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1 **Search for top-down and bottom-up drivers of latitudinal trends in insect** 2 **herbivory in oak trees in Europe**

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80 financial interests.

81

82 **Biosketch**

83 *Elena Valdés-Correcher*: Interested on plant-herbivore interactions. More specifically, she
84 investigate the effect of different drivers of plant herbivore interactions including the effect of
85 landscape composition, climate and tree genotype on plant-herbivore relationships.

86

87 *Bastien Castagneyrol*: Interested on citizen science and on the ecology of plant-herbivore
88 interactions including predation, insect herbivory and leaf traits and how these relationships are
89 influenced by factors that act at different scales.

90

91 *Xoaquín Moreira*: Interested on plant-herbivore interactions. More specifically, interested on the
92 effect of latitude and elevation on biotic relationships.

1 **Title:** Search for top-down and bottom-up drivers of latitudinal trends in insect herbivory in oak
2 trees in Europe

3 **Running title:** Plant-herbivore interactions in oak in Europe

4 **Abstract**

5 **Aim**

6 The strength of species interactions is traditionally expected to increase toward the Equator.
7 However, recent studies have reported opposite or inconsistent latitudinal trends in the bottom-
8 up (plant quality) and top-down (natural enemies) forces driving herbivory. In addition, these
9 forces have rarely been studied together thus limiting previous attempts to understand the effect
10 of large-scale climatic gradients on herbivory.

11 **Location**

12 Europe

13 **Time period**

14 2018-2019

15 **Major taxa studied**

16 *Quercus robur*

17 **Methods**

18 We simultaneously tested for latitudinal variation in plant-herbivore-natural enemy interactions.
19 We further investigated the underlying climatic factors associated with variation in herbivory, leaf
20 chemistry and attack rates in *Quercus robur* across its complete latitudinal range in Europe. We
21 quantified insect leaf damage and the incidence of specialist herbivores as well as leaf chemistry
22 and bird attack rates on dummy caterpillars on 261 oak trees.

23 **Results**

24 Climatic factors rather than latitude *per se* were the best predictors of the large-scale
25 (geographical) variation in the incidence of gall-inducers and leaf-miners as well as in leaf
26 nutritional content. However, leaf damage, plant chemical defences (leaf phenolics) and bird
27 attack rates were not influenced by climatic factors or latitude. The incidence of leaf-miners
28 increased with increasing concentrations of hydrolysable tannins, whereas the incidence of gall-

29 inducers increased with increasing leaf soluble sugar concentration and decreased with increasing
30 leaf C:N ratios and lignins. However, leaf traits and bird attack rates did not vary with leaf damage.

31 **Main conclusions**

32 These findings help to refine our understanding of the bottom-up and top-down mechanisms
33 driving geographical variation in plant-herbivore interactions, and urge for further examination
34 of the drivers of herbivory on trees.

35 **Key words:** leaf chemistry, plant defences, avian insectivory, climate, artificial prey

36 **Introduction**

37 Ecological theory predicts that the strength of species interactions increases toward the Equator
38 due to warmer temperatures, longer growing seasons, and higher species abundance and
39 diversity at lower latitudes (Janzen, 1970; Schemske *et al.*, 2009). Plant species at lower latitudes
40 commonly experience higher rates of herbivory than plants growing further from the equator
41 (Coley & Barone, 1996; Schemske *et al.*, 2009; Lim *et al.*, 2015; Moreira *et al.*, 2018) and thus
42 tropical plant species may evolve higher levels of anti-herbivore defences (Johnson & Rasmann,
43 2011; Pearse & Hipp, 2012; Abdala-Roberts *et al.*, 2016; Hahn *et al.*, 2019). While early reviews
44 reported patterns supporting these predictions (Coley & Aide, 1991; Coley & Barone, 1996; Dyer
45 & Coley, 2002), several studies in recent decades have found either no evidence for a latitudinal
46 gradient in herbivory and plant defences (Moles & Westoby, 2003; Gaston *et al.*, 2004; Moles *et al.*,
47 2011) or increase in herbivory and defences with latitude (Gaston *et al.*, 2004; Stark *et al.*,
48 2008; Adams *et al.*, 2009; Martz *et al.*, 2009; Pennings *et al.*, 2009; Del-Val & Armesto, 2010;
49 Woods *et al.*, 2012; Moreira *et al.*, 2018, 2020). Given these inconsistencies, it is of great
50 importance to identify the mechanisms underlying the substantial variation in herbivory and plant
51 defences across latitudes, as herbivory is an important ecological process that modulates primary
52 productivity by altering the recruitment, mortality and growth of plants.

53 Latitudinal gradients can be used as 'natural laboratories' to study the relationship between
54 climate and plant-herbivore interactions (De Frenne *et al.*, 2013; Kozlov *et al.*, 2015; Lim *et al.*,
55 2015; Moreira *et al.*, 2018). In the northern extratropical hemisphere, mean annual temperature
56 drops by 0.73 °C and mean annual precipitation by 4.04 mm per degree of latitude northward (De
57 Frenne *et al.*, 2013). Latitudinal variation in plant-herbivore interactions is therefore generally
58 associated with large-scale variability in climatic conditions (Moreira *et al.*, 2018) and numerous
59 studies demonstrate an effect of temperature and precipitation on plant traits (e.g. leaf N,
60 phenolic compounds) (Chen *et al.*, 2013; Holopainen *et al.*, 2018; Gely *et al.*, 2019) and herbivory
61 (Jamieson *et al.*, 2015; Gely *et al.*, 2019). However, many regions deviate from the global trend in
62 temperature and precipitation toward higher latitudes due to their proximity to oceans or the

63 presence of mountains (De Frenne *et al.*, 2013), which can markedly change the relationship
64 between latitude and plant-herbivore-predator interactions (Roslin *et al.*, 2017; Loughnan &
65 Williams, 2019; Moreira *et al.*, 2019).

66 Recent work identified several potential sources of variation in the reported directions and
67 strengths of latitudinal gradients in herbivory and plant defences (Johnson & Rasmann, 2011;
68 Anstett *et al.*, 2016). First, theory on latitudinal gradients in herbivory and plant defences assumes
69 a plant-centred equilibrium in which plants at low latitudes have adapted to higher herbivory
70 levels by evolving stronger defences. However, most studies have measured either herbivory
71 patterns or plant defences, but not both (but see Anstett *et al.*, 2015; Moreira *et al.*, 2018),
72 leading to an incomplete understanding of the relationship between latitudinal clines and plant-
73 herbivore interactions. Second, little attention has been paid to latitudinal variation in tritrophic
74 dynamics (Roslin *et al.*, 2017). Herbivore natural enemies, however, can drastically modify
75 tritrophic interactions by suppressing herbivore populations or reducing herbivore feeding
76 (Rosenheim, 1998; Maguire *et al.*, 2015). In the few published studies exploring latitudinal
77 patterns in natural enemy activity, authors have found no variation in parasitism (Dyer & Coley,
78 2002; Moreira *et al.*, 2015), lower attack rates on artificial prey by ants (Roslin *et al.*, 2017), and
79 higher (Zvereva *et al.*, 2019) or no variation (Roslin *et al.*, 2017) in attack rates on artificial prey
80 by birds with increasing latitude. Third, while external feeders are directly exposed to enemies
81 and adverse abiotic conditions, internal feeders (e.g., leaf-mining and gall-inducing insect
82 herbivores) benefit from a buffered microhabitat and relative protection against enemies. It is
83 therefore likely that latitudinal trends in tritrophic interactions would vary across herbivore
84 feeding guilds. Thus, considering bottom-up and top-down forces simultaneously could be crucial
85 for a comprehensive understanding of latitudinal clines in tritrophic interactions.

