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RESEARCH ARTICLE

Testing the contribution of vertebrate predators and leaf traits to mainland–island differences in insect herbivory on oaks

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Abstract

1. Ecological theory predicts that herbivory should be weaker on islands than on mainland based on the assumption that islands have lower herbivore abundance and diversity. However, empirical tests of this prediction are rare, especially for insect herbivores, and those few tests often fail to address the mechanisms behind island–mainland divergence in herbivory. In particular, past studies have not addressed the relative contribution of top-down (i.e. predator-driven) and bottom-up (i.e. plant-driven) factors to these dynamics.
2. To address this, we experimentally excluded insectivorous vertebrate predators (e.g. birds, bats) and measured leaf traits associated with herbivory in 52 populations of 12 oak (*Quercus*) species in three island–mainland sites: The Channel Islands of California vs. mainland California, Balearic Islands vs. mainland Spain, and the island Bornholm vs. mainland Sweden ($N = 204$ trees). In each site, at the end of the growing season, we measured leaf damage by insect herbivores on control vs. predator-excluded branches and measured leaf traits, namely: phenolic compounds, specific leaf area, and nitrogen and phosphorous content. In addition, we obtained climatic and soil data for island and mainland populations using global databases. Specifically, we tested for island–mainland differences in herbivory, and whether differences in vertebrate predator effects or leaf traits

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between islands and mainland contributed to explaining the observed herbivory patterns.

3. Supporting predictions, herbivory was lower on islands than on mainland, but only in the case of Mediterranean sites (California and Spain). We found no evidence for vertebrate predator effects on herbivory on either islands or mainland in any study site. In addition, while insularity affected leaf traits in some of the study sites (Sweden-Bornholm and California), these effects were seemingly unrelated to differences in herbivory.
4. *Synthesis*. Our results suggest that vertebrate predation and the studied leaf traits did not contribute to island–mainland variation patterns in herbivory, calling for more nuanced and comprehensive investigations of predator and plant trait effects, including measurements of other plant traits and assessments of predation by different groups of natural enemies.

KEYWORDS
bottom-up effects, chemical defences, island–mainland comparisons, multi-trophic interactions, plant–herbivore interactions, top-down effects, vertebrate predators

1 | INTRODUCTION

Islands provide valuable settings to study the ecological and evolutionary drivers of biodiversity (Gillespie et al., 2008; MacArthur & Wilson, 2001; Ricklefs & Bermingham, 2007), species interactions (Spiller & Schoener, 1990; Traveset et al., 2013), and trait evolution and speciation (Barrett et al., 1997; Burns, 2019; Carvajal-Endara et al., 2020; Grant & Grant, 2007). To address insularity effects, studies have either compared islands differing in historical and physical features (e.g. island size, isolation, geological age), or insular systems with their closest mainland counterparts (Moreira & Abdala-Roberts, 2022). Within this body of research, work on plant–herbivore interactions poses that herbivory should be weaker on islands than on mainland as a result of lower herbivore abundance and diversity owing to processes such as species dispersal constraints and environmental filtering (Carlquist, 1974; Losos & Ricklefs, 2009; Ricklefs & Bermingham, 2007). This hypothesis has primarily been formulated and tested for mammalian herbivory, given the general absence of mammals in most insular systems (Burns, 2014; Cubas et al., 2019; Salladay & Ramirez, 2018; Vourc'h et al., 2001). Alternatively, insect herbivory could be potentially higher in islands than on mainland due to reduced predation pressure (Schoener et al., 2016; Terborgh, 2010), which may lead to overconsumption by phytophagous insects. In this regard, a recent meta-analysis found no overall significant differences in herbivory by invertebrates (i.e. insects and molluscs) between islands and mainland (Moreira et al., 2021). However, these results were based on a limited number of studies (only three on insects), underscoring the need for additional research on insect herbivory on islands and calling for further work to reassess predictions and test underlying mechanisms.

A critical gap in our understanding of insularity effects on insect herbivory has been the lack of experimental studies on top-down effects by natural enemies, that is predators and parasitoids (Abdala-Roberts et al., 2019; Hairston et al., 1960; Price et al., 1980). There are good examples of such tests involving inter-island comparisons (Henneman & Memmott, 2001; Holt, 2010; Kolbe et al., 2023; Spiller & Schoener, 1990), but mainland vs. island comparisons of natural enemy effects are virtually absent (Moreira & Abdala-Roberts, 2022). Analogous to studies comparing islands with different features, some authors have argued that top-down effects of predators should be weaker on islands than on mainland (Holt, 2010; Schoener & Spiller, 2010), presumably because islands have lower predator abundance and diversity or even entirely lack higher trophic levels (Holt, 2010; Terborgh, 2010). However, some vertebrate predators (e.g. birds, bats, lizards) known to exert strong top-down control of insects (Bael et al., 2008; Maas et al., 2016; Mooney et al., 2010; Van Bael et al., 2003; Whelan et al., 2008) can exhibit high population densities on islands partly due to the lack of top predators (Jones et al., 2009; Presley & Willig, 2022; Terborgh, 2023), thereby potentially intensifying the top-down regulation of insect herbivory. Yet, manipulative field studies testing for island–mainland differences in predation are needed to formally test whether top-down trophic forcing contributes to island–mainland differences in herbivory.

Herbivory patterns can also be influenced by bottom-up control through plant physical and chemical defensive traits (Agrawal, 2011; Carmona et al., 2011; Marquis, 1992; Rhoades, 1979), but studies analysing plant defences on islands are underrepresented (Moreira et al., 2021). Island–mainland variation in abiotic conditions (e.g. climate or soil) can shape differences in plant traits (e.g. effects of abiotic stress or resource availability) predictive of herbivory, including chemical defences or nutritional traits. For example, islands tend to have wetter and less seasonal climates than their mainland counterparts (Weigelt et al., 2013), that is favourable growing conditions that may result in higher growth and nutrient content at the expense of defence allocation (Coley et al., 1985). At the same time, islands may be characteristic of soil types with low productivity (e.g. ultramafic soils; Pillon et al., 2010), which could lead to predictions in the opposite direction, that is lower plant growth and higher defences leading to lower herbivory. Furthermore, the extent and nature of climate- and soil-related variability is often strongly site-specific, thus cautioning against generalizing about the direction of abiotically mediated island–mainland differences in plant traits. Although limited by a low number of studies, a recent meta-analysis was unsupportive of this abiotic forcing paradigm, as there was no overall island–mainland difference in chemical or physical plant traits putatively associated with herbivory (Moreira et al., 2021). Nonetheless, more island–mainland comparisons jointly measuring herbivory, multiple plant traits (e.g. Moreira et al., 2019) and abiotic correlates of plant–herbivore interactions are needed to robustly test these mechanisms of insularity effects on herbivory.

In this study, we explored island–mainland differences in insect leaf herbivory using 52 populations of 12 oak (*Quercus*) species distributed across three distant island–mainland sites, namely: The Channel Islands of California vs. mainland California, the Balearic Islands vs. mainland Spain, and the island Bornholm vs. mainland Sweden. Additionally, we tested for predator- and plant-driven island–mainland differences in herbivory. To this end, we conducted a field experiment in which we excluded vertebrate predators (birds, bats) and measured herbivory and leaf traits putatively associated with herbivory, namely: physical traits (measured as specific leaf area, a proxy of leaf thickness), secondary metabolites (phenolic compounds) and nutritional traits (nitrogen and phosphorus content). Additionally, we characterized abiotic conditions (climate and soil characteristics) for each population by using data from global datasets to explain differences in leaf traits associated with herbivory. Specifically, we asked: (i) Do levels of leaf herbivory differ between islands and mainland? (ii) Do vertebrate predators affect herbivory and does such effect contribute to explaining islands vs. mainland differences in herbivory (i.e. a top-down mechanism)? (iii) Does the expression of leaf traits differ between islands and mainland and is any such difference related to variation in abiotic conditions (i.e. climate and soil)? and (iv) do island–mainland differences in leaf traits contribute to explaining herbivory variation (i.e. a bottom-up mechanism)? We hypothesized that oak trees on islands would have lower herbivory than mainland trees. In addition, predictions on top-down and bottom-up effects can act in different ways. On the one hand, stronger herbivore predation by vertebrates on islands would be consistent with, and contribute to explaining, lower herbivory on islands. On the other hand, weaker predation on islands would favour higher herbivory and therefore counter other forces driving lower herbivory on islands, thus leading to weaker island–mainland differences, no overall difference, or even greater herbivory on islands. Lastly, a similar rationale can be applied for bottom-up effects. Less favourable climatic or soil conditions on islands would result in lower plant quality (i.e. lower nutrient content and higher defence) for herbivores and contribute to explaining lower herbivory on islands. More favourable conditions, however, would lead to higher plant quality on islands, which would promote herbivory and therefore counter other factors driving lower herbivory in islands. Overall, by jointly addressing predator effects and plant traits across different study sites, this study provides a novel test of bottom-up and top-down drivers of plant–herbivore interactions, shedding light on the mechanisms underlying differences in herbivory between islands and mainland.

