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Research Article

From mainland to islands: the evolution of resistance and tolerance to herbivory in long-lived oaks

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Island biogeography theory predicts that island plants should exhibit reduced defences compared with their mainland relatives due to relaxed herbivory pressure. However, growing empirical evidence challenges this prediction, revealing substantial variation among systems, plant lineages and defence types. These inconsistencies suggest that simple expectations of reduced defence on islands overlook the diversity of selective agents and strategies plants use to cope with herbivores. A more integrative perspective proposes that island – mainland comparisons should simultaneously consider multiple defensive mechanisms, including resistance – both constitutive and inducible – and tolerance-related traits. In this study, we conducted two complementary greenhouse experiments to examine resistance and tolerance responses in seven island–mainland species pairs of oaks *Quercus* across three biogeographical regions: Bornholm Island versus mainland Sweden, the Balearic Islands versus mainland Spain, and Lesbos Island versus mainland Greece. Seedlings were exposed to controlled foliar herbivory by the generalist *Lymantria dispar*, with undamaged plants serving as controls. Resistance was quantified by measuring key chemical defences – namely total phenolic content and volatile organic compounds – assessed both at constitutive levels and in terms of inducibility following herbivore damage. Tolerance, in contrast, was evaluated as the plant's capacity for growth compensation, quantified through height regrowth after

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herbivory. Our results show that, contrary to traditional expectations, island and mainland oak seedlings did not differ significantly in either chemical resistance or growth-based tolerance to herbivory. These results suggest that the evolution of plant defences on islands may not be universally reduced and that both island and mainland oaks maintain comparable strategies to cope with herbivory, highlighting the importance of considering multiple defence mechanisms and local ecological contexts when assessing insularity effects.

Keywords: island–mainland comparisons, Lymantria dispar, phenolics, Quercus, regrowth capacity, volatile organic compounds

Introduction

Since the pioneering studies of Darwin and Wallace, islands have been recognized as exceptional systems for studying ecological and evolutionary processes such as adaptive radiations, ecological release, and community assembly (Vitousek et al. 1995, MacArthur and Wilson 2001). In particular, islands offer simplified yet dynamic ecological contexts in which species interactions and evolutionary pressures can be more readily traced than in more biotically complex continental systems (MacArthur and Wilson 2001, Abdala-Roberts and Moreira 2024). Herbivory provides a clear example of this. Herbivore pressure has been shown to differ between islands and mainlands, with many studies reporting lower diversity and abundance of herbivores on islands – a consequence of geographic isolation, smaller land area, and dispersal constraints that limit herbivore colonization (Carlquist 1974, Ricklefs and Bermingham 2008, Burns 2019). If herbivory rates are generally lower on islands owing to these constraints, island plants would be expected to invest less in defensive traits such as physical barriers (e.g. spines, leaf toughness) and chemical compounds (e.g. defensive metabolites) than their mainland relatives (Adsersen and Adsersen 1993, Vourc'h et al. 2001, Burns 2019). Yet, biogeographical tests of island–mainland differences in plant defences remain in their infancy.

Challenging these predictions, a meta-analysis by Moreira et al. (2021) found no consistent reduction in plant defence on islands; in several cases, island species exhibited equal or even higher levels of chemical or physical defences than their mainland relatives. However, the number of studies included in that analysis was still low (n =16), and available research has been strongly restricted to specific systems and plant taxa, often focusing on single traits or defensive strategies (Moreira et al. 2021). Accordingly, an important conclusion of that study was the need for research simultaneously considering multiple defensive strategies to disentangle island–mainland variation in plant traits. Plant defence encompasses any trait that enhances fitness under herbivory and can be broadly categorized into resistance and tolerance mechanisms (Karban and Baldwin 2007). Resistance mechanisms reduce the damage suffered by plants and include structural or chemical traits that may be constitutive or inducible (Karban and Baldwin 2007). Constitutive resistance provides continuous protection but incurs metabolic costs that can constrain growth and reproduction, whereas inducible resistance is activated only after herbivore attack, allowing plants to conserve resources when herbivory is low (Stamp 2003, Karban and Baldwin 2007). In contrast, tolerance mechanisms enable plants to recover after damage through increased growth or resource reallocation (Strauss et al. 1999). Persistent herbivory, often characteristic of mainland habitats, is expected to favour higher constitutive resistance, whereas more variable herbivory regimes – frequently reported on islands – may select for inducible resistance or tolerance strategies. However, although these mechanisms have been extensively studied, constitutive and inducible resistance are rarely analysed separately, and resistance and tolerance are often treated independently (Moreira et al. 2021), a limitation that has carried over into island herbivory research. Failing to consider multiple traits underlying defence strategies may obscure the complex ways in which plant defences evolve on islands, underscoring the need for comprehensive studies that evaluate multiple defence axes simultaneously to reach more robust conclusions.

In this study, we conducted two controlled greenhouse experiments to examine differences in resistance and tolerance responses to herbivory between island and mainland plants. Seedlings from seven oak species *Quercus* spp., representing three biogeographical regions – Bornholm Island versus mainland Sweden, the Balearic Islands versus mainland Spain, and Lesbos Island versus mainland Greece (Fig. 1) – were used. Plants were exposed to foliar herbivory by the generalist caterpillar *Lymantria dispar*, a widespread native herbivore and common pest of oak species occurring in both island and mainland populations (Milanović et al. 2014, Boukouvala et al. 2022), while control plants were left undamaged. Resistance-related traits included total phenolics and volatile organic compounds (VOCs), which were measured in both control and damaged plants to assess inducibility. Tolerance was evaluated as the degree of regrowth in the weeks following herbivore damage. Our study addressed two central questions: 1) do island and mainland plants differ in constitutive levels and inducibility (i.e. the difference between control and damaged plants) of chemical compounds associated with resistance to herbivory? 2) Does regrowth capacity differ between insular and mainland populations, thereby indicating variation in tolerance-related defensive capacity? By integrating resistance and tolerance traits across multiple species and regions, this study provides a more comprehensive and nuanced perspective on how insularity shapes plant defensive phenotypes.

