

1 **Title**

2 Landscape diversity and local temperature, but not climate, affect arthropod predation among habitat types

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## 19 **Abstract**

20 Arthropod predators are important for ecosystem functioning by providing top-down regulation of insect  
21 herbivores. As predator communities and activity are influenced by biotic and abiotic factors on different  
22 spatial scales, the strength of top-down regulation ('arthropod predation') is also likely to vary.  
23 Understanding the combined effects of potential drivers on arthropod predation is urgently needed with  
24 regard to anthropogenic climate and land-use change. In a large-scale study, we recorded arthropod  
25 predation rates using artificial caterpillars on 113 plots of open herbaceous vegetation embedded in  
26 contrasting habitat types (forest, grassland, arable field, settlement) along climate and land-use gradients in  
27 Bavaria, Germany. As potential drivers we included habitat characteristics (habitat type, plant species  
28 richness, local mean temperature and mean relative humidity during artificial caterpillar exposure),  
29 landscape diversity (0.5–3.0-km, six scales), climate (multi-annual mean temperature, 'MAT') and  
30 interactive effects of habitat type with other drivers. We observed no substantial differences in arthropod  
31 predation rates between the studied habitat types, related to plant species richness and across the Bavarian-  
32 wide climatic gradient, but predation was limited when local mean temperatures were low and tended to  
33 decrease towards higher relative humidity. Arthropod predation rates increased towards more diverse  
34 landscapes at a 2-km scale. Interactive effects of habitat type with local weather conditions, plant species  
35 richness, landscape diversity and MAT were not observed. We conclude that landscape diversity favours  
36 high arthropod predation rates in open herbaceous vegetation independent of the dominant habitat in the  
37 vicinity. This finding may be harnessed to improve top-down control of herbivores, e.g. agricultural pests,  
38 but further research is needed for more specific recommendations on landscape management. The absence  
39 of MAT effects suggests that high predation rates may occur independent of moderate increases of MAT  
40 in the near future.

## 41 **Introduction**

42 Predation and parasitism are frequent causes of mortality to many herbivorous insect species (1) and hence  
43 can exert strong impact on herbivore communities (2,3). Through their impact on herbivores, natural  
44 enemies can also indirectly affect plant damage, vegetation structure and composition, and nutrient cycling  
45 (2–4). This renders natural enemies and their biotic interactions essential to ecosystem functioning.  
46 Important natural enemies for the regulation of herbivorous insects are arthropod predators (5). Predation  
47 intensity can differ between habitat types (6,7), albeit direct comparisons among typical habitat types in  
48 temperate regions (forest, grassland, arable fields and settlements) are lacking. Besides, arthropod activity  
49 is influenced by local weather conditions (8), while plant species richness (9), climate (10) and regional  
50 land use (11) affect arthropod communities, with potential consequences for top-down suppression of  
51 herbivores (12,13). However, the combined effects of these drivers on arthropod predation in different  
52 habitats are largely unknown, albeit urgently needed with regard to anthropogenic climate and land-use  
53 change.

54 Local habitat characteristics such as habitat type, plant species richness and weather conditions affect  
55 predator richness, activity or both with possible implications on predation rates. With respect to habitat  
56 type, Ferrante et al. (7) observed higher predation rates in forests than in maize fields. This may be related  
57 to on average higher natural enemy richness in natural than agricultural ecosystems (14), which possibly  
58 translates into higher and lower predation rates, respectively (12). Plant species richness was described both  
59 to benefit natural enemies (15) and predation rates (16), which could result from correlation of the latter  
60 (12,14). Besides, higher plant species richness can also lead to higher structural complexity of the  
61 vegetation (9), which may alter predator behaviour with positive effects on predation rates, e.g. reduced  
62 intraguild predation (17). However, knowledge of plant richness effects on natural enemies and their  
63 services originate almost exclusively from plant diversity experiments (e.g. 9,15,16), while complementing  
64 field studies are lacking. Similar applies to weather conditions. Temperature and humidity modify arthropod  
65 activity in terms of catchability by traps (8), but little is known about their effects on predation rates. For

66 instance, activity of predatory carabid beetles increases with temperature (8,18), and, depending on species  
67 traits, decreases towards higher relative humidity (8), while too low temperatures can restrict carabid  
68 activity (19). Thus, the richness and activity of predators are affected through habitat characteristics, yet  
69 the consequences for predation rates are much less clear.

70 At a regional scale, landscape complexity and climatic factors impact predators. In complex landscapes,  
71 both species richness and abundance of generalist enemies are higher, and top-down control of herbivorous  
72 arthropods is commonly increased (11,20,21). Considering landscape diversity as an aspect of landscape  
73 complexity (20), diverse landscapes can provide complementary or supplementary resources to organisms  
74 moving between habitat patches with beneficial effects on their population size (22). Thus, predation rates  
75 may increase towards more diverse landscapes. In addition, climate change, and in particular a warmer  
76 climate, is expected to affect arthropods in many aspects, for instance, in their geographic distribution and  
77 life history traits (10,23). Consequently, this may impact predation rates. Indeed, the efficacy of predators  
78 to suppress herbivores can increase with mean annual temperatures (24) as well as predation rates increase  
79 towards lower altitudes and latitudes (25). Thus, both diverse landscapes and warm climates may favour  
80 higher predation rates.

81 Here we use arthropod attack marks on artificial caterpillars to study the combined effects of local habitat  
82 type, plant species richness, weather, landscape diversity and multi-annual mean temperature on arthropod  
83 predation, and ask whether effects differ among habitat types. This study advances the understanding of  
84 top-down regulation of herbivores and natural pest control services in the context of climate and land use.

