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Regional Variation in Insularity Effects on Acorn Herbivory in European Oaks Challenges Predictions of Lower Herbivory on Islands

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ABSTRACT

Aim: Ecological theory predicts lower herbivory on islands. However, most island-mainland comparisons have focused on vegetative tissues, while reproductive structures remain understudied despite their direct influence on plant fitness and recruitment. This study investigates how insularity affects insect herbivory in oak (*Quercus*) acorns across multiple island-mainland regions and explores the role of acorn traits (chemical defences and nutrients) and climate as potential drivers.

Location: Three island-mainland regions in Europe: Lesbos Island—mainland Greece, the Balearic Islands—mainland Spain, and Bornholm Island—mainland Sweden.

Time Period: Acorns were collected in autumn 2023. Climatic data are long-term averages for each population.

Major Taxa Studied: Seven oak (*Quercus*) species across regions.

Methods: We aimed to sample up to three island and three mainland populations per species, with four trees per population, but logistical constraints reduced these numbers, resulting in a total of 150 sampled trees. We assessed acorn damage by insect herbivores and analysed chemical defences (phenolics) and nutrients (nitrogen and phosphorus) to test their influence on island–mainland differences in herbivory. Climatic data from the WorldClim database were used to assess climate-mediated insularity effects on acorn traits and herbivory.

Results: Acorn damage did not differ overall between mainland and island populations. However, in the Balearic Islands, damage was higher than in mainland Spain, while no significant differences were found in the other regions. There were no general insularity effects on acorn traits, but a region-by-insularity interaction influenced phosphorus levels, with higher values

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in mainland Sweden than Bornholm Island, while the reverse was observed in Greece. Climate influenced acorn traits, but trait differences did not explain herbivory patterns.

Main Conclusions: Our findings challenge the expectation that insularity reduces herbivory, highlighting region-specific processes. While climate influenced acorn traits, these traits did not mediate insularity effects on herbivory, suggesting local ecological factors drive variation across regions.

1 | Introduction

Islands serve as natural laboratories that provide powerful insights into ecological and evolutionary processes shaping biodiversity (Gillespie et al. 2008; MacArthur and Wilson 2001; Ricklefs and Bermingham 2008). They comprise only 5% of Earth's land area, but serve as critical biodiversity hotspots, harbouring nearly one-third of the world's total species and exhibiting remarkable levels of endemism (Myers et al. 2000). In particular, their geographic isolation and diverse biogeographical histories make them ideal for studying processes such as trait evolution and speciation (Barrett 1997; Burns 2019; Carvajal-Endara et al. 2020; Grant and Grant 2007; Losos and Ricklefs 2009), spatial variation in biodiversity (Borregaard et al. 2017; Kreft et al. 2008; MacArthur and Wilson 2001), drivers of ecosystem function (Oksanen et al. 2010; Terborgh 2010), and species interactions (Moreira and Abdala-Roberts 2022; Spiller and Schoener 1990; Traveset et al. 2013).

Herbivory is predicted to be lower on islands due to reduced herbivore abundance and diversity owing to dispersal constraints and environmental filtering (Carlquist 1974; Losos and Ricklefs 2009; Ricklefs and Bermingham 2008). Within this body of work, most research has focused on herbivory by vertebrates (Moreira, Castagneyrol, et al. 2021). Insects, however, can also be strongly shaped by island-specific factors, but these effects may not operate in the same way as for vertebrate herbivores due to differences in population sizes, species diversity and functional traits (Burns 2019; Moreira and Abdala-Roberts 2022). On the one hand, mainland insect species pools are highly diverse and may have greater species redundancy (i.e., multiple species having overlapping niches) than vertebrate pools (Gillespie and Roderick 2002). This redundancy could increase the chance that islands receive herbivore species from the mainland capable of feeding on insular plant species, mitigating the effects of species loss or dispersal limitations—i.e., a sampling effect (Schoener 2009). On the other hand, trait differences, particularly in diet breadth, may lead to an opposing prediction. Invertebrate herbivores are, on average, more specialist than vertebrates (Dearing et al. 2000; Forister et al. 2015), and may therefore be more affected by lower host plant diversity on islands than vertebrates (Moreira and Abdala-Roberts 2022). We are yet to test these patterns for insect herbivory and build an empirical body of work to address such hypotheses.

Island-mainland tests of herbivory have largely focused on vegetative tissues, particularly leaves, whereas much less work has focused on herbivory on plant reproductive structures such as fruits and seeds (Burns 2019; Carpenter et al. 2020; Heinen and Borregaard 2024; Nogales et al. 2024). However, frugivory and seed predation have strong impacts on plants by directly affecting their fitness and population dynamics (Chen et al. 2017; Herrera and Pellmyr 2009; Janzen 1971). Within this context, insect frugivores and seed predators are particularly abundant and diverse (Janzen 1971; Kolb et al. 2007; Ortegón-Campos et al. 2009; Thein et al. 2021), and importantly, have been shown to play a key role in shaping plant population and community dynamics on islands (Costa et al. 2024; Lewis and Gripenberg 2008), as well as plant trait evolution and species diversification (Kolb et al. 2007). Increased attention to insularity effects on herbivory on plant reproductive structures can contribute to a better understanding of divergent patterns of plant evolution in response to herbivory on islands relative to the mainland.