2 | MATERIALS AND METHODS

2.1 | Natural history

We measured leaf damage by insect herbivores and quantified leaf traits in a total of 12 oak species. Six of these species are distributed on both islands and mainland (*Q. agrifolia*, *Q. ilex*, *Q. suber*, *Q. coccifera*, *Q. petraea* and *Q. robur*), three are endemic species, which are only found on the Channel Islands of California (*Q. pacífica*, *Q. tomentella* and *Q.* × *macdonaldii*), and the remaining three species are the closest phylogenetically related congeneric species of these insular endemisms in mainland (*Q. berberidifolia*, *Q. chrysolepis and Q. lobata*, respectively). Eight of the oak species are evergreen (*Quercus ilex*, *Q. coccifera*, *Q. suber*, *Q. agrifolia*, *Q. pacífica*, *Q. berberidifolia*, *Q. tomentella* and *Q. chrysolepis*) and four are deciduous (*Q.* × *macdonaldii*, *Q. lobata*, *Q. petraea* and *Q. robur*).

Common leaf chewing insect herbivores (immature lepidopterans) feeding on oaks in our study sites include: in the Channel Islands and mainland California species such as the California oakmoth (*Phryganidia californica*), the Pacific tent caterpillar (*Malacosoma constricta*) and the Western tussock moth (*Orgyia vetusta*) (Swiecki & Bernhardt, 2006), in the Island Bornholm and mainland Sweden, species such as the winter moth (*Operophtera brumata*), the oak processionary (*Thaumetopoea processionea*) and the pale tussock (*Calliteara pudibunda*) (Aarvik et al., 2017), and in the Balearic Islands and mainland Spain, species such as the gypsy moth (*Lymantria dispar*), and the purple hairstreak (*Favonius quercus*) (Boukouvala et al., 2022).

Common generalist insectivorous vertebrate predators in our insular study sites include: in the Channel Islands and mainland California bird species such as the orange-crowned warbler (*Oreothlypis celata sordida*), Bewick's wren (*Thryomanes bewickii*), Hutton's Vireo (*Vireo huttoni*) and blue-grey gnatcatcher (*Polioptila caerulea*) (Diamond & Jones, 1980) and bat species such as the pallid bat (*Antrozous pallidus*) (Brown & Rainey, 2018), in the Island Bornholm and mainland Sweden bird species such as the European robin (*Erithacus rubecula*), the marsh warbler (*Acrocephalus palustris*) or the coal tit (*Periparus ater*), and bat species such as the whiskered bat (*Myotis mystacinus*) (Ahlén, 1983), and in the Balearic Islands and mainland Spain, bird species such as Balearic warbler (*Sylvia melanocephala*) or the great tit (*Parus major*) (Casas-Riutord, 2022) and bat species such as the common pipistrelle (*Pipistrellus pipistrellus*) (Serra-Cobo et al., 2011).

Oaks display several traits that have been shown to be predictive of insect herbivore damage, in many cases serving as deterrent or toxic anti-herbivore defences. Some of the best-studied traits in leaves include physical traits such as toughness, fibre content and trichomes (Abdala-Roberts et al., 2018; Moreira & Pearse, 2017; Pearse & Hipp, 2009), secondary metabolites such as phenolic compounds (e.g. flavonoids, tannins; Forkner et al., 2004; Lill & Marquis, 2001; Moreira, Castagneyrol, et al., 2018; Pearse & Hipp, 2009) as well as nutritional traits (e.g. nitrogen, phosphorous; Abdala-Roberts et al., 2018; Moreira, Castagneyrol, et al., 2018).

2.2 | Experimental design, leaf sampling and herbivory measurement

Our study included both inter- (congeneric) and intraspecific (conspecific) island–mainland comparisons. Specifically, we included six conspecific comparisons consisting of local oak species that were present both in islands and in mainland, and three congeneric comparisons consisting on insular endemic species (i.e. species only present in islands). In cases of insular endemism where comparison with the same species on mainland was not possible, we selected the closest phylogenetically related species: we paired *Quercus pacifica* with *Q. berberidifolia* (Backs & Ashley, 2016); *Q. chrysolepsis* with *Q. tomentella* (Ashley et al., 2018) and *Q.* × *macdonaldii* (a stabilized hybrid between *Q. pacifica* and *Q. lobata*) with *Q. lobata* (Nixon, 2002). This represented a total of 12 oak species (see above) across three study sites differing in climate and soil conditions, as well as evolutionary and geological history; The Channel Islands of California vs. mainland California and the Balearic Islands vs. mainland Spain were representative of Mediterranean ecosystems, the island Bornholm vs. mainland Sweden comparison was representative of a boreal ecosystem (Figure 1; Table S1).

For each of the nine oak species that were present on islands, we selected three populations in one or two islands and three paired conspecific or congeneric mainland populations (Figure 1), except for *Q. agrifolia* and *Q.* × *macdonaldii* for which we only sampled two island populations, for a total of 52 populations (Table S1; Figure 1). Populations were at least 5 km apart and consisted of at least 15 reproductive trees, except for island populations of *Q. Chrysolepsis* and *Q.* × *macdonaldii* in the Channel Islands of California, and for island populations of *Q. coccifera* in the Balearic Islands, which consisted of fewer individuals. At the beginning of the growing season (late February to early June 2022 depending on the study site; Table S1), we selected four adult trees (*N* = 208) in each population and experimentally excluded vertebrate predators (e.g. birds, bats) from two opposing, low-hanging accessible branches (twigs) at 1–2.5 m above-ground. Vertebrate predator exclusions consisted of 1.5 × 1.5 m wide agricultural mesh netting (1.9 cm mesh diameter, Feitore®) installed on each branch. For each tree, these predator-excluded branches were then paired with two adjacent control branches (i.e. no exclusion netting) of similar height and orientation. At the end of the growing season, after the peak insect abundance and activity (late May to late August 2022 depending on the study site; Table S1), we randomly collected 10 fully expanded leaves from

