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

Elena Valdés-Correcher¹ | Xoaquín Moreira² | Laurent Augusto³ | Luc Barbaro^{4,5} | Christophe Bouget⁶ | Olivier Bouriaud⁷ | Manuela Branco⁸ | Giada Centenaro⁹ | György Csóka¹⁰ | Thomas Damestoy¹ | Jovan Dobrosavljević¹¹ | Mihai-Leonard Duduman⁷ | Anne-Maïmiti Dulaurent¹² | Csaba B. Eötvös¹⁰ | Maria Faticov¹³ | Marco Ferrante^{14,15} | Ágnes Fürjes-Mikó¹⁰ | Andrea Galmán² | Martin M. Gossner¹⁶ | Arndt Hampe¹ | Deborah Harvey¹⁷ | Andrew Gordon Howe¹⁸ | Yasmine Kadiri¹ | Michèle Kaennel-Dobbertin¹⁶ | Julia Koricheva¹⁷ | Alexander Kozel¹⁹ | Mikhail V. Kozlov²⁰ | Gábor L. Lövei¹⁴ | Daniela Lupaştean⁷ | Slobodan Milanović^{11,21} | Anna Mrazova^{22,23} | Lars Opgennoorth^{24,25} | Juha-Matti Pitkänen²⁶ | Anna Popova²⁰ | Marija Popović¹¹ | Andreas Prinzing²⁷ | Valentin Queloz¹⁶ | Tomas Roslin²⁶ | Aurélien Sallé²⁸ | Katerina Sam^{22,23} | Michael Scherer-Lorenzen²⁹ | Andreas Schuldt³⁰ | Andrey Selikhovkin^{31,32} | Lassi Suominen³³ | Ayco J. M. Tack¹³ | Marketa Tahadlova^{22,23} | Rebecca Thomas¹⁷ | Bastien Castagneyrol¹

¹BIOGECO, INRAE, University Bordeaux, Cestas, France²Misión Biológica de Galicia (MBG-CSIC), Pontevedra, Spain³INRAE, Bordeaux Sciences Agro, UMR 1391 ISPA, Villenave-d'Ornon Cedex, France⁴DYNAFOR, University of Toulouse, INRAE, Castanet-Tolosan, France⁵CESCO, Sorbonne University, MNHN, CNRS, Paris, France⁶Forest Ecosystems' Research Unit – Biodiversity team Domaine des Barres, INRAE, Nogent-sur-Vernisson, France⁷Applied Ecology Laboratory, Forestry Faculty, "Ştefan cel Mare, University of Suceava, Suceava, Romania⁸Instituto Superior de Agronomia, Centro de Estudos Florestais, Universidade de Lisboa, Tapada de Ajuda, Portugal⁹Department of Land, Environment, Agriculture and Forestry, University of Padova, Legnaro, Italy¹⁰Department of Forest Protection, NARIC Forest Research Institute, Mátrafüred, Hungary¹¹Faculty of Forestry, University of Belgrade, Belgrade, Serbia¹²UniLaSalle, AGHYLE, UP.2018.C101, SFR Condorcet FR CNRS 3417, Beauvais, France¹³Department of Ecology, Environment and Plant Sciences, Stockholm University, Stockholm, Sweden¹⁴Department of Agroecology, Flakkebjerg Research Centre, Aarhus University, Slagelse, Denmark¹⁵Azorean Biodiversity Group, cE3c – Centre for Ecology, Evolution and Environmental Changes, University of the Azores, Azores, Portugal¹⁶Forest Entomology, Swiss Federal Research Institute WSL, Birmensdorf, Switzerland¹⁷Department of Biological Sciences, Royal Holloway University of London, Egham, UK¹⁸Department of Geosciences and Natural Resource Management, University of Copenhagen, Frederiksberg, Denmark¹⁹Department of Forest Protection and Wood Science, Belarusian State Technological University, Minsk, Belarus²⁰Department of Biology, University of Turku, Turku, Finland²¹Faculty of Forestry and Wood Technology, Mendel University, Brno, Czech Republic²²Entomology Institute, Biology Centre of Czech Academy of Sciences, Ceske Budejovice, Czech Republic²³Faculty of Science, University of South Bohemia, Ceske Budejovice, Czech Republic²⁴Biodiversity and Conservation Biology, Ecological Genetics, Swiss Federal Research Institute WSL, Birmensdorf, Switzerland

²⁵Department of Ecology, Philipps-Universität Marburg, Marburg, Germany

²⁶Department of Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden

²⁷Research Unit "Ecosystems, Biodiversity, Evolution", Centre National de la Recherche Scientifique, Rennes, France

²⁸Laboratoire de Biologie des Ligneux et des Grandes Cultures, INRAE, Université d'Orléans, Orléans, France

²⁹Geobotany, Faculty of Biology, University of Freiburg, Freiburg, Germany

³⁰Forest Nature Conservation, Georg-August-University Göttingen, Göttingen, Germany

³¹St. Petersburg Forest Technical University, St. Petersburg, Russia

³²St. Petersburg State University, St. Petersburg, Russia

³³Salo Upper Secondary School, Salo, Finland

Correspondence

Elena Valdés-Correcher and Bastien Castagnérol, BIOGECO, INRAE, Univ. Bordeaux, 33610 Cestas, France.
Email: elena.valdes.correcher@gmail.com (E. V.-C.) and bastien.castagnérol@inrae.fr (B. C.)

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Abstract

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

Location: Europe.

Time period: 2018–2019.

Major taxa studied: *Quercus robur*.