Differences in damage by insect herbivores between islands and the mainland can be driven by differences in plant traits that affect herbivore performance, including both defensive and nutritional traits (Agrawal 2011; Carmona et al. 2011; Marquis 1992; Rhoades 1979). Conducting island-mainland comparisons for such plant traits is a key first step that can help elucidate drivers of herbivory differences between islands and the mainland (Moreira and Abdala-Roberts 2022). At the same time, however, variation in plant traits may also be driven by abiotic factors, such as climate (Moreira et al. 2019). In this case, research has shown that islands tend to be, on average, wetter and warmer than the mainland (Weigelt et al. 2013) with such conditions (water or nutrient availability) potentially affecting plant growth, which in turn may influence plant nutrient levels and allocation to chemical defences (Coley et al. 1985; Endara and Coley 2011). Accordingly, this could result in abiotically mediated indirect effects on herbivory mediated by plant traits (Moreira et al. 2018). To date, however, studies testing for island-mainland differences in herbivory including plant trait measurements and investigating abiotically mediated bottom-up effects on herbivory remain scarce (but see Vázquez-González et al. 2025). Further, to our knowledge, no study has been conducted on seed predation, the latter despite the existence of often strong correlations between seed traits, abiotic factors and seed predation (Janzen 1971; Lewis and Gripenberg 2008), possibly underlying island-mainland differences in this herbivory type.

This study builds on recent work showing lower insect leaf herbivory and leaf putative defensive trait levels on island oak trees relative to their mainland counterparts (Vázquez-González et al. 2025). Here, we expand and complement this body of work by conducting island–mainland comparisons of seed (acorn) predation by insects on oaks. Specifically, we assessed acorn damage caused by insect herbivores for populations found on islands and the mainland across seven oak (*Quercus*) species, for each of three distant island–mainland systems (hereafter 'regions'): Lesbos Island vs. mainland Greece, the Balearic Islands vs. mainland Spain and Bornholm Island vs. mainland Sweden. We also tested for island–mainland differences in acorn chemical defences (phenolics) and nutrient content (nitrogen and phosphorus), and whether these traits correlated with abiotic conditions and acorn damage. Specifically, our study addresses three questions: (i) Does acorn damage by insects differ between island and mainland

oaks? (ii) Are there differences in acorn traits between island and mainland oaks, and are these differences associated with climatic variation? (iii) Is any such climatically driven variation in acorn traits associated with observed island–mainland differences in acorn damage? By including plant trait and abiotic factor measurements to our study of insularity effects on acorn predation, this study provides mechanistic insight into the mechanisms behind insularity effects on seed predation, a poorly studied interaction within this body of literature.

2 | Material and Methods

2.1 | Natural History

We measured acorn damage by insect herbivores and traits across seven oak species (*Quercus*, Fagaceae) distributed across each of the island–mainland paired regions: Lesbos Island vs. mainland Greece, the Balearic Islands (Mallorca and Menorca) vs. mainland Spain, and Bornholm Island vs. mainland Sweden (Figure 1). For Lesbos, we used mainland Greece rather than the geographically closer mainland Turkey due to logistical constraints. Specifically, we selected the following European oak species: *Q. robur* L. (pedunculate oak) and *Q. petraea* (Matt.) Liebl. (sessile oak) on Bornholm Island and on mainland Sweden; *Q. ilex* L. (holm oak), *Q. coccifera* L. (kermes oak), and *Q. suber* L. (cork oak) in the Balearic Islands and on mainland Spain; and *Q. pubescens* Willd. (pubescent oak) and *Q. ithaburensis* Decne. (Tabor oak) on Lesbos Island and on mainland Greece.

Oak acorns, which act as both fruits and seeds, are damaged by larvae of a diverse community of insect herbivores, among which weevils (*Curculio* spp., Curculionidae) and moths (*Cydia* spp., Tortricidae) are particularly common (Branco et al. 2002). These insects develop and feed inside the acorns. Upon maturing, larvae exit the acorns, drop to the ground and burrow into the soil where they overwinter (Otvos et al. 2012). As a result, acorn damage can in some cases reach very high levels and substantially reduce oak seedling establishment and growth (Branco et al. 2002; Espelta et al. 2009; Xiao et al. 2007). In most cases, however, damaged acorns can still germinate (Oliver and Chapin 1984; Kaushal and Kalia 1989; Weckerly et al. 1989; Xiao et al. 2007) and establish as viable seedlings (Kaushal and Kalia 1989; Xiao et al. 2007). Accordingly, viability and successful establishment likely depend on acorn defensive mechanisms, making them more able to resist, tolerate, or entirely escape predation (Leiva and Fernández-Alés 2005; Xiao et al. 2007).

Oaks display several traits that are predictive of insect herbivore damage, often acting as deterrents or toxic defences against herbivores. Well-studied leaf traits include secondary metabolites, such as phenolic compounds (e.g., flavonoids, tannins), which play a key role in plant defence (Forkner et al. 2004; Lill and Marquis 2001; Moreira et al. 2018; Pearse and Hipp 2009). Nutritional traits, including nitrogen and phosphorus content, are also significant in influencing herbivore damage (Abdala-Roberts et al. 2018; Moreira et al. 2018). For acorns, similarly, phenolic content has also been linked to reduced acorn damage by insects (Xiao et al. 2007), and nutrient content has been shown to be a reliable predictor of insect acorn damage (Moreira et al. 2020; Shi et al. 2018).

