

Convocatoria AEET-SIBECOL de ayudas a proyectos de investigación ERC en ecología (11ª ed., 2021)

1. Datos de identificación.

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| Título de la propuesta | The role of insectivorous birds at mediating insularity effects on plant-herbivore interactions |
| Categoría | Ganando independencia |
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2. Memoria Técnica. Actividades y resultados de investigación

2.1. Introducción (Planteamiento, objetivos y justificación)

Theoretical background and justification

Insular systems represent valuable settings to study the ecological and evolutionary factors shaping biodiversity (Darwin, 1909; MacArthur and Wilson, 1967; Gillespie *et al.*, 2008; Ricklefs and Bermingham, 2008) species interactions (Spiller and Schoener, 1990; Traveset *et al.*, 2013) and trait evolution (Grant and Grant, 1998), either by comparing islands with contrasting features within an archipelago or an insular system against close by mainland sites. Within this literature, plant-herbivore interactions have received considerable attention, with theory and early empirical work posing that herbivore pressure should be weaker on islands than on mainland as a result of lower herbivore abundance and diversity due to dispersal constraints and environmental filtering (Carlquist, 1974; Ricklefs and Bermingham, 2008). Consequently, plant taxa found on islands are expected to have evolved less defences or completely lost them, a prediction that was supported by early observational studies (Bowen and Van Vuren, 1997; Vourc'h *et al.*, 2001). However, recent systematic island-mainland comparisons have shed mixed findings, with some studies reporting either no difference between islands and mainland (Monroy and García-Verdugo, 2019) or increased herbivory and/or plant defences on islands (Pardo *et al.*, 2018; Moreira *et al.*, 2019; Moreira *et al.*, 2022). For example, a recent meta-analysis based on 21 published studies found that insularity was associated with higher

herbivory by introduced mammals, whereas no association was found with invertebrate herbivory (Moreira *et al.*, 2021). In addition, insularity tended to be associated with higher levels of plant physical defences whereas no association was found for chemical defences (Moreira *et al.*, 2021). Current data, albeit limited, is therefore unresponsive of predictions about insularity effects on herbivory and plant defences, warranting further research to derive robust patterns, re-assess theoretical frameworks and predictions and test underlying mechanisms.

Insularity research has been simplistic by addressing plant-herbivore interactions without considering effects of herbivore natural enemies (e.g. predators, parasitoids). Research has shown that addressing plant-herbivore interactions without considering these top-down effects (and associated food webs) can lead to an incomplete or even erroneous understanding of the causes underlying variation in herbivory rates, herbivore traits, and plant defence evolution (Abdala-Roberts *et al.*, 2019) and to ignore the degree to which insularity effects on herbivory and plant defences are explained by altered tri-trophic interactions. The few empirical and theoretical studies conducted to date have argued that top-down effects of predators on herbivores should be weaker on islands than on mainland (Terborgh and Feeley, 2010; Terborgh *et al.*, 2010). Among the reasons for this is that low-diversity insular systems are more likely to lack predators because they are more prone to extinction due to smaller population sizes (Holt, 2010). In addition, herbivores feeding on new host plants (e.g. endemics) in insular systems but not mainland may be able to sequester novel plant toxins to which predators or parasitoids are not adapted (Spiller and Schoener, 1990; Schoener and Spiller, 2010), and consequently be better able to escape from natural enemies in islands (Denno *et al.*, 1990). However, these predictions have seldom been tested and require a push towards research addressing insularity effects on plant-herbivore interactions under multi-trophic settings (Moreira and Abdala-Roberts, 2022).

Project objectives

In this study, we investigated the role of herbivore natural enemies (i.e., insectivorous birds) at driving island-mainland patterns of variation in insect herbivory and plant defences using oak (*Quercus*) species as model system. To this end, at the beginning of the growing season we experimentally manipulated the presence (vs. absence) of birds in four oak species inhabiting the California Channel Islands and their congeneric or conspecific counterparts in mainland California. At the end of the growing season, we collected leaves to measure leaf damage by

chewing insects and quantified physical (specific leaf area, correlated with leaf thickness or toughness) and chemical (phenolic compounds) defences known to affect herbivory in oaks. Specifically, **the objectives of this study are:** to test **(1)** whether insect herbivory and plant defences in oaks differ between islands and mainland and **(2)** whether insularity effects on herbivory and plant defences are mediated by the third trophic level (presence vs. absence of insectivorous birds). By incorporating multi-trophic interactions, we contribute to achieve a more robust understanding of the causes behind island-mainland patterns in herbivory and plant defences.