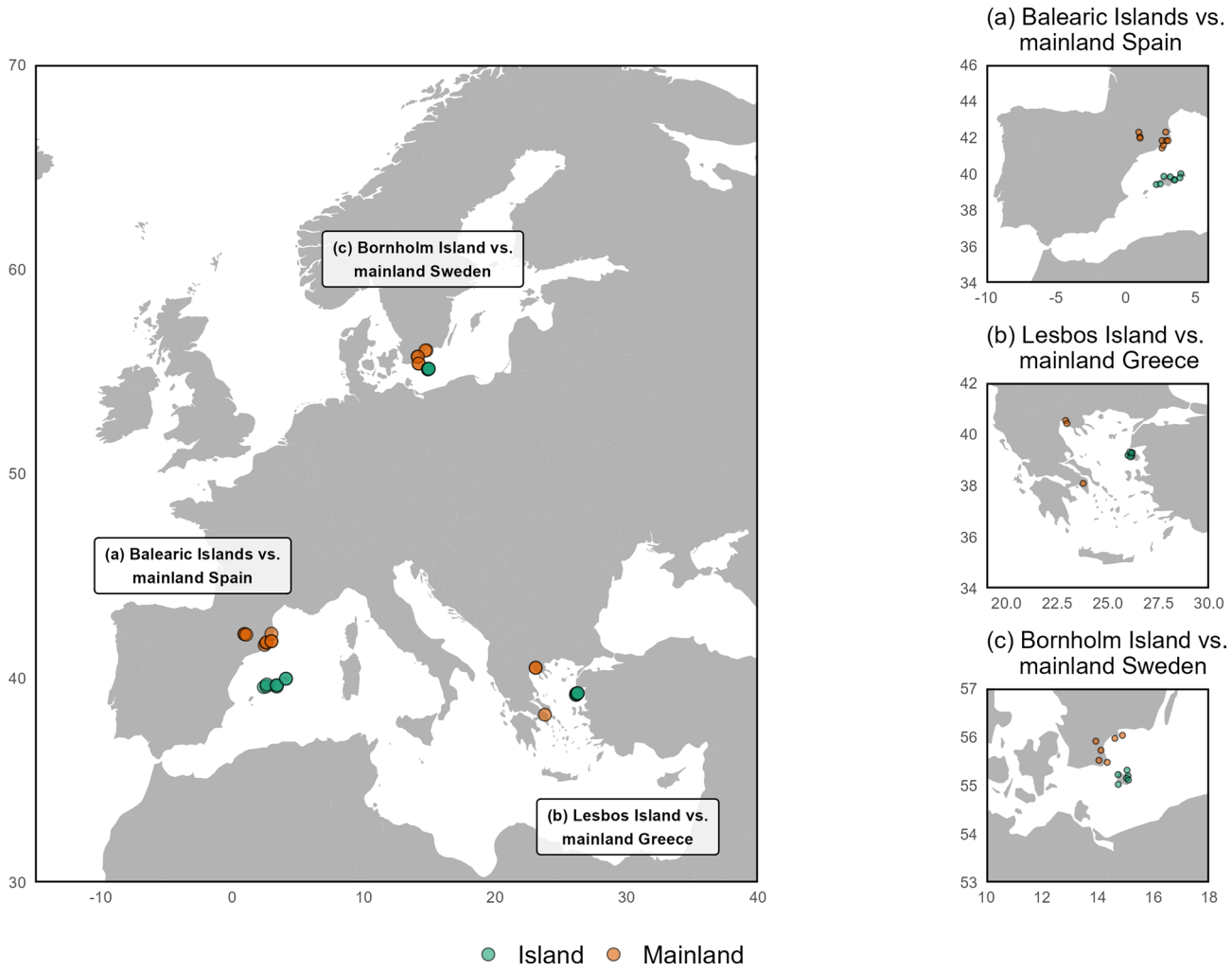

Figure 1. Map showing the locations of mainland and island oak populations across three study regions: Lesbos Island versus mainland Greece, the Balearic Islands versus mainland Spain, and Bornholm Island versus mainland Sweden.

Material and methods

Study system

We studied seven oak species (*Quercus*, Fagaceae) distributed across three island–mainland systems in Europe: Bornholm Island versus mainland Sweden (hereafter the 'northern region'), the Balearic Islands (Mallorca and Menorca) versus mainland Spain (hereafter the 'western Mediterranean region'), and Lesbos Island versus mainland Greece (hereafter the 'eastern Mediterranean region') (Fig. 1). For each focal species, we sampled both island and mainland populations within the same study region. The species included *Q. robur* and *Q. petraea* in the northern region; *Q. ilex*, *Q. coccifera* and *Q. suber* in the western Mediterranean region; and *Q. pubescens* and *Q. ithaburensis* in the eastern Mediterranean region.

European oaks support diverse communities of insect herbivores, including both dietary specialists and generalists, within which folivore guilds such as leaf chewers and miners are often dominant (Roslin and Salminen 2008, Pearse and Hipp 2009, Tack and Roslin 2011, Moreira et al. 2017, 2018a). Among generalist folivores, *L. dispar* (Lepidoptera) is one of the most damaging defoliators of broadleaf forests across western Europe (Milanović et al. 2014). Feeding by larvae of these insects produce irregular holes that can lead to severe defoliation during population outbreaks (Miller and Hanson 1989). Given its widespread distribution and long evolutionary association with Palearctic oaks, *L. dispar* serves as a relevant model herbivore for studying inducible defences and tolerance (Elkinton and Liebhold 1990).

Oak species deploy multiple resistance-related traits against insect herbivores, including chemical traits such as specialized metabolites that deter or are toxic to herbivores (Moreira et al. 2020). These chemical traits can be expressed constitutively or induced upon attack. Inducibility – the ability to upregulate chemical defences following herbivory – is quantified as the difference between induced and constitutive levels (Morris et al. 2006). In this study, we focused on phenolic compounds as a measure of resistance, given their widespread occurrence in *Quercus* and their well-documented capacity to reduce insect performance and preference (Feeny

1970, Roslin and Salminen 2008, Pearse and Hipp 2009, Abdala-Roberts et al. 2016, Moreira et al. 2018a). Phenolics occur at high constitutive concentrations in oak tissues, often up to 100 mg g^{-1} dry weight, and can be upregulated following herbivory (Pearse and Hipp 2009, Moreira et al. 2017, 2018a). In addition, oaks emit volatile organic compounds (VOCs), which are highly inducible and can repel herbivores or attract natural enemies (Staudt and Lhoutellier 2007, Amo et al. 2022). Finally, we evaluated tolerance mechanisms, focusing on regrowth capacity, defined as a plant's ability to restore lost biomass following foliar damage (Strauss et al. 1999). In particular, regrowth represents a compensatory response in which plants allocate resources to produce new tissues after herbivory, thereby mitigating the negative effects of leaf loss on growth and overall fitness (Strauss et al. 1999).

