


BRIEF COMMUNICATION

Effects of latitude and conspecific plant density on insect leaf herbivory in oak saplings and seedlings

Xoaquín Moreira^{1,11} , Luis Abdala-Roberts², Pieter De Frenne³, Andrea Galmán¹, Álvaro Gaytán⁴, Raimo Jaatinen⁵, Beatriz Lago-Núñez¹, Camille Meeussen³, Pertti Pulkkinen⁵, Pii U. Rasmussen⁶, Jan P.J.G. Ten Hoopen⁷, Bart G.H. Timmermans⁸, Carla Vázquez-González¹, Nick Bos⁹, Bastien Castagneyrol^{10,*}, and Ayco J.M. Tack^{4,*}

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¹ Misión Biológica de Galicia (MBG-CSIC), Apdo. 28, Pontevedra, Galicia, Spain

² Departamento de Ecología Tropical, Campus de Ciencias Biológicas y Agropecuarias, Universidad Autónoma de Yucatán, Apartado Postal 4-116, Itzimmá. 97000. Mérida, Yucatán, Mexico

³ Forest and Nature Lab, Ghent University, Geraardsbergsesteenweg 267, BE-9090 Gontrode-Melle, Belgium

⁴ Department of Ecology, Environment and Plant Sciences, Stockholm University, Svante Arrhenius väg 20A, Stockholm, Sweden

⁵ Natural Resources Institute Finland. Haapastensyrjä Breeding Station, FI-16200 Läyliäinen, Finland

⁶ The National Research Centre for the Working Environment, 2100 Copenhagen, Denmark

⁷ OneNature Ecology, Bachlaan 30, 6815 DE Arnhem, The Netherlands

⁸ Department of Agriculture, Louis Bolk Institute, Kosterijland 3-5, 3981 AJ Bunnik, The Netherlands

⁹ Section for Ecology and Evolution, University of Copenhagen, 2200 Copenhagen, Denmark

¹⁰ BIOGECO, INRAE, Univ. Bordeaux, 33610 Cestas, France

¹¹ Author for correspondence (e-mail: xmoreira1@gmail.com)

*These authors are joint for last authorship.

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PREMISE: Abiotic factors and plant species traits have been shown to drive latitudinal gradients in herbivory, and yet, population-level factors have been largely overlooked within this context. One such factor is plant density, which may influence the strength of herbivory and may vary with latitude.

METHODS: We measured insect herbivory and conspecific plant density (CPD) of oak (*Quercus robur*) seedlings and saplings along a 17° latitudinal gradient (2700 km) to test whether herbivory exhibited a latitudinal gradient, whether herbivory was associated with CPD, and whether such an association changed with latitude.

RESULTS: We found a positive but saturating association between latitude and leaf herbivory. Furthermore, we found no significant relationship between CPD and herbivory, and such lack of density effects remained consistent throughout the sampled latitudinal gradient.

CONCLUSIONS: Despite the apparently negligible influence of plant density on herbivory for *Q. robur*, further research with other plant taxa and in different types of plant communities are needed to investigate density-dependent processes shaping geographical variation in plant–herbivore interactions.

KEY WORDS density dependence; latitudinal gradients; plant–herbivore interactions; *Quercus robur*; saplings; seedlings.

Warmer temperatures, longer growing seasons, and higher plant and animal diversity are some of the main factors argued to result in more intense plant–herbivore interactions toward the equator (Schemske et al., 2009). As a result of increased rates of herbivory, higher levels of anti-herbivore defenses are predicted for equatorward plants relative to their poleward counterparts (Coley and

Aide, 1991). While this set of predictions constitutes a central paradigm in ecology, it has been subjected to greater scrutiny in recent years due to evident inconsistencies in the strength and direction of latitudinal gradients in herbivory (Moles et al., 2011; Anstett et al., 2016). Recent efforts have addressed factors likely responsible for variation in latitudinal gradients in herbivory by examining the role

of abiotic factors (e.g., climate; Moreira et al., 2018), and plant or herbivore species-level traits (e.g., herbivore diet breadth or plant defenses; Anstett et al., 2014, 2015). While such work has increased our understanding of how focal species-level traits and abiotic conditions jointly determine latitudinal gradients, population- and community-level factors have received less attention.

