

Climate, Land use and Plant Richness Differently Shape Herbivory on Major Plant Functional Groups

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1 **Title**

2 Climate, land use and plant richness differently shape herbivory on major plant functional groups

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19 **Abstract**

20 Interactions between plants and herbivorous invertebrates drive the nutritional quality of resources for
21 higher trophic levels, nutrient cycling and plant-community structure. Thereby, shifts in functional
22 composition of plant communities particularly impact ecosystem processes. However, the current
23 understanding of herbivory is limited concerning climate, land use and plant richness, as comparative
24 studies of different plant functional groups are lacking. This study was conducted on 81 plots covering large
25 climatic and land-use gradients in Bavaria, Germany. We investigated foliar invertebrate herbivory rates
26 (proportional leaf-area loss, following ‘herbivory’) in three major plant functional groups (legumes, non-
27 leguminous forbs, grasses). As drivers we considered multi-annual mean temperature (range: 6.5–10.0 °C),
28 local habitat type (forest, grassland, arable field, settlement), local plant richness (species and family level,
29 ranges: 10–50 species, 5–25 families) and landscape diversity (0.2–3-km scale). Our results largely confirm
30 higher herbivory on legumes than on forbs and grasses. However, herbivory in forests was similar across
31 plant functional groups since herbivory on legumes was low, e.g. lower than on legumes in grasslands. We
32 also observed differential responses of herbivory among plant functional groups in response to plant
33 richness (family level only), but not to landscape diversity. Temperature did not affect overall herbivory,
34 but in grasslands higher temperature decreased herbivory on legumes and increased on forbs and grasses.
35 We conclude that climate, habitat type and family-level plant richness likely assert different effects on
36 herbivory among plant functional groups. This emphasises the importance of functional groups for
37 understanding community-level herbivory and ecosystem functioning.

38 **Keywords**

39 Ecosystem functions, habitat types, landscape diversity, plant guilds, plant-insect interactions

40 **Introduction**

41 Herbivores feeding on living plant tissue make essential contributions to ecosystem functioning
42 (Biedermann et al. 2005). When becoming prey or through defecating, herbivores provide nutrients to other
43 trophic levels and release nutrients which otherwise would be retained in plant material for a longer time.
44 Despite its key role in food webs and nutrient cycles, herbivory generally causes negligible total biomass
45 loss (Schowalter 2016). Nonetheless, herbivory affects growth, phenology, productivity and competitive
46 ability of individual plants (Crawley 1989; Schowalter 2016). Therefore, different intensities of herbivory
47 on neighbouring plants bear the potential to alter plant community composition (Crawley 1989; Kempel et
48 al. 2015; Schowalter 2016). Shifts in plant community composition – particularly with respect to plant
49 functional groups (e.g. legumes, grasses) – may in turn affect ecosystem's productivity, plant total nitrogen
50 content, top-soil moisture and associated arthropod communities (Tilman et al. 1997; Siemann et al. 1998;
51 Fischer et al. 2019; Barneze et al. 2020). In many ecosystems, insect herbivores are among the major
52 contributors to herbivory (Schowalter 2016). Thus, a deeper understanding of the environmental drivers
53 affecting insect herbivory (in this study addressed by invertebrate herbivory) on plant functional groups is
54 pivotal to mitigate detrimental consequences for ecosystem functioning under anthropogenic climate and
55 land-use change.

56 Herbivory pressure strongly depends on the nutritious quality and palatability of plants (Loranger et al.
57 2012; Njovu et al. 2019), which varies substantially among major plant functional groups – namely
58 legumes, non-leguminous forbs and grasses (Scherber et al. 2006). Legumes contain more nitrogen, e.g.
59 higher crude plant protein content and lower leaf C:N ratio, than forbs and grasses (Perez Corona et al.
60 1995; Leingärtner et al. 2014), whereas lignin content is higher in grasses (Perez Corona et al. 1995).
61 Consequently, high, medium and low foliar herbivory intensities are frequently observed on legumes, non-
62 leguminous forbs and grasses, respectively (Scherber et al. 2006; Leingärtner et al. 2014). Furthermore,
63 plant functional groups encompass food plants of specialist herbivores since insect herbivores are often

64 specialized in feeding within plant genera or families (Haddad et al. 2001). Therefore, different herbivore
65 species may be involved in herbivory among plant functional groups.

66 Temperature impacts life cycles, population dynamics and geographic distributions of invertebrate
67 herbivores and their interaction partners, such as plants and natural enemies (Bale et al. 2002; Rasmann and
68 Pellissier 2015). In warmer climates ectothermic invertebrates have relatively higher energy demands,
69 potentially resulting in uptake of resources with higher C:N ratios (Rasmann and Pellissier 2015; Malzahn
70 et al. 2016; Zhang et al. 2020). For instance, omnivores choose a more plant-based diet to meet changed
71 C:N demands at higher temperatures (Zhang et al. 2020). Yet our study is (among) the first to investigate
72 whether higher temperatures may also trigger invertebrate herbivores to shift diet away from legumes (low
73 C:N ratio) towards plants with higher C:N ratios, such as non-leguminous forbs and grasses.

74 Local drivers such as plant richness and habitat type affect herbivory. However, both positive (Ebeling et
75 al. 2014, Loranger et al. 2014, Dinnage 2013) and negative (Jactel and Brockerhoff 2007) effects of plant
76 species richness on herbivory have been reported. The degree of plant phylogenetic diversity, which can be
77 approximated by plant richness at family level (= plant familial richness), may serve as an explanation for
78 contrasting effects of plant species richness on herbivory (Dinnage 2013). Besides, herbivory depends on
79 the surrounding habitat. While larger impacts of herbivores were reported for herbaceous plants in open
80 rather than forested habitats (Maron and Crone 2006), studies comparing a large range of typical habitat
81 types in temperate regions (forest, grassland, arable field, settlement) are lacking.

82 High landscape diversity (Shannon Index) indicates the presence of more different habitat types, more
83 similar proportions of habitat types or both. This can increase richness and abundance of insect herbivores,
84 particularly of generalist species that benefit from resources of multiple habitats (Jonsen and Fahrig 1997).
85 Higher herbivore abundances, in turn, may increase intensity of herbivory (Ebeling et al. 2014; Njovu et al.
86 2019).