Field sampling

In September 2023, we selected up to three island and three mainland populations for each of the seven oak species, with a few exceptions: only one and two mainland populations were sampled for *Q. ithaburensis* and *Q. pubescens* in Greece, respectively, and two populations were included for *Q. suber* in the Balearic Islands (Supporting information). This resulted in a total of 38 oak populations across island and mainland sites. Populations were chosen based on the presence of at least 15 reproductively mature trees and were separated by a minimum of 2 km from any other population of the same species. The only exception was one *Q. suber* population in Menorca, which contained only 10 reproductive individuals. For each population, we randomly sampled four individual trees ('maternal trees'), except in Menorca's *Q. suber* populations, where only two maternal trees were available. In total, 150 maternal trees were sampled, and from each, 15 acorns were haphazardly collected from the ground beneath the canopy. Acorns were stored in plastic bags with local soil at cool temperatures, shipped to the Misión Biológica de Galicia (Spain), and sown under controlled greenhouse conditions.

Experimental design

In November 2023, we sowed six randomly selected acorns from each of the 150 maternal trees in a greenhouse under controlled conditions. The greenhouse maintained a minimum photoperiod of 10 h per day (photosynthetically active radiation = 725 ± 19 µmol m^{-2} s^{-1}), day/night temperatures of 25/10°C, and regular irrigation twice per week. By April 2024, germination reached approximately 72%, and seedlings had developed sufficient leaf area and size to begin the experiments, with heights ranging from 0.5 to 39.5 cm and 3–10 leaves per seedling. All seedlings belonged to the same cohort and were at comparable phenological stages at the start of the experiment, bearing 5–20 fully expanded leaves at the time of sampling, thereby minimizing potential confounding effects of developmental variation (i.e. phenophases) on plant trait responses. Two complementary greenhouse experiments were conducted: 1) one to test island–mainland differences in resistance-related traits, specifically constitutive levels and inducibility of phenolic compounds and volatile organic compounds (VOCs), and 2) the other to assess tolerance, quantified as regrowth capacity following herbivore damage. This design allowed controlled comparison of resistance and tolerance strategies across multiple island–mainland oak species pairs.

Experiment 1 – measurement of resistance traits

To assess island–mainland differences in chemical traits associated with herbivore resistance, we conducted an experiment in April 2024 using a split-plot design replicated across four blocks. Each block was divided into two main plots corresponding to control and herbivore-induced treatments, the latter applied using *L. dispar*. Main plots were further subdivided into two subplots representing island and mainland populations. Within each subplot, and for each species, we included one individual per population (n = 3), ensuring that induced plants were paired with control individuals derived from the same maternal tree to control for genetic background. Two mainland *Q. coccifera* seedlings were removed to ensure that all control–induced pairs originated from the same maternal tree. When the number of available populations or mother trees was insufficient to complete the experimental structure, additional seedlings from the same population or the same mother tree were incorporated to fill blocks, resulting in some degree of over-representation. The experimental design comprised a total of 334 seedlings, spanning seven oak species, two induction treatments, two insularity origins, and three populations per species (with minor exceptions), across four replicated blocks (Supporting information).

For the herbivory treatment, we collected egg masses of *L. dispar* from the bark of *Q. ilex* trees in two natural populations in the Balearic Islands (Mallorca and Menorca). After hatching in mid-April, larvae were reared in the laboratory on foliage of *Betula pendula*, a common host plant of *L. dispar* (Soukhovolsky et al. 2023). We chose *B. pendula* to avoid larval habituation to any particular oak species and thereby prevent bias when later exposing larvae to *Quercus* seedlings. Once larvae reached the third instar, we applied the herbivory treatment. For each seedling assigned to herbivory, a single larva was placed on the largest leaf and enclosed within a nylon mesh bag to prevent dispersal; feeding was allowed to proceed for 24–48 h until approximately 15% of the leaf area was consumed, after which the herbivores were removed.

Immediately after herbivore removal, we collected VOCs from one of the four experimental blocks following Rasmann et al. (2011), yielding a total of 84 seedlings representing 7 oak species × 2 induction treatments × 2 insularity origins × 3 populations × 1 block. Each seedling was enclosed in a 1-l Nalophan bag, and VOCs were trapped on a charcoal filter by pulling air through the filter with an air-sampling pump for 2 h at 250 ml min^{-1}. Filters were stored at −80°C until chemical analysis. Identical filters, pumps, flow rates and bag volumes were used, and equivalent leaves at comparable developmental stages were sampled across oak genotypes and species.

Immediately after VOC collection, damaged and undamaged leaves from all seedlings across the four blocks were

harvested to quantify phenolics. Leaves were dried at 40°C for 48 h before analysis. Leaf damage in the herbivory treatment was quantified using the BioLeaf-FoliarAnalysis mobile application (Machado et al. 2016) and included as a covariate in the statistical models.

Quantification of phenolic compounds

We ground the leaves of the seedlings to obtain sufficient material, using liquid nitrogen for samples with limited tissue. 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). The extracts were transferred to chromatographic vials. For phenolic quantification, we used an ultra-high-performance liquid chromatography system (UPLC/UHPLC Acquity H-Class PLUS; Waters) equipped with a photodiode array detector (ACQUITY PDA eλ Detector, Waters). We separated the compounds on a Kinetex Core-Shell C18 column (2.6 µm, 100 × 4.6 mm; Phenomenex), protected by a C18 guard cartridge. The flow rate was 0.4 ml min−1, and the column oven temperature was set to 25°C. The mobile phase consisted of two solvents: water (A) and acetonitrile + formic acid (0.01%) (B), starting with 5% B and using a gradient to reach 30% B at 16 min, 60% B at 25 min, 100% B at 27 min, at 5% B at 28 min. The injection volume was 5 µl. Phenolic compounds were measured at 280 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), using the same chromatographic conditions as for quantification analysis but with a lower injection volume (5 µl). Mass spectra was acquired in full scan mode and negative ionization mode. We identified compounds by comparing the acquired MS/MS spectra with reference spectral libraries and previously published data. Identification was based on matching fragmentation patterns, diagnostic mass-to-charge (m/z) ions, and consistent chromatographic retention times. We identified four groups of phenolic compounds: 1) flavonoids; 2) ellagitannins and gallic acid derivatives ('hydrolysable tannins' hereafter); 3) proanthocyanidins ('condensed tannins' hereafter); and 4) hydroxycinnamic acids, based on the comparison of their parent ion mass, fragmentation patterns, UV spectra, and retention times 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 (Hagerman and Butler 1978, Moreira et al. 2018b) using external calibration curves. We calculated the total phenolic concentration as the sum of the four groups and expressed phenolic compound concentrations in mg g^{-1} dry tissue.