Conspecific plant density (CPD) is a well-studied population-level feature of terrestrial plant communities which has important effects on herbivore communities and plant–herbivore interactions (Underwood et al., 2014). Increased CPD can lead to concomitant increase in herbivory on focal plants if herbivores exhibit positive density-dependent attack (resulting in a so-called “resource concentration effect”; e.g., Kim and Underwood, 2015). In other cases, increasing CPD can lead to reduced herbivory if herbivore attack shows negative density dependence such as a Type II (saturating) functional response (i.e., leading to a resource dilution effect; Abdala-Roberts and Mooney, 2013). Provided that these outcomes are strongly contingent on both plant and herbivore traits such as mobility and diet breadth (Castagneyrol et al., 2014), then geographic variation in species traits would be expected to result in concomitant variation in plant density–herbivory associations. Insect herbivore traits are known to vary with latitude (e.g., higher dietary specialization at lower latitudes; Forrister et al., 2015), and recent work found that negative density dependence in tree species seedling recruitment strengthens with decreasing latitude (LaManna et al., 2017)—a pattern that is thought to be largely due to a greater pervasiveness or strength in positively density-dependent herbivory at low latitudes (Janzen, 1970; Bagchi et al., 2014; Comita et al., 2014). To date, however, latitudinal tests of plant density–herbivory associations are rare (see Comita et al., 2014), limiting our understanding of how density-mediated mechanisms shape spatial variation in plant–herbivore interactions.

In this study, we measured both insect herbivory (percentage of leaf area removed) and CPD for oak (*Quercus robur* L., Fagaceae) seedlings and saplings from 23 populations distributed along a 17° temperate latitudinal gradient (2700 km) in Europe. In doing so, our aim was to investigate whether herbivory exhibited a latitudinal gradient, whether herbivory was associated with CPD, and whether such an association varied in strength (i.e., rate of change in herbivory with CPD) and/or sign (i.e., decrease or increase in herbivory with CPD) along the sampled gradient. We predicted that herbivory would increase toward lower latitudes, and that herbivory would be associated with plant density but that the relationship would be contingent on latitude, i.e., shifting from decreasing herbivory with increasing CPD at high latitudes (i.e., negative density-dependent attack) to increasing herbivory with CPD at low latitudes (i.e., positive density-dependent attack). Alternatively, the association would be absent at high latitudes but emerge and strengthen (i.e., an increasing rate of positive density-dependent herbivory) toward lower latitudes. In taking into account plant density along the sampled

gradient, we shed light on density-mediated mechanisms shaping latitudinal clines in herbivory. Furthermore, by focusing on tree seedlings, we can link our findings to the broader literature on density dependent patterns of tree species seedling recruitment.

MATERIALS AND METHODS

Natural history

The English oak *Q. robur* is a long-lived, deciduous tree native to most of Europe, and is distributed from northern Portugal (40°N) to southern Scandinavia (62°N) (Schwarz, 1964). This species is a dominant light-demanding tree, which tolerates an extremely wide range of climatic conditions (Jones, 1959). It is one of the most economically and ecologically important deciduous forest tree species in Europe. Leaves flush in April in southern Europe, and in May for northern Europe. Leaf senescence and leaf drop typically start in September for northern Europe and in October for southern Europe. Leaves are approximately 8–12 cm long with four to seven pairs of lobes and have almost no petiole. In its native range, *Q. robur* supports a large community of insect herbivores, mainly leaf chewers, miners, and galls (Moreira et al., 2018).

Field sampling and leaf herbivory measurements

We selected 23 *Q. robur* populations distributed along a 17° latitudinal gradient from northern Spain to southern Finland (43°N to 60°N, Fig. 1) spanning most of the latitudinal distribution of this species. Each study population included at least 10 mature,

