Phenotypic Plasticity of Pest and Biological Control Agents: Contrasting Mainland and Insular Coastal Ecosystems

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Phenotypic Plasticity of Pest and Biological Control Agents: Contrasting Mainland and Insular Coastal Ecosystems

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Abstract

Islands have long served as natural laboratories for studying the mechanisms that shape biodiversity, ecological interactions, and adaptive evolution. This thesis explores how isolation, environmental heterogeneity, and trophic structure influence the organisation, functioning, and adaptive potential of arthropod communities, comparing coastal grassland ecosystems from the Azores Archipelago and mainland Portugal. Through an integrative approach combining taxonomic, functional, and genetic analyses, this work examines how ecological simplification and limited resource diversity shape community dynamics and species adaptability in insular environments.

In the first part of the study, arthropod communities were systematically sampled across coastal grasslands in both regions. Standardised protocols were applied to ensure data comparability, and all records were structured according to Darwin Core standards and made publicly available through the GBIF platform. These datasets formed the basis for biodiversity and abundance analyses, which revealed marked differences between the two systems. Mainland communities exhibited higher species richness, consistent with greater environmental heterogeneity and resource diversity, whereas insular communities displayed lower richness but showed an abundance compensation for certain species, along with a strong dominance of a few adaptable taxa, particularly within the Coccinellidae. These findings confirm that ecological isolation promotes community simplification and reduces functional redundancy.

Subsequent analyses focused on the trophic structure and functional interactions among ladybirds, ants, aphids, and host plants. Continental networks revealed a greater number of connections, whereas insular networks were characterised by fewer links and higher dependence on dominant species. This simplification suggests that island ecosystems, though stable in the short term, may be more vulnerable to disturbance and species loss due to their limited ecological buffering capacity.

To assess adaptive potential at the population level, laboratory assays were conducted using *Scymnus nubilus*, a key predatory species. Individuals were reared under controlled conditions and fed aphids of different nutritional suitability. The results revealed clear phenotypic plasticity—the ability of a single genotype to express distinct phenotypes under varying environmental conditions—in developmental and reproductive traits,

allowing adjustment to diverse food resources. However, these responses were accompanied by evolutionary trade-offs: individuals performing better on optimal prey showed reduced flexibility when exposed to alternative resources. These results highlight the interaction between genetic variability and phenotypic flexibility as fundamental drivers of adaptation.

Taken together, the evidence demonstrates that ecological isolation and environmental filtering shape both community composition and adaptive capacity. Phenotypic plasticity emerges as a compensatory mechanism that enables persistence under restricted ecological conditions, while simultaneously imposing evolutionary constraints in simplified systems. The integration of ecological, functional, and genetic perspectives in this thesis provides a deeper understanding of how insularity influences biodiversity patterns and resilience, offering valuable insights into the processes that govern adaptation, conservation, and ecosystem stability in a changing world.

Keywords: Life-history traits; Phenotypic plasticity; Ladybirds; Aphids; Trophic networks; Species diversity; Specialization; Density compensation; Coastal grasslands; Insular ecosystems.

Resumo

As ilhas têm, desde há muito, servido como laboratórios naturais para o estudo dos mecanismos que moldam a biodiversidade, as interações ecológicas e a evolução adaptativa. Esta tese explora de que forma o isolamento, a heterogeneidade ambiental e a estrutura trófica influenciam a organização, o funcionamento e o potencial adaptativo das comunidades de artrópodes, comparando ecossistemas de pastagens costeiras do Arquipélago dos Açores e de Portugal continental. Através de uma abordagem integradora que combina análises taxonómicas, funcionais e genéticas, este trabalho examina como a simplificação ecológica e a limitada diversidade de recursos moldam a dinâmica comunitária e a adaptabilidade das espécies em ambientes insulares.

Na primeira parte do estudo, as comunidades de artrópodes foram amostradas de forma sistemática em pastagens costeiras de ambas as regiões. Aplicaram-se protocolos padronizados para garantir a comparabilidade dos dados, que foram estruturados de acordo com os padrões Darwin Core e disponibilizados publicamente através da plataforma GBIF. Estes conjuntos de dados constituíram a base para as análises de biodiversidade e abundância, que revelaram diferenças marcadas entre os dois sistemas. As comunidades continentais apresentaram maior riqueza específica, em consonância com uma maior heterogeneidade ambiental e diversidade de recursos, enquanto as comunidades insulares exibiram menor riqueza, mas uma compensação de abundância em algumas espécies, além de uma forte dominância de poucos taxa adaptáveis, particularmente dentro dos Coccinellidae. Estes resultados confirmam que o isolamento ecológico promove a simplificação comunitária e reduz a redundância funcional.

As análises subsequentes centraram-se na estrutura trófica e nas interações funcionais entre joaninhas, formigas, afídeos e plantas hospedeiras. As redes continentais revelaram um maior número de ligações, ao passo que as redes insulares se caracterizaram por menos conexões e maior dependência de espécies dominantes. Esta simplificação sugere que os ecossistemas insulares, embora estáveis a curto prazo, poderão ser mais vulneráveis a perturbações e à perda de espécies devido à sua reduzida capacidade de amortecimento ecológico.

Para avaliar o potencial adaptativo a nível populacional, foram realizados ensaios laboratoriais com *Scymnus nubilus*, uma espécie predadora-chave. Os indivíduos foram

criados em condições controladas e alimentados com afídeos de diferente adequação nutricional. Os resultados revelaram uma clara plasticidade fenotípica — a capacidade de um único genótipo expressar fenótipos distintos sob diferentes condições ambientais — em características de desenvolvimento e reprodução, permitindo o ajustamento a diversos recursos alimentares. Contudo, estas respostas foram acompanhadas por compromissos evolutivos (trade-offs): indivíduos com melhor desempenho em presas ótimas demonstraram menor flexibilidade quando expostos a recursos alternativos. Estes resultados evidenciam a interação entre variabilidade genética e flexibilidade fenotípica como motores fundamentais da adaptação.

No seu conjunto, as evidências demonstram que o isolamento ecológico e a filtragem ambiental moldam tanto a composição das comunidades como a sua capacidade adaptativa. A plasticidade fenotípica surge como um mecanismo compensatório que permite a persistência sob condições ecológicas restritas, mas que simultaneamente impõe constrangimentos evolutivos em sistemas simplificados. A integração das perspetivas ecológica, funcional e genética nesta tese contribui para uma compreensão mais profunda de como a insularidade influencia os padrões de biodiversidade e a resiliência, oferecendo valiosos contributos para os processos que regem a adaptação, a conservação e a estabilidade dos ecossistemas num mundo em mudança.

Palavras-chave: traços de história de vida; plasticidade fenotípica; joaninhas; afídeos; redes tróficas; diversidade específica; especialização; compensação de densidade; pastagens costeiras; ecossistemas insulares.

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To the best of my knowledge, this thesis contains no material previously published or written by another person, except where referenced or quoted in the text.

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Chapter 1. General introduction

1.1. Contributing Factors to Speciation

Due to their unique characteristics and geographic isolation, island regions are frequently used as natural laboratories for the study of environmental and evolutionary processes (Alhmedi et al., 2018; Stuessy, 2020). The interest in these regions stems from the fact that they host unique organisms that have established themselves over long periods, many of them in complete geographic isolation (MacArthur and Wilson, 1963; Whittaker et al., 2017). Thus, understanding the mechanisms that lead a given population to speciation has been the focus of study for several decades (Chen and He, 2009; Warren et al., 2015; Borregaard et al., 2017; Beierkuhnlein, 2024).

Several factors have been identified as drivers of evolution in isolated environments, including climate, geographic distance, area size, genetic drift, and the founder effect (MacArthur and Wilson, 1963; Petalas et al., 2024). In parallel, biotic factors such as competition for resources and the absence of predators may also lead to speciation (Hembry et al., 2021; Ponti et al., 2023).

It is well established that intra- and interspecific interactions largely depend on fluctuations in these two sets of factors – abiotic and biotic – which directly influence developmental rates (Singh et al., 2024). At the individual level, these rates show high plasticity in response to environmental conditions, with temperature being a determining factor, particularly in coccinellids (Jalali et al., 2014; Singh et al., 2016; Singh et al., 2024). Temperature also affects interspecific interactions, and the fate of a species often depends on indirect thermal effects mediated by adjacent species within the food web (Bideault et al., 2019; Abarca and Spahn, 2021; Ushio et al., 2023) .

1.2. Islands versus Continents

It is widely accepted that, in islands or isolated environments, biodiversity tends to be lower than in continental ecosystems, mainly due to their smaller size (Chisholm et al., 2016; Whittaker et al., 2017). Furthermore, food webs in these systems are expected to have a simpler structure compared with those of continental areas with similar characteristics (Massol et al., 2017). In contrast, continental regions generally exhibit

higher biological diversity and consequently more complex trophic networks (Jønsson and Holt, 2015).

One way to understand ecosystem structure is through the analysis of food webs. Simple bipartite networks – such as predator-prey, plant-herbivore, or mutualistic relationships – provide a general overview of how a more complex community may be organised. Food webs are a highly informative tool for exploring the complex network of interdependencies that link species into functional and resilient communities (Roubinet et al., 2018; Heleno et al., 2020).

Insular environments face a greater risk of vulnerability to external disturbances, such as anthropogenic actions and climate change, which can easily alter the composition of their ecological communities. Such disturbances can be so profound that they may lead to the collapse of entire communities, further limiting the available resources (Tylianakis et al., 2008; Heleno et al., 2020; Harvey et al., 2020). Conversely, in continental regions, such losses may go unnoticed due to the scale and complexity of the ecosystems, as certain organisms may assume the role of others that have disappeared, albeit not always with the same efficiency (Biggs et al., 2020; Henderson et al., 2020; Stadler et al., 2022). Altogether, these findings highlight the importance of considering species interactions to better understand and predict the consequences of rapid environmental change.