86 We aimed to test for latitudinal variation in plant-herbivore-natural enemy (*i.e.*, tritrophic)
87 interactions, as well as the underlying climatic factors associated with variation in herbivory,
88 bottom-up and top-down forces in the pedunculate oak (*Quercus robur*), a long-lived, common
89 European tree. In particular, we asked the following questions: (1) Are there latitudinal clines in
90 herbivory? (2) Is latitudinal variation in leaf chemical traits (bottom-up effects) and/or bird attack
91 rates (top-down effects) on herbivorous insects associated with latitudinal variation in herbivory?
92 (3) Are climatic correlates of latitude associated with clines in herbivory, leaf chemical traits and
93 attack rates? We used data collected by professional scientists and schoolchildren across major
94 parts of the geographical distribution range of *Q. robur*. We quantified insect leaf herbivory, leaf
95 chemical traits (soluble sugars, nutrients and phenolics) and attack rates on dummy caterpillars
96 placed on mature oak trees. Overall, our study attempted to refine our understanding of bottom-
97 up and top-down mechanisms that may drive geographical variation in plant-herbivore
98 interactions.

99 **Material and methods**

100 The present study involved 30 professional scientists from 14 countries and 82 school teachers
101 (with their pupils) from 10 countries, giving a total of 112 partners from 17 European countries
102 and covering most of the native geographic range of the pedunculate oak (**Figure 1**). Every partner
103 received detailed instructions at the beginning of the project (Castagneyrol *et al.*, 2019). Here, we
104 only provide a summary of these instructions. Only project partners who provided data that could
105 be used in the present article were included.

106 **Target species**

107 The pedunculate oak is one of the dominant deciduous tree species in European forests and is of
108 high ecological, economic and symbolic importance (Eaton *et al.*, 2016). Its distribution ranges
109 from Central Spain (39°N) to southern Fennoscandia (62°N), thus this species experiences variable
110 climatic conditions (Petit *et al.*, 2002). Pedunculate oak supports a large community of specialist
111 and generalist herbivorous insects; especially suckers, chewers, skeletonizers, gall-inducers and
112 leaf-miners (Southwood *et al.*, 2005; Moreira *et al.*, 2018), as well as xylophagous species
113 (Marković & Stojanović, 2011). The wide distribution of pedunculate oak and the high diversity of
114 associated herbivorous insects make it a suitable model species for research on the effect of
115 climate on biotic interactions.

116 In total, the study included 261 mature oak trees surveyed by professional scientists (n = 115) and
117 schoolchildren (n = 146) in 2018 (n = 148) and 2019 (n = 113) (**Figure 1**). However, not every
118 partner measured or provided material allowing measurement of herbivory, bird attack rates and
119 leaf chemistry simultaneously on every tree (Figure S1.1a, b and c, supplementary material).

120 **Attack rates on dummy caterpillars**

121 To control for latitudinal variation in environmental conditions, we matched the start of the
122 experiment in each locality to the phenology of local oak trees. Six weeks after oak budburst,
123 partners installed 20 dummy caterpillars per tree, *i.e.*, five caterpillars on each of four branches
124 (facing north, south, east and west) with a minimum distance of 15 cm between caterpillars.

125 The project coordinators provided the same green plasticine (Staedler, Noris Club 8421, green[5])
126 to all partners to make the caterpillars. In order to standardize caterpillar size among partners,
127 we made caterpillars from a 1 cm diameter ball of plasticine, and gently pressed/rolled this along
128 a 12 cm long metallic wire until a 3 cm long caterpillar was obtained, with the wire in its center.
129 Partners attached the caterpillars to branches by twisting the wire and left the caterpillars on
130 trees for 15 days before recording predation marks. A second survey using the same procedure
131 immediately followed the first one. In 2018, schoolchildren photographed every caterpillar with
132 the suspected attack marks from any potential predatory taxon. In 2019, both schoolchildren and
133 professional scientists sent caterpillars back to the project coordinators.

134 In order to be consistent and reduce bias due to multiple observers, photos and dummy
135 caterpillars were screened by a single trained observer (first author, EVC). For each oak tree and
136 survey period, we assessed attack rate as the proportion of dummy caterpillars with at least one
137 attack mark. Although we asked partners to record attack rate marks left by different types of
138 predators (in particular birds and arthropods), attacks by arthropod predators could not be
139 verified on photos because of their low resolution. In addition, the relevance of marks left by
140 arthropods on plasticine model prey has recently been questioned, in particular after mandibular
141 marks were observed on lizards or frog models (Rößler *et al.*, 2018). For these reasons, we
142 decided to discard arthropod attack rate from the study and focused on marks that were
143 unambiguously attributed to birds, *i.e.*, conic holes or V-shaped beak marks. Attack marks left by
144 reptiles or rodents were also disregarded, because only a few caterpillars were attacked by these
145 potential predators. Most bird marks were directed towards the head or the body centre of the
146 dummy caterpillars, which is typical to bird attacks and indicates prey recognition (Rößler *et al.*,
147 2018). We therefore refer to the proportion of dummy caterpillars with such marks as bird attack
148 rate.

149 Between 2018 and 2019, 137 partners installed 12,760 dummy caterpillars on 319 oak trees.
150 Despite clear instructions regarding caterpillar installation, removal and conditioning prior to
151 shipping, the material sent by 22 school partners was of poor quality (with no particular
152 geographic bias) such that only caterpillars returned by 115 partners (*i.e.*, 78.4%, collected on 254
153 oak trees) were screened for attack marks and included in subsequent analyses (**Table S1.1;**
154 **Figure 1**).

155 Leaf herbivory

156 Professional scientists and schoolchildren were instructed to collect oak leaves after the second
157 bird attack rate survey, *i.e.*, roughly 10 weeks after oak budburst, on the same branches where
158 dummy caterpillars were installed. They haphazardly collected 30 leaves per branch, totalling 120
159 leaves from which they blindly drew 60 leaves. Professional scientists oven-dried leaves for a
160 minimum of 48 h at 45°C immediately after collection, and leaves collected by schoolchildren
161 were oven dried upon receipt by the project coordinators, to ensure optimal conservation prior
162 to herbivory assessment.

163 We used three response variables to characterise leaf herbivory: leaf damage (the percentage of
164 leaf area that was consumed or mined by insect herbivores), incidence of leaf-miners (the
165 proportion of leaves with leaf-mines) and incidence of gall-inducers (the proportion of leaves with
166 galls). For each leaf, we visually assessed leaf damage (attributed to ectophagous chewing and
167 leaf-mining organisms) following eight levels of defoliation (0%, >0-5%, >5-10%, >10-15%, >15-
168 25%, >25-50%, >50-75%, and >75%). We then averaged leaf damage at the tree level using the
169 midpoint of each percentage class to obtain a mean value per tree. While this measurement also
170 included the surface covered by leaf mines (*i.e.*, internally chewed by mining larva), it excluded

171 both galls and punctures made by sap feeders. Leaf assessment was made by two trained
172 observers who were blind to leaf origin to reduce unconscious bias. We expect that most of the
173 leaf damage will be attributable to insects, as in our experience, mollusc herbivory (e.g. snails and
174 slugs), although possible, is rare in adult oak trees. As of mites, they mostly cause discolouration
175 that can easily be differentiated from insect herbivory. There are also few mammals consuming
176 oak leaves, mostly rodents and ungulates, but usually they mostly consume seedlings and
177 saplings.