87 Climate, land use and plant richness affect invertebrate herbivory, but knowledge is lacking on – potentially
88 differential – responses of herbivory among plant functional groups. Furthermore, this is the first study
89 comparing herbivory in a wide range of typical habitat types in temperate regions (forest, grassland, arable
90 field and settlement) across large climatic gradients, and also taking into account plant richness effects. In
91 particular, we addressed the following questions:

- 92 1. How do land use at local (habitat type) and landscape scale (landscape diversity), and local plant
93 richness (at species and family level) affect invertebrate herbivory on plant functional groups?
- 94 2. Do climate and land use jointly affect invertebrate herbivory on plant functional groups?

95

96 **Materials and methods**

97 Study area and plot selection

98 Research was conducted on 179 plots (complete data sets acquired for 81 plots) across Bavaria, Germany.
99 To disentangle the combined effects of climate and land use on herbivory in three different plant functional
100 groups, we used a novel multi-scale study design which combined climate zones, landscape-scale land-use
101 types, and a wide range of local habitat types (Redlich et al. 2021). Fifteen combinations of climate zones
102 (multi-annual mean temperature range of 81 plots: 6.5–10.0 °C) and landscape-scale land-use types (near-
103 natural, agriculture and urban) were chosen from 5.8 km x 5.8 km grid cells covering Bavaria, each with
104 four replicates (= 60 ‘regions’). In each selected grid cell, plots were placed in three out of four possible
105 dominant, contrasting habitat types (forest, grassland, arable field, settlement) with at least 50 m distance
106 to larger roads and other habitat types. Furthermore, heat maps guided selection of plots with low correlation
107 between climatic and landscape-scale land-use variables (Redlich et al. 2021). Plots consisted of 30 m x 3
108 m strips located on open herbaceous vegetation, such as forest glades and clearings, grazed, mown and
109 mulched grasslands, field margins and grasslands in proximity to crop fields, and parks and meadows within
110 settlement areas.

111 Herbivory assessment

112 Herbivory was measured in the plots once in the period from end-May until mid-June 2019 (spring season).
113 We assessed mean leaf-area loss by chewing invertebrates for three herbaceous plant functional groups:
114 legumes, non-leguminous forbs (following ‘forbs’) and grasses. Legumes contained representatives of the
115 plant family Fabaceae only. Forbs encompassed species of various herbaceous angiosperm families except
116 for the plant family Fabaceae and for plant families within the order Poales. Grasses included graminoids
117 of the plant family Poaceae and occasionally species of the Cyperaceae family. These three plant functional
118 groups are commonly distinguished due to their differences in several traits and their effect on ecosystem

119 processes (Roscher et al. 2004), sometimes additional groups are distinguished e.g. small and tall forbs
120 (Scherber et al. 2006, Fischer et al. 2019) or C₃ and C₄ grasses (Siemann et al 1998).

121 Per plant functional group, three plant individuals of three plant species were randomly selected for the
122 collection of three leaves (total of 27 plant individuals and 81 leaves per plot). Plant species assessed for
123 herbivory differed among plots, since not even a single plant species occurred across all plots (**Table S1**),
124 but represent herbivory of the local herbaceous vegetation. Leaves from the apical, middle and basal nodes
125 of each plant were pinched off, mounted in a notebook with transparent tape, pressed and dried for later
126 assessment. Both leaf position as selection criterion and digital assessment in the lab were chosen to
127 minimize observer bias and also to include leaves of different ontogenetic stages that may be
128 disproportionately affected by herbivory (Sand-Jensen et al. 1994). Mean leaf-area loss was determined
129 using the BioLeaf app (Machado et al. 2016), which automatically transforms colour images to binary
130 images (only black and white pixels) and calculates proportional mean leaf-area loss based on white parts
131 enclosed by black leaf area. Therefore, some prior image adjustments were needed: i) Nibbled leaf margins
132 were straightened or adjusted to restore the pre-damage leaf contour with a thin black line in order to capture
133 nibbled leaf margins as missing leaf area; and ii) overlapping leaf parts were separated with a thin white
134 line connecting the white space to the surroundings of the leaf to not falsely be assigned as missing leaf
135 area by the Bioleaf app. Images were adjusted using GIMP software (The GIMP Development Team 2017).

136 Measures of plant richness

137 Vegetation surveys were conducted between May and July 2019 (seven subplots on each plot, adding up to
138 10 m² total sampling area per site). Recorded plant species and families were summed up per plot to achieve
139 plant richness at species and family level. Ferns, horsetails and woody plants as part of the herb layer were
140 considered for total plant richness measures but not for herbivory assessment. A list of plant species and
141 families present on plots can be found in the supplement (**Table S1**).

142 Measures of local and landscape-scale land use

143 Local habitat-specific similarities among plots were captured by habitat type (forest, grassland, arable field
144 and settlement).

145 At landscape-scale, we calculated landscape diversity as Shannon Index from detailed land-cover maps
146 distinguishing six land-use categories: natural/semi-natural, forest, grassland, arable field, settlement and
147 water (combination of ATKIS 2019, CORINE 2018 and IACS 2019; for details see **Fig. S1**). Since different
148 insect species can be affected by landscape-scale land use at various spatial scales (Thies et al. 2003;
149 Chaplin-Kramer et al. 2011), we included landscape diversity at multiple scales (0.2 km, 0.5–3.0 km in 0.5-
150 km steps; seven spatial scales) around the centre point of the plots.

151 Measure of climate (temperature)

152 We retrieved 30-year multi-annual mean temperatures per plot based on gridded monthly averaged mean
153 daily air temperatures with a horizontal resolution of 1 km from 1981–2010 (Deutscher Wetterdienst 2020).
154 This climate variable was chosen to study climate and land-use effects in a space-for-time framework (Blois
155 et al. 2013, Redlich et al. 2021).