2.2 | Field Sampling and Acorn Damage Assessment

In September 2023, at the end of the growing season, we selected oak populations from both island and mainland locations

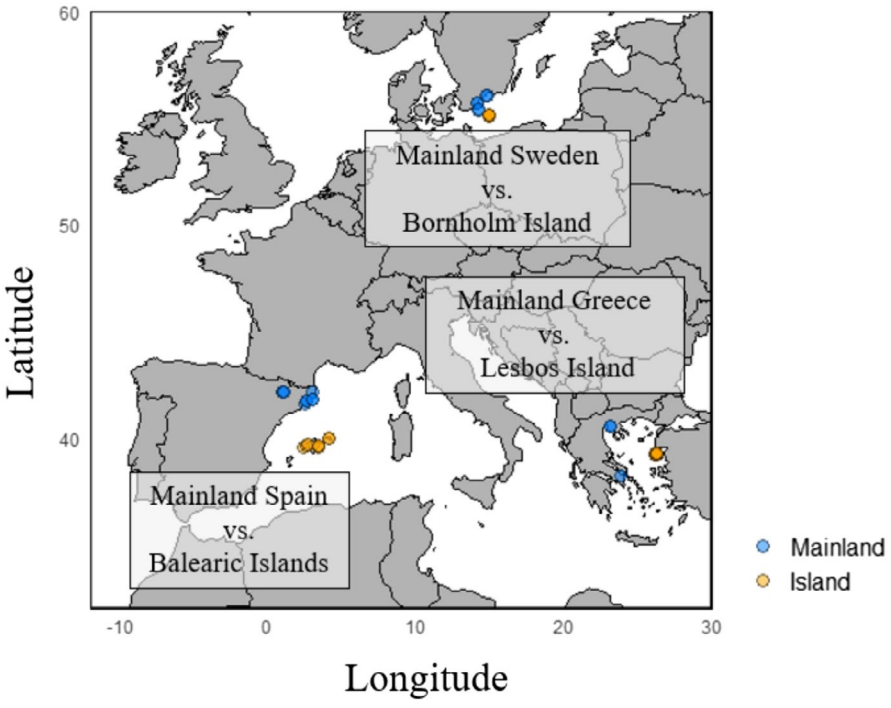

FIGURE 1 | Map of the study region showing the location of mainland and island oak populations in each study region, namely (1) Greece (Lesbos Island vs. mainland Greece), (2) Spain (Balearic Islands vs. mainland Spain), and (3) Sweden (Bornholm Island vs. mainland Sweden).

(Table S1). For each species, we chose up to three island and three mainland populations, except for *Q. ithaburensis* and *Q. pubescens* in mainland Greece for which we sampled only one and two populations, respectively, as well as for *Q. suber* in the Balearic Islands for which we sampled two populations. This resulted in a total of 38 oak populations. Each population consisted of at least 15 reproductive trees and was at least 2 km away from any other study population of the same species. The only exception was the *Q. suber* population in Menorca, which is estimated to comprise approximately 10 reproductive individuals. For each population, we randomly selected four individual trees, except for one population of *Q. suber* in the Balearic Islands where only two trees were sampled. To minimise any confounding factors and reduce variation, we chose trees of similar size and morphology within each population, avoiding isolated individuals and sampling under similar habitat conditions at each site (amount of shading, slope, etc.). Although the number of trees per population is relatively low, this sample size has proven sufficient to detect significant leaf herbivory patterns when comparing islands and the mainland in previous work that has followed a similar sampling design (Moreira et al. 2019; Vázquez-González et al. 2025). The total number of sampled trees resulting from this sampling scheme was 150 (see Table S1 for details per population). Then, for each tree we haphazardly collected 10 acorns found below the tree canopy. The acorns were oven-dried at 40°C for 48 h. After drying, we assessed the presence of insect herbivore (e.g., weevils, moths) damage in each acorn (Xiao et al. 2007; Moreira et al. 2020). Acorns were categorised as either 'damaged' or 'undamaged', based on the presence of larvae or exit holes (Figure S1) (Xiao et al. 2007). We then used the proportion of acorns damaged by insect herbivores per tree ('acorn damage' hereafter) - i.e., the number of damaged acorns divided by the total number of acorns - as a response variable in the statistical analyses (see Section 2.5 below).

2.3 | Acorn Traits

We analysed acorn traits putatively associated with acorn damage, namely phosphorus and nitrogen content as proxies for nutritional value, and total phenolic concentration as a proxy for chemical defences. Two to three acorns per tree with little to no insect herbivore damage were selected for the analyses. Attacked acorns were excluded to avoid variability introduced by local induction from herbivory. Values obtained therefore likely represented constitutive levels, though some degree of systemic induction cannot be ruled out (Moreira et al. 2020). Although the number of acorns for traits is relatively low, based on our previous trials, we assume that intra-individual variability (variation among acorns within the same tree) in chemical composition is relatively low compared to inter-individual and population-level variability.

To quantify nitrogen and phosphorus content, we ground acorns from each tree together using liquid nitrogen and digested 0.1 g of the ground acorn material in a mixture of selenic-sulphuric acid and hydrogen peroxide (Moreira et al. 2012). Diluted aliquots of the digestion were then analysed by colorimetry. We quantified nitrogen content using the indophenol blue method whereas phosphorus content was quantified with the molybdenum blue method, in both cases using a Bio-Rad 650 microplate reader (Bio-Rad Laboratories, Philadelphia, PA, USA) at 650 and 700 nm, respectively (Walinga et al. 1995). We expressed nitrogen and phosphorus concentrations in mg g^{-1} tissue on a dry weight basis.

To quantify the concentration of total phenolic compounds, we used the same ground acorn material as for nutritional trait analyses. Briefly, we incubated 20 mg with 1 mL of 70% methanol in an ultrasonic bath for 15 min (Moreira et al. 2012). Total phenolic content was determined colorimetrically using the Folin–Ciocalteu assay, with a Bio-Rad 650 microplate reader (Bio-Rad Laboratories, Philadelphia, PA, USA) at 740 nm. We quantified total phenolic content with a tannic acid standard curve and expressed the results as mg of tannic acid equivalents per gram of dry plant tissue (mg g^{-1}) (Sampedro et al. 2011).