178 Leaf chemical traits

179 We used leaves collected in 2018 to quantify several leaf chemical traits typically recognized as
180 important determinants of plant quality for insect herbivores associated with oaks. Details of
181 procedures used to analyse chemical leaf traits are reported in online Appendix S1.1.

182 We quantified leaf phenolics as oak defensive metabolites (Moreira *et al.*, 2018). We used only
183 leaves collected by professional scientists in 2018. Unfortunately, we were not able to quantify
184 other leaf defences that need to be estimated on fresh leaves (e.g. leaf toughness) because leaves
185 were oven dried after collection to ensure optimal conservation. From each tree, we selected 10
186 mature, dried leaves with no evidence of insect damage and ground them to fine powder. We
187 identified four groups of phenolic compounds: flavonoids, ellagitannins and gallic acid derivatives
188 (“hydrolysable tannins” hereafter), proanthocyanidins (“condensed tannins” hereafter) and
189 hydroxycinnamic acid precursors to lignins (“lignins” hereafter) (see Appendix S1.1 for further
190 details).

191 We quantified C:N ratio, N:P ratio, cellulose and soluble sugars as proxies for leaf nutritional
192 content to herbivores (Moreira *et al.*, 2019) as in many plant taxa these variables are correlated
193 with herbivory (Mattson, 1980; Schoonhoven *et al.*, 2005; Smilanich *et al.*, 2016). We measured
194 these traits on leaves collected by both professional scientists and schoolchildren. We ground the
195 50 oven dried leaves on which we scored herbivory to fine powder such that leaf nutritional traits
196 reflected the content of leaves with different amounts of herbivore damage (see Appendix S1.1
197 for further details).

198 Statistical analysis

199 We were primarily interested in testing the effect of latitude on herbivory and in identifying the
200 underlying ecological forces. We aimed to test whether the effect of latitude was driven by
201 latitudinal gradients in climatic conditions, and by their direct and indirect consequences on leaf
202 chemistry, herbivory and bird attack rate. We obtained temperature and precipitation data from
203 the WorldClim database (Hijmans *et al.*, 2005) based on oak coordinates as retrieved on Google
204 maps by project partners. Specifically, we extracted the mean temperature and precipitation
205 from April to June, which roughly corresponded to the period when caterpillars were present on
206 trees, irrespective of latitudinal cline in moth phenology. Yet, latitude was correlated with both

207 temperature (Pearson's $r = -0.85$) and precipitation ($r = -0.72$). To avoid spurious estimates of
208 model coefficients caused by collinearity among predictors, we tested the effects of latitude and
209 climate separately.

210 Specifically, we built three types of Linear Mixed-effects Models (LMM): (i) geographic models
211 analysing the effect of latitude on herbivory, leaf chemistry and bird attack rate, (ii) climatic
212 models in which we substituted latitude with climatic data (temperature and precipitation) and
213 (iii) abiotic and biotic models analysing the effects of leaf chemistry and bird attack rate together
214 with temperature and precipitation or latitude (both linear and quadratic) on herbivory. As
215 latitudinal gradients in plant-herbivore interactions can be non-linear (following Rodríguez-
216 Castañeda 2013 and Kozlov *et al.*, 2015), we complemented our linear analyses with quadratic
217 models. As leaf chemistry was only measured on a subset of trees ($n = 64$), we used a subsample
218 of the dataset to quantify relationships between herbivory with its top-down and bottom-up
219 drivers (Table S1.1).

220 In every LMM, we used Partner ID as a random factor to account for the fact that some partners
221 surveyed multiple trees. For instance, the geographic models were of the form:

$$222 \quad Y = \beta_0 + \beta_1 \times \text{Year} + \beta_2 \times \text{Partner} + \beta_3 \times \text{Latitude} + \beta_4 \times \text{Latitude}^2 + \gamma + \epsilon + \sigma^2_{\text{Partner ID}}$$

223 where Y was the response variable, β_i model coefficient parameter estimates, Partner was the
224 effect of partner type (the estimate for schoolchildren being compared with the estimate for
225 professional scientists that was included in the intercept), Year was the effect of each year (2019
226 contrasted with 2018), Latitude (and their quadratic terms) the geographic conditions around
227 sampled oak trees, $\sigma^2_{\text{Partner ID}}$ the random effect of Partner ID (assuming that $\gamma \in N(0, \sigma^2_{\text{Partner ID}})$
228 and ϵ the residuals (assuming $\epsilon \in N(0, \sigma^2_{\epsilon})$). When Y was bird attack rate, we added the survey
229 (first vs. second) as a fixed effect and Tree ID as a random effect nested within Partner ID to
230 account for repeated measurements on the same trees. When needed, we used arcsine square-
231 root (bird attack rate) or $\ln(x + 1)$ transformation (leaf damage, soluble sugars, N:P ratio and leaf
232 defences) of the response variable to satisfy model assumptions.

233 We ran geographic and climatic models on the complete dataset including 2018 and 2019 data
234 collected by both professional scientists and schoolchildren. Note that because not every partner
235 provided reliable data on both bird attack rates and herbivory, the sample sizes differed between
236 models using bird attack rate or herbivory as response variables (**Figure 1, Figure S1.1a and b**).
237 We ran the geographic and climatic models on leaf phenolics as well as the biotic model on the
238 2018 data collected by scientific partners only, as we did not quantify leaf defences on leaves
239 collected and sent by schoolchildren.

240 The tree-level response variables for each year and survey period (Y) were either leaf damage (%
241 of leaf area removed and mined by herbivores), the incidence of leaf-miners or gall-inducers

242 (proportions), mean bird attack rate (ratio of % attacked caterpillars on exposition period) or leaf
243 chemistry (C:N ratio, N:P ratio, soluble sugar content [g L^{-1}], cellulose content (g), concentrations
244 of condensed or hydrolysable tannins, flavonoids or lignins [mg g^{-1} d.m.]). We scaled and centred
245 every continuous predictor prior to modelling to facilitate comparisons of their effect sizes, and
246 made sure that none of the explanatory variables were strongly correlated using the variance
247 inflation factor (VIF) (all VIFs < 5). We used LMM with a Gaussian error distribution, with the
248 exceptions of geographic, climatic and process-based models with the incidence of leaf-miners or
249 gall-inducers as response variables. In these cases, we used Generalized LMM with a binomial
250 error distribution and logit-link.

251 We analysed the data within the information theory framework (Burnham & Anderson, 2002).
252 We first built a set of geographic and climatic models as well as nested models for each response
253 variable separately. Biotic models (models including also leaf chemistry and bird attack rates as
254 explanatory variables) were run on the subset of samples where all data were measured
255 simultaneously. We then applied a procedure of model selection based on AIC corrected for small
256 sample size (AICc). In the first step, we ranked the models according to the difference in AICc
257 between a given model and the model with the lowest AICc (ΔAICc). Models within 2 ΔAICc units
258 of the best model (*i.e.*, the model with the lowest AICc) are generally considered as equally likely.
259 We also computed AIC weight (w_i) that is the probability a given model to be the best model
260 among the set of candidate models examined, as well as the relative variable importance (RVI) as
261 the sum of w_i of every model including this variable. When several models competed with the
262 best model (*i.e.*, when multiple models were such that their $\Delta\text{AICc} < 2$), we applied a procedure
263 of multimodel inference building a consensus model including the variables in the set of best
264 models. We then averaged their effect size across all the models in the set of best models, using
265 variable w_i as a weighting parameter (*i.e.*, model averaging). We considered that a given predictor
266 had a statistically significant effect on the response variable when its confidence interval excluded
267 zero.

