did not significantly influence herbivory (except for herbivory on specialist plants and two specific plant species). These findings are in line with previous studies in fragmented forests, where neither connectivity (Levey et al. 2016) nor fragment size (Schnitzler et al. 2011) affected insect herbivory. Such neutral responses of herbivory to habitat fragmentation can occur when multiple herbivore species play similar ecological roles (Yachi and Loreau 1999). Such functional redundancy among species would allow to maintain herbivory processes through herbivore species that are little or not affected by habitat fragmentation (Elmqvist et al. 2003, Tschardt et al. 2012). A recent review has shown negative effects of fragmentation only on host specialist herbivores, but not on generalist ones (Rossetti et al. 2017). In our study, landscape variables were more important for herbivory by chewers (all landscape variables were included in the best models) than for suckers, contrary to our expectation of chewing insects as less vulnerable and affected by habitat fragmentation. One explanation could be that chewing herbivores depend on widespread resources and need to move more among grassland fragments. In this sense, previous work in our study sites showed negative impacts of isolation and arable land cover only on

habitat generalist leafhoppers which are more likely to move between fragments, while specialists were unaffected (Rösch et al. 2013).

Herbivory on both grassland generalist and specialist plants was similarly affected by local and landscape variables. This is in contrast to the expectation that herbivores on plants with a more continuous and probably wider distribution range (habitat generalist plants) should be less affected by habitat fragmentation (Cornell and Lawton 1992). However, herbivory on specialist plants significantly increased in smaller grasslands which could be a consequence of changes in natural enemy communities. Release from natural enemies, which are often more vulnerable to habitat fragmentation than herbivores because of their higher trophic position (Holt 2010), has been recently identified as the cause of increased herbivory in smaller fragments (Genua et al. 2017). Another explanation may be related to changes in plant community composition that influence herbivore responses (Wirth et al. 2008). Higher insect damage may be due to an increase in the proportion of habitat generalist plants in small fragments, which may be more palatable to herbivores compared to specialist plants that are specialized on living in a hot and dry environment (often with small or hairy leaves). However, previous evidence in the study area does not support the idea of changes in the proportion of generalist and specialist plants with fragment size (Rösch et al. 2015). We also found plant identity patterns, supporting Levey et al. (2016), who also observed dissimilarities in herbivory responses to connectivity and edge distance among plant species, which were attributed to different herbivore communities in taxonomically distant plant species.

In summary, this study examines the relative effects of local vegetation characteristics and landscape variables on insect herbivore, evaluating for the first time whether these effects vary according to herbivore and plant traits. Vegetation characteristics at the local scale were the most important drivers of herbivory in fragmented calcareous grasslands. Functional redundancy among herbivore species would allow to maintain herbivory processes (Elmqvist et al. 2003, Tschardt et al. 2012) in isolated and small grasslands that are surrounded by a high percentage of arable land. Results indicate that resource quantity and

vegetation structure at local scale and herbivore feeding traits are key factors for driving herbivore communities and herbivory in calcareous grasslands. This finding highlights the need to consider different herbivore and plant traits for a better understanding of herbivory responses to local and landscape factors.

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