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

Results: Climatic factors rather than latitude per se were the best predictors of the large-scale (geographical) variation in the incidence of gall-inducers and leaf-miners as well as in leaf nutritional content. However, leaf damage, plant chemical defences (leaf phenolics) and bird attack rates were not influenced by climatic factors or latitude. The incidence of leaf-miners increased with increasing concentrations of hydrolysable tannins, whereas the incidence of gall-inducers increased with increasing leaf soluble sugar concentration and decreased with increasing leaf C : N ratios and lignins. However, leaf traits and bird attack rates did not vary with leaf damage.

Main conclusions: These findings help to refine our understanding of the bottom-up and top-down mechanisms driving geographical variation in plant–herbivore interactions, and indicate the need for further examination of the drivers of herbivory on trees.

KEYWORDS

artificial prey, avian insectivory, climate, leaf chemistry, plant defences

1 | INTRODUCTION

Ecological theory predicts that the strength of species interactions increases toward the Equator due to warmer temperatures, longer

growing seasons, and higher species abundance and diversity at lower latitudes (Janzen, 1970; Schemske et al., 2009). Plant species at lower latitudes commonly experience higher rates of herbivory than plants growing further from the Equator (Coley & Barone, 1996;

Lim et al., 2015; Moreira et al., 2018; Schemske et al., 2009) and thus tropical plant species may evolve higher levels of anti-herbivore defences (Abdala-Roberts et al., 2016; Hahn et al., 2019; Johnson & Rasmann, 2011; Pearse & Hipp, 2012). While early reviews reported patterns supporting these predictions (Coley & Aide, 1991; Coley & Barone, 1996; Dyer & Coley, 2002), several studies in recent decades have found either no evidence for a latitudinal gradient in herbivory and plant defences (Gaston et al., 2004; Moles et al., 2011; Moles & Westoby, 2003) or increase in herbivory and defences with latitude (Adams et al., 2009; Del-Val & Armesto, 2010; Gaston et al., 2004; Martz et al., 2009; Moreira et al., 2018, 2020; Pennings et al., 2009; Stark et al., 2008; Woods et al., 2012). Given these inconsistencies, it is of great importance to identify the mechanisms underlying the substantial variation in herbivory and plant defences across latitudes, as herbivory is an important ecological process that modulates primary productivity by altering the recruitment, mortality and growth of plants.

Latitudinal gradients can be used as 'natural laboratories' to study the relationship between climate and plant-herbivore interactions (De Frenne et al., 2013; Kozlov et al., 2015; Lim et al., 2015; Moreira et al., 2018). In the extratropical northern hemisphere, mean annual temperature drops by 0.73°C and mean annual precipitation by 4.04 mm per degree of latitude northward (De Frenne et al., 2013). Latitudinal variation in plant-herbivore interactions is therefore generally associated with large-scale variability in climatic conditions (Moreira et al., 2018) and numerous studies demonstrate an effect of temperature and precipitation on plant traits (e.g., leaf N, phenolic compounds; Chen et al., 2013; Gely et al., 2019; Holopainen et al., 2018) and herbivory (Gely et al., 2019; Jamieson et al., 2015). However, many regions deviate from the global trend in temperature and precipitation toward higher latitudes due to their proximity to oceans or the presence of mountains (De Frenne et al., 2013), which can markedly change the relationship between latitude and plant-herbivore-predator interactions (Loughnan & Williams, 2019; Moreira et al., 2019; Roslin et al., 2017).

Recent work identified several potential sources of variation in the reported directions and strengths of latitudinal gradients in herbivory and plant defences (Anstett et al., 2016; Johnson & Rasmann, 2011). First, theory on latitudinal gradients in herbivory and plant defences assumes a plant-centred equilibrium in which plants at low latitudes have adapted to higher herbivory levels by evolving stronger defences. However, most studies have measured either herbivory patterns or plant defences, but not both (but see Anstett et al., 2015; Moreira et al., 2018), leading to an incomplete understanding of the relationship between latitudinal clines and plant-herbivore interactions. Second, little attention has been paid to latitudinal variation in tritrophic dynamics (Roslin et al., 2017). Herbivore-natural enemies, however, can drastically modify tritrophic interactions by suppressing herbivore populations or reducing herbivore feeding (Maguire et al., 2015; Rosenheim, 1998). In the few published studies exploring latitudinal patterns in natural enemy activity, authors have found no variation in parasitism (Dyer & Coley, 2002; Moreira et al., 2015), lower attack rates on artificial

prey by ants (Roslin et al., 2017), and higher (Zvereva et al., 2019) or no variation (Roslin et al., 2017) in attack rates on artificial prey by birds with increasing latitude. Third, while external feeders are directly exposed to enemies and adverse abiotic conditions, internal feeders (e.g., leaf-mining and gall-inducing insect herbivores) benefit from a buffered microhabitat and relative protection against enemies. It is therefore likely that latitudinal trends in tritrophic interactions would vary across herbivore feeding guilds. Thus, considering bottom-up and top-down forces simultaneously could be crucial for a comprehensive understanding of latitudinal clines in tritrophic interactions.

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

2 | MATERIAL AND METHODS

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

2.1 | Target species

The pedunculate oak is one of the dominant deciduous tree species in European forests and is of high ecological, economic and symbolic importance (Eaton et al., 2016). Its distribution ranges from central Spain (39°N) to southern Fennoscandia (62°N), thus this species experiences variable climatic conditions (Petit et al., 2002). Pedunculate oak supports a large community of specialist and generalist herbivorous insects; especially suckers, chewers, skeletonizers, gall-inducers and leaf-miners (Moreira