2.4 | Climatic Data

We characterised climatic conditions at each sampled site (i.e., population) using eight bioclimatic variables from the WorldClim database version 2.1 at a 2.5-min resolution (Fick and Hijmans 2017). These were: BIO1 (annual mean temperature, °C), BIO4 (temperature seasonality, expressed as the standard deviation of temperature among months ×100), BIO5 (maximum temperature of the warmest month, °C), BIO6 (minimum temperature of the coldest month, °C), BIO12 (annual precipitation, mm), BIO13 (precipitation of the wettest month, mm), BIO14 (precipitation of the driest month, mm) and BIO15 (precipitation seasonality, expressed as the standard deviation of precipitation across months). We then summarised these population-level climatic data using principal component analysis (PCA) with the *FactoMineR* package in R software (Husson et al. 2006). Using the default parameter *scale.unit = TRUE*, variables were scaled to unit variance, ensuring that all climatic variables contributed equally to the PCA regardless of their original units or scales. This standardisation prevents variables with larger numerical ranges from exerting a disproportionate influence on the resulting principal components. We used the first principal component for subsequent analyses (PC1 climate, explaining 61.28% of the climatic variation), namely the PC1 scores for each population, which were positively correlated with temperature and precipitation seasonality, and negatively correlated with precipitation during the driest month (Figure S2).

2.5 | Statistical Analyses

We conducted all analyses using R version 4.2.1 (R Core Team 2013). First, we ran a generalised linear mixed model with a beta-binomial distribution (logit-link function) to test the effects of insularity (two levels: mainland or island), region (three levels: Lesbos Island-mainland Greece, Balearic Islands-mainland Spain and Bornholm Island-mainland Sweden), and their interaction (all treated as fixed factors) on the proportion of damaged acorns per tree using the *glmmTMB* function from the *glmmTMB* package (Brooks et al. 2017). We also included oak species and population within species as random factors. We assessed the significance of fixed effects using Wald χ^2 tests implemented via the *Anova* function from the *car* package (Fox et al. 2001). In the event of a significant interaction ($p < 0.05$)

between insularity and region, we ran post hoc mean contrasts for island vs. mainland within each region, using the *lsmeans* function from the *lsmeans* package (Lenth 2016), with Sidak correction for multiple comparisons and degrees of freedom estimated using the Kenward–Roger approximation. Pseudo-R^2 values for this model were calculated using the *performance* package (Lüdecke et al. 2021).

Second, we ran generalised linear mixed models with Gaussian error distribution to test the effects of insularity, region, and their interaction on each acorn trait, again using the *glmmTMB* function from the *glmmTMB* package. We also included species and population within species as random factors. We log-transformed phosphorus and nitrogen content to achieve normality of residuals. For these Gaussian models, we specified a variance structure to account for heteroscedasticity between insularity groups. Including this variance structure allowed us to explicitly model group-specific residual variance, thereby improving model fit and ensuring valid estimation of fixed effects and standard errors. We applied the same procedure described above to assess fixed effects, using Wald χ^2 tests for fixed effects. Again, in the case of significant interactions ($p < 0.05$) between insularity and region, we ran post hoc contrasts between means for island vs. mainland within each region, using the same *lsmeans* procedure as described above. For all models, we conducted residual diagnostics using the *DHARMa* package (Hartig et al. 2017) and present these diagnostics in Figure S3.

Next, we ran a piecewise structural equation model (pSEM) (Lefcheck 2016) using population means for all variables in which we tested for associations between insularity, climatic variation (PC1 climate scores), acorn traits, and acorn damage. Specifically, we included the following direct effects: (1) effect of insularity, coded as a dummy variable (mainland = 0, islands = 1) on PC1 climate, acorn traits, and acorn damage; (2) effect of PC1 climate on each acorn trait (nitrogen, phosphorus and total phenolics) and on acorn damage (i.e., the latter to test for direct abiotic forcing on herbivores, an alternative to plant trait-mediated abiotic effects); and (3) effect of each acorn trait on acorn damage. Additionally, we also tested the indirect effects of (4) insularity on acorn traits mediated by climate and, (5) insularity on acorn damage mediated by acorn traits. The pSEM was implemented using the *psem* function from the *piecewiseSEM* package (Lefcheck 2016). The component models in the pSEM included Gaussian models and one non-Gaussian (binomial) model for acorn damage fitted with the *lmer* and *glmer* functions respectively, both from the *lme4* package (Bates et al. 2015). Direct effects were calculated as standardised path coefficients between variables, while indirect effects were calculated as the product of the intervening direct effects for the specified causal pathway (Lefcheck 2016). To estimate indirect effects with 95% confidence intervals, we used the *semEff* function from the *semEff* package (Murphy 2019), which applies bootstrap resampling to provide robust estimates. We evaluated global model fit of the pSEM using both the χ^2 statistic and Fisher's C statistic, following the direct separation procedure (Shipley 2009). These tests evaluate whether the set of conditional independence claims implied by the hypothesised model are consistent with the observed data. A non-significant result indicates that the hypothesised causal structure adequately accounts for the observed associations, whereas a significant result indicates that the model omits one or more associations that would improve statistical fit. To maintain conceptual clarity and parsimony, we constrained the pSEM to a priori hypothesised pathways addressing our research questions, rather than adding additional links solely to improve fit. For transparency, we also provide in Table S2 the list of conditional independence claims tested during the procedure.