VOC analyses

We eluted the previously collected charcoal traps with 150 µl of dichloromethane (CAS no.75–09-2; Merck), to which we had previously added a naphthalene internal standard (CAS no.91–20-3, 200 ng in 10 µl of dichloromethane). Then, following the method described by Rasmann et al. (2011), we injected 1.5 µl of each sample extract into an Agilent 7890B gas chromatograph (GC) coupled to a 5977B mass selective detector, equipped with a 30 µm × 0.25 mm × 0.25 µm film thickness HP-5MS fused silica column (Agilent). We performed the injection in pulsed splitless mode (250°C, 15 psi injection pressure) using helium as the carrier gas. The GC oven temperature program began with a 3.5 min hold at 40°C, followed by a ramp of 5°C min^{-1} to 230 °C, and concluded with a 3 min hold at 250°C. We maintained the transfer line at 280°C. On the mass spectrometer (MS) operating in electron ionization (EI) mode, we scanned a mass range of 33–350 m/z, with the MS source and quadrupole set at 230 and 150°C, respectively. We primarily identified VOCs using the NIST database and confirmed them by comparing their Kováts retention indices with those of n-alkanes (C8–C20, Sigma Aldrich, Merck KGaA; Supporting information) analysed under the same chromatographic conditions, or by using commercially available standards. We quantified the emission of individual VOCs by measuring normalized peak areas and expressed the results in nanograms per hour (ng h^{-1}). We obtained the normalized peak area for each compound by dividing its integrated peak area by the integrated peak area of the internal standard (naphthalene) (Abdala-Roberts et al. 2022), which corrected for variations in sample volume during the elution process. Therefore, we reported the values for individual VOCs as naphthalene-equivalent nanograms of compound released by each plant per hour. Finally, we calculated the total VOC emission as the sum of all individual VOCs.

Experiment 2 – assessment of tolerance-related responses

To assess island–mainland differences in tolerance to herbivory, we conducted a second greenhouse experiment in May 2024 using seedlings from experiment 1 that had not been previously sampled. As in experiment 1, the study followed a split-plot design replicated across two blocks, each divided into control and herbivore-induced main plots (using *L. dispar*) and further subdivided by insularity origin (island versus mainland). Induced plants were paired with control individuals derived from the same maternal tree, and herbivory was applied following the same protocol described for experiment 1. Due to limited seedling availability, *Q. suber* and *Q. ithaburensis* were excluded. The final design included 100 seedlings, spanning five oak species, two induction treatments, two insularity origins, and three populations per species (with minor exceptions), across two replicated blocks. Tolerance was quantified as compensatory growth based on weekly height measurements over 11 consecutive weeks following herbivore removal (Strauss et al. 1999).

Statistical analysis

We conducted all analyses using R ver. 4.2.1 (www.r-project.org). We first tested the effects of insularity separately on constitutive levels of chemical traits associated with resistance

and on their inducibility across study regions. For constitutive phenolics, generalized linear mixed models (GLMMs) were fitted using the *glmmTMB* function from the 'glmmTMB' package (Brooks et al. 2017) to test the effects of insularity (island versus mainland), study region (Balearic Islands versus mainland Spain, Bornholm versus mainland Sweden, Lesbos versus mainland Greece), and their interaction on concentrations of phenolic compound groups – flavonoids, hydrolysable tannins, condensed tannins, hydroxycinnamic acids – and total phenolics. Only control plot data were used, with seedling height included as a covariate. Random factors included population, oak species, block, and the insularity × block interaction. GLMMs were fitted with a Gamma distribution and log link due to non-normal, right-skewed residuals (Zuur et al. 2009). For condensed tannins, a Tweedie distribution was used to account for zero inflation (Dunn and Smyth 2005). The significance of fixed effects was assessed using Wald χ^2 tests via the *Anova* function from the 'car' package (Fox et al. 2001), and post hoc mean contrasts for significant factors were conducted using the *emmeans* function from the 'emmeans' package (Lenth 2023).

To test insularity effects on the inducibility of phenolics, we applied a bootstrap approach following Moreira et al. (2013). For each seedling in the induced treatment, inducibility was calculated as the difference between its induced value and that of each of the four control plants from the same population (one from the same maternal tree and three from other maternal trees within the population). This procedure yielded four estimates per induced seedling, which were treated as repeated measures in the analysis. When fewer than four control seedlings were available per population, we randomly duplicated values to obtain four estimates. This occurred in one island population of *Q. coccifera* and one of *Q. ilex*, where only two viable control seedlings were available. This procedure was applied to each phenolic group and to total phenolics as well. We then fitted repeated-measures GLMMs using *glmmTMB* with a Gaussian distribution and identity link function (Faraway 2006), including insularity, study region, and their two-way interaction as fixed factors. Seedling height and herbivory damage (to account for variation in feeding) were included as covariates. Random factors included population, oak species, block, the interaction between insularity and block, and seedling ID (the latter accounting for repeated measures). The significance of fixed effects and post hoc contrasts were assessed as described above. To account for multiple comparisons, p-values for constitutive and inducible phenolics were adjusted using the false discovery rate method (Benjamini and Hochberg 1995), with significance set at $p < 0.05$.

We then tested insularity effects on constitutive VOC emissions using data from one block. For constitutive VOCs, we fitted a GLMM on total VOC emissions using *glmmTMB* with a Gamma distribution and log link function (Zuur et al. 2009). Fixed factors included insularity, study region, and their two-way interaction, using only control plants. Seedling height was included as a covariate, and population and oak species were included as random factors. The significance of

Table 1. Results from generalized linear mixed models testing the effects of insularity (island versus mainland), study region (Lesbos Island versus mainland Greece; Balearic Islands versus mainland Spain; Bornholm Island versus mainland Sweden), and their interaction on phenolic compound groups, including flavonoids, hydrolysable tannins, condensed tannins, hydroxycinnamic acids and total phenolics. Results are presented for both (a) constitutive levels and (b) inducibility. Seedling height and herbivory damage (for inducibility only) were included as covariates. χ^2 statistics from Wald tests and the corresponding p-values are presented, with p-values adjusted for multiple comparisons using the false discovery rate method.

(a) Constitutive levels

	Flavonoids		Hydrolysable tannins		Condensed tannins		Hydroxycinnamic acids		Total phenolics	
	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p
Insularity (I)	1.34	0.540	4.39	0.703	3.69	0.430	1.98	0.480	3.12	0.430
Region (R)	4.91	0.430	0.17	0.934	2.86	0.540	1.18	0.812	4.17	0.480
I × R	1.82	0.704	0.51	0.934	1.99	0.704	0.22	0.934	0.22	0.934
Height	0.15	0.934	0.68	0.704	1.91	0.480	0.02	0.934	0.38	0.812

(b) Inducibility

	Flavonoids		Hydrolysable tannins		Condensed tannins		Hydroxycinnamic acids		Total phenolics	
	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p
Insularity (I)	4.01	0.286	0.00	0.99	0.03	0.876	1.38	0.699	3.08	0.972
Region (R)	2.90	0.537	8.13	0.286	0.69	0.778	3.63	0.487	4.95	0.286
I × R	1.51	0.714	1.14	0.714	0.36	0.994	0.15	0.876	1.76	0.714
Height	2.10	0.451	0.52	0.714	0.83	0.714	0.51	0.714	3.14	0.286
Herbivory	0.23	0.876	0.05	0.876	0.00	0.984	0.34	0.778	0.06	0.972

fixed effects and post hoc contrasts were assessed as described above.