268 In the results section, we report the degrees of freedom, log-likelihood, AICc, ΔAICc (delta), w_i
269 and the variance explained by fixed and fixed plus random factors (R^2m and R^2c , respectively)
270 (Nakagawa & Schielzeth, 2013) for every model, as well as averaged coefficient parameter
271 estimates and RVI for all variables present in the set of competing best models. When
272 appropriate, we plotted the relationship between raw data and explanatory variables together
273 with the predictions of simplified models, holding undisplayed predictors constant. All analyses
274 were run in the R language environment (Team, 2018) with packages *MuMIn* (Bartoń, 2018) and
275 *lme4* (Bates *et al.*, 2018).

276 **Results**

277 *Latitudinal and climatic gradients in herbivory, leaf chemistry and bird attack rates*

278 Herbivores damaged on average (\pm se) 8.7 ± 0.4 % of leaf area ($n = 182$ trees, see **Table S1.1** for
279 details). Model simplification identified the null model as the best model given the model set,
280 indicating that none of the predictors had a consistent effect on leaf damage (**Figure 2j, k and l**,
281 **Table S2.1**).

282 Insect galls were present on 7.1 ± 0.6 % of the inspected leaves ($n = 182$, **Table S1.1**). In the set of
283 best models (**Table S2.1; Figure S1.3**), the incidence of gall-inducers increased linearly with
284 increasing spring temperature (**Figure 2e**) and peaked at intermediate levels of spring
285 precipitation (**Figure 2f**). It was on average higher in 2018 than in 2019 (**Figure S1.2**). Other
286 predictors had no significant effects on the incidence of gall-inducers (**Figure 2d**).

287 Leaf-miners were present on 18.2 ± 1.3 % of the inspected leaves (**Table S1.1**). In the set of best
288 models (**Table S2.1; Figure S1.3**), the incidence of leaf-miners peaked at intermediate mean
289 spring temperatures (**Figure 2h**) and decreased linearly with increasing spring precipitation
290 (**Figure 2i**). It was significantly higher in 2018 than in 2019 (**Figure S1.2**), and higher in leaves
291 sampled by professional scientists than in those sampled by schoolchildren.

292 Some oak traits related to nutritional content, but not phenolic compounds, covaried with climate
293 and latitude (**Table S1.1**). Specifically, leaf soluble sugar content (3.7 ± 0.2 g·L⁻¹, $n = 114$, **Table**
294 **S1.1**) decreased with increasing precipitation (**Figure 3a**). Leaf C:N ratio (18.6 ± 0.2 , $n = 114$, **Table**
295 **S1.1**) increased non-linearly with latitude (with concave up shape, **Figure 3b**) and was on average
296 lower in leaves collected by professional scientists than those collected by schoolchildren. None
297 of the predictors had a significant effect on N:P or cellulose content (**Table S1.1**).

298 From a total of 10,000 exposed dummy caterpillars, 2,390 had bird beak marks (*i.e.*, 23.9%).
299 Model selection identified the null model as the best model, with no other competing model
300 within two units of Δ AICc of the best model.

301 *Mechanisms underlying latitudinal and climatic variation in herbivory*

302 Using a data subset limited to trees for which information on herbivory, leaf traits and bird
303 predation rates was available, model selection identified the null model as the best model,
304 indicating that none of the examined biotic and abiotic predictors had a significant effect on leaf
305 damage (**Table S2.2**).

306 When leaf chemistry was included in the model, the incidence of gall-inducers increased with
307 increasing soluble sugar concentration and decreased with increasing C:N ratio and lignin
308 concentration (**Figure 4**), whereas the positive relationship between temperature and gall-
309 inducers disappeared. When leaf traits were included in the models, the incidence of gall-inducers
310 increased non-linearly with increasing latitude. The relative importance of leaf chemistry
311 predictors (RVI = 0.65) was however higher than that of latitude (RVI = 0.05) or temperature (RVI
312 = 0.30, **Figure S1.4**).

313 Leaf-miner incidence increased with increasing concentration of hydrolysable tannins. The
314 relationship between temperature and leaf-miners remained significant, suggesting independent
315 effects of leaf defences and temperature on leaf-miners. Other predictors had no significant
316 effects on leaf-miners (**Figure 4; Table S2.2**).

317 **Discussion**

318 We found no evidence that either herbivory, oak chemical traits or bird attack rates varied with
319 latitude linearly or non-linearly. Our work therefore supports the growing number of studies that
320 have recently questioned the common view that biotic interactions are generally stronger at
321 lower latitudes (Moles *et al.*, 2011; Mottl *et al.*, 2020). Several arguments may explain the absence
322 of latitudinal patterns in herbivory or plant defences. On the one hand, Moles & Ollerton (2016)
323 argued that the latitudinal herbivory-defence hypothesis should simply be dismissed because it is
324 not convincingly supported despite decades of research. On the other hand, Anstett *et al.* (2016)
325 called for a refinement of the concepts and methods in the field. We align with the latter
326 perspective and henceforth discuss ecological sources of variation that may have obscured
327 latitudinal patterns, and argue these could be real rather than methodological artefacts.

328 **Herbivory responded to climate rather than to latitude, but in a guild-specific manner—**
329 Variation in the incidence of gall-inducers and leaf-miners, but not in leaf damage, was associated
330 with variation in temperature and precipitation, rather than with latitude *per se* (Anstett *et al.*,
331 2018; Moreira *et al.*, 2018; Loughnan & Williams, 2019). The absence of a climatic or geographic
332 effect on leaf damage is in line with previous reviews and meta-analyses that have shown
333 herbivory does not vary consistently along climatic or geographic gradients (Moles *et al.*, 2011;
334 Moles & Ollerton, 2016). Our analysis suggests that different herbivore species or guilds may be
335 differently affected by abiotic conditions, such that grouping different types of herbivores may
336 prevent the detection of patterns for each herbivore type (Abdala-Roberts *et al.*, 2015; Moreira
337 *et al.*, 2015; Anstett *et al.*, 2016).

338 In line with this explanation, we found that the incidence of gall-inducers and leaf-miners was
339 associated with broad scale climatic conditions. Specifically, the incidence of both gall-inducers
340 and leaf-miners increased with increasing temperature, but the shape of this relationship was
341 accelerating for gall-inducers and decelerating (*i.e.*, convex) for leaf-miners (**Figure 5**). Although
342 we did not identify species of leaf-miners, this result is in line with that of Kozlov *et al.* (2013) who
343 found that in northern Europe, the diversity of leaf miners on birch trees increased linearly toward
344 lower latitudes and was most likely associated with the direct impact of temperature, especially
345 during cold years. We also found that the incidence of gall-inducers peaked at intermediate
346 precipitation (Blanche & Ludwig, 2001; Leckey *et al.*, 2014) whereas leaf-miners decreased
347 significantly with precipitation. It has been hypothesized that endophagous feeding modes such
348 as galling and mining have evolved partly as adaptation to abiotic factors such as UV radiation

349 and desiccation (Fernandes & Price, 1992; Connor *et al.*, 1997; Danks, 2002). If so, gall-inducers
350 and leaf-miners may be expected to be more common in the warmest and driest parts of the
351 pedunculate oak range and at low latitudes where the light intensity is markedly higher
352 (Fernandes & Price, 1992; Lara & Fernandes, 1996; Price *et al.*, 1998; Cuevas-Reyes *et al.*, 2004).
353 However, even within the gall-inducer and leaf-miner groups, relationships to climate are highly
354 variable among species and years (Blanche, 2000; Sinclair & Hughes, 2010; Kozlov *et al.*, 2013,
355 2016), thus suggesting that other factors are also important in the incidence of gall-inducers and
356 leaf-miner herbivores.