Variation in the use of food resources among populations can reveal patterns of local adaptation and indicate responses to past selective forces (Allen et al., 2010; Meek et al., 2023). On the other hand, the process of evolutionary change depends on the amount of genetic variation maintained within the population (Lai et al., 2019; Agashe et al., 2023). When monitoring ladybird populations, it is therefore essential to collect information on their trophic context, for instance by assessing the diversity and abundance of their resources.

1.3. Ladybirds as Model Species

Terrestrial arthropods, and insects in particular, stand out as one of the most successful groups in colonising new habitats and are widely used in evolutionary studies and models (Borges et al., 2011; Hembry et al., 2021). They occur on almost every continent, except for continental Antarctica (Chown and Convey, 2016), and can disperse via wind, other animals, or by their own means.

Arthropods are present in all types of habitats and represent the most abundant taxonomic group in the world (Wilson, 1987). Grasslands, for instance, are diverse and dynamic ecosystems that have been extensively studied due to their ecological importance. They are particularly relevant for supporting rich and varied arthropod communities (Jones and Donnelly, 2004; Feher et al., 2021). In addition, they provide several ecosystem services, such as nutrient cycling, carbon sequestration, and pollination, which are of great importance to humans (Peters et al., 2016).

However, coastal grasslands remain poorly studied, including those located in insular regions. As these coastal communities host many exotic species, they may serve as reservoirs of potential agricultural pests or invasive species (Boieiro et al., 2024).

Species such as coccinellids are widely used as model organisms in these types of studies, as most of them are top predators of major agricultural pests, including aphids, mealybugs, scale insects, mites, and whiteflies (Weber and Lundgren, 2009; Michaud, 2012). Within this group, the tribe Scymnini is of particular importance. The genus *Scymnus*, the most diverse within the family Coccinellidae, includes more than 800 species (Chen et al., 2015), many of which exhibit high potential as biological control agents (Borges et al., 2013; Rosagro et al., 2020).

1.4. Trade-offs and Specialisation

In theory, species exhibiting a more generalist feeding pattern tend to be more successful in colonising new habitats (Clavel et al., 2011; Ducatez et al., 2015). This aspect is particularly relevant when considering species that provide important ecosystem services within their ecosystems and whose life cycles may be deeply affected by external pressures — whether they are predators, phytophagous, or mutualistic — with their plasticity in response to new environmental conditions being decisive for their success (Devictor et al., 2008; Clavel et al., 2011).

The ecological characteristics of food resources are considered one of the main driving forces behind the evolution of prey specialisation, through multiple trade-offs that form a central principle of evolutionary biology (Levins, 1968; Stearns, 1992). The *trade-off* hypothesis postulates that improved performance on a given resource entails a cost in performance on other resources (Levins, 1968; Østman et al., 2014). In simple terms, such adaptation may also entail evolutionary costs. That is, if adaptation occurs to a

particular type of food due to the absence of the preferred food to which the species was originally adapted, a short-term adjustment to a new food resource may occur, resulting in a *trade-off* in which future generations may no longer be able to utilise the original resource as efficiently as their ancestors.

To verify the existence of such *trade-offs*, it is necessary to conduct a comparative measurement of resource suitability and its effect on life-history traits, distinguishing between essential food resources (those that allow completion of larval development and oviposition) and alternative food resources (those that serve only as an energy source and, consequently, prolong survival) (Hodek et al., 2012).

Genetic variability within populations provides the foundation for evolutionary change, allowing individuals to respond differently to environmental challenges (Hoffmann and Parsons, 1989; Devictor et al., 2008). When combined with phenotypic plasticity – the ability of a single genotype to express distinct phenotypes under varying environmental conditions – this variability enhances the adaptive potential of populations (Ward-Fear et al., 2024). Such plastic responses may buffer short-term environmental fluctuations while maintaining the genetic diversity necessary for long-term adaptation. Consequently, both genetic variation and phenotypic plasticity are key mechanisms underlying ecological flexibility and the evolution of specialisation and trade-offs in natural populations (Stearns, 1992; Clavel et al., 2011; Gibert et al., 2019).

In many ladybird species, studies on *trade-offs* have confirmed their existence, such as in *Harmonia axyridis* (Pallas) and *Scymnus subvillosus* (Goeze), demonstrating that aphids are essential resources but differ in their degree of suitability as prey (Soares et al., 2004; Noriyuki and Osawa, 2012; Sebastião et al., 2015). Nevertheless, these studies remain limited, as most have been conducted exclusively on *H. axyridis*, have focused mainly on immature stages, and lack field studies to test these predictions (Grill et al., 1997; Noriyuki and Osawa, 2012).

1.5. General aims and objectives

This thesis aims to explore the general question of what factors account for the evolution of broader or narrower tolerance of resource use, evolving in two contrasting biogeographical environments, continental vs insular coastal ecosystems.

More specifically, the work aims to compare the geographical variation in food resource availability as well as ladybirds' food niche breadth, to compare the phenotypic variation of life-history traits in *Scymnus nubilus* Mulsant, 1850, in continental and insular environments, to test whether a predator exposed during a long period to a less biodiverse habitat entails a loss of phenotypic variation in life-history traits, to determine life-history trade-offs that arise after long-term exposure to contrasting biogeographic environments.

In regions where agriculture plays a vital role in the economy, such as the Azorean archipelago, prior knowledge of the ecology of these organisms – including feeding habits, fecundity, developmental time, and plasticity – provides a general understanding of how a given species may respond to current external pressures.

These results will contribute to a better understanding of colonisation processes, as well as to the identification of species with invasive potential or the improvement of others with the capacity to act as biological control agents.

Finally, this knowledge will enable the development of more effective pest management strategies and the implementation of species reintroduction projects in degraded habitats.

In order to carry out this study, the thesis has been divided into several chapters, each of which focuses on a different aspect of the analysis.

In Chapter 2, entitled "**Arthropod communities of insular (São Miguel Island, Azores) and mainland (Portugal) coastal grasslands**", aims to make a first attempt at characterising and comparing arthropod diversity across biotic communities in coastal ecosystems. The present work provides an inventory of the arthropods recorded in two coastal grassland ecosystems: the mainland Portugal and the Azores. It also aims to present the main arthropod dataset used to carry out this investigation.

The third Chapter is entitled "**A Comparative Analysis of Island vs. Mainland Arthropod Communities in Coastal Grasslands Belonging to Two Distinct Regions:**

São Miguel Island (Azores) and Mainland Portugal". Here, we address a first analysis at a taxonomic level considering each ecosystem (the Azores and mainland Portugal). We aim to (a) investigate the arthropod community composition in both locations; (b) compare the diversity profiles in both locations; (c) investigate potential abundance compensation in the island's arthropod communities.

Chapter 4, entitled "**Coastal vegetation records from São Miguel Island (Azores) and Mainland Portugal**", aims to characterising and comparing plants diversity across biotic communities in coastal ecosystems. The present work provides an inventory of the plant species recorded in coastal vegetations in the Azores Archipelago (São Miguel Island) and Portugal mainland (Sesimbra and Sines regions – Setúbal district).

Chapter 5, entitled "**Contrasting structure of trophic networks from the Azores and mainland Portugal**", aims to contrast the structure of bipartite networks (antagonistic/mutualistic) of the of the aphidophagous coccinellid guilds from coastal grasslands of the Azores and those of mainland Portugal.

Chapter 6, entitled "**Consequences of slow and fast development in *Scymnus nubilus*: effect of prey type**", aims to explore the existence of slow and fast developers in the immature stages of *Scymnus nubilus* Mulsant when fed on two different aphid species, with different levels of suitability, and the potential effects of slow and fast developmental rates on sex-ratio, adult body weight and reproductive attributes.

1.6. References

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Chapter 2. Arthropod communities of insular (São Miguel Island, Azores) and mainland (Portugal) coastal grasslands

Abstract

Background

The data presented here is part of a doctoral project aimed at characterising and comparing arthropod diversity across biotic communities in coastal ecosystems. The present work provides an inventory of the arthropods recorded in two coastal grasslands ecosystems: the Portugal mainland and the Azores. Sampling was conducted on São Miguel Island (Azores Archipelago) as well as in the Sesimbra and Sines regions (Setúbal District, mainland Portugal). Thirty-one plots were set and visited four times, in spring and summer of 2022.

New information

The specimens collected were sorted and catalogued into a total of 534 arthropod species and morphospecies. In total, 67 species were common to both ecosystems. A total of 13,515 specimens were counted in the two coastal grasslands. We registered three new records for the Azores (in São Miguel Island), all being exotic: *Aritranis director* (Thunberg, 1822) (Hymenoptera, Ichneumonidae), *Draeculacephala bradleyi*, Van Duzee, 1915 (Hemiptera, Cicadellidae) and *Isodontia* sp. Patton, 1880 (Hymenoptera, Sphecidae). This publication demonstrates the importance of coastal grasslands as reservoirs for some potentially invasive arthropod species.

Keywords: arthropods, Azores, mainland, coastal grasslands, sweeping net, invasive species

2.1. Introduction

Grasslands are diverse and dynamic ecosystem that have been extensively studied due to their ecological significance. They are particularly important for supporting rich and varied arthropod communities ((Jones and Donnelly, 2004; Feher et al., 2021). Arthropods in this ecosystem provide diverse ecosystem services, such as nutrient cycling, carbon sequestration and pollination (amongst others) which are extremely important for humans (Peters et al., 2016). In turn, coastal grasslands are also home to

many communities which are still poorly studied in their composition (but see Calado et al., 2024).

In island environments, monitoring is crucial due to their vulnerability to anthropogenic impacts (Borges et al., 2018; Delgado and Riera, 2020; Boieiro et al., 2024). Studying the distribution and abundance of arthropod communities in coastal grasslands, alongside consistent monitoring, provides valuable insights into the extent and nature of human-induced effects on these fragile ecosystems.

Grasslands across Europe and North America have suffered extensive degradation, leading to a substantial decline in the ecosystem services they provide and the loss of many associated species (Peters et al., 2016; Wick et al., 2016; Bardgett et al., 2021). The same happens in different parts of the world. For example, the rapid economic growth in China over the last 30 years resulted in massive construction activities that have altered landforms, vegetation and waterways, leading to surface runoff, soil erosion, sedimentation and land degradation (Dai et al., 2022).