## 85 **Material and Methods**

### 86 **Study area and plot selection**

87 This study was conducted within the LandKlif project in Bavaria, Germany, which used a novel multi-scale  
88 study design to disentangle the combined effects of climate and land use on biodiversity and ecosystem  
89 functions (26), here on arthropod predation rates. From grid cells (5.8 km x 5.8 km) covering Bavaria  
90 (Germany), 60 grid cells were selected encompassing four replicates of 15 combinations of climate zones  
91 (multi-annual mean temperature) and landscape-scale land-use types (near-natural, agriculture and urban).  
92 In each selected grid cell ('region'), plots were established in three different habitat types (out of four  
93 possible: forest, grassland, arable field or settlement) typical for the respective region. Plots were installed  
94 as 30 m x 3 m experimental strips on open herbaceous vegetation with at least 50 m distance to larger roads  
95 and other habitat types. Research on predation rates was realised on 147 out of 179 LandKlif plots, yet  
96 complete data sets were acquired for 113 plots (data exclusion criteria, see below).

### 97 **Predation rate assessment**

98 Arthropod predation rates were assessed using standardised green artificial caterpillars (diameter 3 mm;  
99 length 20 mm) made from plasticine (Weible Fantasia KNET grün, Weible GmbH & Co. KG, Germany),  
100 as suggested for rapid ecosystem function assessment with large geographic extent (27). Brown pieces of  
101 paper (size 40 x 19 mm; 100 g m<sup>-2</sup>, hazelnut brown, paper type "Paperado", Rössler Papier GmbH & Co.  
102 KG, Germany) served as carrier onto which the artificial caterpillars were glued (UHU Alleskleber extra  
103 tropffrei gel, UHU GmbH & Co. KG, Germany); 20 artificial caterpillars were placed on every plot at  
104 ground level below vegetation but above litter to standardize position. The artificial caterpillars were spread  
105 across the 30 m x 3 m experimental strip with at least 1-m spacing between two caterpillars and other  
106 experimental items (e.g. Malaise trap). Bamboo sticks with a red tip were punched through a hole in the  
107 paper carrier to fix and mark the position of each artificial caterpillar. The collection of the caterpillars  
108 started after 48 ± 6 hours (range: 42–54 hours). The presence or absence of arthropod attack marks was  
109 assessed in the field using reference images provided by Low et al. (28). Arthropod attack marks were not

110 further differentiated into finer taxonomic level as this is error prone and hence not recommended (28). We  
111 calculated predation rates per plot as the proportion of artificial caterpillars with arthropod attack marks  
112 after 2-d exposure relative to the total number of caterpillars per site. We call the obtained measure  
113 ‘predation rate’, as ground-active arthropods, particularly carabids (Coleoptera: Carabidae), are among the  
114 most frequent attackers of artificial caterpillars at ground-level and as attack marks of parasitoids are rare  
115 (16, Personal observation UF). Arthropod predation rates were assessed in May (starting dates between 10<sup>th</sup>  
116 and 25<sup>th</sup> May 2019).

## 117 **Measures of habitat characteristics**

118 Plots were established in different local habitat types (forest, grassland, arable field and settlement).  
119 Through establishing plots in forest glades, extensive grasslands, crop field margins and green areas in  
120 settlements within the different local habitat types, exposure of artificial caterpillars was standardized to  
121 open herbaceous vegetation.

122 Plant species richness per plot was derived between May and July 2019 from plant species records in seven  
123 subplots (10 m<sup>2</sup> total sampling area). Further details and a species list are provided in Fricke et al. (29).

124 Local weather conditions during caterpillar exposure were derived from thermologgers (ibutton, type  
125 DS1923). Those were attached north-facing to a wooden pole, at 1.1 m above ground and roughly 0.15 m  
126 below a wooden roof, which prevented direct solar radiation. One thermologger was established per plot.  
127 We extracted mean temperature and mean relative humidity (in the following referred to as ‘local mean  
128 temperature’ and ‘mean relative humidity’) during the study-site specific exposure period of the artificial  
129 caterpillars from hourly measurements of the thermologgers.

## 130 **Measures of regional land use and climate**

131 Landscape diversity was calculated as Shannon Index from detailed land-cover maps (combination of  
132 ATKIS 2019, CORINE 2018 and IACS 2019, see (29)) based on six main land-cover types (semi-natural

133 habitat, forest, grassland, arable, urban, water). Thus, high landscape diversity indicates more different  
134 land-cover classes, more similar proportions of them or both. Landscape diversity was calculated in radii  
135 around the centre point of the plots at six spatial scales (0.5–3.0 km, in 500-m steps). At 2-km scale, low  
136 landscape diversity equated a dominance of forest or arable land, and the land-cover proportions of semi-  
137 natural habitat and water were below 7.5% and 10.2%, respectively.

138 We retrieved 30-year multi-annual mean temperatures (1981–2010, MAT) per plot based on gridded (1-km  
139 resolution) monthly averaged mean daily air temperatures (30).

## 140 **Data analysis**

141 Prior to data analysis, data exclusion criteria were applied to standardize data. We excluded artificial  
142 caterpillars exposed to attack for more than 54 hours (exceeding  $48 \pm 6$  h limit), ‘released’ later than 25<sup>th</sup>  
143 May, and recovered incomplete with a loss of more than 20% (<16 artificial caterpillars per plot). In total,  
144 we achieved standardized data on 113 plots. Artificial caterpillars from 58 of these plots (51%) were  
145 transported to the lab to double-check the assessments done in the field. Field and lab assessments of  
146 arthropod predation rates were positively correlated (Pearson’s  $r = 0.79$ ; S1 Fig). In the following, arthropod  
147 predation rates refer to the field observations (113 plots).

148 Arthropod predation rate data were analysed with binomial generalized mixed effect models to cope with  
149 proportional data (derived from absence-presence data) using the R-package ‘glmmTMB’ (31) with R  
150 version 4.0.3 (32). Region was included as a random term to account for the nested study design and was  
151 retrieved throughout the model selection process (33). Due to zero-inflation (complete absence of attack  
152 from 17% of plots), confirmed using the R-package ‘DHARMA’ (34), we added a zero-inflation term. We  
153 did not account for exposure duration of the artificial caterpillars in the models, since data were standardized  
154 by exposure duration ( $48 \pm 6$  h limit) and similar exposure durations of  $48.2 \pm 1.7$  h (mean  $\pm$  SD) were  
155 realized among plots.