156 Data analysis

157 Proportional mean leaf-area loss data were averaged per plant individual, plant species and plant functional
158 group for each plot to equally account for individuals and species despite missing leaves and plant
159 individuals (e.g. nine leaves available of one plant species but only seven leaves of another). This approach
160 was favoured over a multiple-nested random term accounting for nested sampling structure (plant functional
161 group, species, individual, leaf position) to avoid model fitting issues in the presence of missing values.
162 Missing leaves occurred due to processing damage (e.g. dry leaf clung to opposite page and broke in
163 multiple pieces) or unidentifiable third leaves belonging to the same plant individual (e.g. bottom grass leaf
164 in dense vegetation). Missing plant species or individuals occurred when too few species or individuals
165 were available in a plot or, exceptionally, also due to processing damage. To minimize bias through single
166 herbivory events and to assure sampling of at least two different plant species per plant functional group,

167 we excluded data from all plots of which we obtained proportional mean leaf-area loss data of <10 leaves
168 of each plant functional group prior to herbivory analysis. Taking also seven plots into account where no
169 herbivory sampling could be realized due to time constraints, this yielded 81 plots in 40 regions.

170 Herbivory data were analysed with beta regression to cope with continuous proportional data
171 (Yellareddygaru et al. 2016; Douma and Weedon 2019). In preparation of beta regression, zeros were
172 replaced through a small value (0.00001; slightly lower than the smallest value) to allow for model
173 comparison with Akaike's information criterion (AIC), which is inappropriate for scaled data (Douma and
174 Weedon 2019). Proportional mean leaf-area loss data on legumes and forbs contained only a single zero
175 and data on grasses two zeros (2.5%).

176 As candidate predictors, we included plant functional group, multi-annual mean temperature as climatic
177 variable, land use at local (habitat type) and landscape-scale (landscape diversity; seven spatial scales in
178 separate models), and local plant richness (species and family level). Predictor values were z-transformed
179 prior to analysis, while the selected best models are presented with untransformed predictor variables. Ten
180 separate models were created, each of them containing plant functional group, multi-annual mean
181 temperature, one of the four land-use and plant-richness variables (at different spatial scales, if applicable)
182 and all interactions up to the three-way interaction term. Separate models were preferred over one model
183 containing all land-use and plant-richness variables to avoid over-parameterization.

184 The model including the three-way interaction of plant functional group, multi-annual mean temperature
185 and habitat type indicated a trend in grassland, which was further explored using a data subset of grassland
186 plots. An additional model containing multi-annual mean temperature, habitat type and their interaction
187 term was fitted to the subset with the rest of the analysis approach being equal to that of the other models.

188 A nested random term for 'plot' in 'region' (three plots per region) was included to account for plant
189 functional groups on the same plots and clustering of plots, which were located in closer vicinity than other

190 plots due to the nestedness of the study design (Redlich et al. 2021). This nested random term was retained
191 throughout the model selection process (Bolker et al. 2008).

192 The majority of maximum variance inflation factors were <4 , which falls below the commonly applied
193 threshold for collinearity of variance inflation factor >10 (Chatterjee and Price 1991). The few cases in
194 which the variance inflation factor exceeded the threshold were in models containing interaction terms with
195 habitat type. Additionally, a correlation matrix of continuous predictor variables was calculated (**Table S2**)
196 and continuous predictors were plotted by habitat type (**Fig. S2**) to visually assess relationships between
197 continuous and categorical predictor variables. Continuous predictors were not or only weakly correlated
198 except for a strong positive correlation between plant richness at species and family level (Pearson's $r =$
199 0.76 , $P < 0.001$, **Table S2**) and both plant richness measures were highest in forest habitats (**Fig. S2**).

200 Models with all possible predictor combinations were compared by the goodness of fit based on Akaike's
201 information criterion corrected for small sample size (AICc). The lower AICc, the better the relative
202 goodness of model fit. Competing multivariate models with a difference of less than two ($\Delta\text{AICc} < 2$) were
203 considered equal (Burnham and Anderson 2002), and then the more parsimonious model was chosen.
204 Model selection of fixed effects (predictors) was done with models fitted by maximum likelihood, while
205 the selected best model was fitted and is presented by restricted maximum likelihood (Zuur et al. 2009).
206 Tukey posthoc analysis was used to compare herbivory between levels of categorical variables (i.e. plant
207 functional groups, habitat types) and to correct for multiple comparisons.

208 Data analysis was done with R version 4.0.3 (R Core Team 2020) using the packages 'glmmTMB' (Brooks
209 et al. 2017), 'emmeans' (Russell 2020), 'Hmisc' (Harrell 2020), 'MuMin' (Barton 2020), 'ggeffects'
210 (Lüdecke 2018), 'DHARMA' (Hartig 2020), and 'performance' (Lüdecke et al. 2020).

211

212 **Results**

213 Effects of plant functional group, land-use and plant-richness on herbivory

214 We observed an overall proportional leaf-area loss due to invertebrate chewing across plant functional
215 groups of $1.35 \pm 0.10\%$ (mean \pm se). Foliar herbivory on legumes was on average 2.3 times higher than on
216 forbs and 5.4 times higher than on grasses (**Fig. 1a**). Besides, plant functional group and habitat type
217 interactively affected herbivory (**Fig. 1b**). Herbivory on legumes was higher than herbivory on forbs except
218 in forests, where herbivory on legumes and forbs was similar. In forests, herbivory on legumes was also
219 lower than in grassland, and intermediate in settlements and agricultural fields. Herbivory on forbs and
220 grasses was similar across all habitat types.

221 Invertebrate herbivory did not depend on plant richness at species level (**Fig. 2a**). However, with increasing
222 total numbers of plant families, herbivory on legumes decreased while herbivory on forbs and grasses
223 increased (**Fig. 2b**). At the landscape-scale, invertebrate herbivory was similar across the covered landscape-
224 diversity gradient (**Fig. 2; Table S3**).

225 Interactive effects of plant functional group, climate and land-use (or plant richness) predictors on herbivory

226 Mean-annual temperature did not substantially affect overall herbivory and three-way interactions of plant
227 functional group, climate and single land-use or plant richness predictors were not supported by Δ AICc and
228 parsimony (**Fig. 3, Table S3**). Yet in grasslands, herbivory on legumes, forbs and grasses decreased,
229 increased and slightly increased with higher multi-annual mean temperature, respectively (**Fig. 3**, dashed
230 line: grassland subset, **Table S4**).

231

232 **Discussion**

233 In this study, we compared herbivory among three major plant functional groups in a wide range of typical
234 habitat types in temperate regions across large climatic gradients, and also taking into account land use at
235 local and landscape scale, and local plant richness. Herbivory differed between plant functional groups and
236 local habitat types as well as with plant richness at family level, but showed no significant response to plant
237 richness at species level, landscape diversity and multi-annual mean temperature at the studied gradients,
238 except for differential temperature effects among plant functional groups in grasslands (significant effect
239 in grassland subset).