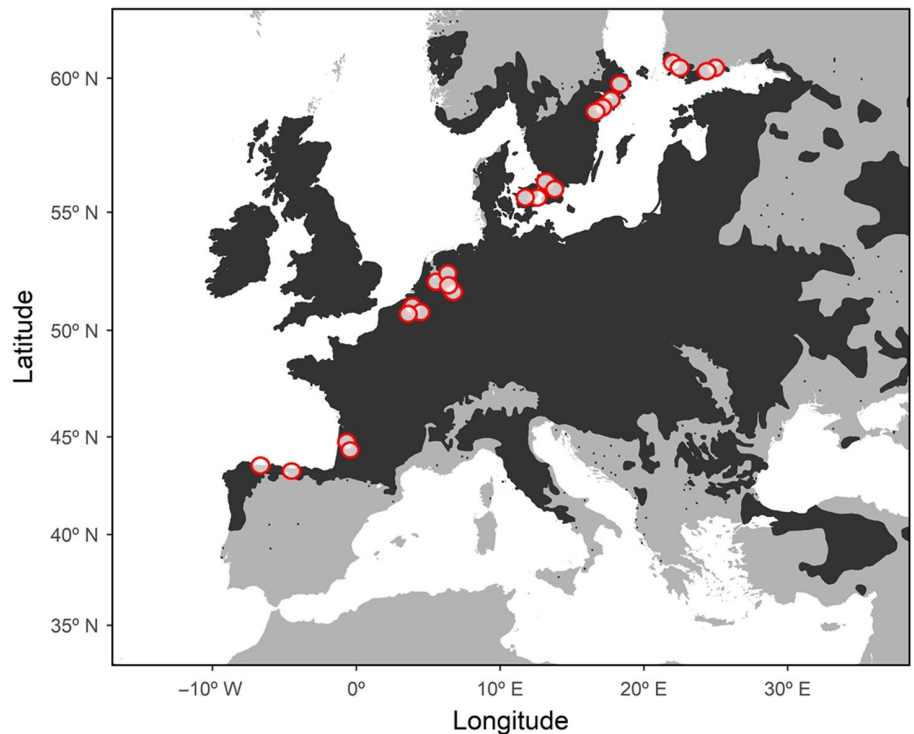


FIGURE 1. Map showing the location of the 23 populations of *Quercus robur* sampled along a 17° latitudinal gradient from northern Spain to southern Finland. The black shaded area represents the distribution range of this species.

reproductive *Q. robur* trees and approximately 30% of the adult trees at each site were of *Q. robur*. At each site, we selected a 40 × 40 m area within which we sampled all *Q. robur* seedlings and saplings. To minimize phenological differences among populations and measure end-of-season cumulative herbivory, the sampling time was adjusted to the growing season at each site. We sampled from late August to early September in northern populations and from late September to early October in southern populations. The number of plants sampled per population ranged from 13–166 (865 total) (Appendix S1). For each focal plant, we measured total height (mean ± SE: 74.12 ± 5.06 cm) and the number of conspecific plants (i.e., CPD) in a 5-m radius around each focal plant. For each plant, we also collected up to 10 leaves randomly selected throughout the canopy to assess herbivore attack.

Collected leaves were mostly damaged by chewing insects, and to a much lesser extent by leaf miners and other insect herbivore guilds (<5% of sampled leaves). For each leaf, we visually estimated the percentage of leaf area removed by chewing insects (“leaf herbivory” hereafter) using the ordinal following scale: 0 = undamaged; 1 = 1–5% damaged; 2 = 6–10% damaged; 3 = 11–25% damaged; 4 = 26–50% damaged; 5 = 51–75% damaged; 6 = >75% damaged) (Moreira et al., 2018). For each focal plant, we averaged values across leaves to obtain a mean value for statistical analyses. To avoid biases in herbivory, the same person (B. Lago-Núñez) scored all the plants.

Statistical analysis

We ran a general linear mixed model with a Gaussian distribution and identity-link function (residuals were normally distributed upon previous inspection) to test for the effects of the linear and quadratic terms of latitude, CPD, and two-way interactions between the latitude terms and CPD (all fixed factors) on leaf herbivory. The interaction terms tested whether the rate of change in herbivory with density (in either magnitude or sign, measured by the slope) varied with latitude. We also included country (because populations were clustered by country) and population nested within country as random effects to account for the nonindependence between individuals sampled at each site. We previously ran this model additionally including plant height, the quadratic term for CPD, and the interaction between each of these and latitude as predictors, but these were not significant and were therefore removed to simplify the model. There was no collinearity between latitude and plant density, as shown by a quadratic regression using population means where CPD was predicted by the linear ($F_{1,20} = 2.46, P = 0.132$) and quadratic ($F_{1,20} = 2.07, P = 0.166$) terms of latitude. For all these analyses, we used the *lmer* function in the *lme4* package (Bates et al., 2015) in R ver. 3.4.1 (R Core Team, 2019). In addition, we also run population-level linear models testing the effect of CPD on insect herbivory separately for each population. For this analysis, we used the *lm* function in the *lme4* package in R.