357 **Leaf chemical traits had an inconsistent response to latitude and climate—**

358 We did not find detectable latitudinal and climatic gradients in plant chemical defences. This
359 contradicts the Latitudinal Herbivory Defence Hypothesis which predicts that plant species at
360 lower latitudes experience higher mean rates of herbivory than their temperate counterparts
361 (Coley & Barone, 1996; Schemske *et al.*, 2009; Lim *et al.*, 2015) and, for this reason, should have
362 evolved higher levels of anti-herbivore defences (Rasmann & Agrawal, 2011; Pearse & Hipp,
363 2012). However, the generality of this hypothesis is currently under debate (Moles & Ollerton,
364 2016). Several studies found no evidence for a latitudinal gradient in herbivory and plant defences
365 (Moles *et al.*, 2011) while others did (Salgado & Pennings, 2005; Woods *et al.*, 2012); there is also
366 mixed evidence when comparing different herbivore species or plant defensive traits (Anstett *et al.*,
367 2015; Moreira *et al.*, 2015, 2018). A plausible explanation for the lack of latitudinal gradients
368 in oak defences may be that there is no latitudinal gradient in leaf damage, hence there is no
369 reason for latitudinal gradient for defences to exist either. It could also be that we sampled leaves
370 at the middle of the growing season rather than at the end, and we did not measure constitutive
371 and induced defences separately. This is an insightful point because oak leaves may have
372 differentially accumulated phenolics in response to herbivory (*i.e.*, induced defences) or have
373 experienced marked differences in light intensity toward the end of the growing season
374 (Karolewski *et al.*, 2013). Furthermore, despite attempts to synchronize phenology across sites,
375 seasonal changes in oak chemical defences (Salminen & Karonen, 2011) might have masked
376 latitudinal patterns in defences. Therefore, further studies should include measurements at
377 multiple time points during the growing season and distinguish between different types of
378 defences, including physical vs. chemical defences (Wang *et al.*, 2018) as well as constitutive vs.
379 induced defences (Anstett *et al.*, 2018) in order to address latitudinal gradients in plant defence
380 more comprehensively.

381 Some leaf traits related to leaf nutrient content were associated with latitude or climatic
382 conditions, but their overall response was inconsistent. Leaf C:N ratio and sugar content varied
383 along latitudinal and climatic gradients, respectively. The leaf C:N ratios were lowest at
384 intermediate latitudes. This outcome may be due to temperature-related plant physiological
385 stoichiometry and biogeographical gradients in soil substrate age (limitation of soil N at higher

386 latitudes) (Reich & Oleksyn, 2004). Leaf soluble sugar content decreased with increasing
387 precipitation (Cao *et al.*, 2018). Soluble sugars, especially glucose and fructose, accumulate
388 together with other osmolytes during drought (Nio *et al.*, 2011), resulting in high concentration
389 in areas where precipitation is low.

390 **Predation rate was not influenced by latitude or climatic conditions—**

391 We found no latitudinal or climatic gradients in bird attack rates on dummy caterpillars (**Figure**
392 **5**). These results agree with the large-scale study performed by Roslin *et al.* (2017) who found an
393 increase of the activity of predatory arthropods in several plant species toward the Equator, but
394 no significant trend in avian predation. Several factors may explain the lack of response of avian
395 predation to latitudinal or climatic gradients. First, some bird species are distributed through
396 migration allowing them to breed at higher latitudes, resulting in a constant predation rate across
397 climatic and geographical clines (Dufour *et al.*, 2020). In contrast, other predators with lower
398 mobility such as arthropods (e.g. ants, ladybirds) are much more abundant at lower latitudes,
399 resulting in a higher selection pressure toward the Equator (Roslin *et al.*, 2017). Second, bird
400 communities are more influenced by forest habitat composition at lower latitudes, and more by
401 food availability at higher latitudes (Charbonnier *et al.*, 2016) where the diet variability is lower
402 (Barnagaud *et al.*, 2019), suggesting a stronger effect of local habitat features (e.g. resource
403 availability and habitat suitability) than climatic gradients. Third, we cannot exclude that the lack
404 of latitudinal trend in bird attack rates resulted from methodological limitations due to the fact
405 that we only exposed green dummy caterpillars in low hanging branches. Birds depend more on
406 food accessibility than abundance *per se*, so that the exact location of dummy caterpillars
407 regarding factors such as edge, light contrast and shrubby understory may have modified the
408 perception and the accessibility to the prey (Zvereva *et al.*, 2019).

409 **Mechanisms underlying latitudinal and climatic variation in herbivory—**

410 We did not find any statistically significant relationship between leaf damage and leaf chemical
411 traits. Although we cannot exclude that unmeasured traits (e.g. leaf toughness, inducible
412 defences) may have correlated with herbivory, our results disqualify large-scale variation in
413 bottom-up forces as important drivers of overall leaf damage at a continental scale. In contrast,
414 the incidence of gall-inducers and leaf-miners was partially related to the variability in several leaf
415 chemical traits (**Figure 5**). For instance, the incidence of gall-inducers increased with increasing
416 leaf soluble sugars and N concentrations, which is consistent with gall-inducers being metabolic
417 sinks (Huang *et al.*, 2014). However, the effect of precipitation on leaf-miners was likely indirectly
418 mediated by climatic variation in defences, as such an effect became non-significant once
419 hydrolysable tannins were included in the model. Similarly, the effects of temperature and
420 precipitation on gall-inducers were indirectly mediated by climatic variation in defences, as such
421 effects were also non-significant after soluble sugars, N concentrations and lignins were included

422 in the models. These results agree with previous studies reporting indirect effects (via leaf
423 defences) of climate on herbivory (Anstett *et al.*, 2018; Moreira *et al.*, 2018). For instance, Anstett
424 *et al.* (2018) found indirect effects of climate on herbivory in 80 species of evening primroses,
425 which were mediated by leaf chemicals (total phenolics and oenothien A). However, these
426 conclusions need to be considered with caution because the dataset used to test the effect of
427 bottom-up and top-down forces on herbivory along large-scale latitudinal and climatic gradients
428 of the biotic and abiotic models only consisted of a subset of the complete dataset used in the
429 geographic and climatic models.

430 We found no evidence that bird attack rate drove large-scale variability in herbivory. This result
431 is in line with a recent study by Zverev *et al.* (2020) who found that birds are unlikely to shape the
432 spatial patterns of insect herbivory in an Arctic ecosystem. More generally, associations between
433 bird insectivory and insect herbivores can be positive (Mäntylä *et al.*, 2014; Gunnarsson *et al.*,
434 2018), negative (Maguire *et al.*, 2015; Kozlov *et al.*, 2017) or non-significant (Moreira *et al.*, 2019;
435 Valdés-Correcher *et al.*, 2019), depending on the study and methods used. Arthropod predators
436 (e.g. ants, ladybirds) play an important role in limiting herbivore populations and may respond to
437 large-scale variation in climatic conditions at greater extent than vertebrate predators (Roslin *et al.*,
438 2017; Zvereva *et al.*, 2019). For example, a meta-analysis conducted by Rodríguez-Castañeda
439 (2013) found that ant predation on herbivores significantly increase at higher temperatures and
440 precipitations, indicating that plants growing under warmer and wetter conditions exhibit lower
441 levels of herbivory. Besides, birds are considered intraguild predators that not only eat insect
442 herbivores but also arthropod predators (Gunnarsson, 2007) and intraguild predation may
443 weaken herbivore suppression (Finke & Denno, 2005). Unfortunately, we were not able to
444 quantify predation rates by such arthropods nor intraguild predation, which weakens our
445 conclusions about the potential role of predators across climatic gradients.