2.2. Descripción de la ejecución- Metodología

Experimental design and leaf sampling

Our study was conducted in the Channel Islands off the coast of California and in mainland California, and included four conspecific or congeneric island-mainland comparisons representing a total of seven oak species. Only one of these species is distributed in the islands and the mainland (*Q. agrifolia*), three are endemic species which are only found in the islands (*Q. pacifica*, *Q. tomentella*, and *Q. xMcdonaldii*) and the remaining three species are their closest congeneric relatives in the mainland (*Q. berberidifolia*, *Q. chrysolepis* and *Q. lobata*, respectively). Five species are evergreen (*Q. agrifolia*, *Q. pacifica*, *Q. berberidifolia*, *Q. tomentella*, and *Q. chrysolepis*) and two are deciduous (*Q. xMcdonaldii*, *Q. lobata*).

For oak species that were present in islands, we selected three populations in two islands (Santa Cruz and Santa Catalina Islands) of the archipelago (Fig. 1A), and paired them to three conspecific (or congeneric in the case of island endemism; see above) populations in the mainland. In the case of *Q. agrifolia* and *Q. xMcDonaldii* we were only able to select two populations in islands, making a total of 22 populations. Neighbouring populations were at least five km apart and consisted of at least 15 reproductive trees. At the beginning of the growing season (late February to early March 2022), we selected four adult trees (N = 88) in each population and experimentally excluded birds from two opposing, low-hanging accessible branches (1-2 m from the ground) (Fig. 1B). Exclusions consisted in installing 1.5 × 1.5-m wide agricultural mesh netting (1.9 cm mesh diameter, Feitore®) on each branch. For each tree, these bird-excluded branches were then paired with two adjacent control (i.e., no bird netting) branches of similar height and orientation. At the end of the growing season, after the peak in bird and insect abundance (late May to early June), we randomly collected ten fully expanded leaves for each bird-excluded and control branch per tree. For bird-excluded branches, we

avoided leaves that were in contact with the net to which birds might have had access. For evergreen species, we avoided older leaves not produced during the current growing season. Finally, some mesh nettings were lost due to animal grazing or vandalism at some populations, reducing the final number of experimental bird-excluded branches and/or trees (168 branch pairs across 87 trees). When a bird-excluded branch was lost, we discarded its associated control branch in order to keep the paired design balanced within subjects (i.e., bird excluded vs. control branches in each tree). Immediately after leaf collection, we oven-dried leaves and measured the percentage leaf area removed by leaf chewers (“herbivory” hereafter) in each leaf using the mobile application BioLeaf - Foliar Analysis™ (Brandoli Machado *et al.*, 2016).

Figure 1. (a) Map of Coastal California showing sampling sites in the Channel Islands (Santa Cruz and Santa Catalina islands) and the sampling sites in the mainland. **(b)** Example of a bird exclusion netting installed in an oak branch.

(a) Channel Islands vs. mainland California



● Islands ● Mainland sites

Oak defences

We chose phenolic compounds which have been broadly shown to act against insect herbivores in oaks (Feeny, 1970; Moreira *et al.*, 2018a; Moreira *et al.*, 2018b; Moreira *et al.*, 2020) as a proxy of chemical defences. We selected two leaves without insect leaf damage per branch. For each tree, we pooled into a single sample leaves from bird-excluded vs. control branches separately and ground them with liquid nitrogen. Compounds were then extracted from 20 mg of dry pulverized leaf tissue with 1 mL of 70% methanol in an ultrasonic bath for 15 min, followed by centrifugation. We then transferred the extracts to chromatographic vials. For phenolic quantification, we used Ultra-High-Performance Liquid-Chromatograph (UHPLC Nexera LC-30AD; Shimadzu) equipped with a Nexera SIL-30AC injector and one SPD-M20A UV/VIS photodiode array detector. The compound separation was carried out on a Kinetex™ 2.6 µm C18 82-102 Å, LC Column 100 × 4.6 mm, protected with a C18 guard cartridge. The flow