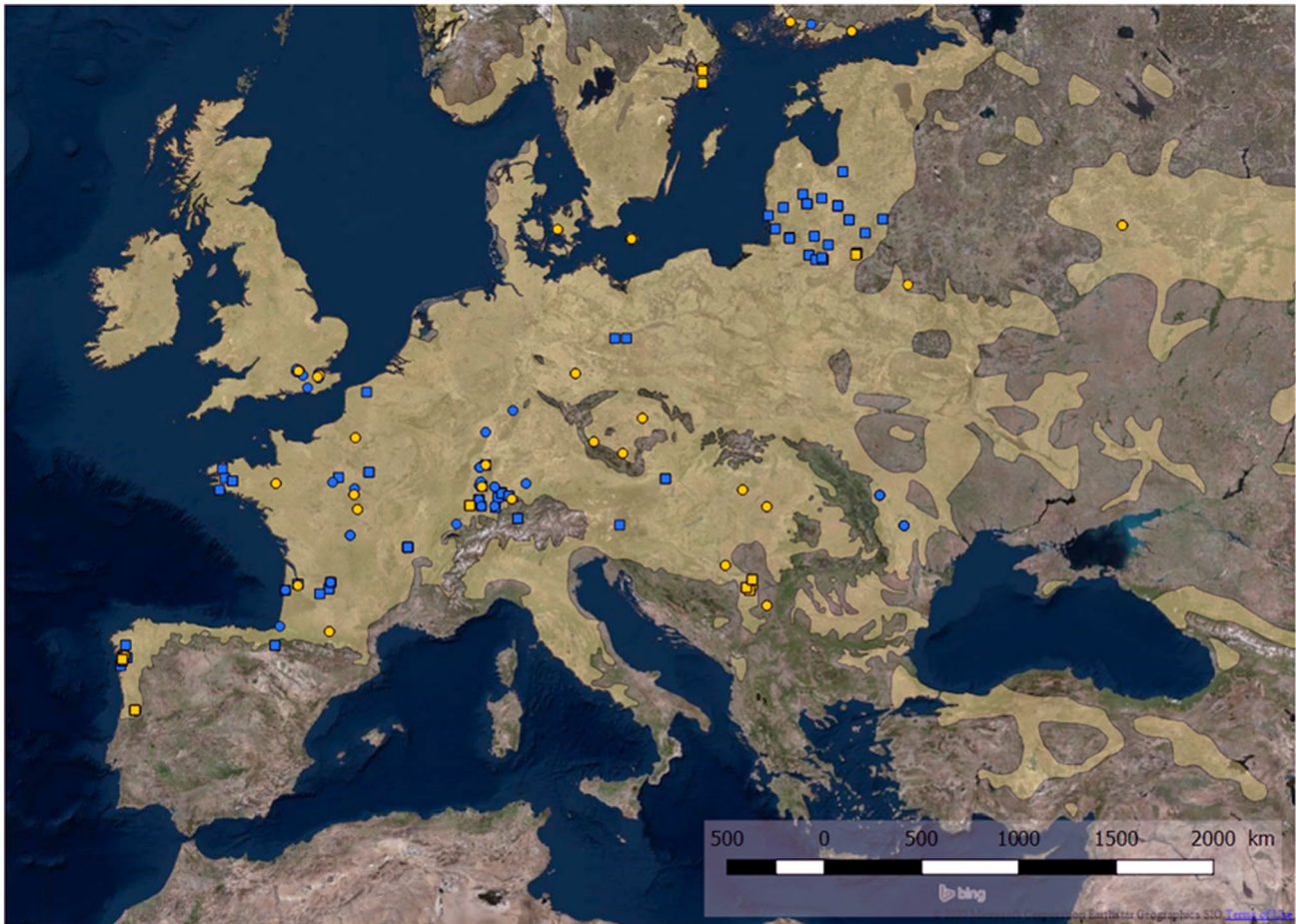


FIGURE 1 Distribution range of *Quercus robur* L. (shaded in yellow) and locations of trees sampled by professional scientists (orange symbols) and schoolchildren (blue symbols) in 2018 (circles) and 2019 (squares). Additional maps showing oak trees used for estimating leaf herbivory, attack rates on dummy caterpillars and trait analyses are provided in Supporting Information Figure S1.1

et al., 2018; Southwood et al., 2005), as well as xylophagous species (Marković & Stojanović, 2011). The wide distribution of pedunculate oak and the high diversity of associated herbivorous insects make it a suitable model species for research on the effect of climate on biotic interactions.

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

2.2 | Attack rates on dummy caterpillars

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

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

In order to be consistent and reduce bias due to multiple observers, photos and dummy caterpillars were screened by a single trained observer (first author, EVC). For each oak tree and survey period, we assessed attack rate as the proportion of dummy caterpillars with at least one attack mark. Although we asked partners to record attack rate marks left by different types of predators (in particular birds and arthropods), attacks by arthropod predators could not be verified on photos because of their low resolution. In addition, the

relevance of marks left by arthropods on plasticine model prey has recently been questioned, in particular after mandibular marks were observed on lizard or frog models (Rößler et al., 2018). For these reasons, we decided to discard arthropod attack rate from the study and focused on marks that were unambiguously attributed to birds, that is, conic holes or V-shaped beak marks. Attack marks left by reptiles or rodents were also disregarded, because only a few caterpillars were attacked by these potential predators. Most bird marks were directed towards the head or the body centre of the dummy caterpillars, which is typical of bird attacks and indicates prey recognition (Rößler et al., 2018). We therefore refer to the proportion of dummy caterpillars with such marks as bird attack rate.