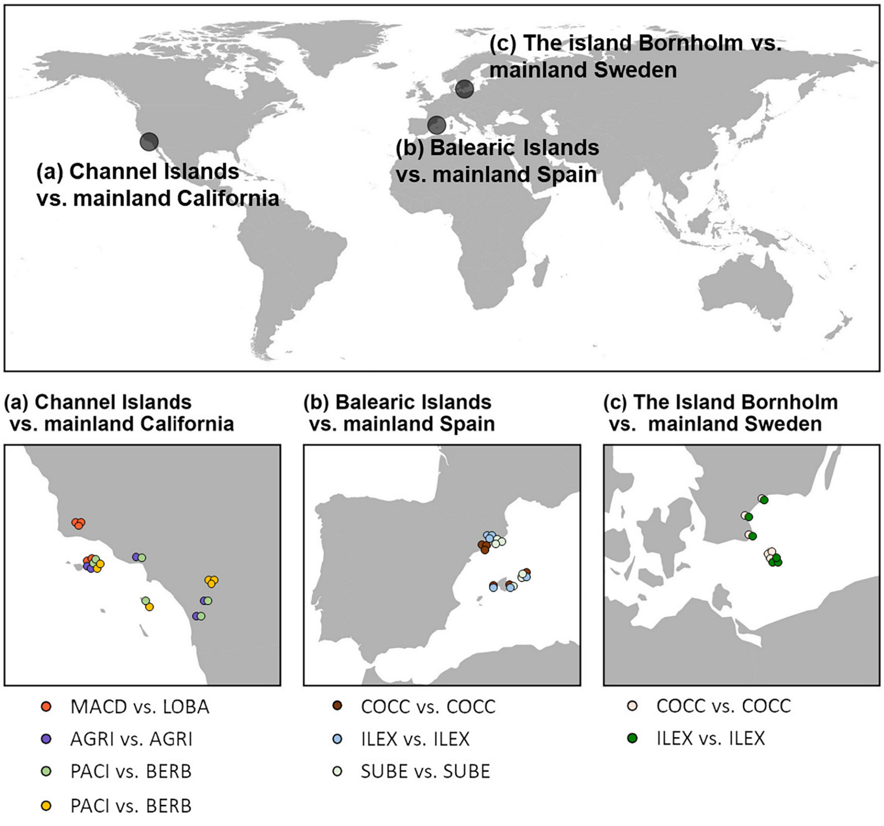

FIGURE 1 Maps showing the three study sites, namely, (a) the Channel Islands of California vs. mainland California, (b) the Balearic Islands vs. mainland Spain and (c) the island Bornholm vs. mainland Sweden, as well as the location of island and mainland populations within each site. See Table S1 in the Supporting Information for specific information about populations. Species codes are: *Quercus ilex* (ILEX), *Q. coccifera* (COCC), *Q. agrifolia* (AGRI), *Q. chrysolepis* (CHRY), *Q. tomentella* (TOME), *Q. suber* (SUBE), *Q. berberidifolia* (BERBE), *Q. pacifica* (PACI), *Q. robur* (ROBU), *Q. lobata* (LOBA), *Q.* × *macdonaldii* (MACD) and *Q. petraea* (PETR). Island populations of insular endemisms where paired to mainland populations of their closest phylogenetically related species: We paired *Q. pacifica* with *Q. berberidifolia*; *Q. chrysolepsis* with *Q. tomentella*, and *Q* × *macdonaldii* with *Q. lobata*.

each predator-excluded and control branch per tree. For predator-excluded branches, we avoided leaves that were in contact with the net to which predators might have had access. For evergreen species, we avoided older leaves not produced during the current growing season. Some mesh nettings were lost due to animal grazing or vandalism, reducing the final number of experimental predator-excluded branches and/or trees (391 branch pairs across 204 trees; Table S1). When a predator-excluded branch was lost, we discarded its associated control branch in order to keep the paired design balanced within subjects (i.e. predator-excluded vs. control branches in each tree). Immediately after leaf collection, we oven-dried leaves at 40°C for 48 h. and then shipped them to Spain (Misión Biológica de Galicia, Pontevedra). Because most of the damage observed on the collected leaves was due to chewing insects (>95% of sampled leaves), we focussed on the percentage leaf area removed by this group ('herbivory' hereafter). Estimates were obtained using the mobile application BioLeaf—Foliar Analysis™ (Brandoli Machado et al., 2016). Most fieldwork was carried out on public lands managed by various institutions, including the University of California Natural Reserve System (Dawson Los Monos Reserve, Emerson Oaks Reserve, Stunt Ranch Reserve, James Reserve, Santa Cruz Island Reserve, Sedgwick Reserve), the Catalina Island Conservancy (Catalina Island), the Danish Nature Agency (Bornholm Island) and the Diputació de Barcelona (Garraf, Montseny, and Montnegre-Corredor Natural Parks), after approval provided by each respective authority. In some instances, such as on mainland Sweden and the Balearic Islands, fieldwork was conducted in areas where formal permits were not required, but all landowners were notified and gave their full support for the sampling activities.

2.3 | Leaf traits

We only quantified leaf traits on the control branches (same ones used for measuring herbivory). We used phenolic compounds as a proxy of chemical defences, which have been broadly shown to act against insect herbivores in oaks (Feeny, 1970; Moreira, Abdala-Roberts, et al., 2018; Moreira et al., 2020; Moreira, Castagneyrol, et al., 2018). We selected two leaves without insect leaf damage in each control branch and ground them together (pooling leaves from the two branches) with liquid nitrogen. We then extracted compounds from 20 mg of dry pulverized leaf tissue with 1 mL of 70% methanol in an ultrasonic bath for 15 min, followed by centrifugation (Moreira et al., 2014). We then transferred the extracts to chromatographic vials. For phenolic quantification, we used an ultra-high-performance liquid chromatography system (UHPLC, Nexera LC-30AD; Shimadzu) equipped with a M20A UV/VIS photodiode array detector (PDA; SPD-M20A Shimadzu). We carried out the compound separation on a Kinetex™ Core-Shell C18 column (2.6 μm, 100 × 4.6 mm; Phenomenex), protected with a C18 guard cartridge. The flow rate was 0.4 mL min^{-1} and the column oven temperature was set at 25°C. The mobile phase consisted of two solvents: water + formic acid (0.1%) (A) and acetonitrile (B), starting with 5% B and using a gradient to obtain 30% B at 4 min, 60% B at 10 min, 80% B at 13 min and 100% B at 15 min. The injection volume was 15 μL. Phenolic compound were measured at 330 nm. For phenolic compound identification, we used an UHPLC-PDA system (Thermo Dionex Ultimate 3000) coupled with an electrospray ionization quadrupole time-of-flight mass spectrometer (QTOF-MS/MS) (Bruker Compact™), suing the same chromatographic conditions as in quantification analysis, but lower injection volume (5 μL). Mass spectra (MS) and MS^2 were acquired in full scan and in negative ionization mode. We identified four groups of phenolic compounds: (i) flavonoids; (ii) ellagitannins and gallic acid derivatives ('hydrolysable tannins' hereafter); (iii) proanthocyanidins ('condensed tannins' hereafter); and (iv) hydroxycinnamic acids, based on the comparison of their parent ion mass and fragmentation pattern, UV spectra and retention time with commercial standards and literature data. We quantified flavonoids as rutin equivalents, condensed tannins as catechin equivalents, hydrolysable tannins as gallic acid equivalents, and hydroxycinnamic acids as ferulic acid equivalents (Moreira, Abdala-Roberts, et al., 2018) by using external calibration curves. We calculated the concentration of total phenolics as the sum of the four groups. We expressed phenolic compound concentrations in mg g^{-1} dry tissue.

We also assessed leaf physical traits and nutrient quality. In the first case, we estimated specific leaf area (SLA) as a proxy of leaf thickness or toughness (Lill et al., 2006; Moreira et al., 2020). Previous work has shown that low SLA correlates with leaf toughness (Hanley et al., 2007; Pearse & Hipp, 2009) and can therefore serve as a measure of physical defence against herbivory. We estimated SLA (mm^2 g^{-1}) for each leaf by dividing the surface area by its dry mass in the same leaves that were used for analysis of phenolic compounds.

In the case of nutrients, we quantified phosphorus and nitrogen concentration, which have been shown to be predictive of herbivory across many plant taxa (Huberty & Denno, 2006; Mattson, 1980), including oaks (Eatough Jones et al., 2008; Forkner & Hunter, 2000). Specifically, we pooled into a single population sample four leaves (two from each of the two control branches) from each tree and ground them with liquid nitrogen. We digested 0.1 g of ground dried leaf material in a mixture of selenic-sulphuric acid and hydrogen peroxide (Moreira et al., 2012). Diluted aliquots of the digestion were analysed by colorimetry for quantification of nitrogen (indophenol blue method) and phosphorus (molybdenum blue method) concentration using a Biorad 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.