At the same time, commerce and tourism can bring many invasive species of plants and animals that are being introduced in several ecosystems and lead to a loss of endemic organisms ((Borges et al., 2022; Boieiro et al., 2024). As an agricultural region, the Azores Archipelago depends on the vital roles played by various organisms, particularly arthropod communities, in supporting crop productivity. The decline or loss of arthropod communities could greatly affect crop productivity, with losses of ecosystem services that could lead to devastating consequences in food security (Calado et al., 2024a). Moreover, as these coastal communities host many exotic species, they could be reservoirs of potential agricultural pests or invasive species (Boieiro et al., 2024; Calado et al., 2024).

Understanding how communities are distributed within a given ecosystem allows us to adopt better and more assertive solutions for the problems they face. In this way, comparative studies are important tools to provide information for conservation and restoration strategies that lead to the mitigation or reversal of the problems caused by anthropogenic actions over the years (Boieiro et al., 2024; Calado et al., 2024).

2.2. General Description

Purpose: The primary objective of this publication is to provide a comprehensive inventory of terrestrial arthropods sampled from grasslands across São Miguel Island (Azores Archipelago), Sesimbra and Sines regions (Setúbal District in Portugal mainland). The dataset includes detailed information on the abundance, diversity and composition of arthropod communities, collected through the project's monitoring surveys.

2.3. Project Description

Title: Phenotypic Plasticity of Pest and Biological Control Agents: Contrasting Mainland and Insular Coastal Ecosystems

Personnel: The project was conducted by Hugo Renato M.G. Calado and led by António O. Soares, Paulo A.V. Borges and Ruben Heleno.

Fieldwork: São Miguel Island: Hugo Renato M.G. Calado; Mainland: Hugo Renato M.G. Calado.

Taxonomists: Paulo A. V. Borges and Hugo Renato M.G. Calado.

Database management: Hugo Renato M.G. Calado and Paulo A. V. Borges.

Darwin Core databases: Hugo Renato M.G. Calado and Paulo A. V. Borges.

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2.4. Sampling Methods

2.4.1. Sampling description

An area of 2,500 m^2 (0.25 ha) was defined for each plot to carry out the sampling programme. Plots were selected in both regions to have a similar general substrate (rocky), latitude and elevation. Thirteen plots on São Miguel Island and eighteen on Portugal's mainland, distributed across the Setúbal District (Sesimbra – 12 and Sines – 6), were visited four times between spring and summer of 2022. A total of 121 samples were collected (50 in São Miguel and 71 on Portugal's mainland).

2.4.2. Step description

Arthropod sampling: Sweeping nets were used to collect arthropods (which included spiders, true bugs, ants, beetles and other insects) on both coastal grasslands (in the Azores and on Portugal's mainland). In each plot, a random sweeping session was carried out using a nylon mosquito net 40 cm in diameter, 50 cm in length, with 0.25 mm mesh and an effort of 15 min. was spent (3 min. for sweeping and 12 min. for processing and labelling of the collected material). All collected specimens were transferred to tubes with 99.8% ethyl alcohol for later sorting and identification in the laboratory.

Morphospecies identification: In the laboratory, all arthropod specimens were sorted into morphospecies and stored in 2 ml Eppendorf tubes with 99.8% ethyl alcohol. For each morphospecies, at least one exemplar was selected and photographed, using a LEICA S9i stereomicroscope with LAS X 5.2.1.27831, to create a photographic database to facilitate taxonomic identification.

All morphospecies of the Azorean samples were identified by the senior author (Paulo A.V. Borges) to species level, when possible. All species collected in the Azores were categorised into three colonisation categories following the last checklist of Azorean arthropods (Borges et al. 2022b): endemic, native non-endemic and introduced. In some cases, the colonisation status was undetermined. A database for both events and occurrences was created following the Darwin Core criteria.

2.5. Geographic Coverage

Description: The study was conducted on the coastal grasslands of the São Miguel Island (Azores Archipelago – North Atlantic) and Portugal Mainland (Setúbal District – Sesimbra and Sines regions) (Figure 1).The Azores Archipelago is in the middle of the

North Atlantic, approximately 1600 km from mainland Portugal, with an extension of about 600 km between Santa Maria and Corvo (37°–40° N latitude; 25°–31° W longitude). Three island groups compose the Archipelago: Eastern (Santa Maria and São Miguel Islands), Central (Terceira, Graciosa, São Jorge, Pico and Faial Islands) and Western (Corvo and Flores Islands). The different islands are aligned in a NW–SE orientation. São Miguel is situated in the oriental islands group (37.7804° N; -25.4970° W) and is the largest archipelago island with 746.8 km², measuring 64.7 km in length and 8–15 km in width and a maximum altitude above sea level of 1,103 m (Elias et al., 2016; Borges et al., 2019).

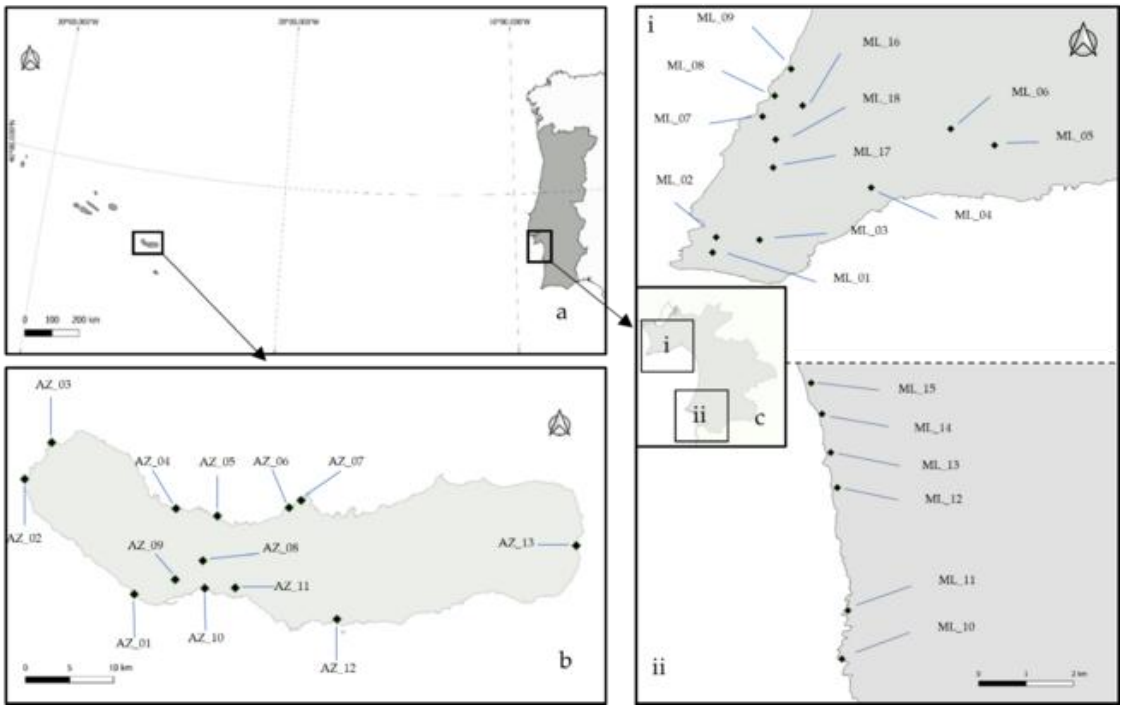

Figure 1. Sampling areas with the plots indicated: (**a**) Azores Archipelago and Portugal mainland; (**b**) São Miguel's Island; (**c**) Setúbal District; (**i**) Sesimbra; (**ii**) Sines (source: Calado et al., 2024).

The Archipelago's climate is affected by the surrounding ocean, namely, the effects of the Gulf Stream, as well as by island topography, being mild and very wet, often reaching an average annual relative humidity of 95% in high-altitude forests (Borges et al., 2019). The oceanic temperate climate is reflected in high annual precipitation, high relative humidity, persistent wind and low thermal amplitude (Pavão et al., 2023).

Mainland Portugal, on the other hand, is located in south-western Europe and is confined between parallels 37°N and 42°N and within the relatively narrow meridional band that develops between 6.5°W and 9.5°W. It lies in the transitional region between the sub-

tropical anticyclone and the sub-polar depression zones. In this territory, the latitude, orography and effect of the Atlantic Ocean are the main driving forces of the climate (De Lima et al., 2015). The Setúbal District is located south of Lisbon, between parallels 37°N and 39°N. Sesimbra is ca. 30 km south of Lisbon and has an area of 194.98 km², whereas Sines is located ca. 150 km south of Lisbon and has an area of 195,47 km². Portugal has a Mediterranean climate characterised by warm and dry summers and cool and wet winters (Carvalho et al., 2014). Precipitation ranges from more than 2,000 mm in the northwest to roughly 400 mm in the most south-eastern part of the country (Santos et al., 2016).

2.6. Taxonomic Coverage

Description: The following classes and orders are covered:

Arachnida: Araneae; Opiliones.

Diplopoda: Julida.

Insecta: Coleoptera; Diptera; Hemiptera; Hymenoptera; Lepidoptera; Mantodea; Neuroptera; Orthoptera; Phasmida; Psocodea; Thysanoptera.

2.7. Temporal Coverage

Notes: The data were collected between March 2022 and 31 July 2022.

2.8. Collection Data

Collection name: Renato_PhD

Collection identifier: PHEPLA

Specimen preservation method: 99.8% ethyl alcohol

2.9. Usage license

Creative Commons Public Domain Waiver (CC-Zero)

2.10. Data resources

Data package title: Arthropod communities of island vs. mainland coastal grasslands: São Miguel Island (Azores) and mainland Portugal.