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

2.3 | Leaf herbivory

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

We used three response variables to characterize leaf herbivory: leaf damage (the percentage of leaf area that was consumed or mined by insect herbivores), incidence of leaf-miners (the proportion of leaves with leaf-mines) and incidence of gall-inducers (the proportion of leaves with galls). For each leaf, we visually assessed leaf damage (attributed to ectophagous chewing and leaf-mining organisms) following eight levels of defoliation (0, >0–5, >5–10, >10–15, >15–25, >25–50, >50–75 and >75%). We then averaged leaf damage at the tree level using the midpoint of each percentage class to obtain a mean value per tree. While this measurement also included the surface covered by leaf mines (i.e., internally chewed by mining larvae), it excluded both galls and punctures made by sap feeders. Leaf assessment was made by two trained observers who were blind to leaf origin to reduce unconscious bias. We expect that most of the leaf damage will be attributable to insects, as in our experience, mollusc herbivory (e.g., snails and slugs), although possible, is rare in adult oak trees. As for mites, they mostly cause discolouration that can easily be differentiated from insect herbivory. There are also a few mammals that consume oak leaves, mostly rodents and ungulates, but usually they mostly consume seedlings and saplings.

2.4 | Leaf chemical traits

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

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

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

2.5 | Statistical analysis

We were primarily interested in testing the effect of latitude on herbivory and in identifying the underlying ecological forces. We aimed to test whether the effect of latitude was driven by latitudinal gradients in climatic conditions, and by their direct and indirect consequences on leaf chemistry, herbivory and bird attack rate. We obtained temperature and precipitation data from the WorldClim database (Hijmans et al., 2005) based on oak coordinates as retrieved on Google Maps by project partners. Specifically, we extracted the mean temperature and precipitation from April to June, which roughly corresponded to the period when caterpillars were present on trees, irrespective of latitudinal cline in moth phenology. Yet, latitude was correlated with both temperature (Pearson's $r = -.85$) and precipitation ($r = -.72$). To avoid spurious estimates of model coefficients caused by collinearity among predictors, we tested the effects of latitude and climate separately.

Specifically, we built three types of linear mixed-effects models (LMMs): (a) geographical models analysing the effect of latitude on herbivory, leaf chemistry and bird attack rate, (b) climatic models in which we substituted latitude with climatic data (temperature and precipitation) and (c) abiotic and biotic models analysing the effects

of leaf chemistry and bird attack rate together with temperature and precipitation or latitude (both linear and quadratic) on herbivory. As latitudinal gradients in plant-herbivore interactions can be nonlinear (following Rodríguez-Castañeda, 2013 and Kozlov et al., 2015), we complemented our linear analyses with quadratic models. As leaf chemistry was only measured on a subset of trees ($n = 64$), we used a subsample of the data set to quantify relationships between herbivory and its top-down and bottom-up drivers (Supporting Information Table S1.1).

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

$$Y = \beta_0 + \beta_1 \times \text{Year} + \beta_2 \times \text{Partner} + \beta_3 \times \text{Latitude} + \beta_4 \times \text{Latitude}^2 + \gamma + \varepsilon + \sigma_{\text{Partner ID}}^2$$

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

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

The tree-level response variables for each year and survey period (Y) were either leaf damage (% of leaf area removed and mined by herbivores), the incidence of leaf-miners or gall-inducers (proportions), mean bird attack rate (ratio of % attacked caterpillars on exposition period) or leaf chemistry [C : N ratio, N : P ratio, soluble sugar content (g/L), cellulose content (g), concentrations of condensed or hydrolysable tannins, flavonoids or lignins (mg/g dry matter)]. We scaled and centred every continuous predictor prior to modelling to facilitate comparisons of their effect sizes, and made sure that none of the explanatory variables were strongly correlated using the variance inflation factor (VIF) (all VIFs < 5).

We used LMMs with a Gaussian error distribution, with the exceptions of geographical, climatic and process-based models with the incidence of leaf-miners or gall-inducers as response variables. In these cases, we used generalized LMMs with a binomial error distribution and logit-link.

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

In the Results section, we report the degrees of freedom, log-likelihood, AICc, ΔAICc (delta), w_i and the variance explained by fixed and fixed plus random factors (R^2_m and R^2_c , respectively; Nakagawa & Schielzeth, 2013) for every model, as well as averaged coefficient parameter estimates and RVI for all variables present in the set of competing best models. When appropriate, we plotted the relationship between raw data and explanatory variables together with the predictions of simplified models, holding undisplayed predictors constant. All analyses were run in the R language environment (R Core Team, 2020) with packages *MuMIn* (Bartoń, 2020) and *lme4* (Bates et al., 2015).

3 | RESULTS

3.1 | Latitudinal and climatic gradients in herbivory, leaf chemistry and bird attack rates

Herbivores damaged on average ($\pm SE$) $8.7 \pm 0.4\%$ of leaf area ($n = 182$ trees, see Supporting Information Table S1.1 for details). Model simplification identified the null model as the best model given the model set, indicating that none of the predictors had a consistent effect on leaf damage (Figure 2j-l, Supporting Information Table S2.1).