446 **Conclusion** — By simultaneously investigating bottom-up and top-down forces driving herbivory
447 along latitudinal and climatic clines in a widespread tree species in Europe, this study brings some
448 new insights into the vivid debate about latitudinal variation in the direction and strength of biotic
449 interactions (Schemske *et al.*, 2009; Moles *et al.*, 2013; Anstett *et al.*, 2016; Roslin *et al.*, 2017).
450 We found no evidence that latitude or climate influenced insect herbivores feeding on oaks, but
451 we found that climatic factors rather than latitude *per se* were the best predictors of the large-
452 scale variation in the incidence of leaf-miner and gall-inducer herbivores as well as in variation in
453 leaf nutritional content. In sharp contrast, we found no evidence that plant chemical defences
454 and bird attack rates were influenced by latitude or climatic factors, which conflicts with the
455 dominant view in ecology (Moles & Ollerton, 2016; Roslin *et al.*, 2017; Zvereva *et al.*, 2019).
456 Because unravelling causes of latitudinal variation in the strength of biological interactions is one
457 of the common approaches for the prediction of biotic interactions under global warming
458 (Verheyen *et al.*, 2019), it is crucial that future studies simultaneously test for effects of latitude

459 *per se* and climate on herbivory by different feeding guilds (Kozlov *et al.*, 2017), as well as
460 investigate the complexity of biotic interactions in which plant-herbivores interactions are
461 embedded.

462 Data accessibility

463 The datasets supporting this article are available
464 via an open-access repository (<https://doi.org/10.5061/dryad.18931zdw0>).

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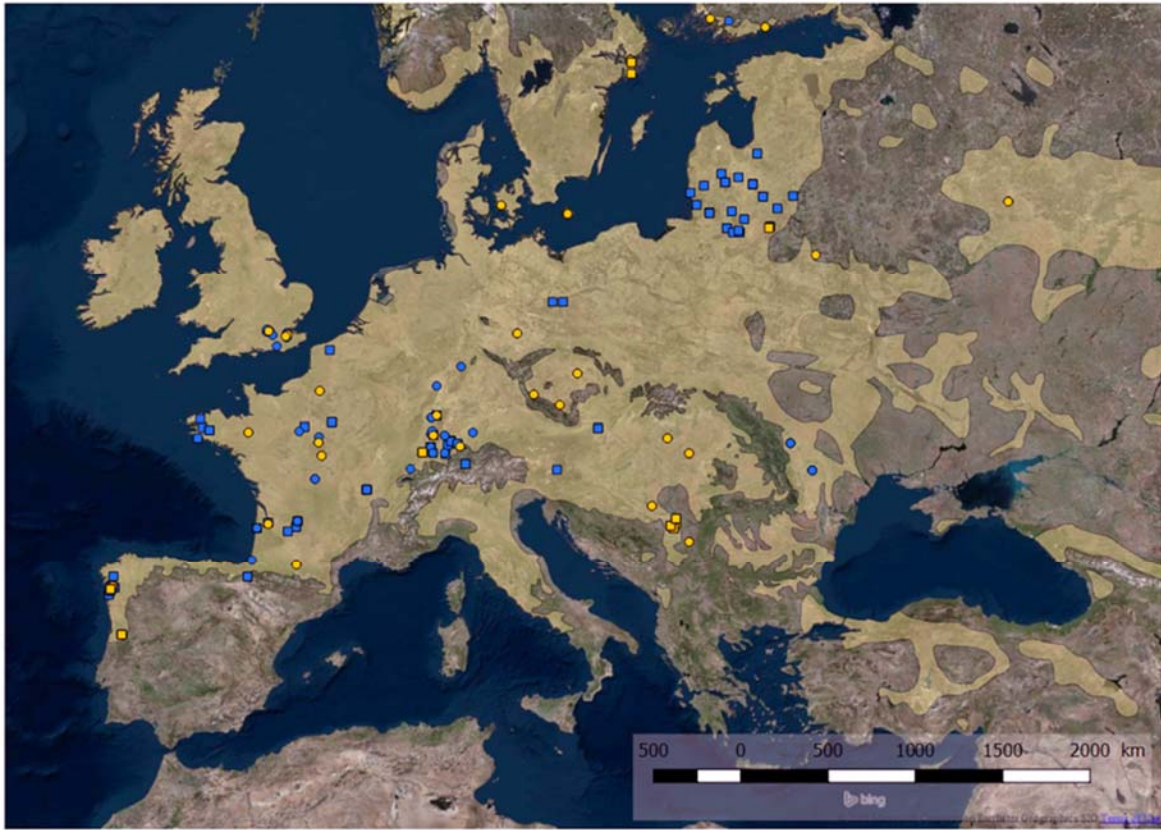
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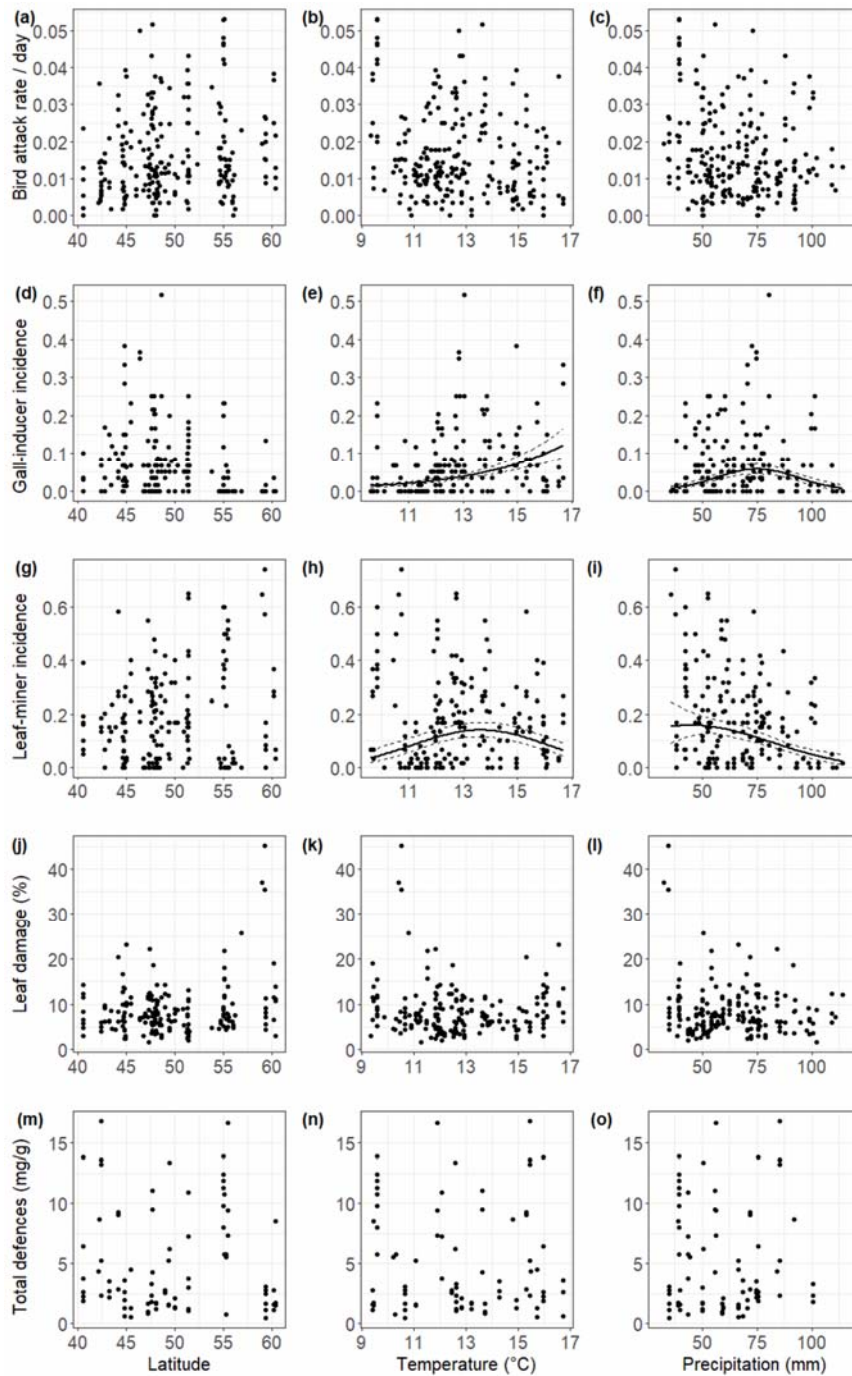
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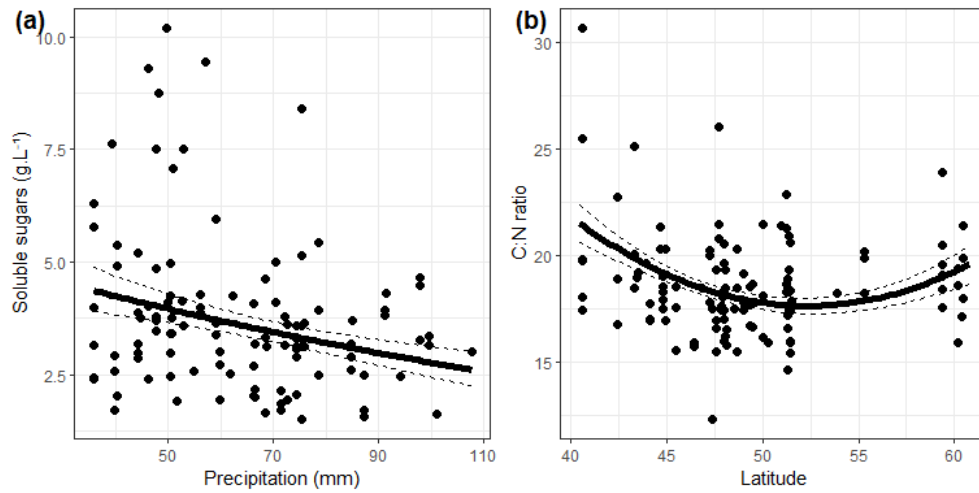
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726 **Figure 1.** Distribution range of *Quercus robur* L. (shaded in yellow) and locations of trees sampled by professional
727 scientists (orange symbols, 30 sites) and schoolchildren (blue symbols, 82 sites) in 2018 (circles, 57 sites) and 2019
728 (squares, 55 sites). Additional maps showing oak trees used for estimating leaf herbivory, attack rates on dummy
729 caterpillars and trait analyses are provided in supplementary material (Figure S1.1).