156 As candidate predictors (fixed effects) of arthropod predation rates, we included habitat type, plant species  
157 richness, local mean temperature and mean relative humidity (during artificial caterpillar exposure),  
158 landscape diversity and MAT. Candidate predictors were z-transformed prior to analysis, while presented  
159 models contain untransformed predictor variables.

160 To parametrize the zero-inflation term, we considered factors which might explain absence of attack on  
161 plot level, e.g. arthropod activity limited by low temperatures (19). Besides, we visually screened the  
162 candidate predictors for accumulation of absence-of-attack events (predation rate = 0) at the extremes of  
163 the predictor ranges. Local mean temperature was the only candidate predictor in which absence of attack  
164 marks was frequently observed at the lower range on a per plot basis. Therefore, local mean temperature  
165 was included as a single candidate predictor in the zero-inflation term. Additionally, we run a separate  
166 analysis on presence-absence of attack on plot level (data extracted from predation rate data; predation rate  
167 > 0 replaced by 1) to investigate how the probability of attack on plot level was affected through local mean  
168 temperature using binomial generalized linear mixed effect models including region as random term (see  
169 S1 Table).

170 When analysing the data, we first conducted multi-model averaging to identify the most relevant predictors  
171 and spatial scales. Models with all possible predictor combinations were created separately for each spatial  
172 scale (0.5–3.0 km, six scales). Akaike weights were computed using the dredge-function from the ‘MuMin’  
173 R-package (35). Achieved Akaike weights ( $w_i$ ) were summed per predictor and spatial scale, whereby high  
174 summed Akaike weights ( $\sum w_i$ ; range: 0 (low) – 1 (high)) indicate a high relative importance of a predictor,  
175 corresponding to high cumulative probability that a predictor occurs in the best model at the respective  
176 spatial scale (36).

177 In a second step, we analysed potential interactive effects of habitat type with plant species richness,  
178 weather conditions during artificial caterpillar exposure (local mean temperature, mean relative humidity),  
179 landscape diversity and MAT. Therefore, we added single interaction terms (e.g. local habitat type \* plant  
180 species richness) to the best model at the most relevant spatial scale derived from multi-model averaging.



181 Model selection was done based on Akaike's information criterion corrected for small sample size (AICc).  
182 Thereby, models with lower AICc were considered better, and models with  $\Delta\text{AICc} < 2$  were considered  
183 equal and the more parsimonious model was chosen.

184 Pearson correlations between continuous candidate predictor variables were rather low  $\leq 0.33$  (S2 Table)  
185 with two exceptions. MAT was positively correlated with local mean temperature (Pearson's  $r = 0.59$ ) and  
186 negatively correlated with mean relative humidity (Pearson's  $r = -0.51$ ). However, all variance inflation  
187 factors (VIF) fell below the commonly applied threshold for collinearity of variance inflation factor  $>10$   
188 (30, see S3 Table), unless interactions with the only categorical variable habitat type were included (S4  
189 Table), which commonly inflates VIF; the latter were calculated using the R-package 'performance' (37).  
190 Local mean temperature (Kruskal Wallis,  $P = 0.070$ ), mean relative humidity (Kruskal Wallis,  $P = 0.219$ )  
191 and landscape diversity (2-km scale, Kruskal Wallis,  $P = 0.187$ ) were similar among habitat types whereas  
192 plant species richness was higher in grasslands than arable plots and intermediate in forests and settlements  
193 (Kruskal Wallis,  $P = 0.022$ ; Bonferroni-corrected Wilcoxon test), and MAT was higher in settlements than  
194 forests and grasslands, and intermediate in arable plots (Kruskal Wallis,  $P = 0.008$ ; Bonferroni-corrected  
195 Wilcoxon test) (S2 Fig).

## 196 **Results**

197 Artificial caterpillars encountered arthropod attack on 83% of the plots. At plot level, absence of arthropod  
198 attack occurred mainly at low local temperatures, while attack (predation rates > 0) was observed with 80%  
199 probability when local mean temperatures were above 7°C (Fig 1, S1 Table). On plots with arthropod attack,  
200 on average 26% (mean; ± 19% SD) of the artificial caterpillars were attacked per plot within 2-d exposure;  
201 across all plots, the average predation rate was 21% (mean± 20% SD).

202 **Fig 1. Probability of arthropod attack relative to local mean temperature during artificial caterpillar exposure.**  
203 Logistic regression curve and dots indicate absence (0) and presence (1) of arthropod attack on artificial caterpillars at  
204 plot level.

205 Due to landscape diversity as landscape parameter, models at intermediate scales (1.5, 2.0 or 2.5-km) –  
206 particularly at 2-km scale – were more important for explaining arthropod predation rates than models at  
207 smaller (0.5 km, 1.0 km) or larger scales (3.0 km), as shown by sum of Akaike weights ( $\Sigma w_i$ , Fig 2A). The  
208 relative importance of candidate predictors for explaining arthropod predation rates revealed a similar  
209 pattern across all spatial scales, with high relative importance of landscape diversity and local mean  
210 temperature as zero-inflation term, intermediate relative importance of mean relative humidity, and low  
211 relative importance of MAT, plant species richness, local mean temperature (as fixed effect) and habitat  
212 type (Figs 2B, 3). Thus, landscape diversity and – as a zero-inflation term – local mean temperature have a  
213 high probability to appear in the best fitting model across spatial scales (Fig 2B), with the most substantial  
214 contribution in models including landscape diversity at the intermediate 2-km scale (Fig 2A, see also S3  
215 Table).