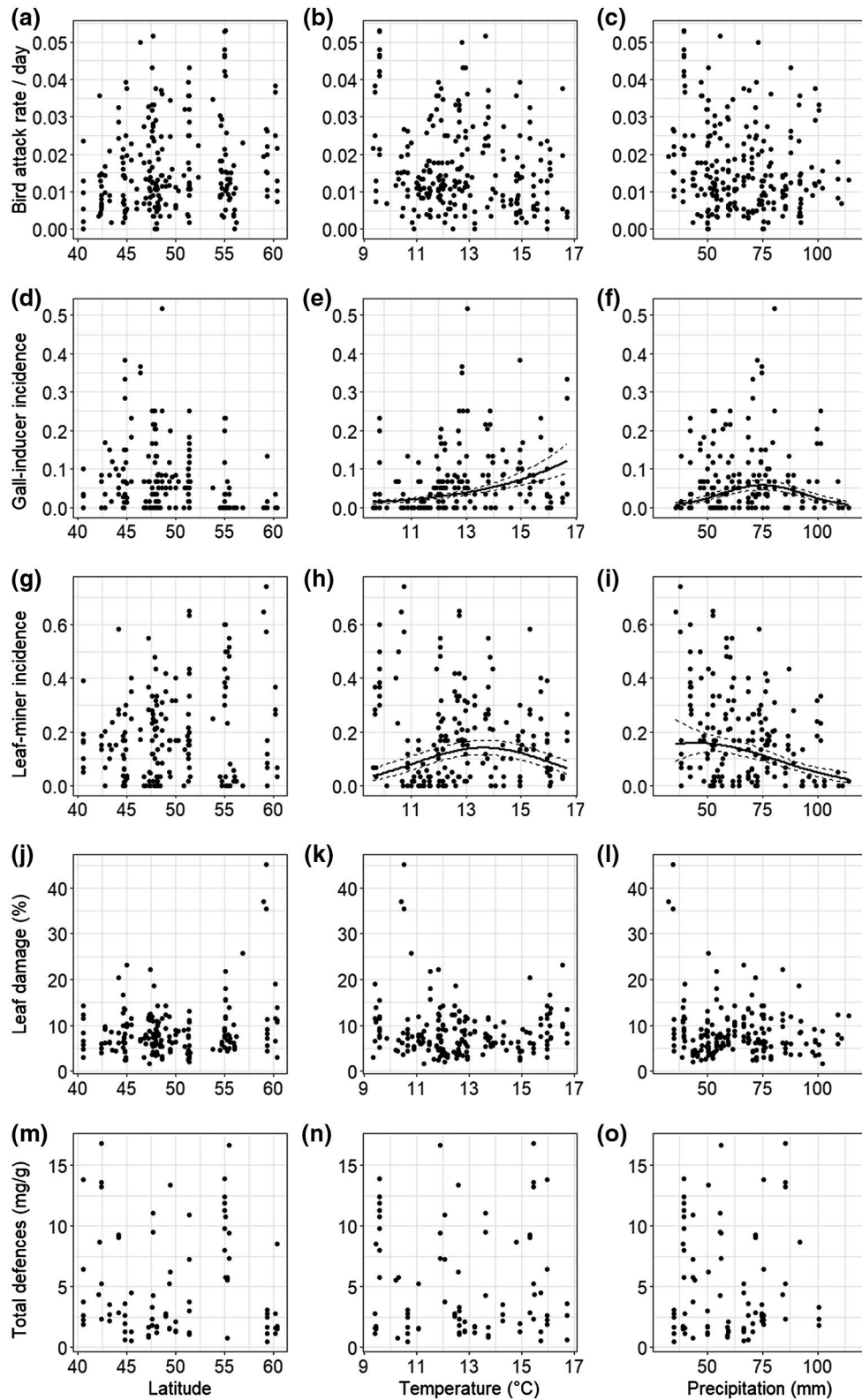


FIGURE 2 Effects of latitude, mean spring temperature and mean spring precipitation on bird attack rates (a, b, c), gall-inducer incidence (d, e, f), leaf-miner incidence (g, h, i), leaf damage (j, k, l) and total defences (m, n, o). Dots represent raw data averaged at the tree level. Solid and dashed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

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

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

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

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

3.2 | Mechanisms underlying latitudinal and climatic variation in herbivory

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

When leaf chemistry was included in the model, the incidence of gall-inducers increased with increasing soluble sugar concentration and decreased with increasing C : N ratio and lignin concentration (Figure 4), whereas the positive relationship between temperature and gall-inducers disappeared. When leaf traits were included in the models, the incidence of gall-inducers increased nonlinearly with increasing latitude. The relative importance of leaf chemistry predictors (RVI = .65) was, however, higher than that of latitude (RVI = .05) or temperature (RVI = .30, Supporting Information Figure S1.4).

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

4 | DISCUSSION

We found no evidence that either herbivory, oak chemical traits or bird attack rates varied with latitude linearly or nonlinearly. Our work therefore supports the growing number of studies that have

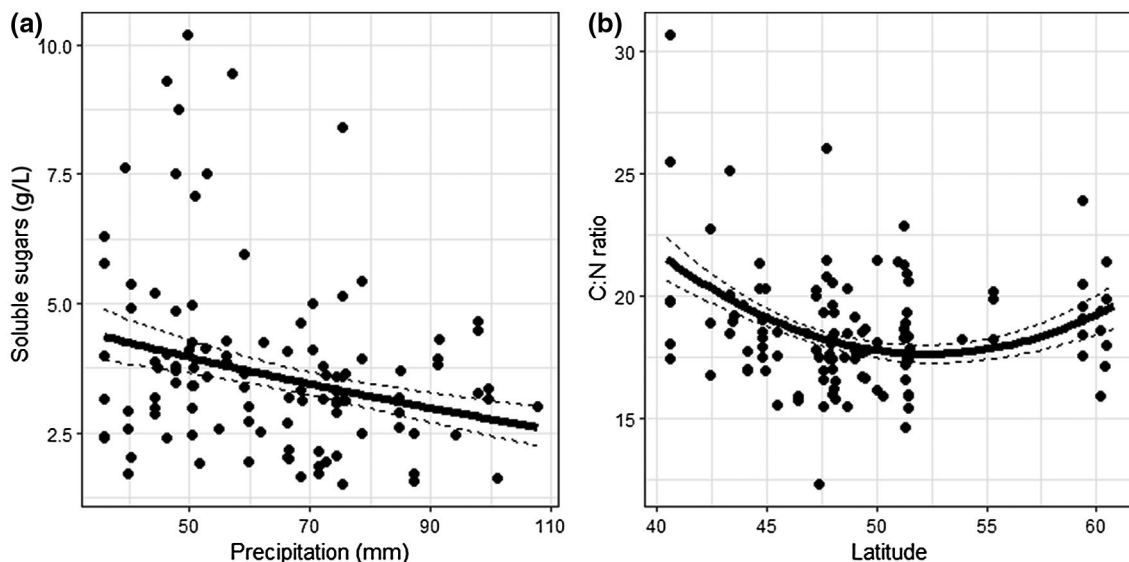


FIGURE 3 Effect of mean spring precipitation and latitude on soluble sugar (a) and C : N ratio (b) on leaves, respectively. Dots represent raw data averaged at tree level. Solid and dashed lines respectively represent model predictions and corresponding standard error for temperature and latitude calculated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