We then estimated VOC inducibility (using total VOCs data) for each seedling as the difference between its induced value and that of the corresponding control seedling from the same maternal tree. Unlike phenolic compounds measurements, VOCs were collected from only one block, so no repeated measures were generated. When a paired control from the same maternal tree was unavailable, a control seedling from a different maternal tree within the same population was used to calculate inducibility. We then fitted GLMMs using *glmmTMB* with a Gaussian distribution and *identity* function (Faraway 2006), including insularity, study region, and their two-way interactions as fixed factors. Inducibility values were standardized (mean = 0, SD = 1) to improve the numerical stability (Faraway 2006). Seedling height and herbivory amount were included as covariates, and population and oak species as random factors. The significance of fixed effects and post hoc contrasts were assessed as above.

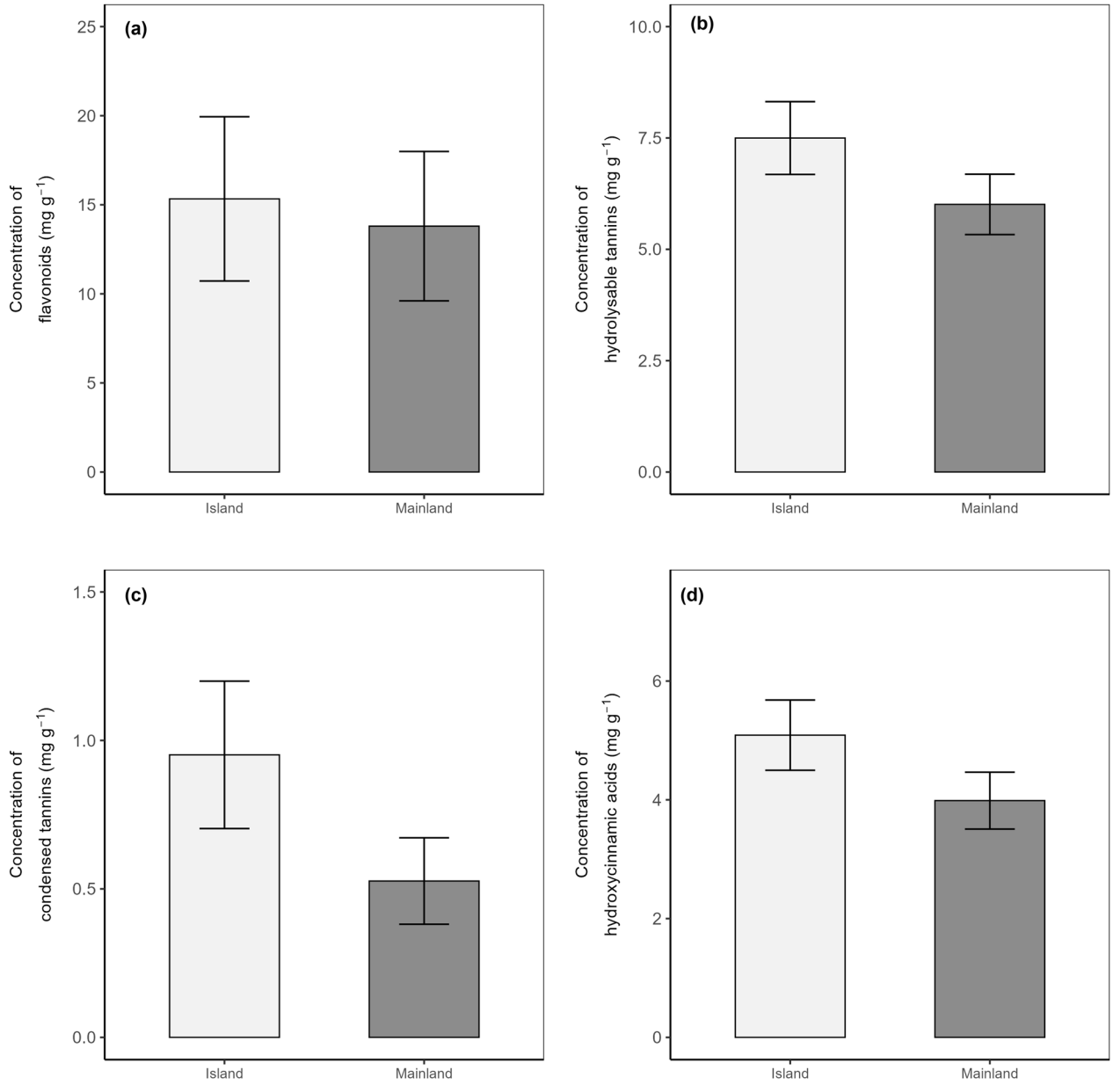

Figure 2. Concentrations (mg g^{-1}) of constitutive phenolic compounds: (a) flavonoids, (b) hydrolysable tannins, (c) condensed tannins, and (d) hydroxycinnamic acids in leaves of oak seedlings from island (n = 83 seedlings) and mainland (n = 84 seedlings) origins across three study regions. Bars represent least-squares means (± SE) estimated from the corresponding generalized linear mixed models.