216 **Fig 2. Relative importance (sum of Akaike weights) for explaining arthropod predation rates of A) spatial scale**  
217 **(i.e. models with all possible predictor combinations at one scale relative to the others) and of B) each**  
218 **candidate predictor per spatial scale.** White symbols refer to habitat characteristics (Habitat: habitat type, SpecNum:  
219 plant species richness, Temp or RH: local mean temperature or mean relative humidity during artificial caterpillar  
220 exposure, zi: included as zero-inflation term) and filled blue symbols to regional factors (LandDiv: landscape diversity,

221 MAT: multi-annual mean temperature). Landscape diversity is the only landscape parameter (value changes with  
222 spatial scale).

223 Multi-model averaging revealed that, arthropod predation rates were similar among habitat types (Fig 3A;  
224 mean  $\pm$  SD, forests  $0.20 \pm 0.20$ , grasslands  $0.22 \pm 0.20$ , arable fields  $0.21 \pm 0.20$ , settlements  $0.21 \pm 0.20$ ),  
225 and across the observed range of plant species richness (Fig 3B) and local mean temperature (Fig 3C), while  
226 higher relative humidity tended to decrease arthropod predation rates (Fig 3D)(S3 Table). Local mean  
227 temperature as zero-inflation term equals a higher probability of arthropod attack at plot level with higher  
228 local mean temperatures (Fig 1). Particularly at 2-km scale (Fig 2A), arthropod predation rates increased  
229 towards diverse landscapes (Fig 3E). Higher maximum predation rates and more frequently high predation  
230 rates were observed in more diverse landscapes than landscapes dominated by a single land cover type (Fig  
231 3E, e.g. compare landscape diversity  $< 0.69$  and  $\geq 0.69$ , landscape diversity value of 0.69 equals an effective  
232 number of two land-cover types). MAT did not substantially affect arthropod predation rates (Fig 3F). We  
233 observed no interaction effects of any predictor on arthropod predation rates depending on habitat type (S4  
234 Table).

235 **Fig 3. Relationship between arthropod predation rates and candidate predictors:** A) Habitat type (For: forest, Gra:  
236 grassland, Ara: arable field, Set: Settlement), B) plant species richness, C+D) local mean temperature and mean  
237 relative humidity during artificial caterpillar exposure, E) landscape diversity at 2-km scale and F) multi-annual mean  
238 temperature (MAT). Light grey dots present values per plot; overlapping dots appear darker. In A) circles indicate  
239 outliers. In B-F) solid lines indicate model predictions of the best model derived through multimodel averaging.

## 240 **Discussion**

241 In this study, we assessed drivers of arthropod predation in open herbaceous vegetation in typical habitat  
242 types of the temperate region. Arthropod predation rates in different habitat types were similar and  
243 responded similarly to both local and regional drivers. Towards diverse landscapes, particularly at 2-km  
244 scale, arthropod predation rates increased, whereas they tended to decrease towards higher mean relative  
245 humidity and were frequently absent from plots with low local mean temperatures. Plant species richness  
246 and MAT did not substantially affect arthropod predation rates.

247 The observed average arthropod predation rate of 21% (in 2 days) in May was in the same order of  
248 magnitude as reported in other studies on artificial caterpillars at ground-level in temperate regions, when  
249 assuming that arthropod predation rates scale linearly with exposure time (see 38) and tend to increase from  
250 spring towards summer (6,16). In open herbaceous vegetation, Hertzog et al. (16) obtained average  
251 arthropod predation rates of 15% (per day) in May, and Meyer et al. (38) determined arthropod attack marks  
252 on 51% of the recovered artificial caterpillars (after 3 days) in summer.

253 Among local habitat types (forest, grassland, arable field, settlement) arthropod predation rates were not  
254 substantially different and high arthropod predation rates were observed in all habitat types. However, large  
255 variation in predation rates among plots of the same habitat type may result from largely different natural  
256 enemy communities due to a selective permeability of habitat edges. This permeability depends both on  
257 characteristics of the habitat edge – e.g. of natural or anthropogenic origin (39) – and on the behaviour of a  
258 predator – e.g. habitat and trophic specialist or generalist (40,41). Thus, large variation in spill-over from  
259 adjoining habitat into open herbaceous vegetation possibly masked differential effects of local habitat types  
260 on arthropod predation rates. This assumption of variation in spill-over from adjoining habitat is supported  
261 by the significant impact of landscape diversity on local predation rates.

262 Towards higher landscape diversity (particularly at 2-km scale), arthropod predation rates increased. Thus,  
263 in more diverse landscapes natural enemy communities were likely denser (40, p. 218), richer in the number  
264 of species (12) or more frequently included effective predators (12,13). However, among plots in diverse

265 landscapes we also observed large variability in predation rates, which may have several reasons. First,  
266 natural enemies may respond variably to diverse landscapes depending on i) the presence, proportion and  
267 combination of certain land-cover types – which may differ in their supply of complementing or  
268 supplementing resources (22,41) –, ii) the permeability of boundaries between land-cover types – but also  
269 at finer scales – (40,41), and therefore iii) the configuration of land-cover types (42). Second, changes in  
270 natural enemy communities likely mediate landscape-diversity effects on predation rates, but it is not yet  
271 fully understood which changes landscape diversity elicits in natural enemy communities (see 40, p. 218),  
272 and how and under which conditions this links to altered predation functions (12,13,43). Thus, landscape  
273 diversity promotes predation rates, but variability in predation rates in diverse landscapes – and elucidated  
274 potential sources of this – point out future research directions to derive more specific recommendations for  
275 landscape management aiming to promote top-down regulation of herbivores and potentially also of  
276 agricultural pests.

277 The absence of habitat type effects but increasing predation rates towards higher landscape diversity does  
278 not mean that directly adjoining habitat type is less important to arthropod predation than general landscape  
279 diversity, yet it suggests that the landscape composition of the intermediate surrounding (i.e. 2-km radius)  
280 impacts natural enemy communities in a way that can alter predation rates independent of the dominant  
281 habitat in the vicinity. Thus, our results provide first evidence that landscape diversity favours high  
282 predation services (in open herbaceous vegetation) across typical habitat types in the temperate region.