240 *How do land use and plant richness affect invertebrate herbivory on plant functional groups?*

241 Although herbivory assessment was conducted on open herbaceous vegetation, the surrounding local
242 habitat types included in this study differ in multiple aspects that may impact invertebrate herbivores.
243 Among habitat types, we did not observe differences in herbivory on forbs and grasses but herbivory on
244 legumes was lower in forests than in grasslands and intermediate in settlements and arable fields. Higher
245 impact of herbivores on herbs in grasslands than forests – not differentiating plant functional groups – was
246 also reported by Maron et al (2006). Our results, however, suggest that herbivory on legumes is more
247 sensitive to local land use (habitat type) than that on forbs and grasses, which emphasises the importance
248 of distinguishing between plant functional groups. One explanation could be that legumes are more prone
249 to specialist herbivory and that herbivore communities on herbaceous-vegetation patches in forests may
250 more frequently lack these herbivore species, since forests may constitute barriers to dispersal (Schmitt et
251 al. 2000) and since small, isolated patches face higher species extinction risk at simultaneously reduced
252 recolonization rate (Rösch et al. 2013). In analogy, highest herbivory intensities on legumes in grasslands
253 may result from larger habitat patches and fewer dispersal barriers. An even simpler explanation of the
254 observed herbivory pattern on legumes provides the ‘habitat amount hypothesis’ put forth by Fahrig (2013).
255 This hypothesis stresses the importance of the total amount of habitat area for species richness (across a
256 broad taxonomic range, including insects). Thus, more herbaceous vegetation in grasslands than forests

257 may have led to higher species richness of herbivores foraging on herbaceous plants and indirectly to higher
258 herbivory rates on legumes, under the assumption that higher herbivore species richness increases the
259 likelihood that herbivore species specialized on legumes are present.

260 While herbivory on legumes differed among habitat types, we observed similar herbivory among habitat
261 types on grasses and forbs. Herbivory on grasses was commonly low, thus when small habitat-type effects
262 occurred, they may have been rendered invisible. Forbs encompass species of several plant families, which
263 increases the likelihood that some of the forb plant families perceive herbivore damage. This suggests to
264 differentiate between more groups of forbs, e.g. distinguishing herbivory on plant-family level for forbs or
265 distinguishing small and tall forbs (see also Roscher et al. 2004). Alternatively, forbs and grasses may be
266 prone to more generalist herbivores, which have the potential to maintain herbivory even at low (generalist
267 herbivore) species number (Rossetti et al. 2017). Further research should elaborate on linking functional
268 invertebrate community compositions, e.g. degree of herbivore generality (Shinohara and Yoshida 2021),
269 to herbivory on plant functional groups (differentiating several groups of forbs) in different habitat types
270 for a deeper understanding of herbivory.

271 Plant richness at family level – but not at species level – decreased herbivory on legumes and increased
272 herbivory on non-leguminous forbs and (slightly on) grasses. Since herbivores are often specialized on
273 feeding within plant families (Bernays and Graham 1988; Haddad et al. 2001), resource concentration and
274 dilution effects are likely stronger at family level. Nonetheless, small effects of plant richness at family
275 level on herbivory on grasses may result from generally very low herbivory intensity on grasses. In the
276 presence of more plant families, lower herbivory rates on legumes may be explained by the reduced
277 likelihood of specialist herbivores to find their host plant (Root 1973, ‘resource concentration hypothesis’).
278 The increased herbivory on forbs (most species- and family-rich functional group) may result from an
279 increased likelihood of palatable plant families being among the forb species present. Family-level plant
280 richness differentially affecting herbivory among plant functional groups, and plant richness effects at
281 family level (higher taxonomic level) may explain contrasting plant species richness effects on herbivory

282 reported in literature (Jactel and Brockerhoff 2007; Dinnage 2013; Ebeling et al. 2014; Loranger et al.
283 2014).

284 Landscape diversity may elicit contrasting effects on invertebrate species – both herbivores and natural
285 enemies – depending on their needs or ability to exploit resources from multiple habitats (Jonsen and Fahrig
286 1997; Martin et al. 2013). However, our results indicate that herbivory at the level of plant functional groups
287 seems to be largely independent of landscape diversity at various spatial scales. Since a small number of
288 common generalist herbivore species have the potential to maintain herbivory (Rossetti et al. 2017), both
289 herbivore and natural-enemy community composition may have changed without immediate changes
290 visible in herbivory. Nevertheless, diverse landscapes may favour resilience of herbivory and predation
291 (Oliver et al. 2015).

292 *Do climate and land use jointly affect invertebrate herbivory among plant functional groups?*

293 Although warmer climates are expected to increase herbivory pressure (Rasmann and Pellissier 2015), we
294 did not observe a general increase of herbivory in response to higher multi-annual mean temperature
295 covered by our study design. In grassland habitats, however, herbivory on legumes decreased towards
296 warmer climates, while herbivory increased on forbs and (slightly on) grasses. Differential climate effects
297 occurring only in grasslands may result from microclimatic buffering effects in forests (De Frenne et al.
298 2019) and potentially overriding effects of anthropogenic disturbance (Danneyrolles et al. 2019) – in arable
299 and settlement habitats. The observed pattern in grasslands may have multiple causes: i) Legume-specialist
300 herbivores might be more sensitive to higher temperatures than generalists or specialists of the other plant
301 functional groups. ii) Metabolic needs of ectotherms may increase more quickly than feeding rate with
302 increasing temperature (Lee et al. 2015; Malzahn et al. 2016; Zhang et al. 2020) and thus generalist
303 invertebrate herbivores may shift from legumes to non-legumes to meet higher energy (less nitrogen)
304 demands. iii) Chemistry and efficacy of plant defences are subject to temperature effects (Lemoine et al.
305 2013; Havko et al. 2020), thus – potentially – plant defence efficacy may be higher or adapt more quickly
306 in legumes than forbs and grasses at higher temperature. More research will be needed to provide further

307 evidence on differential rates of herbivory among plant functional groups towards higher temperature and
308 to identify the major drivers.