2.4 | Climatic and soil data

We characterized climatic and soil conditions for each population. For climatic data, we used a subset of eight bioclimatic variables from WorldClim database version 2.1 at the 2.5 min resolution (Fick & Hijmans, 2017), consisting of historical data from 1970 to 2000, 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), BIO15 (precipitation seasonality, expressed as standard deviation of precipitation across months). For soil data, we used variables from the SoilGrids database version 2.0 at 250-m grid resolution (Poggio et al., 2021), namely bulk density ($kg\,m^{-3}$), cation exchange capacity ($cmolc\,kg^{-1}$), volumetric percentage of coarse fragments, soil organic carbon content (‰), PH, and percentage of clay, silt and sand in the topsoil (5–15 cm). We summarized population level climatic and soil data using principal component analysis (PCA) and retained each of the first PCs for further statistical analyses. The first PC for climatic data (PC1 climate) explained 62.82% of total variation and positive values were associated with warmer and drier climates (i.e. more limiting climatic conditions) (Figures S1a and S2a). The first PC for soil data (PC1 soil), explained 52.24% of total variation and positive values were associated with higher bulk density, clay and silk content, and lower organic matter (i.e. more limiting soil conditions) (Figures S1b and S2b).

2.5 | Statistical analyses

First, we ran a linear mixed model (LMM) testing the effects of insularity (two levels; island and mainland), vertebrate predation (two levels; predator-excluded and control branches), study site (three levels; Channel Islands of California vs. mainland California, Balearic Islands vs. mainland Spain, and island Bornholm vs. mainland Sweden), and their two- and three-way interactions, all treated as fixed factors, on herbivory. We also included the identity of the conspecific (intraspecific) or congeneric (interspecific) island–mainland pair identity (i.e. species identity in the case of conspecific comparison or species pair identity in the case of congeneric comparison Figure S3), the population, and the individual tree as random effects, the latter to account for paired branch design (i.e. repeated measures, see *herbivory measurements* above). Herbivory data was log-transformed to achieve normality of residuals. When we found significant ($p < 0.05$) or marginally significant ($p < 0.1$) interactions, we ran follow-up post hoc mean contrast analyses to examine significant differences between groups for a given factor within each level of the other factor (e.g. differences in average values between islands and mainland for each site). We also performed a likelihood ratio test (LRT) to asses the contribution of random factors to variance explained by the model. It is important to note that we also tested for interactions between comparison type (two levels; inter- or intraspecific comparison) and insularity, as well as comparison type and predation on herbivory in a model with pair identity, study site, population and tree identity as random effects, and both interactions were non-significant ($F = 0.02$; $p = 0.869$ and $F = 0.08$; $p = 0.775$ for interactions with insularity and predation, respectively), suggesting that the observed patterns were not affected by the type of comparison.

Second, we ran LMMs testing the effects of insularity (island vs. mainland), study site (three levels; Channel Islands of California vs. mainland California, Balearic Islands vs. mainland Spain, and island Bornholm vs. mainland Sweden) and their interaction on each measured leaf trait using data from control branches only. Specifically, we ran models for SLA, each group of phenolic compounds (flavonoids, hydrolysable tannins, condensed tannins, and hydroxycinnamic acids), total phenolics (i.e. sum across compound groups) and leaf nutrients (nitrogen and phosphorous content). We included the identity of the conspecific or congeneric island–mainland comparison and population as random factors (except for leaf nutrients, which were obtained at the population rather than individual plant level; see above). We squared root transformed SLA and nutrients, and log-transformed phenolics to achieve normality of residuals. When we found significant ($p < 0.05$) or marginally significant ($p < 0.1$) interactions, we ran follow-up post-hoc mean contrast analyses to examine significant differences between groups for a given factor within each level of the other factor, and performed an LRT to asses the contribution of random factors to variance explained by each model.

Finally, we ran a piecewise structural equation model (PSEM) (Lefcheck, 2016) using population-level data to conduct a cross-site test of causal relationships between insularity, abiotic factors, leaf traits, predation effects and herbivory, and whether abiotically mediated bottom-up forcing, or top-down predation effects, explained island–mainland differences in herbivory. Preliminary analyses based on population-level correlations indicated that the concentration of phenolics and SLA were negatively and positively associated with herbivory respectively (Figure S4a,b), suggesting that these traits conferred resistance to herbivory, therefore justifying their use as predictors of leaf damage. We summarized variation in leaf traits using PCA with population-level data for all traits (total phenolics in the case of chemical defences). The first PC (PC nutrients) explained 57.46% of total variation in leaf traits and positive values were associated with higher SLA and higher concentration of nitrogen and phosphorous (i.e. thinner leaves with higher nutrient content, indicative of higher plant quality via lower physical defence) (Figure S5), whereas the second PC (PC phenolics) explained 32.62% of total variation in leaf traits and positive values were associated with higher concentration of phenolic compounds (i.e. proxy of higher chemical defence) (Figure S5). We used leaf trait PCs z-values rather than individual traits in the PSEM to avoid collinearity among predictors and model overparameterization. In addition, we computed population-level predation effects as Hedges' g effect sizes (Figure S6), where positive values indicated higher herbivory on predator-excluded than on control branches, and negative values indicated lower herbivory on predator-excluded than control branches. We built a PSEM including the direct effects of (1) insularity (coded as a dummy variable; mainland = 0, islands = 1) on abiotic factors (PC1 climate and PC1 soil), predation (Hedges' *g*), leaf trait PCs and herbivory, (2) abiotic factors on predation, leaf trait PCs and herbivory, and (3) predation and leaf trait PCs on herbivory. We also calculated indirect effects of (4) insularity on leaf trait PCs via abiotic factors, and of (5) insularity on herbivory via predation, leaf trait PCs and abiotic factors, and compared them to the corresponding direct effects of insularity on these variables. Direct effects were calculated as standardized model path coefficients for each response variable, while indirect effects were the product of intervening direct effects along the specified causal pathway of interest. The PSEM included the study site and the identity of the conspecific or congeneric island–mainland comparison as random factors. We log-transformed herbivory data.

We conducted all analyses in R version 4.2.1 (R Core Team, 2013). We implemented linear mixed models using the *lmer* function, conducted type III anova based on Satterthwaite approximation for degrees of freedom using the *anova* function, obtained variance estimates for random factors using the *summary* function, and performed LRT for random factors using the *ranova* function; all functions from the *lmerTest* package (Kuznetsova et al., 2017). We performed post hoc mean contrasts with a Sidak test based on Kenward–Roger approximation for degrees of freedom using the *lsmeans* function from the *lsmeans* package (Lenth, 2016). We implemented the PSEM and obtained direct effect coefficients (i.e. standardized path coefficients) using the *psem* function from the *piecewiseSEM* package (Lefcheck, 2016), and obtained bootstrapped indirect effects (i.e. product of intervening path coefficients) and associated 95% confidence intervals using the *semEff* function from the *semEff* package. We implemented PCA analyses using the *PCA* function from the *FactoMineR* package (Husson et al., 2016). We calculated predation effect size (Hedges' *g*) used as an endogenous variable in the PSEM using the *cohen.d* function with the Hedges' *g* correction from the *effsize* package (Torchiano & Torchiano, 2020).

3 | RESULTS

The main effect of insularity (islands vs. mainland) on herbivory was marginally significant but contingent on the study site (i.e. significant insularity × study site interaction; Table 1). There was a significant island–mainland difference in herbivory for both Mediterranean sites, with herbivory being ca. 116% higher on mainland Spain ($3.09 \pm 0.90\%$) than on the Balearic Islands ($1.42 \pm 0.53\%$) and ca. 60% higher on mainland California ($4.35 \pm 1.02\%$), than on the Channel Islands ($2.72 \pm 0.73\%$) (Figure 2). In contrast, there was no significant difference in herbivory between mainland Sweden ($4.48 \pm 1.47\%$) and the island Bornholm ($6.30 \pm 1.96\%$) (Figure 2). In addition, we found no significant effect of vertebrate predation on herbivory (predator-excluded: $3.43 \pm 0.55\%$; control: $3.49 \pm 0.55\%$), and there was no interaction between predation and insularity or study site, indicating consistent non-significant effects of predators on herbivory across island and mainland locations and across study sites (Table 1; Figure 2).