Resource link: http://ipt.gbif.pt/ipt/resource?r=matela_protest&v=1.1

Number of data sets: 2

Data set name: Event Table

Character set: UTF-8

Download URL: http://ipt.gbif.pt/ipt/resource?r=matela_protest&v=1.1

Data format: Darwin Core Archive format

Data format version: 1.2

Description: The following data table includes all the records for which a taxonomic identification of the species was possible. The dataset submitted to GBIF is structured as a sample event dataset that has been published as a Darwin Core Archive (DwCA), which is a standardised format for sharing biodiversity data as a set of one or more data tables. The core data file contains 121 records (eventID). This GBIF IPT (Integrated Publishing Toolkit, Version 2.6.2) archives the data and, thus, serves as the data repository. The data and resource metadata are available for download in the Portuguese GBIF Portal IPT (Calado et al., 2024b).

Column label	Column description
eventID	Identifier of the events, unique for the dataset.
locationID	Identifier of the locations, unique for the dataset.
country	The name of the country or major administrative unit in which the Location occurs (Portugal).
countryCode	The standard code for the country in which the Location occurs (PT).
stateProvince	The name of the next smaller administrative region than country (state, province, canton, department, region etc.) in which the Location occurs.
county	The full, unabbreviated name of the next smaller administrative region than stateProvince (county, shire, department etc.) in which the Location occurs.
municipality	The full, unabbreviated name of the next smaller administrative region than county (city, municipality etc.) in which the Location occurs.
locality	The specific description of the place.
verbatimLocality	The original textual description of the place.
locationRemarks	Comments or notes about the Location.
habitat	The habitat for an Event (coastal grasslands).

minimunElevationInMetres	The lower limit of the range of elevation (altitude, usually above sea level), in metres.
decimalLatitude	Approximate centre point decimal latitude of the field site in GPS coordinates.
decimalLongitude	Approximate centre point decimal longitude of the field site in GPS coordinates.
geodeticDatum	Standard Global Positioning System coordinate reference for the location of the sample collection points.
coordinateUncertaintyInMetres	Uncertain value of coordinate metrics.
coordinatePrecision	Value in decimal degrees to a precision of five decimal places.
georeferenceSources	Navigation system used to record the location of sample collections.
samplingProtocol	The sampling protocol used to capture the species (3 minutes of random sweeping at an area of 2,500 m^2; 12 minutes to vacuum the organisms, put in flasks and label).
sampleSizeValue	A numeric value for a measurement of the size (time duration, length, area or volume) of a sample in a sampling Event.
sampleSizeUnit	The unit of measurement of the size (time duration, length, area or volume) of a sample in a sampling Event.
samplingEffort	The amount of effort expended during an Event (1 person randomly sweeping for 15 minutes on 0.25 ha plot, 4 repeats in spring and summer).
year	Year the sample was collected (2022).
month	The integer month in which the Event occurred.
day	The integer day of the month on which the Event occurred.
eventDate	The date-time or interval during which an Event occurred.
verbatimEventDate	The verbatim original representation of the date and time information for an Event.
dynamicProperties	Climatic conditions at the time of sampling at each location (Weather; Wind; AirTemperatureInCelsius; Nebulosity; Humidity).

Data set name: Occurrence Table

Character set: UTF-8

Download URL: http://ipt.gbif.pt/ipt/resource?r=matela_protest&v=1.1

Data format: Darwin Core Archive format

Data format version: 1.2

Description: The dataset was published in the Global Biodiversity Information Facility platform, GBIF structured as an occurrence table that has been published as a Darwin Core Archive (DwCA), which is a standardised format for sharing biodiversity data as a set of one or more data tables. The core data file contains 3,636 records (occurrenceID).

This GBIF IPT (Integrated Publishing Toolkit, Version 2.6.2) archives the data and, thus, serves as the data repository. The data and resource metadata are available for download in the Portuguese GBIF Portal IPT (Calado et al., 2024b).

Column label	Column description
eventID	Identifier of the events, unique for the dataset.
type	Type of the record, as defined by the Darwin Core Standard. In this case, "PhysicalObject".
licence	Reference to the licence under which the record is published.
institutionID	The identity of the institution publishing the data.
collectionID	The identity of the collection publishing the data.
institutionCode	The code of the institution publishing the data (UAc).
collectionCode	The code of the collection where the specimens are conserved (PHEPLA).
datasetName	Name of the dataset (Renato_PhD).
basisOfRecord	The nature of the data record. In this case, "PreservedSpecimen".
recordedBy	A list (concatenated and separated) of names of people, groups or organisations who performed the sampling in the field.
occurrenceID	Identifier of the record, coded as a global unique identifier.
datasetID	The identifier for the set of data.
organismQuantity	A number or enumeration value for the quantity of Organisms.
organismQuantityType	The type of quantification system used for the quantity of organisms.
kingdom	Kingdom name.
phylum	Phylum name.
class	Class name.
order	Order name.
family	Family name.
genus	Genus name.
specificEpithet	Specific epithet name.
infraspecificEpithet	Infraspecific epithet name.
scientificNameAuthorship	The authorship information for the scientificName formatted according to the conventions of the applicable nomenclaturalCode.
identificationRemarks	Comments or notes about the Identification (Morphospecie's number in Renato PhD Collection).
identifiedBy	A list of names of people, groups or organisations who assigned the Taxon to the subject.
dateIdentified	The date on which the subject was determined as representing the Taxon.
scientificName	The full scientific name, with authorship and date information if known.

taxonRank	Lowest taxonomic rank of the record.
establishmentMeans	The process of establishment of the species in the location, using a controlled vocabulary: 'native', 'introduced', 'endemic', "indeterminate".

2.11. Additional Information

A total of 13,515 specimens were collected in the two coastal grasslands (Azores = 7861; Mainland = 5654) belonging to 534 arthropod species. In the Azores, 210 species were identified. Of those, 143 were found only in the Archipelago. For the mainland, 391 species were identified, with 324 presents only there. A total of 67 species were common in both ecosystems (Figure 2), (Table 1).

Table 1. Common species in the Azores and mainland coastal grasslands.

Class	Order	Family	Species	Total Abundance Azores	Total Abundance Mainland
Arachnida	Araneae	Araneidae	*Mangora acalypha* (Walckenaer, 1802)	16	117
			Neoscona crucifera (Lucas, 1838)	8	1
			Zygiella x-notata (Clerck, 1757)	42	66
		Linyphiidae	*Oedothorax fuscus* (Blackwall, 1834)	11	4
			Prinerigone vagans (Audouin, 1826)	52	15
		Salticidae	*Chalcoscirtus infimus* (Simon, 1868)	73	13
			Macaroeris diligens (Blackwall, 1867)	16	6
			Salticus mutabilis Lucas, 1846	31	28
			Synageles venator (Lucas, 1836)	61	7
		Thomisidae	*Xysticus nubilus* Simon, 1875	90	97
Insecta	Coleoptera	Apionidae	*Aspidapion radiolus* (Marsham, 1802)	72	3
		Chrysomelidae	*Psylliodes marcida* (Illiger, 1807)	11	49
		Coccinellidae	*Rhyzobius litura* (Fabricius, 1787)	38	5
			Scymnus interruptus (Goeze, 1777)	129	2
			Scymnus suturalis Thunberg, 1795	2	1
		Curculionidae	*Mecinus pascuorum* (Gyllenhal, 1813)	286	18
		Nitidulidae	*Brassicogethes aeneus* (Fabricius, 1775)	54	8
		Phalacridae	*Stilbus testaceus* (Panzer, 1797)	14	10
		Staphylinidae	*Tachyporus chrysomelinus* (Linnaeus, 1758)	1	1
	Diptera	Agromyzidae	*Chromatomyia nigra* (Meigen, 1830)	10	1
		Calliphoridae	*Lucilia sericata* (Meigen, 1826)	16	3
		Chloropidae	*Thaumatomyia notata* (Meigen, 1830)	32	35
		Lonchopteridae	*Lonchoptera bifurcata* (Fallén, 1810)	67	69

	Muscidae	*Coenosia humilis* Meigen, 1826	65	8
		Musca osiris Wiedemann, 1830	70	6
		Stomoxys calcitrans (Linnaeus, 1758)	123	71
	Opomyzidae	*Geomyza tripunctata* (Fallén, 1823)	4	3
	Rhinophoridae	*Melanophora roralis* (Linnaeus, 1758)	82	15
	Syrphidae	*Eristalis tenax* (Linnaeus, 1758)	4	3
		Eupeodes corollae (Fabricius, 1794)	15	7
		Sphaerophoria scripta (Linnaeus, 1758)	34	12
	Tephritidae	*Dioxyna sororcula* (Wiedemann, 1830)	220	1
Hemiptera	Anthocoridae	*Orius laevigatus laevigatus* (Fieber, 1860)	44	3
	Aphididae	*Aphis fabae* Scopoli, 1763	58	2
		Aphis nerii Boyer de Fonscolombe, 1841	42	2
		Melanaphis donacis (Passerini, 1862)	257	48
		Myzus persicae (Sulzer, 1776)	127	45
		Therioaphis trifolii (Monell, 1882)	19	10
	Aphrophoridae	*Philaenus spumarius* (Linnaeus, 1758)	285	241
	Cicadellidae	*Macrosteles sexnotatus* (Fallen, 1806)	301	14
	Delphacidae	*Megamelodes quadrimaculatus* (Signoret, 1865)	44	3
		Sogatella nigeriensis (Muir, 1920)	252	45
	Lygaeidae	*Kleidocerys ericae* (Horváth, 1909)	49	6
		Nysius ericae ericae (Blackwall, 1867)	14	15
	Miridae	*Taylorilygus apicalis* (Fieber, 1861)	433	26
	Nabidae	*Nabis capsiformis* Germar, 1838	180	3
	Pentatomidae	*Nezara viridula* (Linnaeus, 1758)	53	13
	Psyllidae	*Acizzia uncatoides* (Ferris & Klyver, 1932)	15	21
	Rhyparochromidae	*Beosus maritimus* (Scopoli, 1763)	1	9
	Saldidae	*Saldula palustris* (Douglas, 1874)	4	1
Hymenoptera	Aphelinidae	*Encarsia formosa* Gahan, 1924	9	2
	Apidae	*Apis mellifera* Linnaeus, 1758	19	6
		Bombus terrestris (Linnaeus, 1758)	16	3
	Encyrtidae	*Pseudaphycus maculipennis* Mercet, 1923	13	2
	Eulophidae	*Baryscapus galactopus* (Ratzeburg, 1844)	69	86
		Diglyphus isaea (Walker, 1838)	6	4
	Formicidae	*Hypoponera eduardi* (Forel, 1894)	5	5
		Lasius grandis Forel, 1909	593	6
		Tetramorium caespitum (Linnaeus, 1758)	20	4
	Ichneumonidae	*Aritranis director* (Thumberg, 1822)	1	1