3 | Results

There were no significant main effects of insularity or region on acorn damage (Table 1), but there was a significant insularity-by-region interaction (Table 1; Figure 2). Specifically, oak trees in the Balearic Islands showed, on average, a significantly (103%) greater proportion of damaged acorns (lsmean ± SE: 0.543 ± 0.089) compared to those on mainland Spain (0.268 ± 0.068) ($z = -2.34$, $p = 0.019$), while for the Greece region there was an inverse trend (albeit non-significant, $z = 1.61$, $p = 0.108$; Lesbos Island: 0.315 ± 0.089, mainland Greece: 0.592 ± 0.140), and for Sweden island vs. mainland values were highly similar ($z = 0.60$, $p = 0.549$; Bornholm Island: 0.210 ± 0.073; mainland Sweden: 0.276 ± 0.083) (Figure 2).

There were no significant main effects of insularity, region, or their interaction on acorn nitrogen content (Table 1; Figure 3a). For phosphorus, there were no significant main effects either (Table 1), but there was a significant insularity-by-region interaction (Table 1; Figure 3b). Oak trees from Lesbos Island had acorns with significantly (29%) more phosphorus (1.236 mg g^{-1} ± 0.148) than those from mainland Greece (0.959 mg g^{-1} ± 0.127), whereas those from Bornholm Island (1.048 mg g^{-1} ± 0.125) had acorns with less (17%) phosphorus than those from mainland Sweden (1.268 mg g^{-1} ± 0.151). There was no island-mainland difference in the Spanish region (Figure 3b). Lastly, there were no significant main effects or interaction on the concentration of phenolic compounds (Table 1; Figure 3c).

The pSEM indicated a significant positive direct effect of insularity on PC1 climate, meaning that island populations experience warmer temperatures and greater precipitation seasonality (i.e., more rain in the wettest month and less rain in the driest) compared to mainland populations (Figure 4). PC1 climate had a significant direct positive effect on phosphorus content, whereby warmer temperatures and greater precipitation seasonality were associated with more acorn phosphorus content (Figure 4). As a result, there was a significant positive indirect effect of insularity on phosphorus content via PC1 climate (indirect effect coefficient = 0.202 ± 0.065; $p < 0.05$). Insularity also had a significant direct effect on phosphorus content, but with opposite (i.e., negative) direction (Figure 4). There were no direct effects of acorn traits (including phosphorus) on acorn damage (Figure 4), and, accordingly, no significant indirect effect of insularity on acorn damage via traits (indirect effect coefficient = 0.070 ± 0.062; $p > 0.05$). The global goodness-of-fit tests were statistically significant ($\chi^2 = 43.81$, df = 3, $p < 0.001$; Fisher's $C = 45.24$, df = 6, $p < 0.001$), indicating that the model omits some associations (particularly among acorn traits; See Table S2) that would improve statistical fit. Nonetheless, the model captures the hypothesised causal pathways central to our

TABLE 1 | Results from generalised linear mixed models testing the effects of insularity (island vs. mainland), study site (Lesbos Island vs. mainland Greece, Balearic Islands vs. mainland Spain, and Bornholm Island vs. mainland Sweden), and their interaction on the proportion of acorns damaged by weevils and moths, as well as on acorn traits, including nitrogen and phosphorus content and the concentration of total phenolic compounds. For fixed effects, χ^2 statistics from Wald tests and the associated *p*-values are reported. For random effects, we provide the estimated variance components (σ^2), which indicate the proportion of variability in the response attributable to population and species.

	Insularity		Study region		Insularity × Study region	
Fixed effects	χ^2	*p*	χ^2	*p*	χ^2	*p*
Acorn damage	0.23	0.631	3.64	0.162	8.14	**0.017**
Nitrogen content	0.01	0.934	3.52	0.171	4.90	0.086
Phosphorus content	0.81	0.367	3.33	0.189	12.33	**0.002**
Phenolic concentration	3.84	0.050	0.99	0.610	2.96	0.228
Random effects			**Population σ^2**		**Species σ^2**	
Acorn damage			0.649		~0	
Nitrogen content			0.012		0.053	
Phosphorus content			0.009		0.022	
Phenolic concentration			0.759		0.603	

Note: Significant *p*-values are shown in bold.