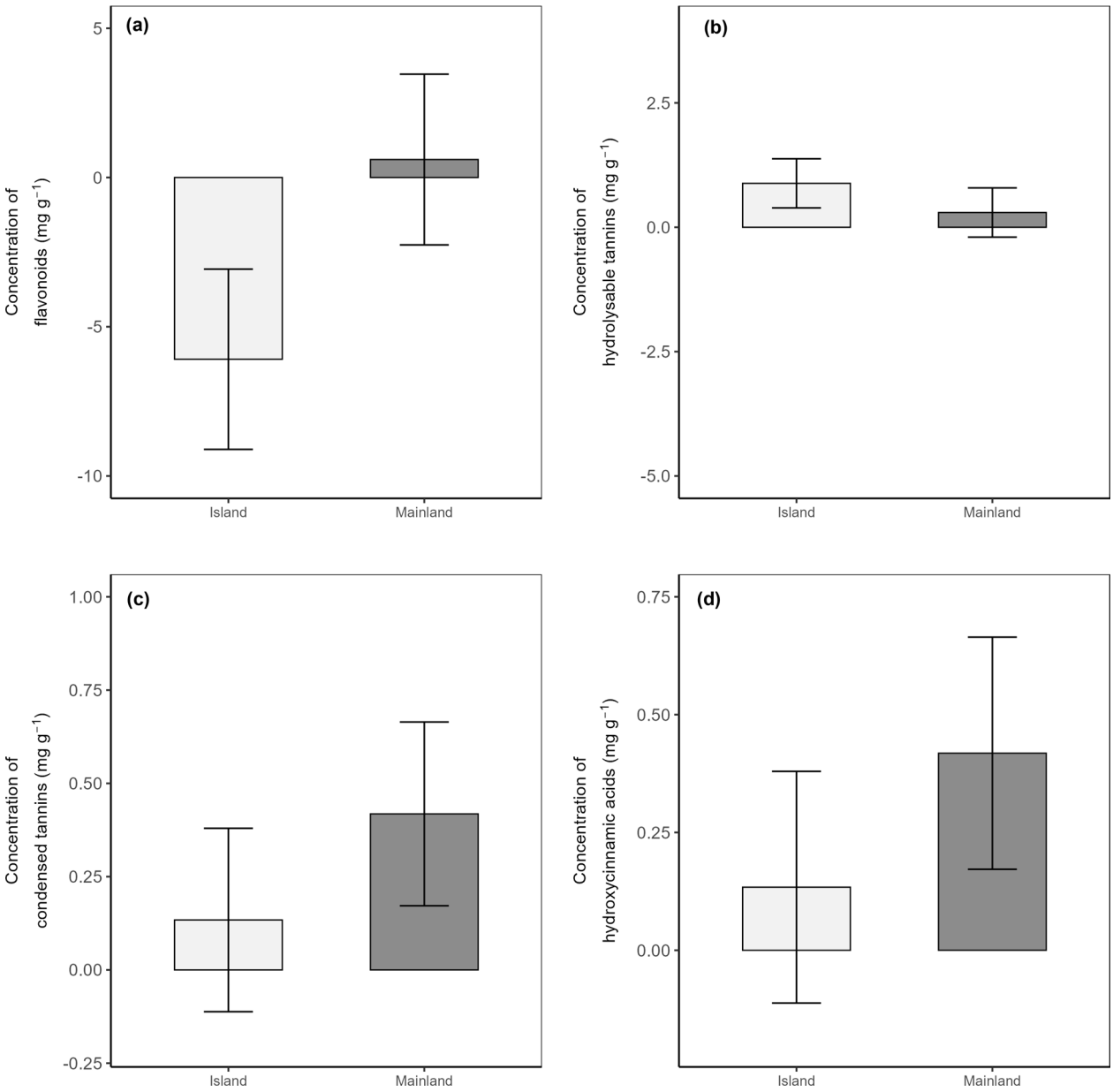

Figure 3. Inducibility of concentrations (mg g^{-1}) of phenolic compounds: (a) flavonoids, (b) hydrolysable tannins, (c) condensed tannins, and (d) hydroxycinnamic acids in leaves of oak seedlings from island (n = 83 seedlings) and mainland (n = 84 seedlings) origins across three study regions. Bars represent least-squares means (± SE) predicted by the corresponding generalized linear mixed model. Inducibility was calculated as the difference between induced and paired control seedlings, where positive values indicate an increase in concentration following herbivory, and negative values indicate a decrease relative to the control.

To test the effects of insularity on regrowth capacity as a proxy for tolerance to herbivory, we applied a bootstrap approach similar to that used for phenolics and VOCs. For each seedling in the induced treatment, inducibility was calculated as the difference in height between its induced value and that of each of the two control plants from the same population (one from the same maternal tree and the other from different maternal trees within the population), yielding two estimates per induced seedling, which were treated as repeated measures in the analysis. Repeated-measures GLMMs were then fitted using *glmmTMB* with a Gaussian distribution and identity link function (Faraway 2006), including insularity, study region, time, and their interactions as fixed factors. Herbivory (% leaf area lost) was included as a covariate, and random factors comprised population, oak species, block, the insularity × block interaction, and seedling ID to account for repeated measurements over time. The significance of fixed effects and post hoc contrasts was assessed as described above.

Detailed descriptions of all statistical analyses are provided in the Supporting information.

Table 2. Results from generalized linear mixed models testing the effects of insularity (island versus mainland), study region (Lesbos Island versus mainland Greece; Balearic Islands versus mainland Spain; Bornholm Island versus mainland Sweden), and their interaction on VOC emissions. Results are presented for both (a) constitutive levels and (b) inducibility. Seedling height and herbivory damage (for inducibility only) were included as covariates. For fixed effects, χ^2 statistics from Wald tests and the corresponding p-values are reported. Significant p-values are indicated in bold.

	(a) Constitutive VOCs		(b) Inducibility of VOCs	
	χ^2	p	χ^2	p
Insularity	1.69	0.194	0.00	0.989
Study region	12.10	**0.002**	0.09	0.958
Insularity × Study region	1.91	0.384	0.25	0.881
Seedling height	16.88	**<0.001**	4.20	**0.040**
Herbivory	–	–	0.82	0.365

Results

Insularity effects on constitutive levels and inducibility of phenolics

We found no significant effects of insularity, study region, or their interaction on either constitutive concentration (Table 1, Fig. 2, Supporting information) or inducibility (Table 1, Fig. 3, Supporting information) on the four phenolic groups or on total phenolics.

Insularity effects on constitutive levels and inducibility of VOCs

We found no significant main effect of insularity on constitutive total VOC emissions, as well as no significant interaction between insularity and study region (Table 2, Fig. 4a, Supporting information)). In contrast, study region had a significant effect (Table 2): oaks from the western Mediterranean region exhibited markedly higher volatile concentrations (351.60 ± 89.71 ng h^{-1}) than those from the eastern Mediterranean (110.52 ± 34.13 ng h^{-1}) and northern regions (110.75 ± 34.17 ng h^{-1}), which had very similar values. In addition, the inducibility of VOCs showed no significant effects of insularity, study region or their interaction (Table 2, Fig. 4b, Supporting information).

Insularity effects on seedling regrowth capacity after herbivore damage

There were no significant effects of insularity, study region, time, or their interactions on seedling regrowth capacity (Table 3, Fig. 5).