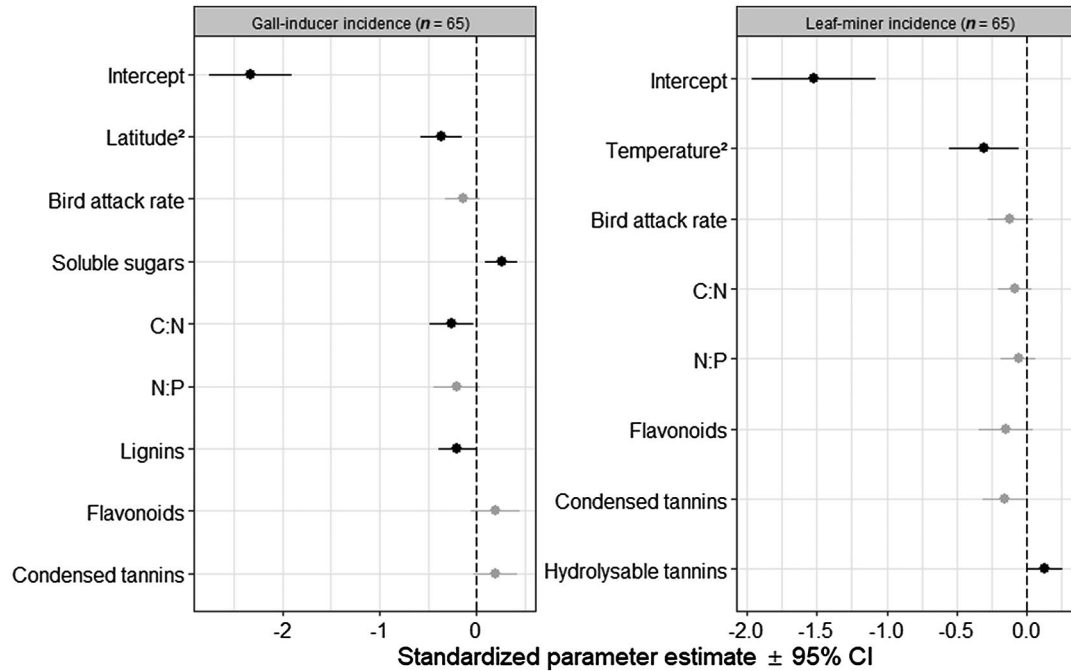


FIGURE 4 Effects of latitude, mean spring temperature, mean spring precipitation and leaf chemistry on gall-inducer (left) and leaf-miner (right) incidences. Circles and error bars represent standardized parameter estimates and corresponding 95% confidence intervals (CI), respectively. The vertical dashed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

recently questioned the common view that biotic interactions are generally stronger at lower latitudes (Moles et al., 2011; Mottl et al., 2020). Several arguments may explain the absence of latitudinal patterns in herbivory or plant defences. On the one hand, Moles and Ollerton (2016) argued that the latitudinal herbivory-defence hypothesis should simply be dismissed because it is not convincingly supported despite decades of research. On the other hand, Anstett et al. (2016) called for a refinement of the concepts and methods in the field. We align with the latter perspective and henceforth discuss ecological sources of variation that may have obscured latitudinal patterns, and argue these could be real rather than methodological artefacts.

4.1 | Herbivory responded to climate rather than to latitude, but in a guild-specific manner

Variation in the incidence of gall-inducers and leaf-miners, but not in leaf damage, was associated with variation in temperature and precipitation, rather than with latitude per se (Anstett et al., 2018; Loughnan & Williams, 2019; Moreira et al., 2018). The absence of a climatic or geographical effect on leaf damage is in line with previous reviews and meta-analyses that have shown herbivory does not vary consistently along climatic or geographical gradients (Moles et al., 2011; Moles & Ollerton, 2016). Our analysis suggests that different herbivore species or guilds may be differently affected by abiotic conditions, such that grouping different types of herbivores may prevent the detection of patterns for each

herbivore type (Abdala-Roberts et al., 2015; Anstett et al., 2016; Moreira et al., 2015).

In line with this explanation, we found that the incidence of gall-inducers and leaf-miners was associated with broad-scale climatic conditions. Specifically, the incidence of both gall-inducers and leaf-miners increased with increasing temperature, but the shape of this relationship was accelerating for gall-inducers and decelerating (i.e., convex) for leaf-miners (Figure 5). Although we did not identify species of leaf-miners, this result is in line with that of Kozlov et al. (2013) who found that in northern Europe, the diversity of leaf-miners on birch trees increased linearly toward lower latitudes and was most likely associated with the direct impact of temperature, especially during cold years. We also found that the incidence of gall-inducers peaked at intermediate precipitation (Blanche & Ludwig, 2001; Leckey et al., 2014), whereas leaf-miners decreased significantly with precipitation. It has been hypothesized that endophagous feeding modes such as galling and mining have evolved partly as adaptations to abiotic factors such as UV radiation and desiccation (Connor et al., 1997; Danks, 2002; Fernandes & Price, 1992). If so, gall-inducers and leaf-miners may be expected to be more common in the warmest and driest parts of the pedunculate oak range and at low latitudes where the light intensity is markedly higher (Cuevas-Reyes et al., 2004; Fernandes & Price, 1992; Lara & Fernandes, 1996; Price et al., 1998). However, even within the gall-inducer and leaf-miner groups, relationships to climate are highly variable among species and years (Blanche, 2000; Kozlov et al., 2013, 2016; Sinclair & Hughes, 2010), thus suggesting that other factors are