283 Local weather conditions during artificial caterpillar exposure shaped arthropod predation. In our study,  
284 higher local mean temperatures made it more likely to observe predation (predation rates > 0), but did not  
285 substantially increase predation rates. This seems to be in contrast to observations from pitfall trap catches,  
286 where numbers of many ground-active arthropod species in the catches increased with temperature (44),  
287 which similarly could have increased the likelihood of encounter with an artificial caterpillar. However, as  
288 we did not study predation rates as time-series but on different plots, natural enemy communities possibly  
289 differed between plots and entailed arthropod species with different temperature preferences (19) and

290 sensitivities (see 44), which can explain the absence of a clear temperature relationship in our study.  
291 Furthermore, local mean temperatures measured 1-m above ground possibly reflected the conditions  
292 experienced by a predator differently depending on the effects of vegetation structure on microclimate and  
293 the daily activity pattern. Thus, local weather conditions may influence predation rates but this effect might  
294 be masked in our study, possibly through differences in natural enemy communities among plots and a  
295 discrepancy between the measured and experienced temperature by ground-active arthropods. However,  
296 we more frequently observed the absence of attack (predation rates = 0) at low local mean temperatures.  
297 Accordingly, temperature thresholds may apply more broadly to arthropod predation, at least in spring.  
298 Both, because emergence after overwintering is temperature-dependent (45) and temperature thresholds of  
299 relevant predators may not have been reached in colder areas of our study region or not long enough for  
300 relevant predators to move onto the plots, and – maybe even more importantly– because initiation of daily  
301 activity seems to depend on certain temperatures (19, p. 13). Thus far only few studies, which quantified  
302 predation, have reported on local weather conditions (46). Our results provide further evidence that local  
303 temperature impacts predation and thus should be considered when interpreting predation functions.

304 MAT did not substantially affect arthropod predation rates. This may have several reasons. First, natural  
305 enemy communities were not substantially altered through long-term temperature along the observed MAT  
306 gradient, or second, different natural enemy communities can provide similar predation rates. Although we  
307 cannot test the first reason, studies reporting on increased predation rates towards lower latitudes and  
308 altitude (25) or towards higher mean annual temperatures (24) were conducted at a global scale. Thus,  
309 various factors may obscure a (weak) climate effect in studies covering a fraction of the global temperature  
310 range, such as our study. Indeed, we observed large variation in predation rates among plots of similar  
311 MAT, which may suggest that other factors impact natural enemy communities more strongly than MAT.  
312 However, even if natural enemy communities change along the MAT gradient, this may not have led to  
313 differences in predation rates. This is supported by the observation that several independent studies using  
314 artificial caterpillars in temperate regions reported predation rates in the same order of magnitude (see

315 above) – which likely encompasses large differences in natural enemy communities –, but also by the  
316 marked relevance of key predators for predation functions, e.g. compared to natural enemy richness (12).  
317 Key predators can be, for instance, particular voracious predator species (47) and predators with specific  
318 feeding traits matching the ‘vulnerability trait’ of the prey (48). Thus, high predation rates across the  
319 covered MAT gradient illustrate the potential to increase predation rates (e.g. through landscape  
320 management) independent of a potential moderate increase of MAT in the near future.

321 Plant species richness did not substantially affect arthropod predation rates in our study, whereas Barnes et  
322 al. (15) reported increasing top-down control and Hertzog et al. (16) increasing invertebrate predation rates  
323 towards higher plant species richness. However, these positive effects of plant species richness on predation  
324 rates were reported from grassland experiments (15,16), whereas we report from a multi-scale field  
325 experiment. This likely included much more variation in natural enemy communities and also considerable  
326 differences in plant species pools between plots. Thus, plant species richness may indirectly affect  
327 arthropod predation rates depending on the natural enemy community composition and the plant species  
328 pool, but our data suggests that this is not a ubiquitous or dominant pattern.

329 Our results provide insights into herbivore regulation through arthropod predators, but are limited by the  
330 method of artificial caterpillars as sentinel prey. Common predators on artificial caterpillars at ground-level  
331 are chewing insects, especially carabids (6). Properties of the artificial caterpillars such as length (49) and  
332 colour (50) act as a filter – with yet unknown specificity – on the interacting predators. Furthermore,  
333 predation rates on artificial caterpillars do not directly translate into successful predation attempts as the  
334 complexity of predator-prey interactions is reduced by e.g. prey mobility (51) and defensive traits such as  
335 cuticular toughness (48). However, predation rates on artificial caterpillars are widely recognised for their  
336 standardisable estimate (27,52) and can provide unique insights into drivers of predation functions through  
337 generalist predators, which are otherwise impossible to obtain.

## 338 **Conclusion**

339 We conclude that landscape diversity favours high arthropod predation rates in open herbaceous vegetation  
340 across typical habitat types in the temperate region, while adjoining habitat type and plant species richness  
341 are of minor importance when studying a large spatial extent with possibly vastly different natural enemy  
342 communities. However, more research is needed on the underlying mechanisms of the landscape diversity  
343 effect to deduce more specific management options for improved top-down control of herbivores and for  
344 enhanced natural pest control in agricultural ecosystems. Besides, local weather conditions impact  
345 predation, e.g. low local mean temperatures can limit predation, and hence should be considered when  
346 interpreting predation rates. With respect to MAT, arthropod predation rates did not substantially change  
347 and high rates were observed across the covered climatic gradient, which highlights the potential to increase  
348 predation rates (e.g. through landscape management) independent of potential moderate temperature  
349 increases in the near future.



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- 481

## 482 **Supporting information**

483 **S1 Table. Model output on the probability of arthropod attack on plot level** (presence-absence of attack from a  
484 plot, binomial generalized linear mixed model) including local mean temperature during artificial caterpillar exposure as  
485 predictor compared to an empty model (null, null model). Bold font highlights the best model based on  $\Delta\text{AICc} < 2$  and  
486 parsimony.