TABLE 1 Results from the linear mixed model testing the effect of insularity (two levels; islands and mainland), predation by vertebrates (two levels; predator-excluded and control branches), study site (three levels; Channel Islands of California vs. mainland California, Balearic Islands vs. mainland Spain, and island Bornholm vs. mainland Sweden), and their two- and three-way interactions on percentage of chewing insect leaf herbivory on oak trees.

Fixed effects	df (num, den)	*F*-value	*p*
Insularity	1, 40	3.73	0.060
Predation	1, 574	0.07	0.787
Study site	2, 6	2.46	0.166
Insularity × predation	1, 573	0.00	0.964
Insularity × study site	2, 40	4.82	**0.013**
Predation × study site	2, 573	0.90	0.408
Predation × study site × insularity	2, 573	0.48	0.618

Random effects	σ^2	LRT	*p*
Tree	0.07	22.52	**<0.001**
Population	0.09	25.05	**<0.001**
Island–mainland comparison identity	0.10	11.00	**<0.001**
Residual	0.35	–	–

Note: *F*-values, degrees of freedom (numerator, denominator) and associated *p*-values for each fixed effect from the corresponding model, as well as variance (σ^2) explained by random factors and significance based on a likelihood ratio test (LRT) are shown. Significant *p*-values are highlighted in bold.

There was no significant main effect of insularity on total leaf phenolics, but there was a significant insularity × study site interaction whereby insularity only had a significant effect on total phenolics at the boreal site, namely, the concentration of total phenolics was ca. 41% higher on mainland Sweden than on the island Bornholm (Figure 3A). Analyses for each group of phenolic compounds indicated significant main effects for condensed tannins and hydroxycinnamic acids (Table 2) with overall greater mean values on mainland than on island locations (Figure S7). In addition, there was a significant (or marginally significant) insularity × study site interaction for all groups of phenolics depicting site-specific patterns, where the concentration of some groups of phenolics was lower on mainland Sweden and mainland California than on their respective islands, but no insularity effect was detected on mainland Spain vs. Balearic Islands (Table 2; Figure S7). Effects on SLA and nutrients followed a similar pattern, with a main effect of insularity on phosphorus content (but not SLA or nitrogen content; Table 2), and insularity × study site interactions for SLA and phosphorus (marginally significant in the latter case) whereby significant Island–mainland differences were only observed for the boreal site (Figure 3). Here, SLA was ca. 20% lower and phosphorus content 36% higher on mainland Sweden than on the island Bornholm (Figure 3B,D).

The PSEM indicated positive direct effects of insularity on PC1 climate and PC1 soil. Specifically, islands were warmer, drier, had higher seasonality in precipitation and had soils with lower organic matter content and higher bulk density than mainland locations (Figure 4a).

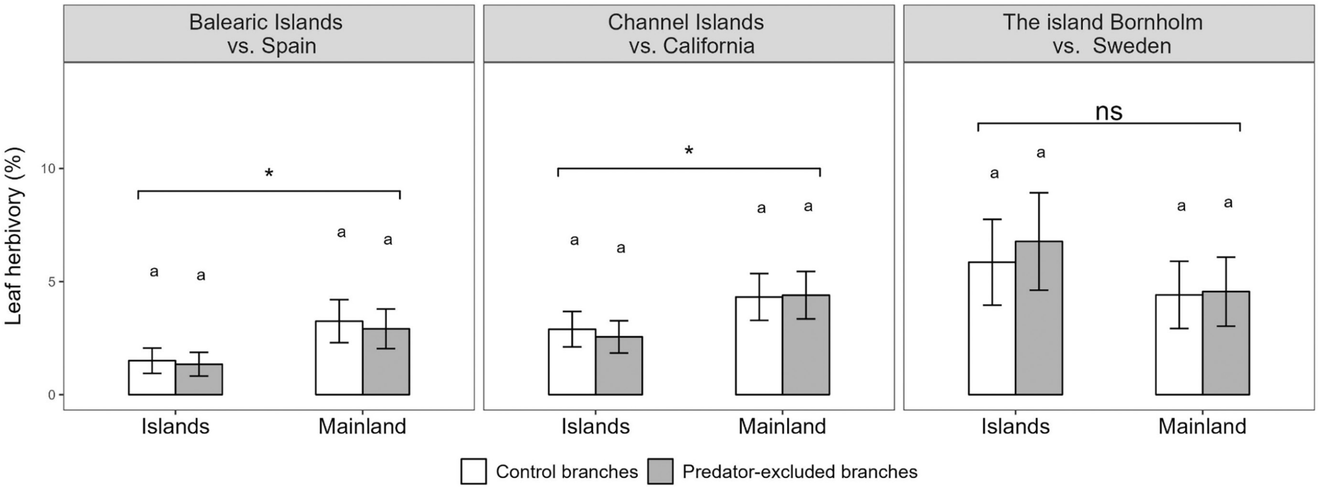

FIGURE 2 Effect of insularity (two levels; islands vs. mainland) and the top-down effect of predation by vertebrates (two levels; predator-excluded vs. control branches) on percentage leaf herbivory in oak trees across study sites. Bars represent least squared means (± SE) as predicted by the corresponding linear mixed model ($N = 204$). Different letters represent statistical differences between least square means of control and predator-excluded branches for each level of insularity and site, while asterisks represent statistical differences between least square means of islands and mainland for each level of site (ns, non-significant; $^{*}p < 0.05$).