Because of the high density of seedlings and saplings at sites in France (>200), we haphazardly sampled only 30 individuals in these populations. To verify that differences in sampling effort did not bias our conclusions, we ran a sensitivity analysis. We randomly selected *N* saplings per population (where *N* is the minimum number of sampled saplings across populations) and recalculated model coefficient parameter estimates for this random sample. We repeated

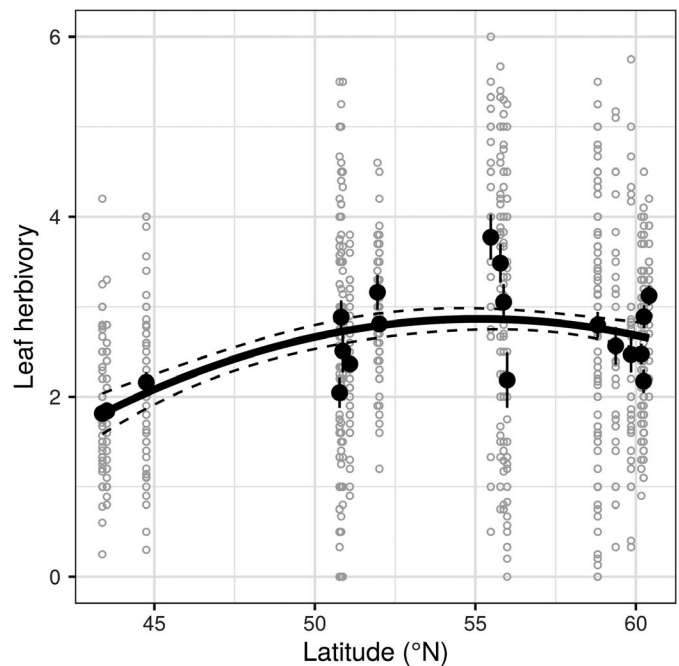


FIGURE 2. Latitudinal variation in insect leaf herbivory on *Quercus robur* seedlings and saplings sampled at 23 populations spanning 17° latitude from northern Spain to southern Finland. Gray dots represent individual plants sampled ($N = 865$) and black dots represent population means ($N = 23$; error bars are standard errors). The black solid curve depicts the predicted nonlinear relationship between herbivory and latitude at the individual plant level (controlling for data nonindependence within populations). The dashed lines represent its 95% confidence interval.

this procedure 1000 times and compared the coefficient parameter estimates of the model based on the full data set with the 95% distribution of the 1000 models based on random data subsets. This analysis indicated that our findings were robust and unbiased by sampling effort.

RESULTS

We found a nonlinear, saturating latitudinal gradient in herbivory whereby the leaf damage increased with latitude initially but leveled off at intermediate-to-high latitudes (Fig. 2). Unexpectedly, we found no significant association between CPD and herbivory, as well as no significant interaction between CPD and either the linear or the quadratic effect of latitude (Table 1). Neither was there any significant association between herbivory and conspecific density in analyses run separately for each population (Appendix S2).

DISCUSSION

Insect leaf herbivory on *Q. robur* seedlings and saplings exhibited a nonlinear (positive) saturating latitudinal gradient. Notably, this result contrasts with the latitudinal pattern found for *Q. robur* adult trees, for which insect leaf herbivory increased linearly toward lower latitudes (Moreira et al., 2018). Together, these contrasting

TABLE 1. Effects of CPD, linear and quadratic terms for latitude, and interactions between latitude terms and CPD (all fixed factors) on leaf herbivory on focal seedlings and saplings of *Q. robur*. The model included country and population nested within country as random factors in order to account for population clustering within each country and for the nonindependence between individuals at each site, respectively. Slope estimates and their standard errors (SE), *F*-values, degrees of freedom (numerator, denominator), and associated significance levels (*P*) are shown. Significant (*P* < 0.05) effects are in bold. Latitude² = quadratic term of latitude.

	Estimate ± SE	<i>F</i> -value	DF _{num}	DF _{den}	<i>P</i> -value
Latitude	1.127 ± 0.367	7.30	1	19.4	0.014
Latitude ²	−0.011 ± 0.004	6.60	1	19.5	0.019
CPD	1.335 ± 0.862	0.29	1	331.8	0.590
Latitude × CPD	−0.055 ± 0.034	2.54	1	659.3	0.111
Latitude ² × CPD	0.0006 ± 0.0003	2.65	1	566.3	0.104

gradients suggests that latitudinal variation in herbivory in *Q. robur* is contingent on plant ontogeny. Mature trees represent a resource that is easier to locate than young plants, and therefore attract more herbivores potentially diverting attack on seedlings and saplings (Moreira et al., 2017). To explain the observed gradient, this protective effect on young plants would be presumably stronger at low latitudes and/or weaker (and stabilizes) at high latitudes, possibly because these effects are realized to a greater extent under longer leafing phenology of trees at lower latitudes. In addition, differences in herbivore species composition or oak defensive mechanisms in the understory vs. canopy could also explain these contrasting ontogenetic patterns.