309 *Conclusion*

310 We conclude that multi-annual mean temperature, plant richness at family level and land-use at local scale
311 (habitat type) – but not at landscape scale (landscape diversity) – assert differential effects on herbivory
312 among plant functional groups, with legume herbivory in grasslands being most affected. Herbivory on
313 legumes was higher in grassland than forest habitats, decreased with temperature in grasslands, and
314 decreased with family-level plant richness. Further research is needed to identify the drivers behind these
315 observations, whereby functional herbivore community composition – along with plant functional groups
316 – may provide valuable insights. Our study emphasises the importance of functional groups (of both plants
317 and herbivores) for understanding the response of community-level herbivory and ecosystem functioning.

318

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328

329 **Declarations**

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333 Ethics approval: Not applicable

334 Consent to participate: Not applicable

335 Consent for publication: Not applicable

336 Availability of data and material: We intend that data will be available from the Dryad Digital Repository.

337 Code availability: R Code is available from the corresponding author upon reasonable request.

338

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483 **Electronic supplementary material**

484 Additional supporting information may be found in the online version of this article:

485 **Fig. S1 (+Text)** Creation of detailed land-cover maps based on six main land-use types within Bavaria (semi-natural
486 habitat, forest, grassland, arable, urban, water). The map was created by combining three different land-cover maps
487 (ATKIS 2019, IACS 2019, CORINE 2018).

488 **Fig. S2** Visual evaluation of relationships between the categorical predictor variable (habitat type) and the continuous
489 predictor variables (a) multi-annual mean temperature, (b) species-level plant richness (= total plant species richness)
490 and (c) family-level plant richness (= total plant familial richness) used for herbivory analysis.

491 **Table S1** List of recorded plant species in vegetation survey and number of plots on which they occurred. Plant species
492 list was used to derive plant richness measures (species and family level). Even though ferns, horsetails and woody
493 plants as part of the herb layer are listed, these were not considered for herbivory assessment. No plant species
494 occurred on all plots (= 179 plots).

495 **Table S2** Pearson correlation coefficients for all continuous variables included in model selection processes on
496 herbivory data (81 plots). Significant correlations based on $\alpha = 0.05$ are indicated as following: $P < 0.05^*$, $P < 0.01^{**}$,
497 $P < 0.001^{***}$

498 **Table S3** Null, “full” and best beta mixed models on mean leaf area loss per plant functional group and plot. “Full”
499 models include different sets of fixed effects but always include plant functional group, one climatic environmental
500 variable, one land-use or plant-richness variable and their interaction terms. Fixed effects encompass: Plant functional
501 group (Plant guild), multi-annual mean temperature (MAT), habitat type (habitat), species-level plant richness
502 (specnum), family-level plant richness (famnum) and landscape diversity (LD) at multiple spatial scales. Continuous
503 predictor variables were z-transformed (s-Fixed effect) prior to modelling. To account for study design, plot nested in
504 region was added as random term. Asterisks (*) between fixed effects indicate that both, all main effects and all
505 interaction terms were included. Bold font indicates the best model based on relative goodness of model fit (lowest
506 AICc).

507 **Table S4** Selection process of beta mixed models on mean leaf area loss per plant functional group and plot on data
508 from grassland habitats only. Fixed effects encompass plant functional group (Plant guild) and z-transformed multi-
509 annual mean temperature (sMAT). To account for study design, plot nested in region was added as random term.
510 Asterisks (*) between fixed effects indicate that both, main effects and all interaction terms were included. Relative

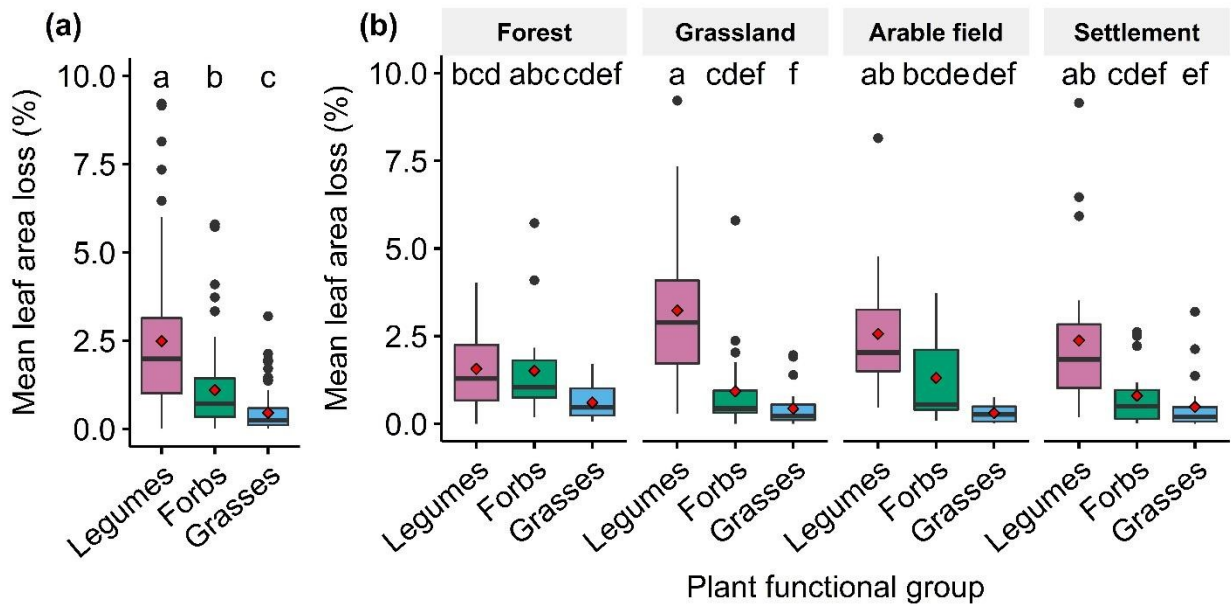
- 511 goodness of model fit is indicated by Akaike's information criterion corrected for small sample size (AICc). Bold font
- 512 highlights the best model based on $\Delta AICc < 2$.