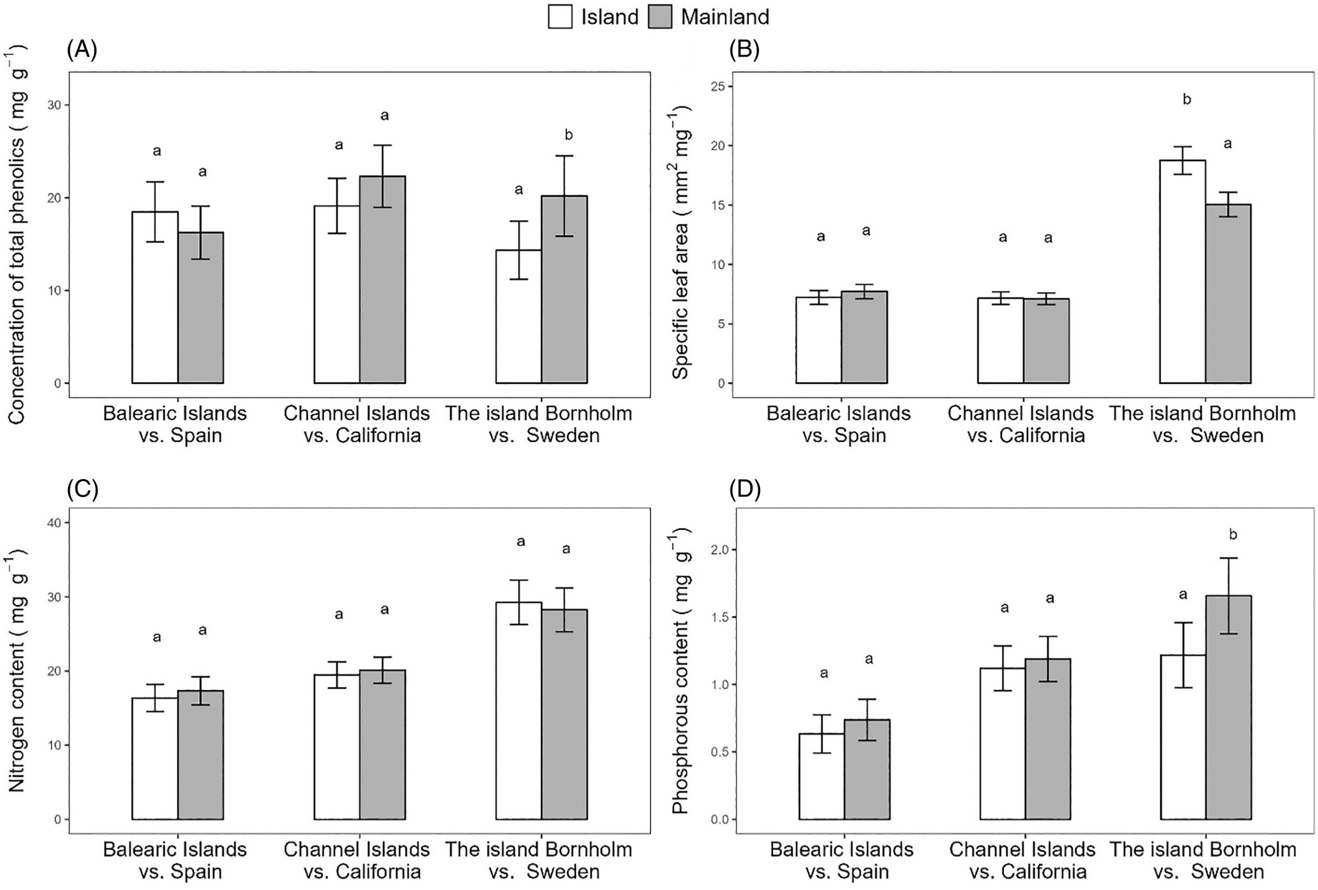

FIGURE 3 Effect of insularity (islands vs. mainland) on individual leaf traits across study sites. Bars represent least squared means (±SE) as predicted by the corresponding linear mixed model for (A) the concentration of total phenolics ($N = 204$), (B) specific leaf area ($N = 204$), and (C) nitrogen and (D) phosphorous content ($N = 52$). Statistical differences between islands and mainland are indicated with different letters.

TABLE 2 Results from the linear mixed models testing the effects of insularity (two levels; islands and mainland), study site (three levels; Channel Islands of California vs. mainland California, Balearic Islands vs. mainland Spain, and island Bornholm vs. mainland Sweden), and their interaction on individual leaf traits in control branches (without predator exclusions).

	Fixed effects			**Random effects**		
	***F*-value**$_{\mathbf{(DenDF,NumDF)}}$			$\sigma^2_{\mathbf{(LRT)}}$		
	Insularity	**Study site**	**Insularity × site**	**Population**	**Pair identity**	**Residual**
Individual leaf traits						
Total phenolics (mg g^{-1})	$3.50_{(1,40)}$	$0.44_{(2,6)}$	$\mathbf{4.13}_{\mathbf{(2,40)}}^{*}$	$0.03_{(21.61)}^{***}$	$0.07_{(19.24)}^{***}$	0.06
Flavonoids (mg g^{-1})	$0.00_{(1,41)}$	$2.92_{(2,6)}$	$\mathbf{4.19}_{\mathbf{(2,41)}}^{*}$	$0.05_{(39.76)}^{***}$	$0.04_{(6.92)}^{**}$	0.07
Hydrolysable tannins (mg g^{-1})	$1.33_{(1,38)}$	$0.22_{(2,6)}$	$\mathbf{3.17}_{\mathbf{(2,38)}}^{\bullet}$	$0.01_{(28.45)}^{***}$	$0.03_{(24.68)}^{***}$	0.02
Condensed tannins (mg g^{-1})	$\mathbf{13.34}_{\mathbf{(1,41)}}^{***}$	$1.05_{(2,6)}$	$\mathbf{4.11}_{\mathbf{(2,41)}}^{*}$	$0.02_{(14.14)}^{***}$	$0.09_{(35.95)}^{***}$	0.04
Hydroxycinnamic acids (mg g^{-1})	$\mathbf{8.67}_{\mathbf{(1,40)}}^{**}$	$0.03_{(2,6)}$	$\mathbf{5.59}_{\mathbf{(2,40)}}^{**}$	$0.04_{(17.37)}^{***}$	$0.14_{(30.09)}^{***}$	0.08
SLA (mm^2 mg^{-1})	$3.81_{(1,39)}$	$\mathbf{56.39}_{\mathbf{(2,6)}}^{***}$	$\mathbf{5.80}_{\mathbf{(2,39)}}^{**}$	$0.02_{(6.46)}^{*}$	$0.02_{(4.64)}^{*}$	0.10
Nitrogen content (mg g^{-1})	$0.20_{(1,40)}$	$\mathbf{6.87}_{\mathbf{(2,6)}}^{*}$	$0.64_{(2,40)}$	–	$0.13_{(25.37)}^{***}$	0.07
Phosphorous content (mg g^{-1})	$\mathbf{11.24}_{\mathbf{(1,40)}}^{**}$	$4.14_{(2,6)}$	$\mathbf{2.44}_{\mathbf{(2,40)}}^{\bullet}$	–	$0.02_{(27.39)}^{***}$	0.01

Note: *F*-values, degrees of freedom (numerator, denominator) and associated significance levels for each fixed effect from the corresponding model, as well as variance (σ^2) explained by random factors and significance based on a likelihood ratio test (LRT) are shown. Significance of fixed and random effects are indicated as: $^{\bullet}p < 0.1$; $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$. Significant or marginally significant fixed effects are highlighted in bold.

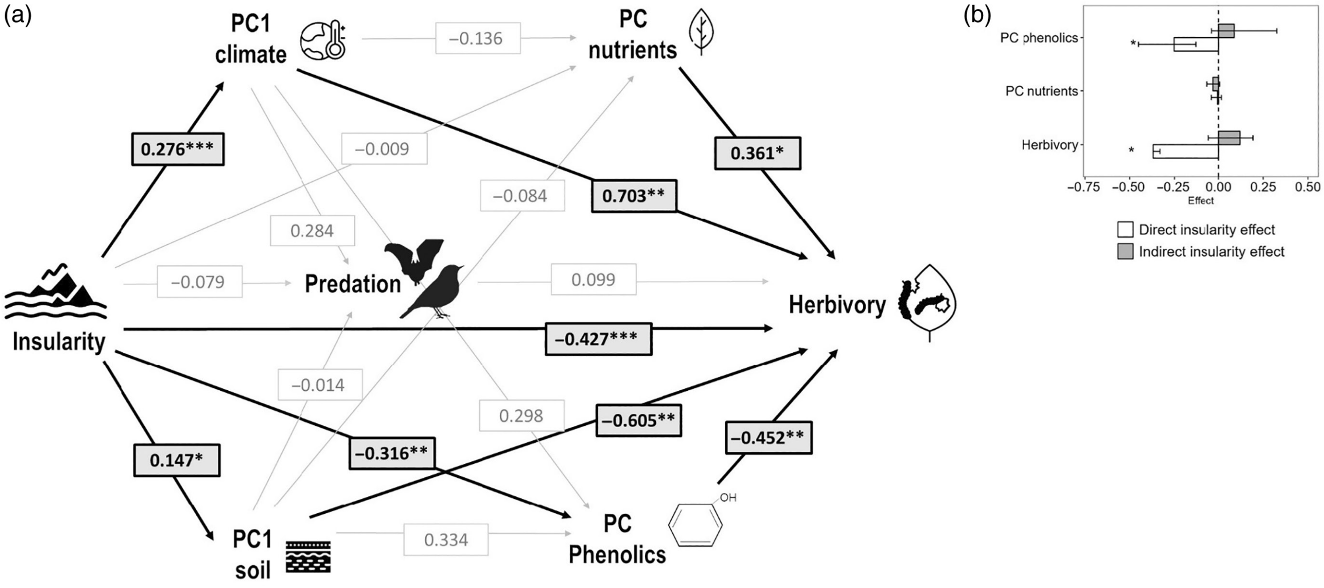

FIGURE 4 (a) Structural equation model showing (1) the direct effects (paths) of insularity (interpreted as the effect of islands over mainland) on abiotic factors (PC1 climate associated with warmer and drier climates and PC1 soil associated with higher bulk density, clay and silk content, and lower organic matter), predation (Hedges' *g* effect size indicating the effect of excluding vertebrate predators), leaf traits (PC nutrients associated with higher SLA and concentration of nitrogen and phosphorous and PC phenolics associated with higher concentrations of phenolic compounds) and herbivory, (2) the direct effects of abiotic factors on predation and leaf trait PCs, and (3) the direct effects of leaf trait PCs on herbivory. Significant paths are in black, while non-significant paths are in grey (both arrows and font). (b) Bar plot depicting (4) the indirect effects of insularity on leaf trait PCs (PC nutrients and PC phenolics) via abiotic factors, and (5) the indirect effect of insularity on herbivory via predation, leaf trait PCs and abiotic factors as compared to corresponding direct effects of insularity on those variables. Bars represent bootstrapped effects ±95% confidence intervals. In both panels, significance levels are indicated with an asterisk: $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$. Explained variance based on marginal R^2: Herbivory = 55%; PC nutrients = 4%; PC phenolics = 28%; PC1 climate = 5%; PC1 soil = 1%; Predation = 1%. Model's AICc = 760.61.