Discussion

We observed that insularity had no significant effect on constitutive chemical traits associated with herbivore resistance, including phenolics and VOCs. Previous studies, however, have reported contrasting patterns. For instance, Monroy and García-Verdugo (2019) found that island populations of *Periploca laevigata* (Apocynaceae) maintain higher concentrations of foliar condensed tannins, and Moreira et al. (2019) reported elevated condensed tannins in island individuals of *Q. ilex* in Mediterranean systems. In contrast, Vázquez-González et al. (2025) observed lower total phenolic concentrations for island oaks relative to mainland plants. Island plants may maintain similar levels of

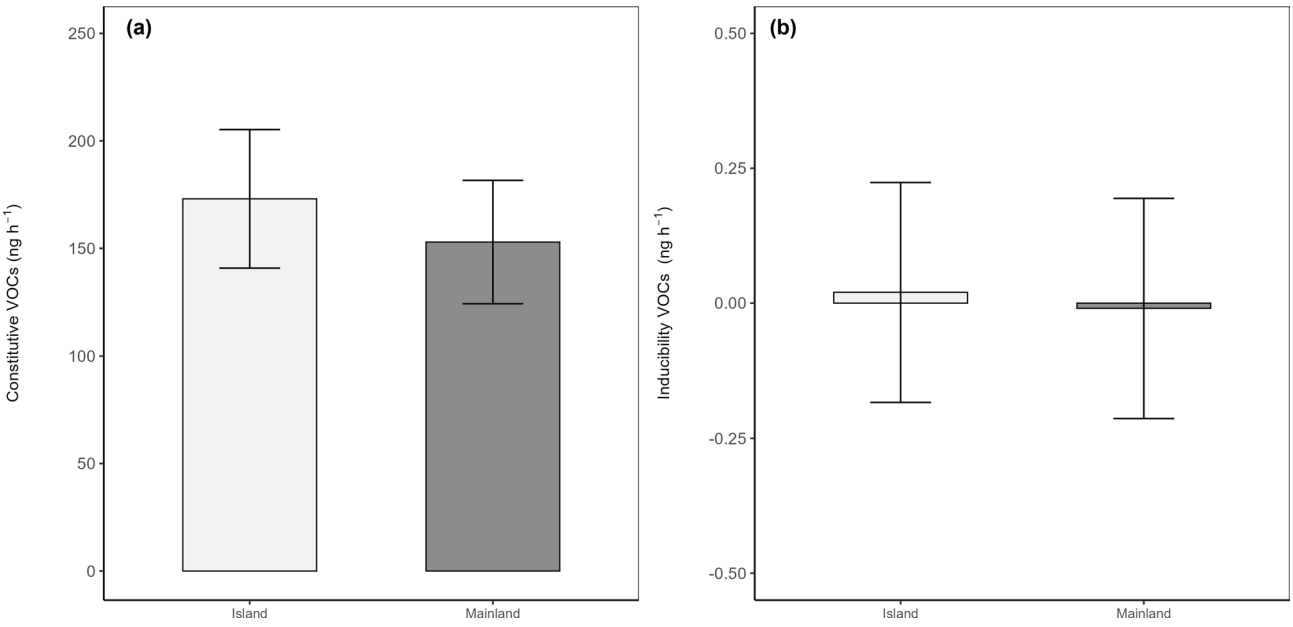

Figure 4. Concentrations (ng h^{-1}) of (a) constitutive volatile organic compounds (VOCs) and (b) their inducibility emitted by oak seedlings from island (n = 40 seedlings) and mainland (n = 42 seedlings) origins across three study regions. Bars represent least-squares means (± SE) predicted by the corresponding generalized linear mixed model.

Table 3. Results from generalized linear mixed models testing the effects of insularity (island versus mainland), study region (Lesbos Island versus mainland Greece; Balearic Islands versus mainland Spain; Bornholm Island versus mainland Sweden), time (weeks; continuous variable), and their interactions on seedling regrowth capacity after damage (induced – control values) as a proxy for tolerance to herbivory. Herbivory damage was included as a covariate. χ^2 statistics from Wald tests and the corresponding p-values are reported.

	χ^2	p
Insularity	0.11	0.742
Study region	1.52	0.469
Time	1.69	0.194
Insularity × Region	1.18	0.554
Insularity × Time	0.18	0.675
Region × Time	1.36	0.507
Insularity × Region × Time	4.08	0.130
Herbivory	0.01	0.940

constitutive resistance traits as their mainland counterparts for several reasons. First, some compounds, such as phenolics or VOCs, serve multiple functions beyond herbivore deterrence, including UV protection, pathogen defence, and structural support (Caldwell et al. 1998, Stamp 2003). As a result, selection may favour their maintenance regardless of herbivore pressure. Second, phylogenetic and evolutionary constraints can limit reductions in these traits, as highly conserved resistance traits may persist due to evolutionary inertia or pleiotropic effects (Blomberg et al. 2003, Kroymann 2011). Third, when island environments provide sufficient nutrients or light, the metabolic cost of maintaining constitutive resistance is reduced (Moreira et al. 2025). Finally, the observed patterns could also reflect underlying genetic differences between populations, an aspect that should be explored in future studies using population genetics tools (García-Verdugo et al. 2015). Overall, these findings highlight the complex and context-dependent factors shaping plant defensive traits on islands.

Our results also indicated that insularity had no significant effect on the inducibility of phenolic compounds or VOCs. This finding aligns with previous work; for example, Pardo et al. (2018) reported no differences in the induction of phenolic compounds in *Prunus lusitanica* (Rosaceae) across Macaronesian island populations and mainland sites in Spain and Morocco. In contrast, Hoan et al. (2014) detected greater inducibility of physical traits associated with herbivore resistance, such as prickle density, in island species compared to their continental sister species. One possible explanation for our findings is that inducible responses are maintained because they provide a flexible, low-cost strategy for coping with temporal and spatial variability in herbivore pressure, a pattern expected on both islands and the mainland (Karban and Baldwin 2007). Additionally, if island herbivore communities include generalists capable of causing strong but unpredictable damage (Blossey and Notzold 1995), plants may retain inducibility as an adaptive buffering mechanism. Another possible mechanism involves physiological constraints: the pathways regulating phenolics and VOCs are deeply integrated into core metabolic networks, potentially limiting evolutionary divergence in their inducibility (Herrmann 1995). Finally, we cannot rule out that gene flow between mainland and island populations has homogenized resistance traits, particularly in species with effective dispersal, such as oaks (Backs and Ashley 2016, Ashley et al. 2018). Overall, our results indicate that the inducibility of phenolics and VOCs does not differ between island and mainland populations, suggesting that these chemical responses are consistently maintained across environments.