			Diplazon laetatorius (Fabricius, 1781)	32	4
		Mymaridae	*Litus cynipseus* Haliday, 1833	6	2
		Pteromalidae	*Pteromalus puparum* (Linnaeus, 1758)	8	7
	Lepidoptera	Pieridae	*Colias croceus* (Fourcroy, 1785)	4	1
	Orthoptera	Acrididae	*Locusta migratoria* (Linnaeus, 1758)	3	1
		Trigonidiidae	*Trigonidium cicindeloides* Rambur, 1838	69	3
	Psocodea	Caeciliusidae	*Valenzuela flavidus* (Stephens, 1836)	48	3
Total				**4848**	**1332**

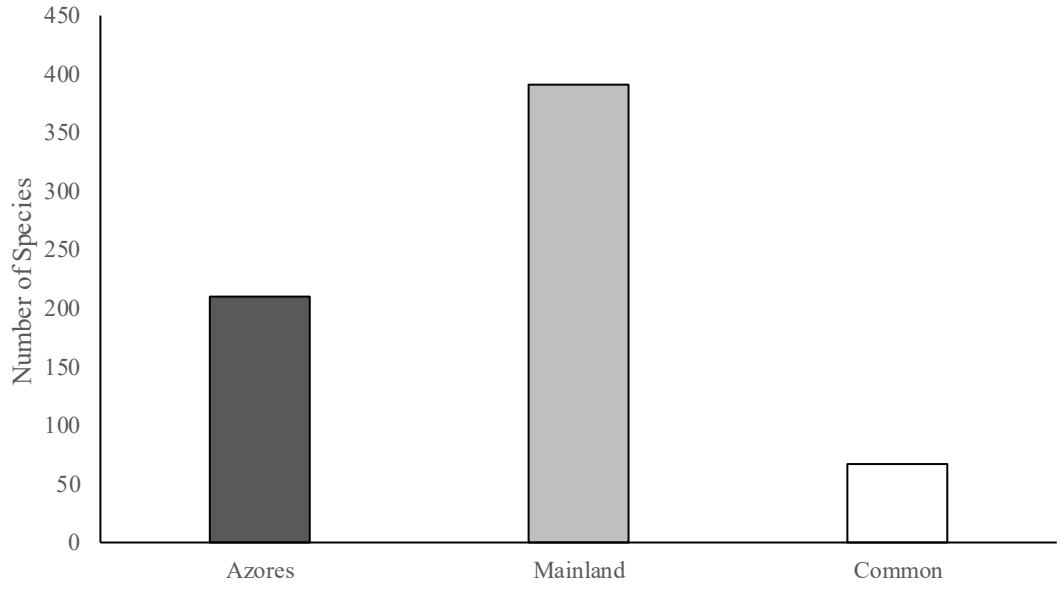

Figure 2. Number of species collected in the Azores and mainland coastal grasslands.

All the 210 taxa collected in the Azores were organised by colonisation category, following the last checklist of Azorean arthropods (Borges et al., 2022a). Of those, only four are endemic, with the others considered introduced (39), native non-endemic (42) or not yet specified (125) (Figure 3).

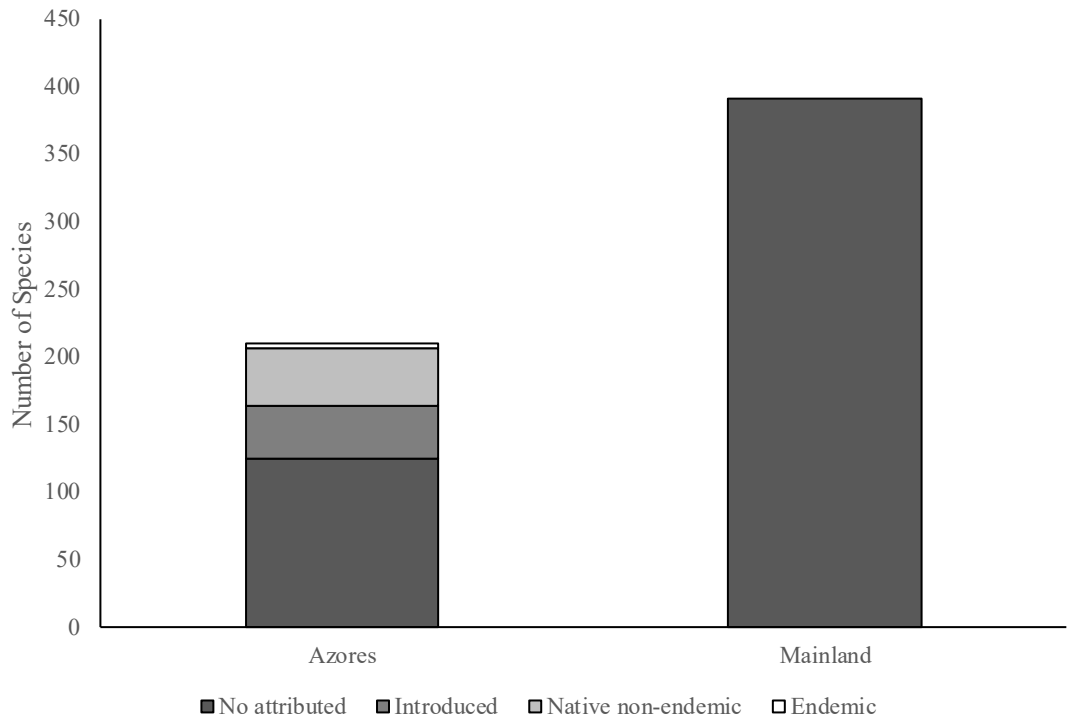

Figure 3. Total of species of terrestrial arthropods, organised by colonisation category, collected in the Azores and mainland coastal grasslands.

2.12. Three new arthropod species were recorded for the Azores

2.12.1. Aritranis director *(Thunberg, 1822) (Hymenoptera, Ichneumonidae)*

The Ichneumonoidea is one of the largest superfamilies of the apocritan wasps with 58,121 described species and is distributed worldwide (Yu, 2024).

This species is native to Europe and considered invasive in North America (Townes and Townes, 1962). The length up to 10 mm, with a black head and thorax. The bulk of the abdomen is orange-red, with the final part black. The female, immediately before the ovipositor, also has a small white band at the tip of the abdomen (Townes and Townes, 1962). Females have a longer and downcurved ovipositor (longer than the metasoma) and the postpetiole is strongly convex (Verheyde et al., 2021).

This species was first found in grassland in São Roque (São Miguel Island), in April 2022, using a sweeping net (Figure 4).

Figure 4. *Aritranis director* (Thunberg, 1822). Photo by Hugo Renato Calado.

2.12.2. Draeculacephala *Ball (Hemiptera, Cicadellidae)*

The genus naturally occurs throughout the temperate and tropical zones of North and South America, including some Caribbean islands, but some species have been introduced into Hawaii (Blanco-Rodríguez and Pinedo-Escatel, 2022). *Draeculacephala* was established by Ball (1901) with Tettigonia mollipes as its type-species (Young, 1977).

Draeculacephala can be easily recognised by its strongly depressed crown, which is typically angularly produced and its forewing, characterised by reticulated venation distally (Dietrich, 1994; Blanco-Rodríguez and Pinedo-Escatel, 2022).

This species was first found in grassland in São Roque (São Miguel Island), in April 2022, using a sweeping net (Figure 5).

Figure 5. *Draeculacephala bradleyi*, Van Duzee, 1915**.** Photo by Hugo Renato Calado.

2.12.3. Isodontia *sp. Patton, 1880 (Hymenoptera, Sphecidae)*

The genus *Isodontia* Patton, 1880 contains 62 described species distributed worldwide (Can, 2024). The first recurrent vein enters the second submarginal cell, the second recurrent vein enters the third submarginal cell; the body is completely black (Notton, 2017; Gladcaia, 2024). This species was first found in grassland in São Roque (São Miguel Island), in April 2022, using a sweeping net (Figure 6).

Figure 6. *Isodontia* sp. Patton, 1880. Photo by Hugo Renato Calado.

2.13. Conclusions

This paper includes the inventory of the species collected in coastal grasslands in the Azores islands and Portugal's mainland in Calado et al. (2024a).

We observed greater arthropod diversity in the mainland coastal grasslands compared to those on São Miguel Island. The total number of species and morphospecies recorded in mainland coastal grasslands was significantly higher, in some cases doubling or exceeding those found in the Azores (e.g. for taxa such as Coleoptera, Hymenoptera and Araneae). These findings align with the well-documented pattern that insular ecosystems tend to be species-poor and exhibit disharmonic species composition (Whittaker et al., 2017).

Comparing different types of ecosystems provides valuable insights into species composition within communities, their distribution patterns and their ecological roles. This understanding is crucial for assessing the complexity of a given ecosystem and evaluating its potential vulnerability to anthropogenic impacts. Additionally, studies like this contribute to the broader understanding of local biodiversity, particularly for taxonomic groups that remain understudied, highlighting the need for further research to fill knowledge gaps (Borges et al., 2022a)

Therefore, through these studies, it will be possible to predict which species can be marked as potential invaders and the risks they may pose to native species. This information can be useful to decide the best preventative measures to impede their spread and mitigate potentially harmful effects. At the same time, this will be helpful for minimising the costs related to eventual pest outbreaks (Nentwig, 2008; Boieiro et al., 2024).

Finally, given the climate changes we are currently experiencing, long-term monitoring of these environments will also allow us to adopt the most effective measures to safeguard some species that are most sensitive to these same changes, as well as trying to predict which will be the results of the losses of their respective habitats.