Consistent with the LMMs, there was no direct effect of insularity on predation (Figure 4a). The PSEM showed a negative direct effect of insularity on PC phenolics (not on PC nutrients) (Figure 4a,b), but no direct effect of abiotic PCs on any trait PCs (Figure 4a). Consequently, we found no indirect effect of insularity on leaf traits via abiotic PCs (Figure 4b). Finally, the PSEM showed a significant negative direct effect of insularity on herbivory (Figure 4a,b), as well as significant negative and positive direct effects of PC phenolics and PC nutrients respectively on herbivory (Figure 4a). However, we found no evidence of overall indirect effect of insularity on herbivory via leaf traits, predation and abiotic factors (Figure 4b).

4 | DISCUSSION

Our findings showed that oaks on Mediterranean islands (the Channel Islands in California and the Balearic Islands in Spain) had lower levels of insect leaf herbivory than their mainland counterparts, whereas no difference was found for the boreal site (the island Bornholm vs. mainland Sweden). However, we found no evidence that either top-down or bottom-up forcing contributed to the observed island–mainland herbivory patterns. On the one hand, predators had no detectable effect on insect herbivory and this was consistent at both island and mainland locations. On the other hand, while there were lower levels of leaf phenolics, nutrients (phosphorous) or SLA for oaks on some island sites (e.g. at the island Bornholm and the Channel Islands) than on mainland and these traits correlated with herbivory, the PSEM analyses showed that abiotic factors were not associated with leaf traits and there were no overall indirect effects of insularity on traits via abiotic factors, or on herbivory via traits, predation and abiotic factors. These findings provide limited support for the proposed roles of top-down and abiotically-mediated bottom-up forcing in shaping island–mainland differences in insect herbivory, but also highlight the need for mechanistic studies to uncover the biotic or abiotic drivers of insularity effects on plant–herbivore interactions.

Past studies have hypothesized that herbivore pressure should be weaker on islands than on mainland (Carlquist, 1974; Losos & Ricklefs, 2009; Ricklefs & Bermingham, 2007), but insularity research has been strongly biased towards vertebrate herbivory (approx. 70% of the studies; Moreira et al., 2021). Although patterns of invertebrate herbivory may not necessarily match those for mammals due to differences in dispersal limitation or inherent responses by each group to insularity-related factors, our results provide support for this prediction, though in a site-specific manner. Specifically, insect leaf herbivory was lower on islands than on mainland at both Mediterranean sites, consistent with a previous study reporting that holm oaks (*Q. ilex*) from Mediterranean insular populations exhibited lower levels of insect leaf herbivory than those on mainland (Moreira et al., 2019). Similarly, Monagan Jr. et al. (2017) found lower fruit damage by insects in coffee agroecosystems on the island of Puerto Rico than on mainland Mexico. In contrast, Pardo and Pulido (2017) found that insect leaf damage in *Prunus lusitanica* was higher in the Macaronesia insular region than on mainland Iberia. However, we did not observe differences in herbivory at the boreal site, underscoring site-specific responses and warranting a more detailed inspection to explain variation across sites.

The observed site-specific differences in herbivory could be explained by historical factors that vary across insular (and mainland) regions. The Mediterranean islands in our study have a longer history of isolation (around 5 Mya the Californian Islands and around 25 Mya the Balearic Islands; Muhs et al., 2014; Rosenbaum et al., 2002), which could lead to stronger island–mainland differences in insect species abundance or richness and resulting herbivore pressure. In contrast, many boreal islands are continental islands and of relatively recent geological age (10,000 years in the case of Börnholm; Andrén et al., 2000), then having experienced less evolutionary time for island–mainland species divergence. The similar environmental conditions and shorter isolation times may thus have led to less pronounced differences in herbivore pressures compared to mainland. In addition, Mediterranean regions typically have high biodiversity, including a wide variety of herbivores and plants (Fady-Welterlen, 2005; Pignatti & Pignatti, 1999), which would set up a stronger Island–mainland contrast. In contrast, boreal sites usually have lower species richness than temperate regions (Gaston, 2000), and the herbivore communities are likely dominated by a few species equally distributed across both mainland and islands. This homogeneity can lead to similar herbivory rates regardless of insularity.

We found no evidence of top-down effects of vertebrate predators on herbivory. This result was surprising and runs counter prevailing evidence that predation by vertebrates reduces insect herbivore abundance and consequently leads to reductions in herbivory (Mooney et al., 2010). In the case of oaks, previous experimental work showed that vertebrate predators, including insectivorous bats and birds, significantly reduced insect abundance and herbivory (Beilke & O'Keefe, 2023; Marquis & Whelan, 1994). However, there is also evidence that these effects can vary among sites and among trees within sites (e.g. due to microhabitat features or as a function of plant ontogeny; Böhm et al., 2011; Giffard et al., 2012; Zehnder et al., 2010), including work reporting an absence of vertebrate predator effects on insect herbivore abundance on adult oak trees (Barber & Marquis, 2011) as well as on seedlings or saplings (Forkner & Hunter, 2000; Giffard et al., 2012). Several factors could be invoked to explain weak vertebrate predator effects or an inability to detect them in our study. First, vertebrate predation effects can vary strongly depending on the herbivore feeding guild (Singer et al., 2014), and there may have been stronger effects on sap-feeding or other insect guilds not studied (Zehnder et al., 2010). Second, while vertebrate predation has been shown to reduce herbivory despite intra-guild predation effects (Mooney et al., 2010), we cannot discard that invertebrate predators (e.g. ants, spiders) benefited from the exclusion of vertebrate predators and this weakened the predator exclusion effect on herbivory (Holt & Polis, 1997; Interian-Aguiñaga et al., 2022; Nell & Mooney, 2019). Third, while we excluded most vertebrate predator from oak branches (e.g. birds, bats), it is possible that smaller vertebrate predators such as lizards were not excluded with netting and compensated for the exclusion of larger vertebrates (Spiller et al., 2024). Fourth, foraging activity of some vertebrate predators (e.g. birds) often exhibits density-dependence, i.e., contingent on prey density (Bridgeland et al., 2010; Singer et al., 2012), such that predation effects could be more difficult to detect at low herbivore abundances (overall low to moderate herbivory rates in our sites would be consistent with this idea). Finally, some studies have found that predation effects were stronger early in the growing season when new foliage is abundant or at sites where leaf turnover is higher (Van Bael & Brawn, 2005). Although we installed the predator exclusions at the beginning of the growing season, a detailed examination of herbivory early in the growing season would allow to detect potential episodes of strong trophic control upon initial stages of plant growth and herbivore community build up.