487 **S2 Table. Predictor variable details and Pearson's correlation coefficients** included in multimodel averaging on  
488 arthropod predation rate models based on 113 study sites. Significant correlations based on  $\alpha = 0.05$  are indicated as  
489 following:  $P < 0.05^*$ ,  $P < 0.01^{**}$ ,  $P < 0.001^{***}$ .

490 **S3 Table. Model output of arthropod predation rate models** (zero-inflated binomial generalized linear mixed model)  
491 with different parametrization (best: best model based on  $\Delta\text{AICc} < 2$  and parsimony;  $\Delta\text{AICc} < 4$ ; full: model containing  
492 all candidate predictors; null: null model with or without temperature as zero-inflation term) at the best spatial scale  
493 identified by multimodel averaging (2-km scale). Best model is highlighted in bold font.

494 **S4 Table. Model output of arthropod predation rate models including interactive effects with habitat type** (zero-  
495 inflated binomial generalized linear mixed model) at the best spatial scales identified by multimodel averaging (2-km  
496 scale). Interaction terms are added to the original best model and to null models containing only temperature during  
497 exposure as zero-inflation term. Asterisks between candidate predictors indicate that both main effects and their  
498 interaction term is included. Best model parametrization is derived based on  $\Delta\text{AICc} < 2$  and parsimony. Best models  
499 are highlighted in bold font.

500 **S1 Fig. Pearson correlation between arthropod predation rates assessed in the field and in the lab.** Dots indicate  
501 values per plot; overlapping dots appear darker. The dashed grey line presents a hypothetically perfect correlation ( $r =$   
502 1) and the solid black line, the observed correlation based on  $\alpha = 0.05$ ,  $P < 0.001^{***}$ .

503 **S2 Fig. Relationship between habitat type and other candidate predictors of arthropod predation rates.** Dots  
504 indicate values per plot; overlapping dots appear darker. Asterisks highlight significance levels of  $P < 0.05^*$  and  $P <$   
505  $0.01^{**}$ . Letters indicate significant differences between habitat types based on Bonferroni-corrected pairwise  
506 comparisons using Wilcoxon rank sum test.



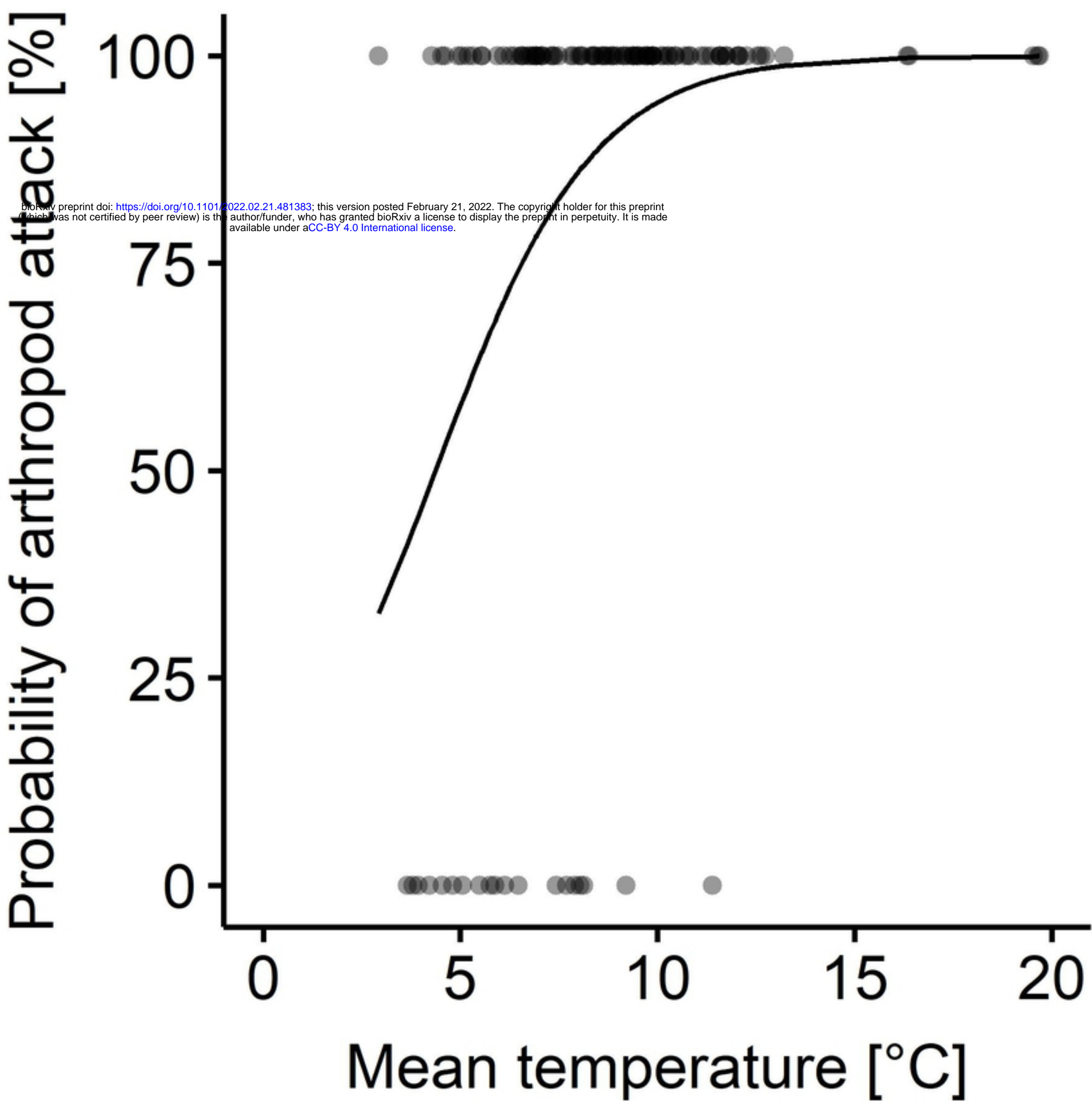
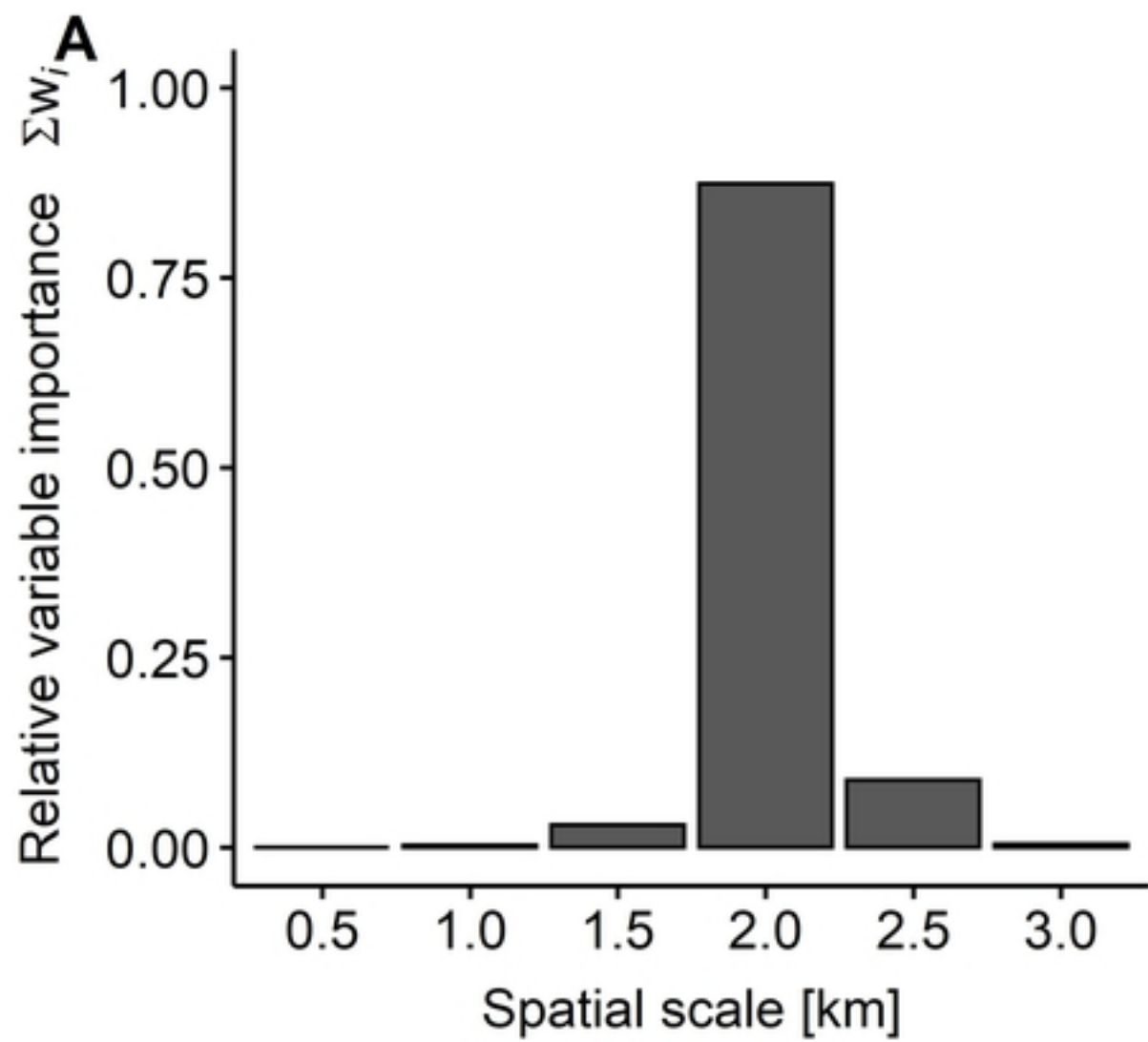