730

731 **Figure 2. Effects of Latitude, mean spring temperature and mean spring precipitation on bird attack rates (a, b, c),**
 732 **gall-inducers incidence (d, e, f), leaf-miners incidence (g, h, i), leaf damage (j, k, l) and total phenolics (m, n, o). Dots**
 733 **represent raw data averaged at the tree level. Solid and dashed lines represent model predictions (and corresponding**
 734 **standard error) calculated after other significant variables (see Table S2.1) were set to their mean value. Only**
 735 **statistically significant relationships are shown. Regression line equations are as follows: e, $y = -3.32 + 0.44 \cdot x$; f, $y =$**
 736 **$-3.32 + 0.32 \cdot x - 0.51 \cdot x^2$; h, $y = -1.98 + 0.37 \cdot x - 0.36 \cdot x^2$; i, $y = -1.98 - 0.44 \cdot x$.**



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738 **Figure 3. Effect of mean spring precipitation and latitude on soluble sugar (a) and C:N ratio (b) on leaves,**
 739 **respectively.** Dots represent raw data averaged at tree level. Solid and dashed lines represent model predictions
 740 (and corresponding standard error) for temperature and latitude calculated after other significant variables (see
 741 Table S2.2) were set to their mean value. Only significant relationships are shown. Regression line equations are as
 742 follows: **a**, $y = 1.53 - 0.10 \cdot x$; **b**, $y = 17.9 - 0.86 \cdot x + 0.70 \cdot x^2$.