A number of correlational and experimental studies have found significant effects of plant density on herbivory (e.g., Abdala-Roberts et al., 2017; Bogdziewicz et al., 2018), and related work has documented density-dependent herbivore responses to plant availability (Abdala-Roberts and Mooney, 2015) and its causative link with negative density-dependent plant recruitment (reviewed by Comita et al., 2014). Despite solid evidence for density-dependence in plant–herbivore interactions, we found no detectable association between herbivory and density of *Q. robur* saplings and seedlings, suggesting that CPD does not influence herbivory during early stages of plant development in this species. Although not directly comparable, this finding contrasts with results from another study, which found that weevil attack rates on acorns of *Q. ilex* depended on CPD (Bogdziewicz et al., 2018). Further work manipulating seedling densities and separating damage by different insect species is needed for a more detailed and rigorous investigation of herbivore density-dependent responses in this system (Brenes-Arguedas, 2012; Abdala-Roberts et al., 2017). Including other sympatric tree species with broad distributions and manipulating species relative frequencies would also be of high value to describe community-level patterns and separate intra- from interspecific associational effects (sensu Kim and Underwood, 2015).

We found that the association between CPD and herbivory remained consistently weak or absent across the sampled gradient. This finding counters the expectation that herbivory responses to variation in plant density change with latitude, specifically that positive density-dependent attack should arise and/or become stronger (i.e., exhibit a higher rate of increase with plant density) at lower latitudes (Bagchi et al., 2014; Comita et al., 2014). However, research addressing latitudinal variation in herbivory density-dependence

has mainly involved temperate–tropical comparisons (see Comita et al., 2014; LaManna et al., 2017), whereas the gradient we sampled was restricted to temperate latitudes for which the importance of negative density dependent attack appears to be negligible. Interestingly, this pattern was observed despite the fact that herbivory increased (up to a saturation point) with latitude, rather than the inverse, from which a parallel increase in the strength of density-dependent attack toward higher latitudes would have been expected. It is also worth noting that while density-dependent patterns of herbivory severity (as measured here in terms of percentage of leaf area removed) would be expected to be related to concomitant patterns of mortality for focal plants, measurements of seedling mortality are necessary to directly link herbivory to density-dependent seedling recruitment. In this sense, our work is conceptually and methodologically closer to work on resource dilution and concentration effects (Underwood et al., 2014), which have involved measurements of herbivory on focal plants under changing conspecific (or heterospecific) densities (Kim and Underwood, 2015). Accordingly, to address both perspectives on density-dependent processes, a necessary step forward is to manipulate plant densities and conduct parallel measurements of herbivory and survival on focal plants at the plot level across the sampled gradient. Experimental removal of insect or vertebrate herbivores would also facilitate separating herbivory effects from intraspecific competition.

Insect herbivore assemblages are generally less specialized in temperate relative to tropical forests (Forrister et al., 2015), and density-dependent processes affecting plant–herbivore interactions are thought to be modulated by herbivore dietary specialization (Comita et al., 2014). Thus, work spanning temperate and tropical systems is needed across more plant taxa. This work would link latitudinal changes in herbivore diversity and traits to these density-dependent mechanisms. At the same time, a more detailed and systematic inspection of patterns within and among temperate and tropical community types is also warranted, given considerable variation in latitudinal gradients across different types of temperate forests (Carmona et al., 2020) or between tropical and subtropical plant communities (Moles et al., 2011; Weissflog et al., 2018).

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AUTHOR CONTRIBUTIONS

Designed the experiment: X.M., A.J.M.T., B.C., L.A.R. Performed the experiment: X.M., P.D.F., A.Gal., A.Gay., R.J., B.L.N., C.M., P.P., P.U.R., J.P.J.G.T.H., B.G.H.T., C.V.G., N.B., B.C., A.J.M.T. Analyzed the data: X.M., B.C. Wrote the manuscript: X.M. All authors edited the manuscript, gave final approval for publication, and agree to be held accountable for the work performed therein.

DATA AVAILABILITY

Appendix S1 reports all data used for statistical analyses.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

APPENDIX S1. Data used for this paper.

APPENDIX S2. Summary of population-specific linear models testing the effect of conspecific sapling density on insect herbivory.

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