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Chapter 3. A Comparative Analysis of Island vs. Mainland Arthropod Communities in Coastal Grasslands Belonging to Two Distinct Regions: São Miguel Island (Azores) and Mainland Portugal

Abstract

Coastal grasslands host diverse arthropod communities and provide important ecosystem services. Islands, being isolated environments, are expected to have simpler ecosystems than continental areas, with the few successful colonizing species often attaining high densities; however, these patterns are still poorly documented for coastal grassland arthropods. We conducted a comparative study of the biodiversity of arthropod communities in two distinct coastal grassland ecosystems (Portugal mainland and the Azores) with the following objectives: (a) to investigate the arthropod community composition in both locations; (b) to compare the diversity profiles in both locations; (c) to investigate potential density compensation in the island's arthropod communities. For four months, arthropods were collected on the Island of São Miguel, Setúbal Peninsula, and Sine's region and subsequently classified into taxonomic groups. With the data collected, Hill Numbers were calculated for each region. We confirmed that the richness on the mainland was higher than in the Azores, and we found some apparent abundance compensation in the Azores. At the same time, we also observed that many species in the Azores are also present in the continental coastal grasslands of mainland Portugal

Keywords: Arthropods; grasslands; diversity; density compensation

3.1. Introduction

Oceanic islands, which are characterized by their geographical isolation and natural barriers, present unique ecosystems with relatively simple architectures compared to mainland counterparts (Graham et al., 2017). This simplicity makes island communities particularly susceptible to environmental perturbations (Fernández-Palacios et al., 2021), including biological invasions (Tylianakis et al., 2008; Heleno et al., 2020) and climate change (Harter et al., 2015; Harvey et al., 2020). The limited diversity and specialized niches in island species often lack the resilience necessary to withstand such disturbances. Consequently, these ecosystems face heightened vulnerability, which makes them crucial

focal points for conservation efforts and scientific research (Kueffer and Kinney, 2017; Harvey et al., 2020; Fernández-Palacios et al., 2021). At the same time, terrestrial arthropods are one of the most widely studied taxonomic groups and are also quite sensitive to environmental changes (Murphy et al., 2020). Although there are several studies of these communities in different island ecosystems, such as pristine and forest areas, crops, or marshes (Marcelino et al., 2013; Marcelino et al., 2016; Borges et al., 2019; Hembry et al., 2021; Marcelino et al., 2021), there is still a lack of studies focused on arthropod communities in coastal island grasslands.

Grasslands are very rich and diverse ecosystems, not only due to their floristic and faunistic biodiversity but also for the diverse ecosystem services they provide (like nutrient recycling, carbon sequestration, and air purification, among others), most of which have already been identified and well-studied over the years (Jones and Donnelly, 2004; Blair et al., 2014; Elizalde et al., 2020; Feher et al., 2021). Often called prairies, grasslands differ from the latter in that they no longer maintain most of their original native plants, having undergone major changes in their plant composition (Holstein, 2011; Mooney and Zavaleta, 2016; Lark, 2020). These environments also differ from their more inland counterparts in terms of temperature and humidity, typically being warmer and more humid (Diamond and Smeins, 1988).

Comparative studies on the composition and diversity of arthropod communities in coastal grasslands, contrasting ecosystems, such as insular and mainland, are very useful to ecology. They may provide greater insights regarding how these communities are organized, enabling us to discern the disparities in biodiversity, relative abundance, and ecosystem services these species provide (Ameixa et al., 2018). In areas where specific richness is lower, an inverse relation to the density of organisms could occur (the so-called density compensation), which partially reduces the higher risk of extinction caused by the less complex communities (McGrady-Steed and Morin, 2000). There are species, such as birds and lizards, which, in island environments, show an increase in their abundance when compared to their continental counterparts (MacArthur et al., 1972; Wright, 1980; Novosolov et al., 2013; Stadler et al., 2022). There are also recent studies that have used trait-based approaches to explain patterns in organism densities (Jonsson et al., 2009; Zakharova et al., 2019). For ladybirds, for example, species richness, diversity, and body mass tended to be lower in insular ecosystems (Soares et al., 2017, 2021).

In arthropods, however, there are still gaps in the knowledge about island coastal grasslands. Moreover, the islands are also seen as excellent places for studies on ecology and evolution (Graham et al., 2017; Kueffer and Kinney, 2017; Fernández-Palacios et al., 2021) and this kind of study should include a comprehensive understanding of the causes of variation in species richness, how ecological communities are distributed, and what are the mechanisms that shape evolutionary processes (Warren et al., 2015; Whittaker et al., 2017; Whittaker et al., 2023). By doing so, we gain insights into whether these distinctions are significant enough to drive ecological and evolutionary processes within existing communities. At the same time, these studies are also important for the establishment of new solutions for conservation and ecological restoration (Heleno et al., 2010).

In this way and considering that current Azorean coastal grasslands are a highly modified ecosystem with a dominance of exotic and naturalized vegetation originating from nearby mainland with very few endemic plant species and, at the same time, have some similar characteristics to their mainland homologs (in terms of latitude and substrate), we investigate how arthropod communities are assembled in comparison with an equivalent mainland habitat. We aim to (a) investigate the arthropod community composition in both locations; (b) compare the diversity profiles in both locations; (c) investigate potential abundance compensation in the island's arthropod communities. Since oceanic islands are species-poor and disharmonic systems, we predict that: (i) local arthropod taxonomic diversity will be lower on the island-modified coastal prairies compared with that from the mainland; (ii) arthropod communities from the Azorean coastal grasslands will be composed mostly of exotic arthropods; and (iii) some density compensation will likely occur in the island arthropod communities.

3.2. Material and Methods

3.2.1. Study Area

The Azores archipelago is in the middle of the North Atlantic, approximately 1600 km from mainland Portugal, with an extension of about 600 km between Santa Maria and Corvo (37°–40° N latitude; 25°–31° W longitude). Three island groups compose the archipelago: Eastern (Santa Maria and São Miguel islands), Central (Terceira, Graciosa, São Jorge, Pico, and Faial islands), and Western (Corvo and Flores islands). The different

islands are aligned in a NW–SE orientation. São Miguel is the largest of the islands of the Azores archipelago and the largest of all the islands that make up the territory of Portugal, with an area of 748.82 km^2, measuring 64.7 km in length and 8–15 km in width (Borges et al., 2019; Elias et al., 2016) (Figure 1a). The archipelago's climate is affected by the surrounding ocean, namely, the effects of the Gulf Stream, as well as by island topography, being mild and very wet, often reaching an average annual relative humidity of 95% in high-altitude forests (Borges et al., 2019). The oceanic temperate climate is reflected in high annual precipitation, high relative humidity, persistent wind, and low thermal amplitude (Pavão et al., 2023).

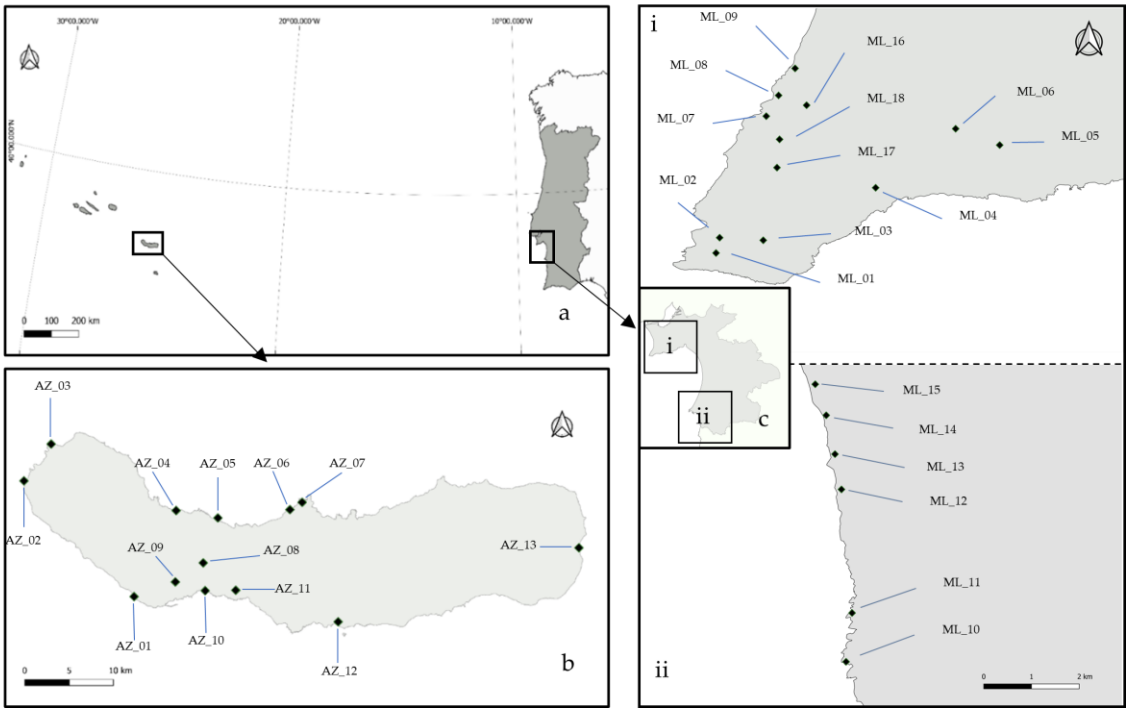

Figure 1. Maps of sampling areas with the plots indicated: (**a**) Azores Archipelago and Portugal mainland; (**b**) São Miguel's Island; (**c**) Setúbal district; (**i**) Sesimbra; (**ii**) Sines.

Mainland Portugal, on the other hand, is located in southwestern Europe and is confined between parallels 37° N and 42° N and within the relatively narrow meridional band that develops between 6.5° W and 9.5° W. It lies in the transitional region between the sub-tropical anticyclone and the sub-polar depression zones. In this territory, the latitude, orography, and effect of the Atlantic Ocean are the main driving forces of the climate (De Lima et al., 2015).

The Setúbal district is located south of Lisbon, between parallels 37° N and 39° N, with an area of 5'034 km^2, and encompasses the regions of Sesimbra and Sines. Sesimbra is c.