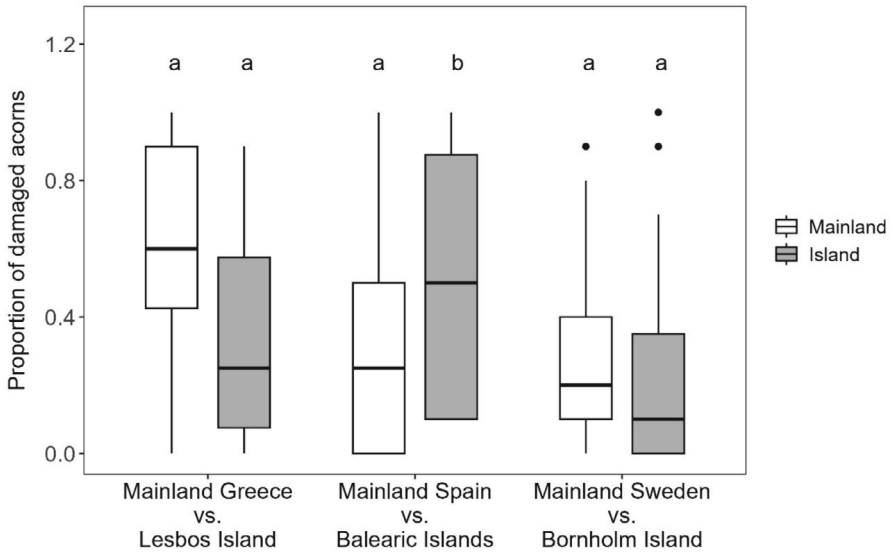

FIGURE 2 | Proportion of acorns damaged by weevils and moths on islands and the mainland across three study regions ($N = 150$ trees). Boxplots show the distribution of observed values per group (island or mainland) within each region; boxes represent the interquartile range (IQR), horizontal lines indicate medians, whiskers extend to 1.5× the IQR, and points outside this range are shown as outliers. Different letters indicate statistically significant differences between island and mainland least-squares means within each region, based on post hoc contrasts from the generalised linear mixed model (beta-binomial) with Sidak correction.

research questions, and thus provides a parsimonious representation of the system.

4 | Discussion

Our findings underscore marked geographical variation in insularity effects on acorn damage and traits. Oaks in the Balearic Islands exhibited higher acorn damage than their counterparts on mainland Spain, but no island-mainland differences were observed in the other two regions. In addition, we found no evidence of island-mainland differences for most acorn traits, except phosphorus content, which exhibited region-specific differences: higher phosphorus in island populations in Greece, whereas the reverse was observed for Sweden vs. Bornholm Island. However, there was no detectable association between acorn traits and herbivory, and although climatic variation associated with insularity was linked to variation in acorn phosphorus content, this had no consequences for acorn damage (i.e., no evidence of an indirect effect of island-associated climatic variation on acorn damage via traits). These findings challenge the prediction of lower herbivory on islands and suggest that

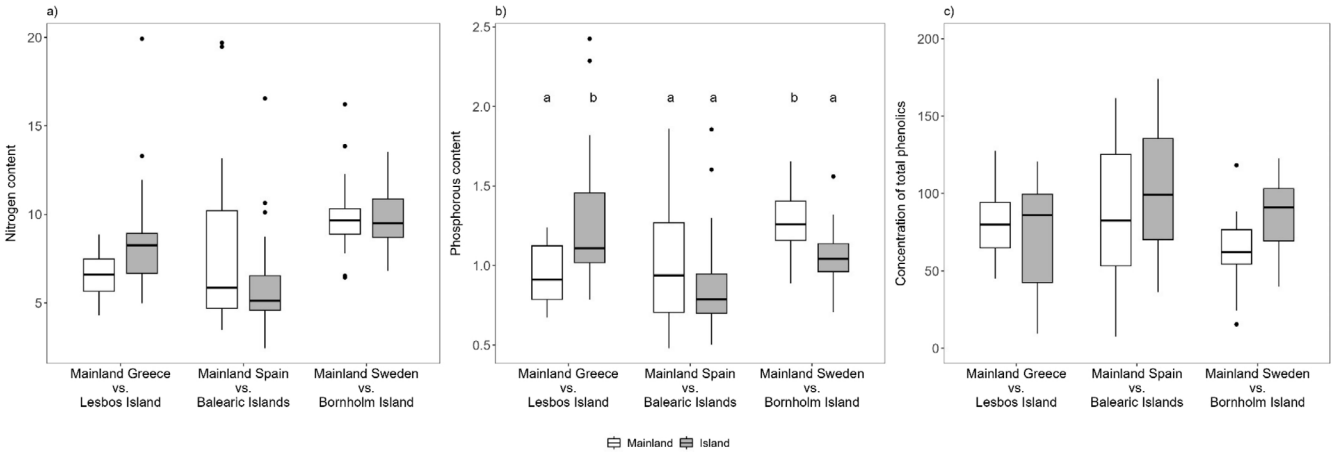

FIGURE 3 | (a) Nitrogen content (mg g^{-1}), (b) phosphorus content (mg g^{-1}) and (c) concentration of total phenolics (mg g^{-1}) in oak acorns on islands and the mainland across three study regions ($N = 150$ trees). Boxplots show the distribution of observed values per group (island or mainland) within each region; boxes represent the interquartile range (IQR), horizontal lines indicate medians, whiskers extend to 1.5× the IQR, and points outside this range are shown as outliers. Different letters indicate statistically significant differences between island and mainland least-squares means within each region, based on post hoc contrasts from the corresponding generalised linear mixed model (Gaussian error distributions), using Sidak correction. Letters are shown only for regions where the insularity × region interaction was significant.

island-mainland patterns of acorn damage are not explained by climatic forcing on acorn traits. In turn, our findings show substantial regional differences in herbivory and trait patterns point to the need for further detailed work to elucidate regional factors that explain observed spatial variation in oak seed predation.

Our results showed that oaks on the Balearic Islands experienced higher acorn damage by insects compared to those on mainland Spain, thus challenging the classical view that herbivory should be weaker on islands (Moreira and Abdala-Roberts 2022; Terborgh 2010). However, this pattern did not hold for the other regions. Although differences were not statistically significant, an inverse trend was observed between mainland Greece and the Island of Lesbos, with acorn damage tending to be higher on the mainland compared to Lesbos Island. Additionally, and in contrast, mean values of acorn damage were very similar between mainland Sweden and Bornholm Island. In contrast to the pattern observed in Spain, in a recent study, insect leaf herbivory across 12 oak species, including some of the same species studied here, was overall lower on islands than on the mainland (Vázquez-González et al. 2025). The same was true for a study on leaf herbivory on holm oak, *Quercus ilex* (Moreira et al. 2019). Taking these findings and our present results into account points to contrasting effects of insularity on folivores and seed predators attacking oaks. We speculate that differences in herbivore guild diversity and diet breadth (which tend to be lower and narrower, respectively, for insects feeding on acorns) do not account for the observed patterns. If they did, one would expect a stronger negative effect of insularity on acorn herbivory in the Spanish region, due to a weaker sampling effect from a less diverse species pool and more restricted host use on islands. For instance, in one of the few studies to date conducting an island–mainland comparison of herbivory on reproductive structures, Monagan Jr. et al. (2017) found lower insect fruit damage on coffee plants in Puerto Rico relative to mainland Mexico. This difference, however, was attributed to stronger top-down control by lizards (*Anolis* spp.) in Puerto Rico, a mechanism that was not tested in our study.