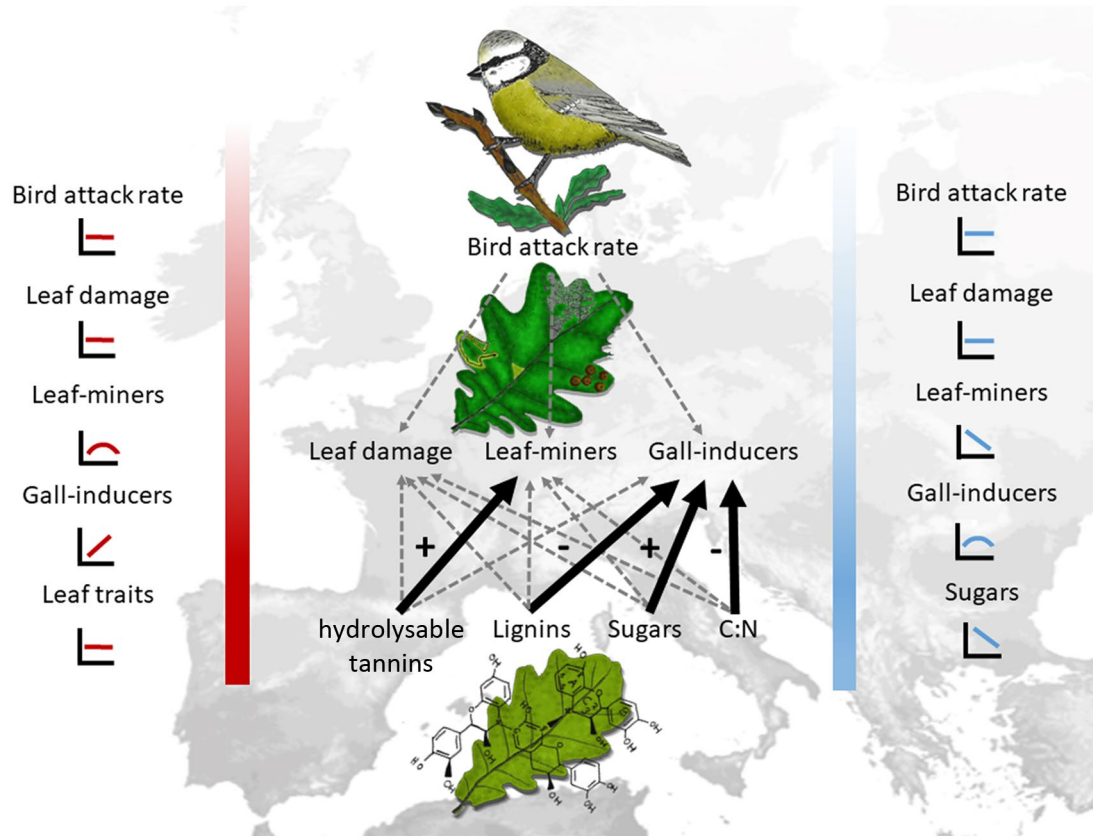


FIGURE 5 Summary illustrating plant-herbivore-predator relationships along a latitudinal gradient in Europe. The red and blue bands denote the variation in mean spring temperature and precipitation, respectively. The five figures on the left represent the correlation between the mean spring temperature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

also important in the incidence of gall-inducers and leaf-miner herbivores.

4.2 | Leaf chemical traits had an inconsistent response to latitude and climate

We did not find detectable latitudinal and climatic gradients in plant chemical defences. This contradicts the latitudinal herbivory-defence hypothesis, which predicts that plant species at lower latitudes experience higher mean rates of herbivory than their temperate counterparts (Coley & Barone, 1996; Lim et al., 2015; Schemske et al., 2009) and, for this reason, should have evolved higher levels of anti-herbivore defences (Pearse & Hipp, 2012; Rasmann & Agrawal, 2011). However, the generality of this hypothesis is currently under debate (Moles & Ollerton, 2016). Several studies found no evidence for a latitudinal gradient in herbivory and plant defences (Moles et al., 2011) while others did (Salgado & Pennings, 2005; Woods et al., 2012); there is also mixed evidence when comparing different herbivore species or plant defensive traits (Anstett et al., 2015; Moreira et al., 2015, 2018). A plausible explanation for the lack of latitudinal gradients in oak defences may

be that there is no latitudinal gradient in leaf damage, hence, there is no reason for a latitudinal gradient in defences to exist either. It could also be because we sampled leaves at the middle of the growing season rather than at the end, and we did not measure constitutive and induced defences separately. This is an insightful point because oak leaves may have differentially accumulated phenolics in response to herbivory (i.e., induced defences) or have experienced marked differences in light intensity toward the end of the growing season (Karolewski et al., 2013). Furthermore, despite attempts to synchronize phenology across sites, seasonal changes in oak chemical defences (Salminen & Karonen, 2011) might have masked latitudinal patterns in defences. Therefore, further studies should include measurements at multiple time points during the growing season and distinguish between different types of defences, including physical versus chemical defences (Wang et al., 2018) as well as constitutive versus induced defences (Anstett et al., 2018) in order to address latitudinal gradients in plant defence more comprehensively.

Some leaf traits related to leaf nutrient content were associated with latitude or climatic conditions, but their overall response was inconsistent. Leaf C : N ratio and sugar content varied along latitudinal and climatic gradients, respectively. The leaf C : N ratios were lowest at intermediate latitudes. This outcome may be due

to temperature-related plant physiological stoichiometry and biogeographical gradients in soil substrate age (limitation of soil N at higher latitudes; Reich & Oleksyn, 2004). Leaf soluble sugar content decreased with increasing precipitation (Cao et al., 2018). Soluble sugars, especially glucose and fructose, accumulate together with other osmolytes during drought (Nio et al., 2011), resulting in high concentration in areas where precipitation is low.