Fig 1



Predictor

- $\triangle$  Habitat
- $\square$  Temp
- $\nabla$  Temp(zi)
- $\bullet$  MAT
- $\diamond$  SpecNum
- $\circ$  RH
- $\blacktriangle$  LandDiv

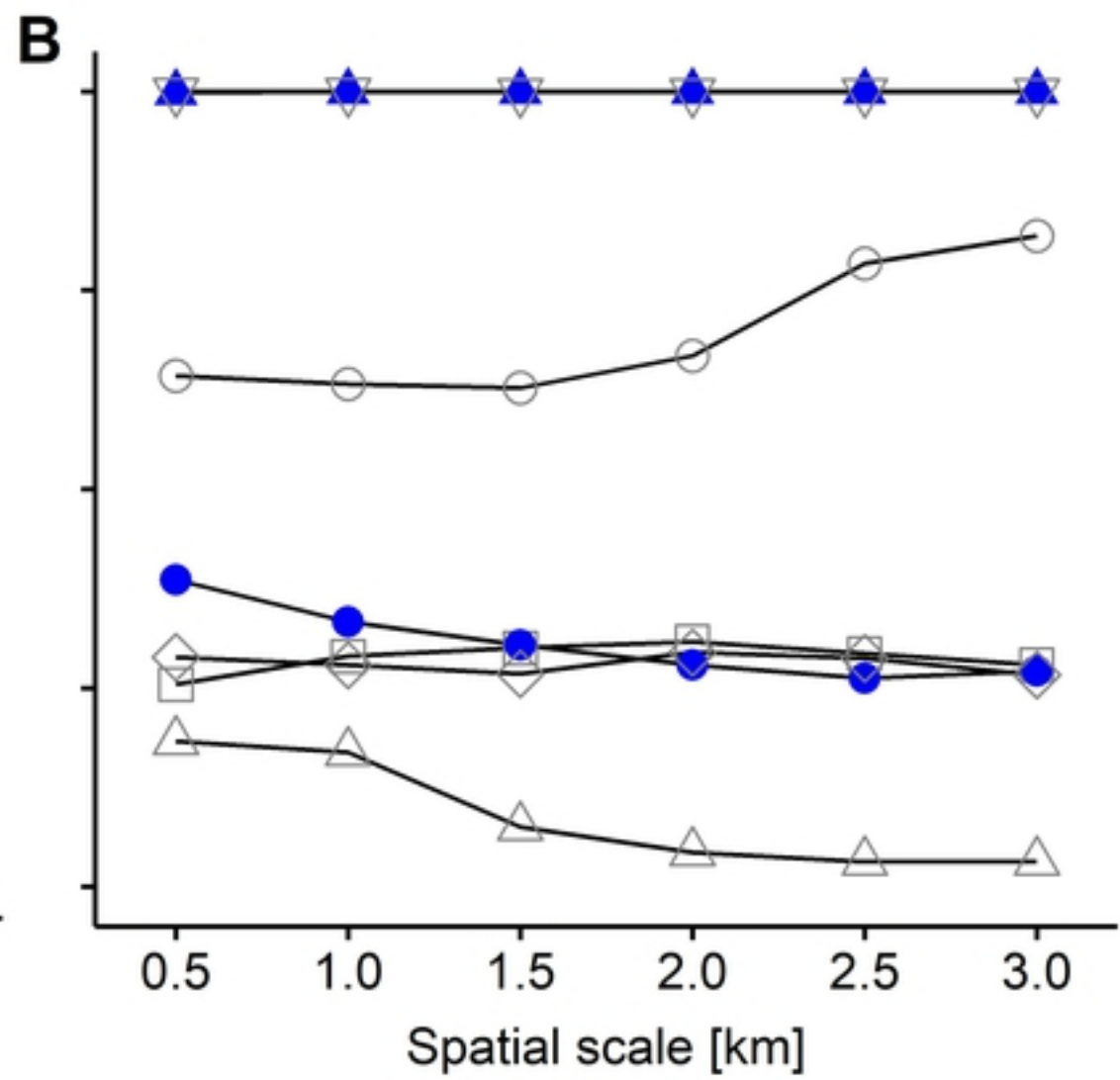


Fig 2

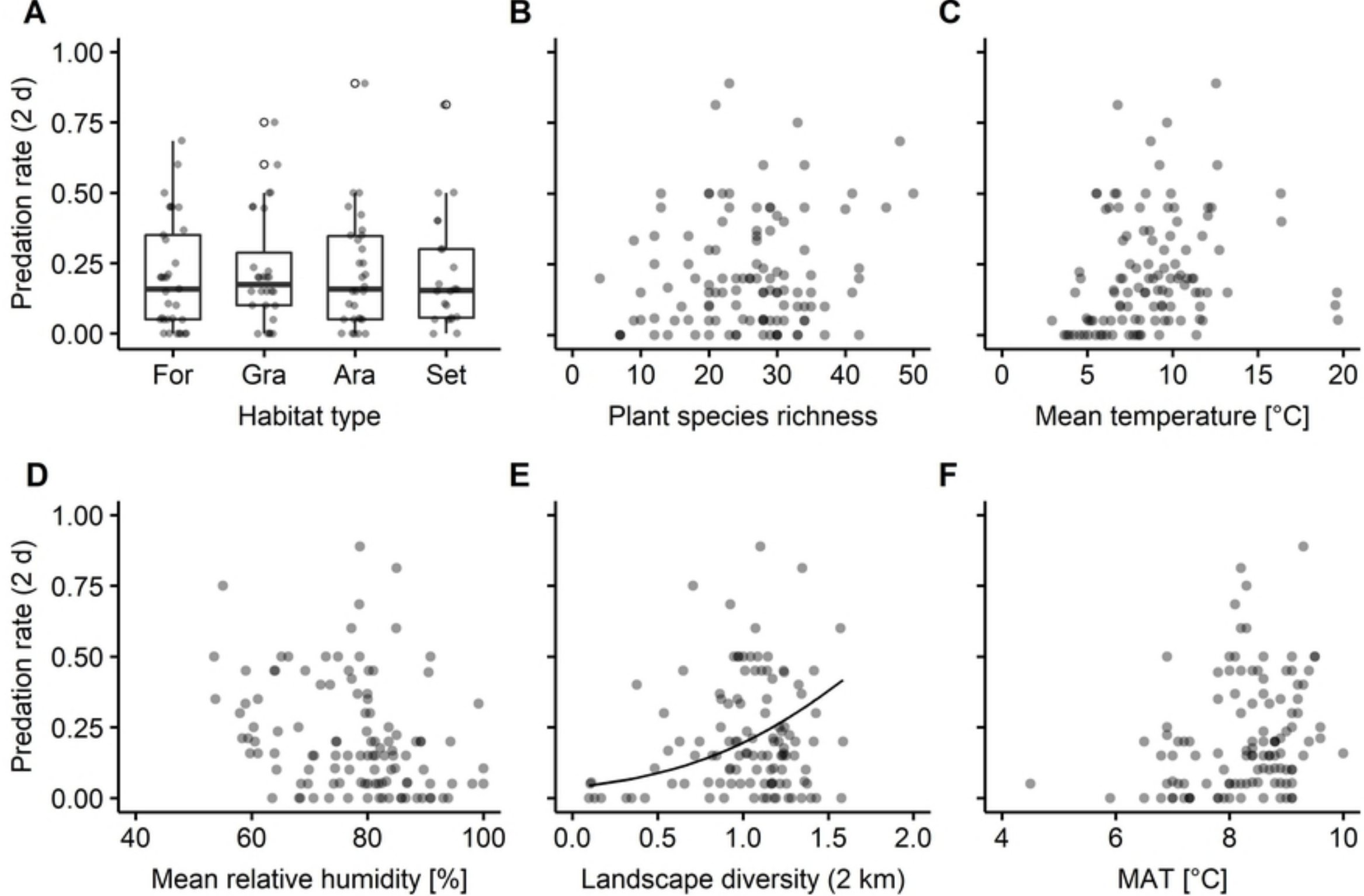


Fig 3