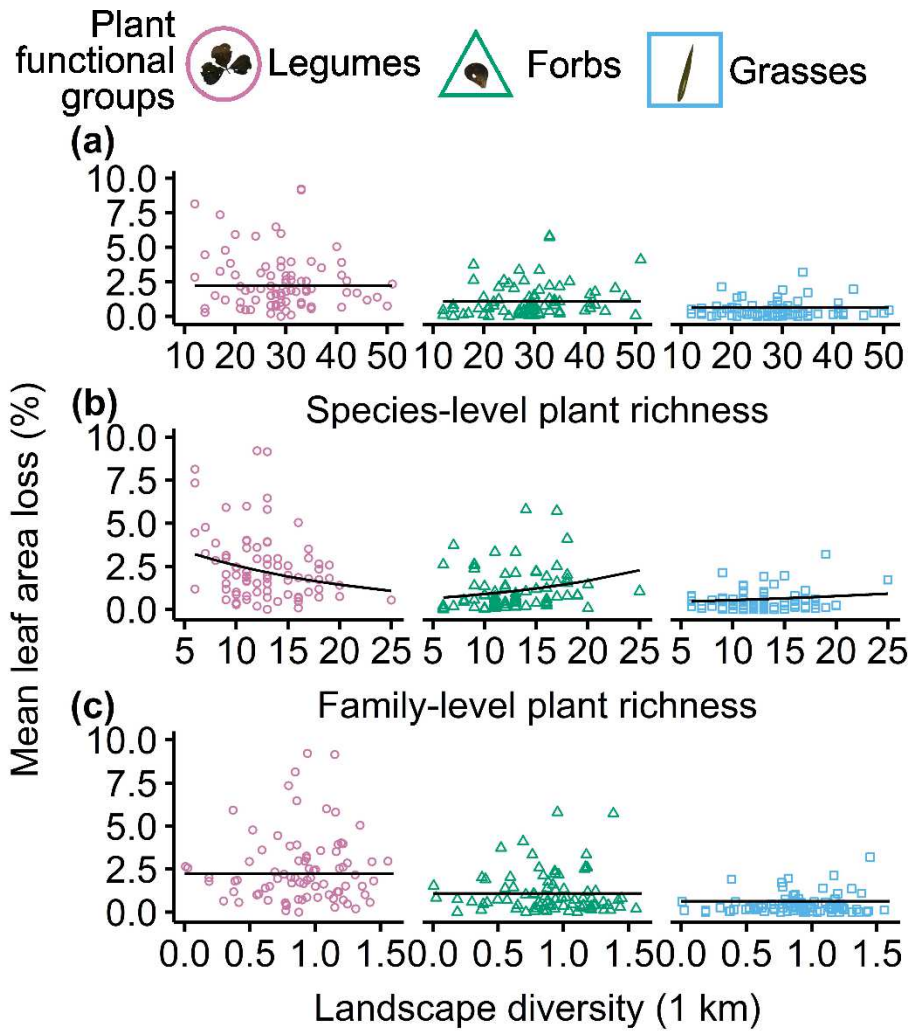
513 **Fig. 1** Mean leaf-area loss per plot (a) for each plant functional group and (b) habitat type and plant functional group.
514 Red diamonds highlight mean values. Lower case letters indicate differences between groups (plant functional groups
515 and habitat types) evaluated by post hoc tests with Tukey correction after evaluation of the overall effects in beta
516 regression models by $\Delta AICc$ and parsimony.

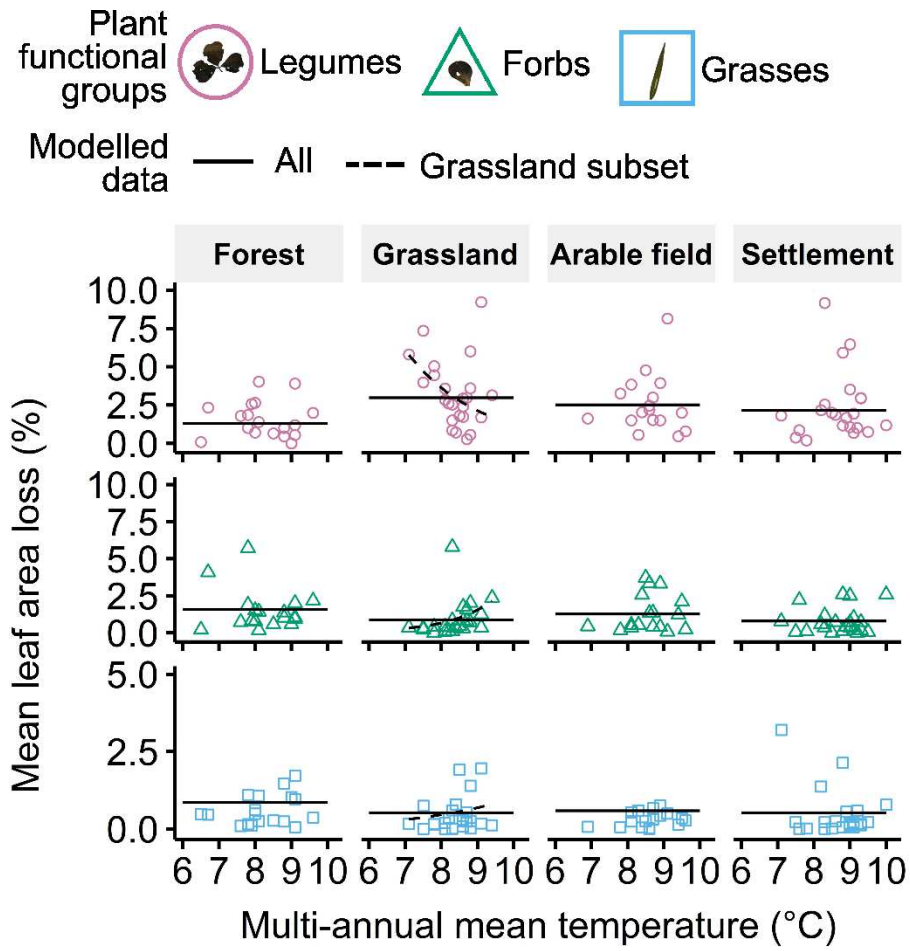
517 **Fig. 2** Mean leaf-area loss to invertebrate herbivory per plot and plant functional group (legumes: pink circles, non-
518 leguminous forbs: green triangles: grasses: blue squares) is presented across plant richness at (a) species level and
519 (b) family level, and (c) landscape diversity at 1-km spatial scale. Solid lines present predictions of best beta mixed
520 models. Model selection was based on $\Delta AICc$ and parsimony.