rate was 0.4 mL min^{-1} and the oven temperature was set at $25 \text{ }^{\circ}\text{C}$. The mobile phase consisted of two solvents: water-formic acid (0.05%) (A) and acetonitrile-formic acid (0.05%) (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 $15 \text{ } \mu\text{L}$. For phenolic compound identification, we used an ultra-performance liquid chromatography coupled with electrospray ionization quadrupole (Thermo Dionex Ultimate 3000 LC) time-of-flight mass spectrometry (UPLC-Q-TOF-MS/MS) (Bruker Compact™). 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. We quantified flavonoids as rutin equivalents, condensed tannins as catechin equivalents, hydrolysable tannins as gallic acid equivalents, and hydroxycinnamic acids as ferulic acid equivalents. We achieved the quantification of these phenolic compounds by external calibration using calibration curves at 0.25, 0.5, 1, 2 and $5 \text{ } \mu\text{g mL}^{-1}$. We expressed phenolic compound concentrations in mg g^{-1} dry tissue.

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 and Hipp, 2009) and can therefore serve as a measure of structural resistance against herbivory. We estimated SLA ($\text{cm}^2 \text{ g}^{-1}$) for each leaf by dividing the surface area by its dry mass in three leaves per tree.

Statistical analysis

First, we tested for insularity effects on the percentage of insect leaf herbivory and on chemical and physical defences (i.e., phenolic compounds and SLA). We estimated insularity effect sizes using Hedges’ g metric and 95% confidence intervals (CI) based on the pooled sample sizes (Hedges, 1981) using the ‘effsize’ package in R software version 4.2.1 (Team, 2013; Torchiano and Torchiano, 2020). Hedges’ g was calculated as the standardized mean difference between island and mainland tree-level values such that negative values indicate that herbivory or leaf traits had lower values on islands than on the mainland, whereas positive values indicate the inverse. We considered effect sizes significant when the 95% confidence intervals did not include zero.

Second, we tested for bird predation effects on herbivory and chemical and physical defences (i.e., phenolic compounds and SLA) on islands vs. mainland. We estimated bird predation

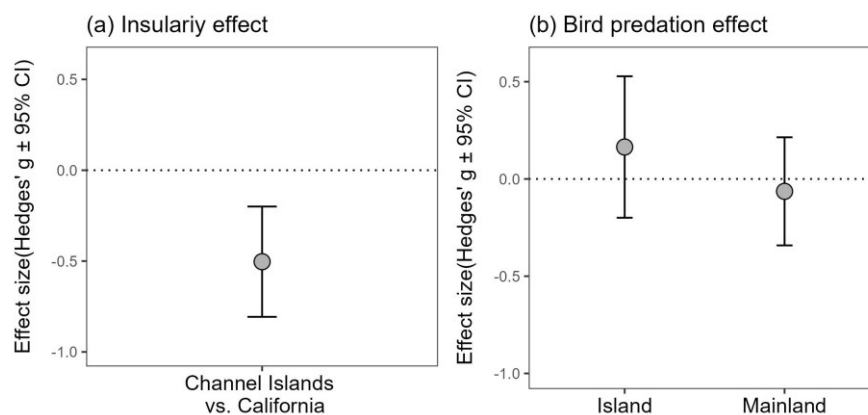
effect sizes using Hedges' g metric and 95% CI based on the pooled sample sizes using the same statistical methods described above for insularity effects. This time, because we compared bird-excluded branches vs. control branches within each tree, we computed effect sizes considering a within subjects (i.e., repeated measures) paired design. Hedges' g was calculated as the standardized mean difference between control and bird-excluded branch-level herbivory values for each pair of branches such that negative values indicate that herbivory was lower on control than on bird-excluded branches, whereas positive values indicate the inverse. Because we wanted to assess contrasting bird predation effects in islands vs. mainland, we computed effect sizes separately for islands and mainland.

2.3. Resultados obtenidos (cumplimiento de objetivos)

Insularity and bird predation effects on insect herbivory

Insularity had a significant negative effect on herbivory (Hedges' g -0.50 [-0.80, -0.20]) Specifically, the percentage of insect leaf herbivory was 37% lower in the Channel Islands (4.05 ± 0.46 %, $n = 40$) than in mainland California (6.43 ± 0.70 %, $n = 40$) (Fig. 2a). Contrary, bird predation did not have a significant effect on insect leaf herbivory neither in islands nor in mainland (Fig. 2b).