The substantial region-specific variation observed in our study may stem from a combination of differences in the islands' biogeographical histories and regional-scale ecological processes, such as masting dynamics and flowering phenology. For instance, island populations with a longer history of isolation, such as those in Spain, which separated from the continent approximately 25 million years ago (Rosenbaum et al. 2002), have had more time for herbivore communities to diverge and for plants and herbivores to co-evolve. This deeper evolutionary separation may help explain why significant or marginally significant effects of insularity were observed in more strongly isolated island–mainland comparisons. In the particular case of Lesbos, our comparison with mainland Greece rather than the geographically closer Turkish mainland may have reduced our ability to detect clear insularity effects, given that floristic and faunistic affinities between Lesbos and western Anatolia are historically stronger than with more distant Greek populations. However, due to logistical constraints, we used populations from mainland Greece as a reference instead. In addition, although not directly evaluated in our study, the effects of oak masting on seed predation also merit discussion. In *Quercus* species, seed production is typically highly variable and synchronised across individuals, displaying pronounced masting dynamics (Kelly 1994; Kelly and Sork 2002; Koenig and Knops 2000; Sork 1993). These episodic mass seed production events can overwhelm seed predators, reducing seed predation in mast years through predator satiation (Espelta et al. 2008; Fox 1974; Janzen 1971). Importantly, masting events in oaks are strongly influenced by climatic conditions (Pearse et al. 2016). Therefore, if island and mainland populations are not synchronised in their seed production and masting cycles (and if such asynchrony varies among regions, likely due to climatic differences) this may lead to contrasting patterns of acorn damage. Moreover, recent research has shown that resource depletion from previous fruiting events can significantly influence flowering phenology in *Quercus* species, with reduced resource availability constraining flower production in subsequent years (Le Roncé et al. 2023). This resource-mediated variation in flowering timing and synchrony may affect acorn

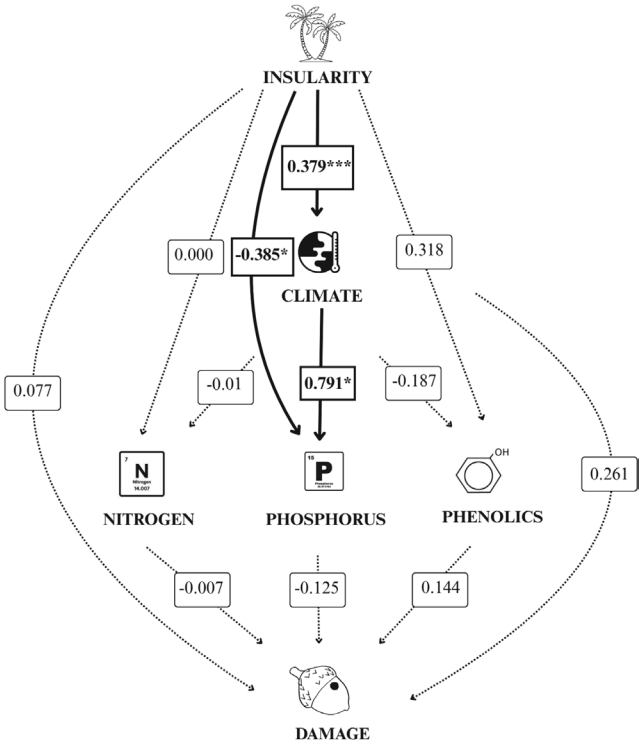

FIGURE 4 | Structural equation model using population level data ($N = 38$) illustrating the direct effects (paths) of (1) insularity, coded as a dummy variable (mainland = 0, islands = 1) on PC1 climate; (2) direct effects of PC1 climate on acorn traits, namely, nitrogen and phosphorus content and the concentration of total phenolics, as well as on acorn damage; and (3) the direct effects of acorn traits on acorn damage. Solid lines indicate statistically significant paths, while dashed lines represent non-significant paths. Significance levels of path coefficients are indicated with stars (***$p < 0.001$). Explained variance based on marginal R^2: Acorn damage = 10%; Nitrogen content = 0%; Phosphorus content = 21%; Phenolics = 7%; PC1 climate = 17%. Model's AIC = 694.888. Model fit was evaluated using the chi-square statistic ($\chi^2 = 43.81$, $p < 0.001$) and Fisher's C statistic ($C = 45.24$, $p < 0.001$); significant values suggest that additional paths not included in the model (particularly among acorn traits) could improve overall model fit (see Table S2 for tested independence claims).

production across populations and further shape seed predator dynamics. Consequently, region-specific differences in flowering phenology, driven by variation in resource dynamics, may also contribute to the geographical variation in acorn damage observed in our study.