521 **Fig. 3** Mean leaf-area loss per plot and plant functional group (legumes: pink circles, non-leguminous forbs: green
522 triangles: grasses: blue squares) is presented per habitat type across the multi-annual mean temperature gradient.
523 Solid lines indicate predictions of the best beta mixed model based on the complete data set. Dashed lines show
524 predictions based on the grassland subset. Model selection was done using $\Delta AICc$ and parsimony.

525







Figures

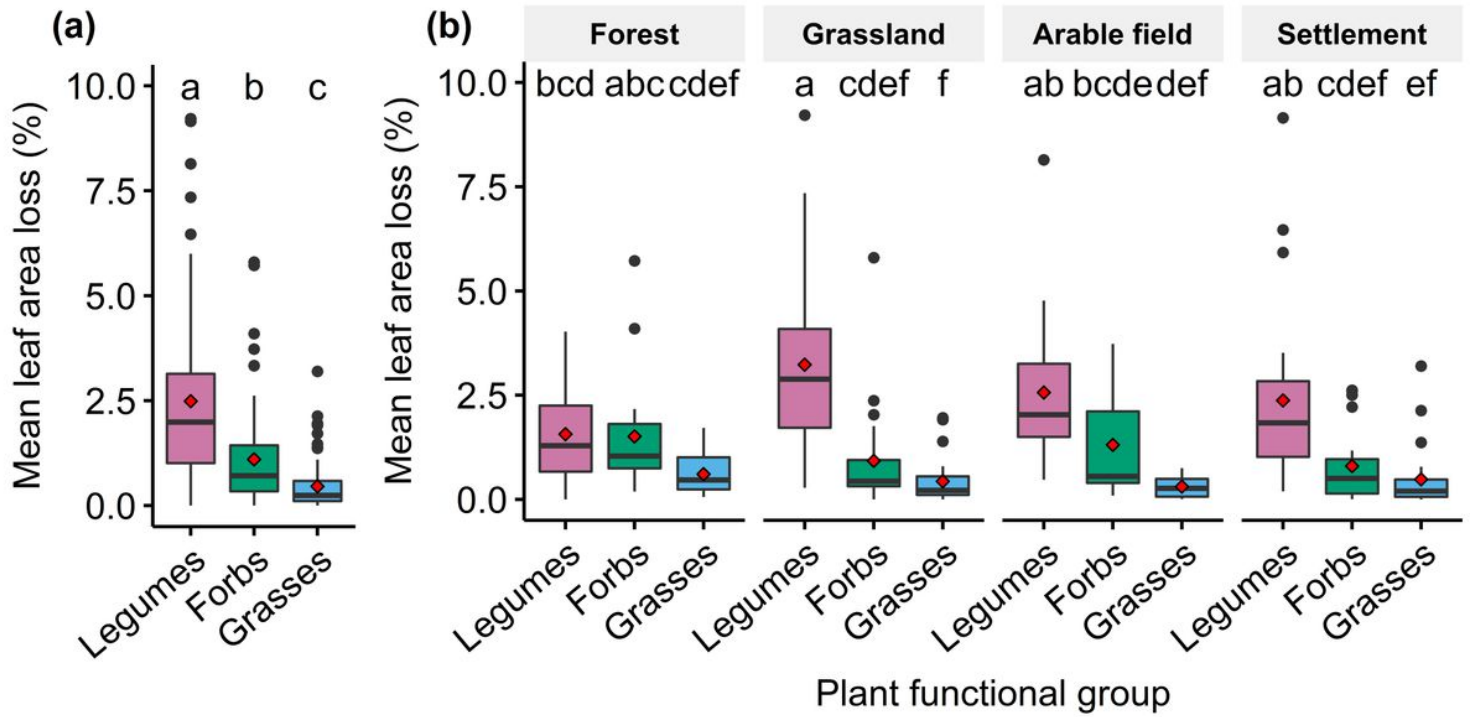


Figure 1

Mean leaf-area loss per plot (a) for each plant functional group and (b) habitat type and plant functional group. Red diamonds highlight mean values. Lower case letters indicate differences between groups (plant functional groups and habitat types) evaluated by post hoc tests with Tukey correction after evaluation of the overall effects in beta regression models by $\Delta AICc$ and parsimony.