Our findings show that insularity did not significantly influence tolerance to herbivory, a pattern that, to our

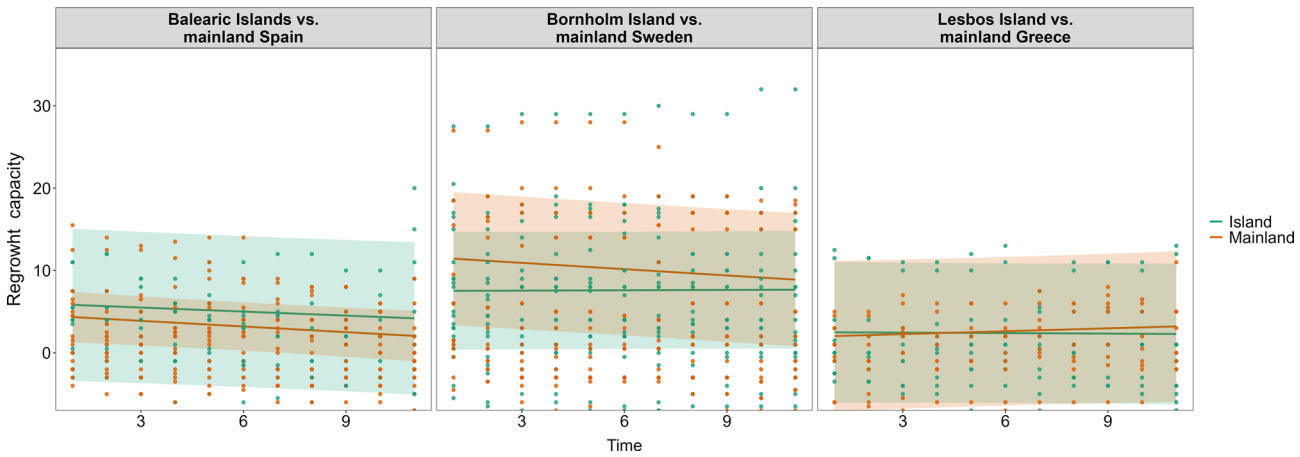

Figure 5. Regrowth capacity, estimated as the inducibility of height (cm), in oak seedlings from island (n = 48 seedlings per time point) and mainland (n = 52 seedlings per point) origins across three study regions (Balearic Islands versus mainland Spain, Bornholm Island versus mainland Sweden, and Lesbos Island versus mainland Greece) over time (weeks). Inducibility was calculated as the difference between induced and paired control seedlings, with positive values indicating an increase in height following herbivory and negative values indicating a decrease relative to the control. Lines depict predicted regrowth capacity values for each insularity level, and shaded areas represent 95% confidence intervals around these predicted trends.

knowledge, has not been previously explored in comparative island–mainland studies, and this pattern was consistent over time. Several mechanisms could underlie these results. First, the 11-week period following damage may not have been sufficient to capture the full extent of compensatory growth, as longer-term responses have been observed in other studies (Haukioja and Koricheva 2000, Boege and Marquis 2005). Second, islands may still host sufficient herbivore diversity or episodic herbivory events to maintain selection for tolerance, preventing its relaxation. Third, tradeoffs between tolerance and other fitness-related traits, such as reproduction or resistance, could stabilize tolerance across environments (Strauss et al. 1999, Salgado-Luarte et al. 2023). It is also important to note that our study did not measure biomass accumulation or specific leaf area, limiting the full interpretation of tolerance. Future studies incorporating these additional metrics could provide a more comprehensive assessment. Collectively, these mechanisms suggest that tolerance evolution on islands is context-dependent, emphasizing the need to integrate multiple ecological and evolutionary factors.

Overall, our results indicate that insularity did not significantly influence constitutive chemical traits associated with herbivore resistance, their inducibility, or tolerance to herbivory. These findings are important because they challenge the traditional expectation from island biogeography theory that island plants should universally exhibit reduced defences due to relaxed herbivory. Instead, our results suggest that both island and mainland oaks maintain comparable defensive strategies, highlighting the potential role of context-dependent ecological and evolutionary processes. Future research should implement field experiments across multiple island–mainland systems to investigate how abiotic factors – such as drought, nutrient limitation, and light stress – interact with herbivore pressure to shape both constitutive and inducible resistance, as well as tolerance mechanisms, providing a more complete understanding of the selective forces driving plant defence evolution on islands. Given that *L. dispar* is a generalist herbivore, some defence mechanisms may not have been fully activated (Ali and Agrawal 2012), so future studies should include both generalist and specialist herbivores. Mechanistic studies on non-structural carbohydrate allocation, meristem availability, and intrinsic growth rates, as well as genomic and transcriptomic analyses, could clarify the basis of defence investment and inducible responses. Together, these approaches will improve our understanding of how islands shape multifunctional plant defence strategies and resilience under changing environmental conditions.

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Author contributions

Xoaquín Moreira and **Carla Vázquez-González** share the senior authorship. **Irene Virseda**: Conceptualization (equal); Data curation (lead); Formal analysis (equal); Investigation (equal); Methodology (equal); Resources (equal); Software (equal); Validation (equal); Visualization (equal); Writing – original draft (lead). **Luis Abdala-Roberts**: Conceptualization (equal); Investigation (equal); Validation (equal); Visualization (equal); Writing – review and editing (equal). **Miquel Capó**: Investigation (equal); Methodology (equal); Validation (equal); Visualization (equal). **Ayco J. M. Tack**: Investigation (equal); Methodology (equal); Validation (equal); Visualization (equal); Writing – review and editing (equal). **Johan A. Stenberg**: Investigation (equal); Methodology (equal); Validation (equal); Visualization (equal); Writing – review and editing (equal). **Finn Hansen**: Investigation (equal); Methodology (equal). **Nikolaos M. Fyllas**: Investigation (equal); Methodology (equal); Validation (equal); Visualization (equal); Writing – review and editing (equal). **Raúl de la Mata**: Investigation (equal); Methodology (equal); Validation (equal); Visualization (equal); Writing – review and editing (equal). **Joana Cursach**: Investigation (equal); Methodology (equal); Validation (equal); Visualization (equal); Writing – review and editing (equal). **Beatriz Lago-Núñez**: Investigation (equal); Methodology (equal). **Carla Pastoriza**: Investigation (equal); Methodology (equal). **Alessio Tei**: Investigation (equal); Methodology (equal). **Cristina Saez-Asensio**: Investigation (equal); Methodology (equal). **Sergio Rasmann**: Investigation (equal); Methodology (equal); Validation (equal); Visualization (equal); Writing – review and editing (equal). **Gregory Roder**: Investigation (equal); Methodology (equal); Validation (equal); Visualization (equal);

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.2ngf1vj37 (Virseda et al. 2026).

Supporting information

The Supporting information associated with this article is available with the online version.

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