Figure 2 (a) Insularity effect sizes (Hedges' $g \pm 95\%$ confidence intervals) computed as the standardize mean difference of the percentage of insect leaf herbivory on islands vs. mainland **(b)** Bird predation effect sizes (Hedges' $g \pm 95\%$ confidence intervals) computed as the standardize mean difference of the percentage of insect leaf herbivory in control vs. bird-excluded branches in islands and mainland. Effects are considered significant when 95% confidence intervals do not overlap the zero dashed line.



Insularity and bird predation effects on oak defences

Regarding results for defences (phenolic compound and SLA), samples are still in the process of being analysed and thus **data is not yet available**. We expect, however, to have this data by February 15th. We contemplate two possible scenarios. If herbivore pressure drives variation in defences, we predict a positive association between herbivory and leaf chemical and physical defences and thus lower defence levels in oaks in islands. Conversely, if variation in defences drives concomitant variation in herbivory, we predict a negative association between herbivory and defences, and thus higher defence levels in islands. Regarding potential effects of bird predation on oak defences, the absence of a significant effect of bird predation on herbivory challenges the assumption of changes in the defensive profile of control vs. bird-excluded branches as we initially hypothesised.

2.4. Conclusiones y valoración de la ejecución

We observed that insect leaf herbivory was lower on islands than on the mainland, being in agreement with our working hypothesis of lowered herbivore pressure in insular systems (Carlquist, 1974; Ricklefs and Bermingham, 2008; Losos and Ricklefs, 2009). However, and contrary to expectations, we did not observe a significant effect of bird predation on herbivory, neither in islands nor in the mainland. This result was surprising and contradicts previous research where bird predation was associated with lower herbivory or arthropod abundance in plants (Van Bael *et al.*, 2008; Mooney *et al.*, 2010; Maas *et al.*, 2016). Our results thus suggest that bird-predation effects are not responsible for island-mainland differences in leaf herbivory. A potential alternative hypothesis is that differences in herbivory between islands and the mainland are influenced by bottom-up (plant-mediated) rather than top-down (predator-mediated) ecological mechanisms. Upcoming data of oak defences will allow to test this hypothesis.

Overall we have successfully completed the oak leaf sampling and herbivory measurements in insular oak populations and their mainland counterpart, and oak defence data will be soon available. Despite non-significant results of bird predation on herbivory data, results obtained from this project obtained so far contribute to understanding the evolution of plant-herbivore interactions in insular systems and highlight the need for rethinking current theoretical frameworks and hypothesis.

2.5. *Publicaciones resultantes*

Results from this project will be presented in the **2023 Gordon Research Conference on Plant-Herbivore Interaction** (February 26th – March 3rd). Tentatively, we aim to publish the results from this project in the upcoming special issue about *Functional Island Biogeography* that will be published by **Journal of Biogeography** (Impact factor 2021: 4.810).

2.6. *Bibliografía*

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1. **Informe de gastos del proyecto.** Relación de partidas de gastos y sus importes. Se deberán aportar justificantes originales de los pagos realizados (tickets, recibos o facturas).

| Concept | Description | Euros* | Dollars |
|---|--|----------------|----------------|
| Materials | Bird netting, nylon cord and Velcro for bird exclusions. Envelopes for leaves. | 605.67 | 663.78 |
| Transportation | Boat Santa Cruz Island (1st field campaign) – 2 persons | 149.58 | 168 |
| Transportation | Boat Santa Cruz Island (2nd field campaign) – 2 persons | 160.95 | 168 |
| Transportation | Boat Catalina Island (1st field campaign) – 2 persons | 139.83 | 154 |
| Transportation | Boat Catalina Island (2nd field campaign) – 1 person | 68.06 | 74 |
| Transportation | Catalina Island – Within island transportation – Shuttle – 1 person | 19.31 | 21 |
| Gasoline | Personal Car | 231.21 | 255.1 |
| Accommodation | Sedgwick reserve (1st field campaign) 2 person – 2 nights | 110.78 | 120 |
| Accommodation (+ UC reserve charges) | Santa Cruz Island (1st field campaign) 3 persons - 2 nights | 449.54 | 472.25 |
| Accommodation | Catalina Island (1st field campaign) 2 person – 2 nights | 147.09 | 160.45 |
| Accommodation | Sedgwick reserve (2nd field campaign) 2 person – 2 nights | 60.31 | 60 |
| TOTAL | | 2142.33 | 2316.58 |
| TAXES (15% of 2500 Euros) | | 375 | |

*Exchange rates are approximate vary across purchase dates

Fdo: Carla Vázquez González

en Irvine (CA), a 30 de Enero de 2023