30 km south of Lisbon and has an area of 194.98 km^2, whereas Sines is located c. 150 km south of Lisbon and has an area of 195.47 km^2. Portugal has a Mediterranean climate characterized by warm and dry summers and cool and wet winters (Carvalho et al., 2014). Precipitation ranges from more than 2000 mm in the northwest to roughly 400 mm in the most south-eastern part of the country (Santos et al., 2019).

3.2.2. Arthropod Sampling

For the study of arthropod diversity, 31 plots were selected in coastal grasslands. Thirteen plots were located on São Miguel Island (Figure 1b) and 18 on the mainland west coast, distributed across Sesimbra and Sines, in Setúbal district (Figure 1c). Plots were selected in both regions to have a similar general substrate (rocky), latitude, and elevation (See Appendix A – Table A1). For each one, an area of 2'500 m^2 (0.25 ha) was defined. All selected plots were visited four times between spring and summer 2022.

In each plot, a randomly sweeping section was carried out using a nylon mosquito net 40 cm in diameter, 50 cm in length, and 0.25 mm mesh. For each section, an effort of 15 min was spent (3 min for sweeping and 12 min for processing and labelling of the collected material). All collected organisms were placed in flasks with 96% ethyl alcohol for later sorting and identification.

Since the climate conditions that occur in spring in the Azores normally begin one month later than in the mainland, we assume, for the purposes of this study, that March, April, May, and June on the mainland will be similar to April, May, June, and July for the Azores, respectively.

3.2.3. Species Sorting, Identification, and Diversity Measurements

In the laboratory, all arthropod specimens were sorted into different morphospecies and stored in 2 ml Eppendorf tubes with 99% absolute alcohol. For each morphospecies, three exemplars were selected and photographed, using a LEICA S9i stereo microscope with LAS X 5.2.1.27831, to create a photographic database to help the taxon identification. The senior author (P.A.V.B.) identified all morphospecies of the Azorean samples to the species level when possible. All species collected in the Azores were categorized into

three colonization categories following the last checklist of Azorean arthropods (Borges et al., 2022a): endemic, native non-endemic, and introduced (See Appendix A – Table A2). In some cases, the colonization status was undetermined. A database for both events and occurrences was created using the Darwin Core criteria.

Accumulation curves were constructed using EstimateS program v. 9.1.0 (Colwell and Elsensohn, 2014), with 100 runs, for the observed number of species, species richness estimates, singletons, and doubletons, using the non-parametric estimators Chao 1 and Jackknife 1. From EstimateS, we also extracted the number of singletons, doubletons, uniques, and duplicates. Common indices of diversity were also calculated for the two geographic areas, following the Hill series: species richness (H_0); Shannon–Wiener exponent (H_1); inverse Simpson´s index (H_2); inverse Berger–Parker index (H_3) (Chao et al., 2014).

H_0 = S (total number of species)

H_1 = exponent of Shannon–Wiener index (H')

Shannon–Wiener index:

$$H' = -\sum_{i=1}^{n} p_i \; Ln \, p_i$$

$$p_i = \frac{n_i}{N_t}$$

n_i = species abundance;
N_t = Total species abundance,
p_i = relative abundance for each species.

H_2 = Simpson inverse = $1/D$

Simpson index:

$$D = \sum_{i=1}^{n} p_i^2$$

H_3 = Berger–Parker inverse = $1/d$

Berger–Parker index:

$$d = \frac{N_{max}}{N_t}$$

Evenness index:

$$E = \frac{H'}{Ln\ (S)}$$

The use of biodiversity indices allows us to analyse and understand in more detail the difference between two distinct ecosystems, as it presents important and simple information on how species are distributed in terms of richness and abundance (dominance or rarity). Hill numbers, in this sense, act as an extremely important tool for research into biodiversity and ecological assessments (Carvalho et al., 2012; Chao et al., 2014). The Fisher's Alpha index was also calculated since it is considered to have low sensitivity to sampling effort.

Fisher's Alpha index:

$$S = \alpha * \ln\ (1 + \frac{N}{\alpha})$$

S = number of taxa;
N = number of individuals,
α = Fisher's alpha.

To verify the dissimilarity between the Azores and Mainland communities, we computed a beta partition framework using the Jaccard index (Carvalho et al., 2012).

Jaccard index:

$$\beta_{Jac} = \beta_{repl} + \beta_{rich}$$

$$\beta_{Jac} = \frac{b + c}{a + b + c} = \frac{2\min\ (b, c)}{a + b + c} + \frac{|b - c|}{a + b + c}$$

a = the number of species common to both sites;

b = the number of species that occur in the first site but not in the second,

c = the number of species that occur in the second site but not in the first.

3.2.4. Data Analysis

The Kolmogorov–Smirnov and Levene's tests were performed to assess the normality and homogeneity of data variances, respectively. When the previous condition was not verified, data were log-transformed. The comparative analysis of arthropod species richness and abundance between the mainland and the Azores utilized either parametric t-tests or non-parametric Kruskal–Wallis tests. Mean values were considered significantly different when $p < 0.05$. All statistical analyses were conducted using SPSS v. 29.0.1 (IBM Corporation, 2023).

For the Hill numbers, Jaccard index, and Fisher's Alpha index calculation, we used only the morphospecies identified at least until the family taxonomic group.

3.3. Results

3.3.1. Species Richness and Abundance

A total of 13,515 specimens were collected in the two coastal grasslands (Azores = 7861; Mainland = 5654) belonging to 534 arthropod species and morphospecies. In the Azores, 210 species and morphospecies belonging to 3 classes were collected: Arachnida (22), Diplopoda (1), and Insecta (187). On the mainland, a total of 391 species and morphospecies were collected, belonging to 2 classes: Arachnida (55) and Insecta (336) (Table 1).

Table 1. Number of morphospecies and species collected in the Azores and mainland coastal grasslands by Class and Order.

Class	Order	Azores	Mainland
Arachnida		**22**	**55**
	Araneae	21	54
	Opiliones	1	1
Diplopoda		**1**	
	Julida	1	
Insecta		**187**	**336**
	Coleoptera	26	109
	Diptera	42	42
	Hemiptera	44	73
	Hymenoptera	51	86

	Lepidoptera	12	12
	Mantodea		1
	Neuroptera	1	
	Orthoptera	7	11
	Phasmida	1	
	Psocodea	3	1
	Thysanoptera		1
Total		**210**	**391**

Of the 210 morphospecies collected in the Azores, only four are endemic, with the others considered introduced (39), native non-endemic (42), or not yet specified (125) (see Appendix A—Table A2). The class with the highest abundance in the Azores coastal grasslands was Class Insecta, with 7313 specimens, of which 2958 belonged to order Hemiptera (44 species and morphospecies). The group with the largest taxa number was the Hymenoptera, with a total of 51 morphospecies. In the mainland coastal grasslands, the class with the greatest abundance was also Insecta, with a total of 4816 specimens. Of these, 1634 belonged to the order Coleoptera, also the one with the largest number of identified morphospecies (109).

In total, 67 species were common in both ecosystems (Table 2), with 54 of these more abundant in the Azores than in the mainland coastal grasslands.

Table 2. Common species in the Azores and mainland grasslands.

Class	Order	Family	Species	Total Abundance Azores	Total Abundance Mainland
Arachnida	Araneae	Araneidae	*Mangora acalypha* (Walckenaer, 1802)	16	117
			Neoscona crucifera (Lucas, 1838)	8	1
			Zygiella x-notata (Clerck, 1757)	42	66
		Linyphiidae	*Oedothorax fuscus* (Blackwall, 1834)	11	4
			Prinerigone vagans (Audouin, 1826)	52	15
		Salticidae	*Chalcoscirtus infimus* (Simon, 1868)	73	13
			Macaroeris diligens (Blackwall, 1867)	16	6
			Salticus mutabilis Lucas, 1846	31	28
			Synageles venator (Lucas, 1836)	61	7
		Thomisidae	*Xysticus nubilus* Simon, 1875	90	97
Insecta	Coleoptera	Apionidae	*Aspidapion radiolus* (Marsham, 1802)	72	3
		Chrysomelidae	*Psylliodes marcida* (Illiger, 1807)	11	49
		Coccinellidae	*Rhyzobius litura* (Fabricius, 1787)	38	5
			Scymnus interruptus (Goeze, 1777)	129	2
			Scymnus suturalis Thunberg, 1795	2	1
		Curculionidae	*Mecinus pascuorum* (Gyllenhal, 1813)	286	18
		Nitidulidae	*Brassicogethes aeneus* (Fabricius, 1775)	54	8
		Phalacridae	*Stilbus testaceus* (Panzer, 1797)	14	10
		Staphylinidae	*Tachyporus chrysomelinus* (Linnaeus, 1758)	1	1
	Diptera	Agromyzidae	*Chromatomyia nigra* (Meigen, 1830)	10	1
		Calliphoridae	*Lucilia sericata* (Meigen, 1826)	16	3