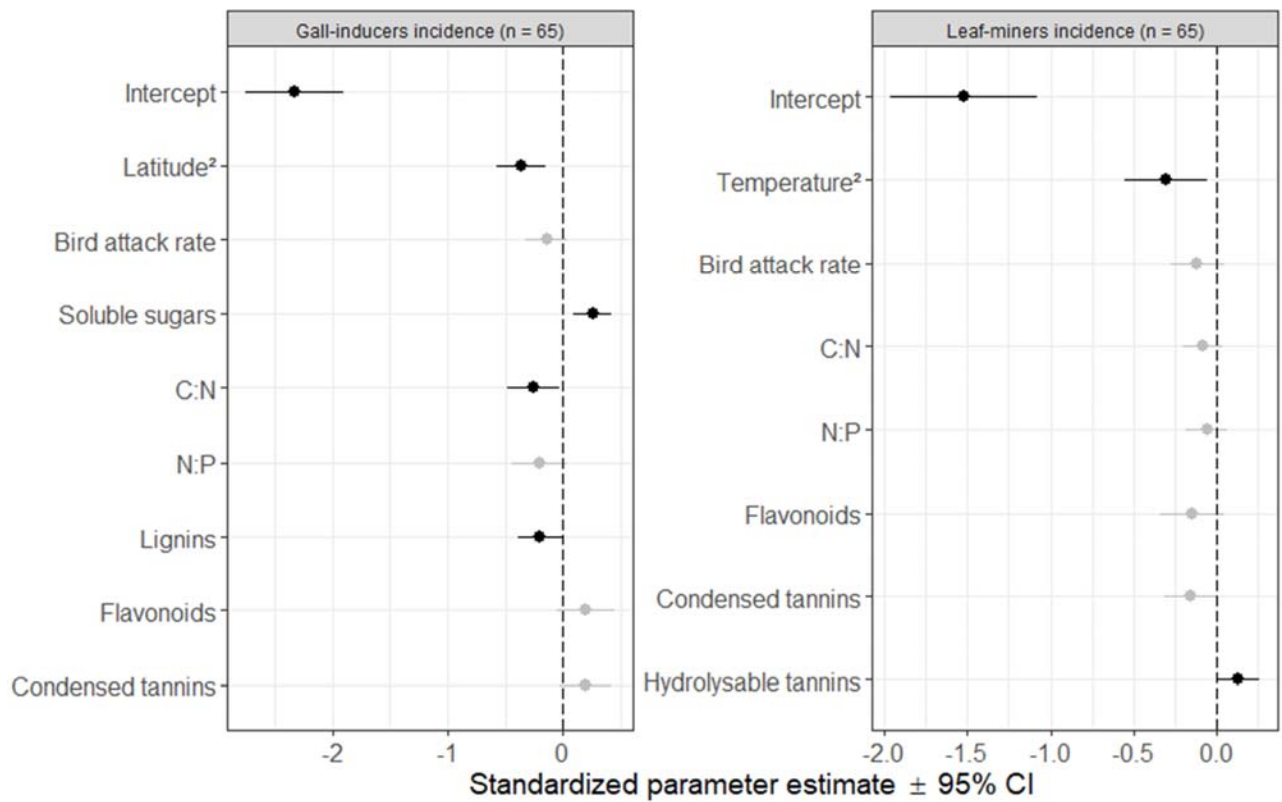
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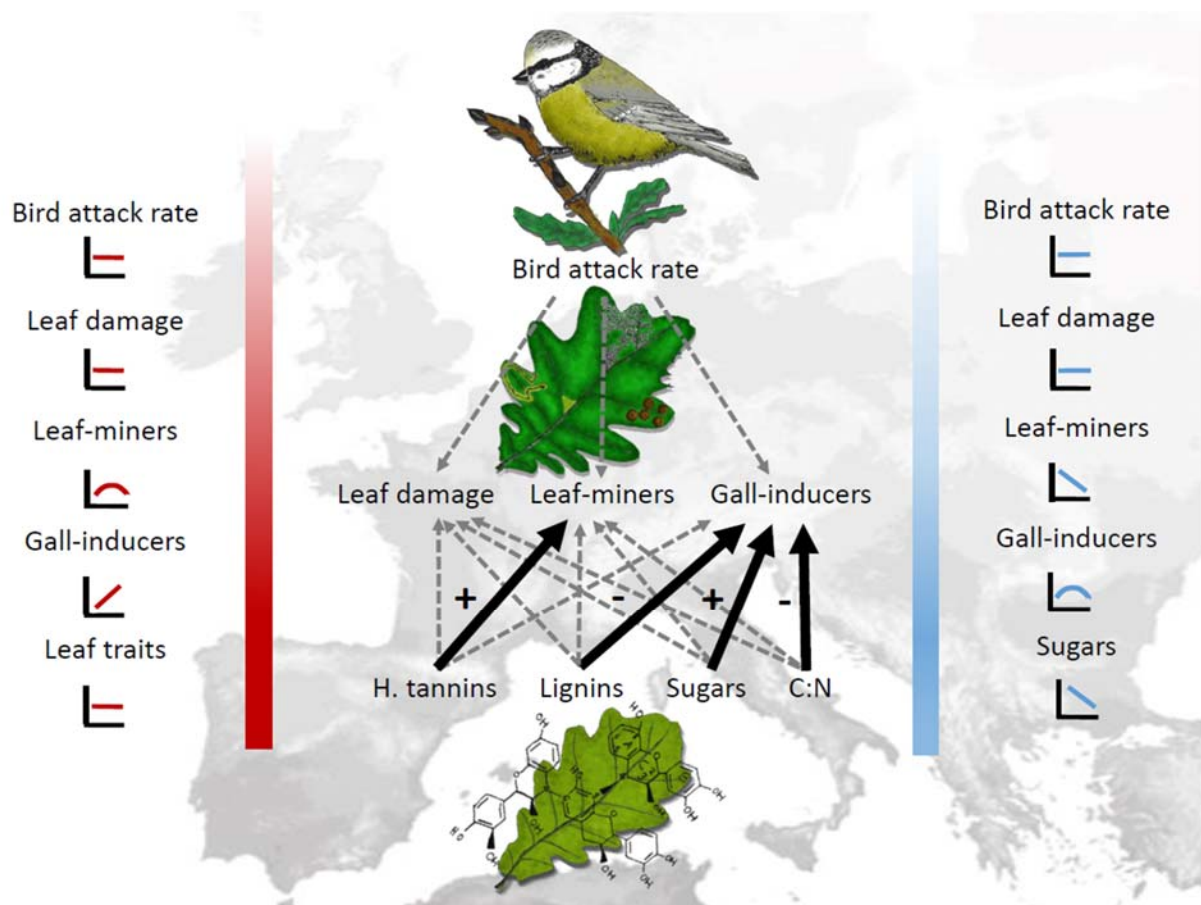
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750 **Figure 4. Effects of latitude, mean spring temperature, mean spring precipitation and leaf chemistry on gall-inducer**
 751 **(left) and leaf-miner (right) incidences.** Circles and error bars represent standardized parameter estimates and
 752 corresponding 95% CI. The vertical dashed line centred on zero represents the null hypothesis. Black and grey circles
 753 represent significant and non-significant effect sizes, respectively.

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758 **Figure 5.** Summary illustrating plant-herbivore-predator relationships along a latitudinal gradient in Europe. The red
 759 and blue bands denote the variation in mean spring temperature and precipitation, respectively. The five figures on
 760 the left represent the correlation between the mean spring temperature and bird attack rate, leaf damage, the
 761 incidence of gall-inducers and leaf-miners and leaf traits. The five figures on the right correspond with the correlation
 762 between mean spring precipitation and bird attack rate, leaf damage, the incidence of leaf-miners and gall-inducers
 763 and the concentration of soluble sugar in leaves. Solid black arrows represent significant positive (+) or negative (-)
 764 relationships; dashed grey lines indicate non-significant relationships.

765

766 **Figure S1.1.** Location of the trees sampled for the assessment of herbivory (a), predation attack rate (b), leaf
 767 nutritional content (c) and leaf defences (d). An interactive version of these maps are also included in the
 768 supplementary material as Figures S1.1a, S1.1b, S1.1c and S1.1D.

769 Interactive version of the maps:

770 **Figure S1.1a.** Trees sampled for the assessment of herbivory.

771 **Figure S1.1b.** Trees sampled for the assessment of predation attack rate.

772 **Figure S1.1c.** Trees sampled for the assessment of leaf nutritional content.

773 **Figure S1.1d.** Trees sampled for the assessment of leaf defences.

774 **Figure S1.2.** Effects of partner type, year, mean spring temperature and mean spring precipitation on gall-inducers
775 and leaf-miners incidences. Circles and error bars represent standardized parameter estimates and corresponding
776 95% CI. The vertical dashed line centered on zero represents the null hypothesis. Black and grey circles indicate
777 significant and non-significant effect sizes, respectively.

778 **Figure S1.3.** Importance of every variable (RVI) included in the geographic and climatic models that considered the
779 effect of longitude, latitude, temperature and precipitation on herbivory (gall-inducers and leaf-miners incidences;
780 $n = 182$) and on leaf chemistry (soluble sugar and C:N ratio; $n = 114$).

781 **Figure S1.4.** Importance of every variable (RVI) included in the biotic model that considered the effect of leaf traits,
782 bird attack rate, climatic variables on gall-inducers and leaf-miners incidence ($n = 65$).

783 **Table S1.1.** Summary of the different variables measured.

784 **Table S2.1.** Summary of model coefficient parameter estimates (i.e., effect sizes), degrees of freedom (df), log-
785 likelihood, AICc, Δ AICc, AICc weight (w_i) and the variance explained by fixed ($R2m$) and fixed plus random factors
786 ($R2c$) of the different climatic models. The gradient of colours from red to green corresponds to the effect size,
787 from large negative (red) to large positive (green) effect sizes. The set of models competing with the best model
788 within 2 units of Δ AICc is highlighted in bold font. *Partner type* is the effect of partner type (the estimate for
789 schoolchildren being compared with the estimate for professional scientists that was included in the intercept) and
790 *Year* is the effect of each year (2019 contrasted with 2018).

791 **Table S2.2.** Summary of model coefficient parameter estimates (i.e., effect sizes), degrees of freedom (df), log-
792 likelihood, AICc, Δ AICc, AICc weight (w_i) and the variance explained by fixed ($R2m$) and fixed plus random factors
793 ($R2c$) of the different climatic models. The gradient of colours from red to green corresponds to the effect size,
794 from large negative (red) to large positive (green) effect sizes. The set of models competing with the best model
795 within 2 units of Δ AICc is highlighted in bold font.

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