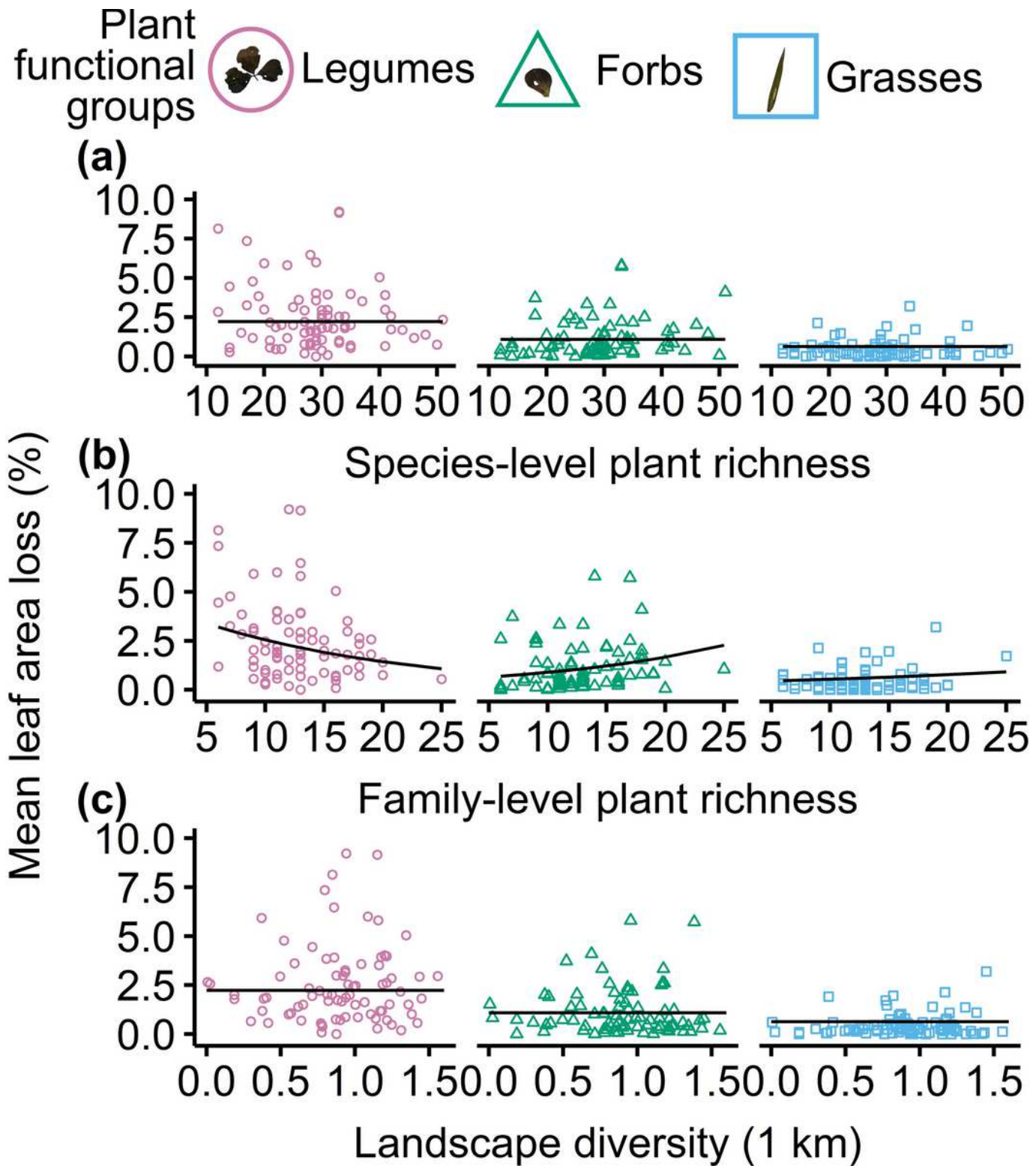


Figure 2

Mean leaf-area loss to invertebrate herbivory per plot and plant functional group (legumes: pink circles, non leguminous forbs: green triangles: grasses: blue squares) is presented across plant richness at (a) species level and (b) family level, and (c) landscape diversity at 1-km spatial scale. Solid lines present predictions of best beta mixed models. Model selection was based on $\Delta AICc$ and parsimony.

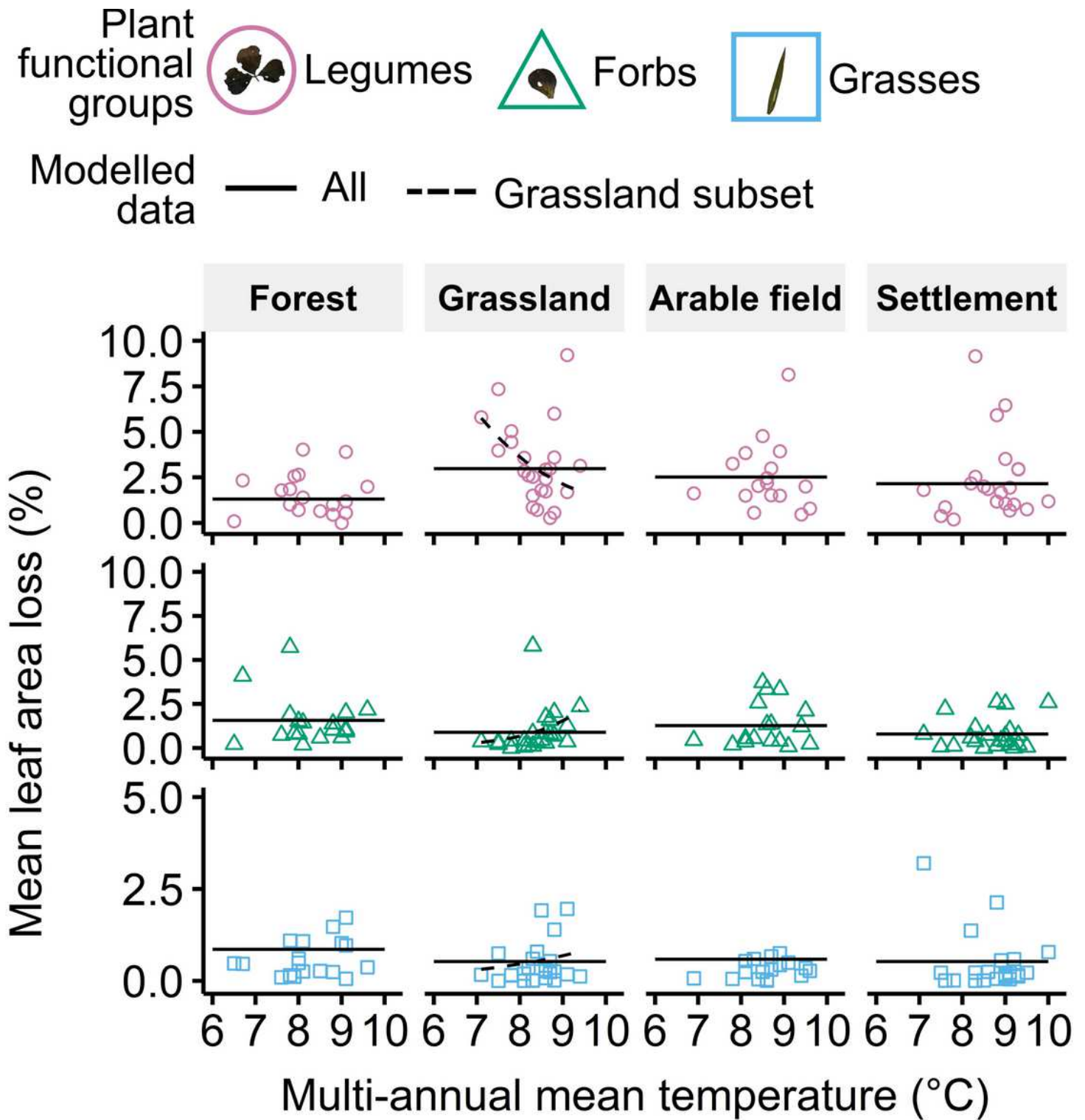


Figure 3

Mean leaf-area loss per plot and plant functional group (legumes: pink circles, non-leguminous forbs: green triangles: grasses: blue squares) is presented per habitat type across the multi-annual mean temperature gradient. Solid lines indicate predictions of the best beta mixed model based on the complete data set. Dashed lines show predictions based on the grassland subset. Model selection was done using $\Delta AICc$ and parsimony.

Supplementary Files

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