Contrary to previous work (Moreira et al. 2019; Vázquez-González et al. 2025), we found no island-mainland differences for most of the acorn traits measured, including nitrogen and phenolic compounds. The only exception was phosphorus, which exhibited region-specific patterns: levels were higher on Lesbos Island compared to mainland Greece, but lower on Bornholm Island compared to mainland Sweden; differences between the Balearic Islands and mainland Spain were negligible and non-significant. In addition, island-mainland differences in acorn phenolics were non-significant across all regions. Previous studies have reported lower levels of plant putative defences on islands (Pardo and Pulido 2017; Vázquez-González et al. 2025), whereas others have found higher levels on islands (Monroy and García-Verdugo 2019; Moreira et al. 2019; Pardo and Pulido 2017) but no previous study has, to our knowledge, reported on differences in plant nutrients. At present, drawing definitive conclusions about the direction and magnitude of variability in acorn chemical traits between island and mainland environments is challenging, highlighting the need for further research.

Our mechanistic (pSEM) analysis showed climatic differences between island and mainland sites, with the former exhibiting higher temperatures and greater seasonality in precipitation. Such variation in climate was also associated with changes in acorn phosphorus content, a finding that is consistent with previous work reporting that climate strongly drives leaf phosphorus content in oaks (Abdala-Roberts et al. 2016, 2018). In turn, we observed a significant indirect positive effect of insularity on phosphorus via climate. The pSEM also showed a significant direct, but negative, effect of insularity on phosphorus. These two opposite effects possibly counteracted each other, leading to the absence of a total effect of insularity on phosphorus, as seen in the linear mixed models. Despite such abiotically driven variation in acorn phosphorus, we found no detectable associations between acorn chemistry and damage, and consequently, no evidence of indirect effects of insularity on acorn damage via acorn traits. This is consistent with previous island–mainland comparisons of leaf chemistry and insect leaf herbivory in oak trees (Moreira et al. 2019; Vázquez-González et al. 2025). Combined, these results do not support the mechanism of bottom-up control as an explanation for island–mainland differences in insect herbivory by either insect herbivore guild (albeit contrasting insularity effects; see above). However, we acknowledge that our trait analyses were based on a relatively small sample of undamaged acorns, a necessary choice to assess constitutive chemical traits, but one that may have limited our ability to detect associations between acorn chemistry and herbivory. It is also possible that unmeasured acorn chemical traits (other types of secondary metabolites) that are putatively associated with acorn damage, or that reproductive traits (phenology or seed output; see above), mediate island–mainland variation in acorn damage. An additional trait worth investigating is acorn size, which has been shown to correlate with insect attack in oak species (Mezquida et al. 2021). Previous research on *Quercus* species has suggested that larger acorns are more likely to be damaged or infested by insects (Espelta et al. 2008; Mezquida et al. 2021). Because seeds tend to be relatively larger on islands than on the mainland (i.e., insular gigantism), larger acorns on islands may increase acorn damage by insects, as seen in some studies (Cox and Burns 2017). Future research should therefore examine a broader suite of physical and chemical acorn traits (e.g., terpenoids, acorn size), along with key reproductive traits (phenology, seed output), to better understand their roles in mediating island–mainland patterns of acorn damage.

Author Contributions

Formulated the idea of the manuscript and designed the experiment: Xoaquín Moreira, Carla Vázquez-González, and Luis Abdala-Roberts; Performed the experiment: Irene Virseda, Carla Vázquez-González, Miquel Capó, Ayco J.M. Tack, Johan A. Stenberg, Finn Hansen, Nikolaos M. Fyllas, Raúl de la Mata, and Joana Cursach; Performed leaf trait analysis and herbivory measures: Irene Virseda, Felisa Covelo, and

Beatriz Lago-Núñez; Obtained funding: Xoaquín Moreira; Analysed the data: Irene Virseda and Carla Vázquez-González; Wrote the first draft of the manuscript: Irene Virseda with input from Carla Vázquez-González, Xoaquín Moreira, and Luis Abdala-Roberts; All authors significantly contributed to revise the manuscript, gave final approval for publication, and agreed to be held accountable for the work performed therein.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study is available in Dryad Digital Repository at https://doi.org/10.5061/dryad.brv15dvm3.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Population information, including island versus mainland location (environment), sampling site (region), species (SP), and population. **Figure S1:** Images showing insect herbivore damage on an oak acorn. **Figure S2:** PCA summarising climate variables, namely, BIO1 (annual mean temperature, °C), BIO4 (temperature seasonality, expressed as the standard deviation of temperature among months ×100), BIO5 (maximum temperature of the warmest month, °C), BIO6 (minimum temperature of the coldest month, °C), BIO12 (annual precipitation, mm), BIO13 (precipitation of the wettest month, mm), BIO14 (precipitation of the driest month, mm), and BIO15 (precipitation seasonality, expressed as standard deviation of precipitation across months). PC1 climate was used for further statistical analyses, and was positively associated with warmer climates that have greater precipitation seasonality, indicating harsher climatic conditions. **Figure S3:** Residual diagnostics for all models used in the study, based on simulated scaled residuals from the DHARMa package. For each model, we present three diagnostic plots: residuals vs. fitted values, uniform quantile-quantile (Q–Q) plot and histogram of scaled residuals. Models include one beta-binomial generalised linear mixed model for acorn damage, and three Gaussian generalised linear mixed models for acorn traits (nitrogen content, phosphorus content and phenolic content). **Table S2:**. Results of direct separation tests for conditional independence claims omitted from the final path model. Significant results indicate potential missing paths that could improve model fit. Test statistics correspond to standardised regression coefficients from linear models, with degrees of freedom (DF), critical values (*t*-values) and associated *p*-values. Significant *p*-values are highlighted in bold.