4.3 | Predation rate was not influenced by latitude or climatic conditions

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

4.4 | Mechanisms underlying latitudinal and climatic variation in herbivory

We did not find any statistically significant relationship between leaf damage and leaf chemical traits. Although we cannot exclude that unmeasured traits (e.g., leaf toughness, inducible defences) may have correlated with herbivory, our results disqualify large-scale variation in bottom-up forces as important drivers of overall leaf damage at a continental scale. In contrast, the incidence of gall-inducers and leaf-miners was partially related to the variability in several leaf chemical traits (Figure 5). For instance, the incidence of gall-inducers increased with increasing leaf soluble sugars and N concentrations, which is consistent with gall-inducers being metabolic sinks (Huang

et al., 2014). However, the effect of precipitation on leaf-miners was likely indirectly mediated by climatic variation in defences, as this effect became non-significant once hydrolysable tannins were included in the model. Similarly, the effects of temperature and precipitation on gall-inducers were indirectly mediated by climatic variation in defences, as these effects were also non-significant after soluble sugars, N concentrations and lignins were included in the models. These results agree with previous studies reporting indirect effects (via leaf defences) of climate on herbivory (Anstett et al., 2018; Moreira et al., 2018). For instance, Anstett et al. (2018) found indirect effects of climate on herbivory in 80 species of evening primroses, which were mediated by leaf chemicals (total phenolics and oenothien A). However, these conclusions need to be considered with caution because the data set used to test the effect of bottom-up and top-down forces on herbivory along large-scale latitudinal and climatic gradients of the biotic and abiotic models only consisted of a subset of the complete data set used in the geographical and climatic models.

We found no evidence that bird attack rate drove large-scale variability in herbivory. This result is in line with a recent study by Zverev et al. (2020) who found that birds are unlikely to shape the spatial patterns of insect herbivory in an Arctic ecosystem. More generally, associations between bird insectivory and insect herbivores can be positive (Gunnarsson et al., 2018; Mäntylä et al., 2014), negative (Kozlov et al., 2017; Maguire et al., 2015) or non-significant (Moreira et al., 2019; Valdés-Correcher et al., 2019), depending on the study and methods used. Arthropod predators (e.g., ants, ladybirds) play an important role in limiting herbivore populations and may respond to large-scale variation in climatic conditions to a greater extent than vertebrate predators (Roslin et al., 2017; Zvereva et al., 2019). For example, a meta-analysis conducted by Rodríguez-Castañeda (2013) found that ant predation on herbivores significantly increased at higher temperatures and precipitation, indicating that plants growing under warmer and wetter conditions exhibit lower levels of herbivory. Besides, birds are considered intraguild predators that not only eat insect herbivores, but also arthropod predators (Gunnarsson, 2007) and intraguild predation may weaken herbivore suppression (Finke & Denno, 2005). Unfortunately, we were not able to quantify either predation rates by arthropods or intraguild predation, which weakens our conclusions about the potential role of predators across climatic gradients.

4.5 | Conclusion

By simultaneously investigating bottom-up and top-down forces driving herbivory along latitudinal and climatic clines in a wide-spread tree species in Europe, this study brings some new insights into the vivid debate about latitudinal variation in the direction and strength of biotic interactions (Anstett et al., 2016; Moles et al., 2013; Roslin et al., 2017; Schemske et al., 2009). We found no evidence that latitude or climate influenced insect herbivores feeding on oaks, but we found that climatic factors rather than

latitude per se were the best predictors of the large-scale variation in the incidence of leaf-miner and gall-inducer herbivores as well as in variation in leaf nutritional content. In sharp contrast, we found no evidence that plant chemical defences and bird attack rates were influenced by latitude or climatic factors, which conflicts with the dominant view in ecology (Moles & Ollerton, 2016; Roslin et al., 2017; Zvereva et al., 2019). Because unravelling causes of latitudinal variation in the strength of biological interactions is one of the common approaches for the prediction of biotic interactions under global warming (Verheyen et al., 2019), it is crucial that future studies simultaneously test for effects of latitude per se and climate on herbivory by different feeding guilds (Kozlov et al., 2017), as well as investigate the complexity of biotic interactions in which plant-herbivore interactions are embedded.

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CONFLICT OF INTEREST

The authors declare no competing financial interests.

DATA AVAILABILITY STATEMENT

The data sets supporting this article are available via an open-access repository (<https://doi.org/10.5061/dryad.18931zwcw0>).

ORCID

Elena Valdés-Correcher  <https://orcid.org/0000-0001-6842-1280>
 Mikhail V. Kozlov  <https://orcid.org/0000-0002-9500-4244>
 Gábor L. Lövei  <https://orcid.org/0000-0002-6467-9812>
 Andreas Prinzing  <https://orcid.org/0000-0002-8736-1946>
 Bastien Castagneyrol  <https://orcid.org/0000-0001-8795-7806>

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BIOSKETCHES

Elena Valdés-Correcheris interested in plant–herbivore interactions. More specifically, she investigates the effects of different drivers of plant–herbivore interactions including the effects of landscape composition, climate and tree genotype on plant–herbivore relationships.

Bastien Castagneyrol is interested in citizen science and in the ecology of plant–herbivore interactions including predation, insect herbivory and leaf traits and how these relationships are influenced by factors that act at different scales.

Xoaquín Moreira is interested in plant–herbivore interactions. More specifically, he is interested in the effects of latitude and elevation on biotic relationships.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

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