Theory predicts that predator top-down effects should be weaker on islands than on mainland as a result of lower predator abundance, diversity, or even an entire lack of carnivores (Holt, 2010; Terborgh, 2010). Countering this view, insectivorous vertebrate predators such as birds, bats and lizards, are common predators on islands where they can exhibit considerably high population densities in some systems (Jones et al., 2009; Terborgh, 2023). For instance, a previous study reported that *Anolis* lizards had stronger pest-suppressing effects on the island of Puerto Rico than on mainland Mexico (Monagan Jr. et al., 2017), and a recent review showed that vertebrate effects on insect herbivory were stronger on islands than on mainland (Sam et al., 2024). However, this was not the case in our study, as the predator exclusion had no detectable effect on leaf herbivory across both island and mainland locations, suggesting that top-down control of herbivory was weak and unaffected by insularity. Further research should incorporate complementary methods to assess predator foraging activity (e.g. placing plasticine caterpillars; Low et al., 2014) that allow for measurements of predation by specific carnivore groups, including lizards and invertebrate predators such as spiders and ladybirds, as well as parasitoids, to fully assess predation pressure and test for potential differences between islands and mainland.

Oaks found on islands (in particular in The Channel Islands of Californian and the island Bornholm) showed lower levels of leaf chemical defences (i.e. total phenolic compounds or specific groups of phenolics) and nutrients (phosphorous) or SLA (in the case of Bornholm island) compared to mainland oaks. These results agree with at least one previous study reporting lower levels of phenolic compounds in *Prunus lusitanica* plants in Macaronesia islands compared to those on mainland (Pardo et al., 2018). However, they counter evidence from other studies reporting higher chemical defences for Mediterranean-distributed plants on islands (e.g. cyanogenics, tannins; Monroy & García-Verdugo, 2019; Moreira et al., 2019; Pardo et al., 2018), including a comprehensive study across the Mediterranean basin with one of the oak species studied here (*Q. ilex*; Moreira et al., 2019). We found no support for the predicted abiotically mediated effect of insularity on leaf traits as there were no associations between abiotic factors and leaf traits, leading to a non-significant indirect abiotic effect of insularity on leaf traits. We acknowledge that further work involving a higher resolution of abiotic data, particularly soil conditions, would allow to test with greater precision associations between physicochemical soil variables and leaf traits. In situ soil sampling would be ideal in this regard. Likewise, climatic data at a higher resolution (to characterize microclimates) would also be useful, combined with on-site measurements of other abiotic or physical factors (e.g. salinity, wind exposure, anthropogenic effects).

We found no significant overall indirect effect of insularity on herbivory, nor any evidence supporting the proposed bottom-up mediated effect of insularity (island vs. mainland) on herbivory through measured leaf traits in our PSEM. While insularity was negatively associated with PC phenolics, which were in turn negatively correlated with herbivory, this suggests a positive, rather than negative, indirect effect of insularity on herbivory through this pathway. Furthermore, the PSEM suggests that insularity had a positive indirect effect on herbivory via PC1 climate and a negative indirect effect via PC1 soil, with significant intervening direct effects along each causal pathway. These opposing individual indirect effects appeared to counterbalance each other, resulting in a negligible and non-significant overall indirect effect of insularity on herbivory. This also suggests that the mediating factors included in our analysis—leaf traits, predation and abiotic factors—did not explain the observed pattern of reduced herbivory on islands. Alternatively, this pattern could be the result of reduced herbivore abundance and diversity on islands, which aligns with ecological theory predicting lower herbivory and, thus, weaker selection for defences on islands (Bryant et al., 1989; Carlquist, 1974; Janzen & Rosenthal, 1979; Vourc'h et al., 2001). The lack of an association between leaf traits and abiotic factors in the PSEM analysis further reinforces this possibility. Further work involving joint measurements of plant traits and herbivory at different points in the growing season (especially after initial build-up of herbivory early in the season) and across several seasons (same applies for predation, see above) are needed to reach stronger conclusions about the bottom-up effects of oak trait variation on island–mainland differences in herbivory.

AUTHOR CONTRIBUTIONS

Formulated the idea of the manuscript and designed the experiment: Carla Vázquez-González, Xoaquín Moreira, Luis Abdala-Roberts, Kailen A. Mooney; Performed the experiment: Carla Vázquez-González, Lydia S. Dean, Miquel Capó, Raúl de la Mata, Ayco J. M. Tack, Johan A. Stenberg, Joana Cursach, Ana Hernández-Serrano, Finn Hansen, Kailen A. Mooney; Performed leaf trait analysis and herbivory measures: Beatriz Lago-Núñez, Felisa Covelo, Ana Cao; Contributed reagents/materials/analysis tools: Xoaquín Moreira, Carla Vázquez-González, Kailen A. Mooney; Analysed the data: Carla Vázquez-González; Wrote the first draft of the manuscript: Carla Vázquez-González with input from Xoaquín Moreira, Luis Abdala-Roberts, Kailen A. Mooney; 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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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad Digital Repository at https://doi.org/10.5061/dryad.t1g1jwtbn (Vázquez-González et al., 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1: Populations' information, including island vs. mainland location (environment), sampling site (site), species (SP), unique population identification code (Population ID), number of trees sampled (#trees), number of total control (#Control) and predator-excluded (#Excluded) branches, date in which the exclusions were installed (time_0), date in which leaves were collected (time_f), latitude and longitude. Species codes are: *Quercus ilex* (ILEX), *Q. coccifera* (COCC), *Q. agrifolia* (AGRI), *Q. chrysolepis* (CHRY), *Q. tomentella* (TOME), *Q. suber* (SUBE), *Q. berberidifolia* (BERBE), *Q. pacifica* (PACI), *Q. robur* (ROBU), *Q. lobata* (LOBA), *Q.* × *macdonaldii* (MACD) and *Q. petraea* (PETR). Island populations of insular endemisms where compared to mainland populations of their closest phylogenetically related species: we paired *Quercus pacifica* with *Q. berberidifolia*; *Q. chrysolepsis* with *Q. tomentella*, and *Q.* × *macdonaldii* (a stabilized hybrid between *Q. pacifica* and *Q. lobata*) with *Q. lobata*.

Figure S1: (a) PCA summarizing 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), BIO15 (precipitation seasonality, expressed as standard deviation of precipitation across months). (b) PCA summarizing soil variables, namely, BLDFIE (bulk density, kg m^{-3}), CECSOL (cation exchange capacity, cmolc kg^{-1}), CRFVOL (volumetric percentage of coarse fragments), ORCDRC (soil organic carbon content, permille), PHIHOX (pH index measured in water solution), PHIKCL (pH index measured in KCl solution), CLYPPT (percentage of clay), SLTPPT (percentage of silt) and SNDPPT (percentage of sand).

Figure S2: (a) Boxplot showing variation in PC1 climate and (b) Boxplot showing variation in PC1 soil across study systems. Each point represents a study population.

Figure S3: Boxplots showing average percentage of insect leaf herbivory (a) and leaf traits (b–e) in islands vs. mainland in each conspecific or congeneric comparison. Species codes are: *Quercus ilex* (ILEX), *Q. coccifera* (COCC), *Q. agrifolia* (AGRI), *Q. chrysolepis* (CHRY), Q. tomentella (TOME), Q. suber (SUBE), Q. berberidifolia (BERBE), *Q. pacifica* (PACI), *Q. robur* (ROBU), *Q. lobata* (LOBA), *Q.* × *macdonaldii* (MACD) and *Q. petraea* (PETR).

Figure S4: Bivariate associations between leaf traits and herbivory. Each point is a different island or mainland population.

Figure S5: PCA showing the correlated expression of leaf trait values in oak trees in islands and mainland. Each dot represents an island or mainland population.

Figure S6: Predation Hedges' *g* effect sizes calculated at the population level (Figure S6). Higher (i.e., more positive) predator effects are indicative of higher herbivory on predator-excluded branches, while lower (i.e., more negative effects) of lower herbivory on predator-excluded branches.

Figure S7: Effect of insularity (islands vs. mainland) on individual groups of phenolic compounds, namely, (a) flavonoids, (b) hydrolysable tannins, (c) condensed tannins and (d) Hydroxycinnamic tannins across study sites. Bars represent least squared means (± SE) as predicted by the corresponding linear mixed models ($N = 204$). Statistical differences between islands and mainland are indicated with different letters. Models included the insularity, the study site, and their interaction as fixed factors, and the identity of the conspecific or congeneric comparison, the population (in case of phenolics and specific leaf area) as random factors.

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