		Chloropidae	*Thaumatomyia notata* (Meigen, 1830)	32	35
		Lonchopteridae	*Lonchoptera bifurcata* (Fallén, 1810)	67	69
		Muscidae	*Coenosia humilis* Meigen, 1826	65	8
			Musca osiris Wiedemann, 1830	70	6
			Stomoxys calcitrans (Linnaeus, 1758)	123	71
		Opomyzidae	*Geomyza tripunctata* (Fallén, 1823)	4	3
		Rhinophoridae	*Melanophora roralis* (Linnaeus, 1758)	82	15
		Syrphidae	*Eristalis tenax* (Linnaeus, 1758)	4	3
			Eupeodes corollae (Fabricius, 1794)	15	7
			Sphaerophoria scripta (Linnaeus, 1758)	34	12
		Tephritidae	*Dioxyna sororcula* (Wiedemann, 1830)	220	1
	Hemiptera	Anthocoridae	*Orius laevigatus laevigatus* (Fieber, 1860)	44	3
		Aphididae	*Aphis fabae* Scopoli, 1763	58	2
			Aphis nerii Boyer de Fonscolombe, 1841	42	2
			Melanaphis donacis (Passerini, 1862)	257	48
			Myzus persicae (Sulzer, 1776)	127	45
			Therioaphis trifolii (Monell, 1882)	19	10
		Aphrophoridae	*Philaenus spumarius* (Linnaeus, 1758)	285	241
		Cicadellidae	*Macrosteles sexnotatus* (Fallen, 1806)	301	14
		Delphacidae	*Megamelodes quadrimaculatus* (Signoret, 1865)	44	3
			Sogatella nigeriensis (Muir, 1920)	252	45
		Lygaeidae	*Kleidocerys ericae* (Horváth, 1909)	49	6
			Nysius ericae ericae (Blackwall, 1867)	14	15
		Miridae	*Taylorilygus apicalis* (Fieber, 1861)	433	26
		Nabidae	*Nabis capsiformis* Germar, 1838	180	3
		Pentatomidae	*Nezara viridula* (Linnaeus, 1758)	53	13
		Psyllidae	*Acizzia uncatoides* (Ferris & Klyver, 1932)	15	21
		Rhyparochromidae	*Beosus maritimus* (Scopoli, 1763)	1	9
		Saldidae	*Saldula palustris* (Douglas, 1874)	4	1
	Hymenoptera	Aphelinidae	*Encarsia formosa* Gahan, 1924	9	2
		Apidae	*Apis mellifera* Linnaeus, 1758	19	6
			Bombus terrestris (Linnaeus, 1758)	16	3
		Encyrtidae	*Pseudaphycus maculipennis* Mercet, 1923	13	2
		Eulophidae	*Baryscapus galactopus* (Ratzeburg, 1844)	69	86
			Diglyphus isaea (Walker, 1838)	6	4
		Formicidae	*Hypoponera eduardi* (Forel, 1894)	5	5
			Lasius grandis Forel, 1909	593	6
			Tetramorium caespitum (Linnaeus, 1758)	20	4
		Ichneumonidae	*Aritranis director* (Thumberg, 1822)	1	1
			Diplazon laetatorius (Fabricius, 1781)	32	4
		Mymaridae	*Litus cynipseus* Haliday, 1833	6	2
		Pteromalidae	*Pteromalus puparum* (Linnaeus, 1758)	8	7
	Lepidoptera	Pieridae	*Colias croceus* (Fourcroy, 1785)	4	1
	Orthoptera	Acrididae	*Locusta migratoria* (Linnaeus, 1758)	3	1
		Trigonidiidae	*Trigonidium cicindeloides* Rambur, 1838	69	3
	Psocodea	Caeciliusidae	*Valenzuela flavidus* (Stephens, 1836)	48	3
Total				**4848**	**1332**

We found a significant difference in the abundance of the common species between the Azores (72.36 ± 13.33) and mainland (19.88 ± 4.53) coastal grasslands (Paired T-test: t = 4.073; df = 66; $p \leq 0.001$) (Figure 2).

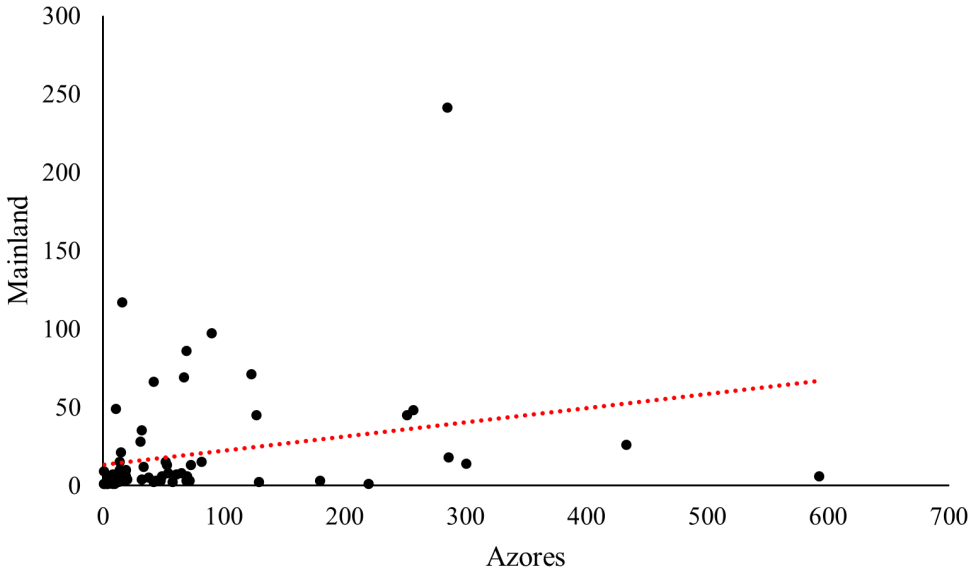

Figure 2. Abundance of common species between the Azores and Mainland coastal grasslands.

In relation to the completeness of the sampling, based on the Chao 1 and JackKnife 1 estimators (Figure 3), both ecosystems present a very high completeness for both estimators.

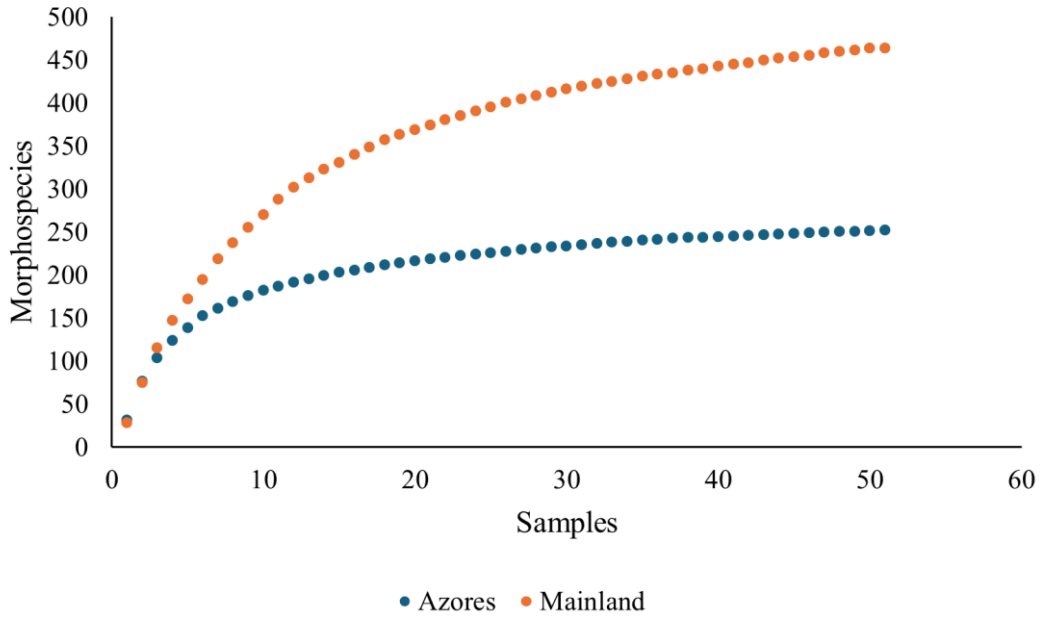

Figure 3. Species accumulation curves for species and morphospecies recorded on the Azores and mainland coastal grasslands based on 100 randomized curves.

However, Uniques (species found in just one sample) and Singletons (species represented by one individual) are superior to Duplicates (species found in two samples) and

Doubletons (species represented by two individuals) (Meredith et al., 2019) in both locations (Table 3). This means that additional species are expected if more effort is applied in future surveys.

Table 3. Diversity metrics for the Azores and Mainland: N—number of individuals; S—number of species.

	Azores	Mainland
N	7861	5654
S	210	392
Chao 1	245.06	464.18
Jackknife1	252.16	491.56
Completeness Chao1	0.86	0.84
Completeness Jackknife1	0.83	0.80
Singletons	34	82
Doubletons	15	45
Uniques	43	101
Duplicates	45	79

Concerning the total abundance of arthropods for communities of both locations, we found out that it was significantly higher in the Azores coastal grasslands (154.14 ± 18.34) than in the mainland (80.77 ± 11.33) (Kruskal–Wallis-test: K-W= 17.635; df = 1; $p \leq 0.001$) (Figure 4).

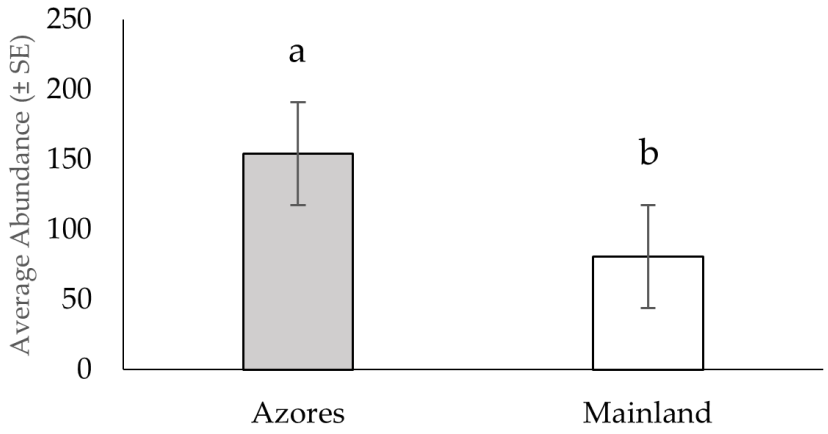

Figure 4. Abundance means for Azores and Mainland. Different letters indicate significant differences (Kruskal–Wallis-test; $p < 0.05$).

3.3.2. Diversity Metrics for the Arthropod Communities of the Azores and Mainland Coastal Grasslands (Hill Series)

When we analyse the differences between species richness (H_0) in coastal grasslands of the Azores (30.9 ± 1.96) and mainland (29.43 ± 2.05), we found no significant differences (Kruskal–Wallis-test: K-W = 0.322; df = 1; p = 0.571) (Figure 5). Concerning the Shannon–Wiener exponent (H_1) for the arthropod communities, also no significant

statistical differences were observed between Azores (16.36 ± 0.87) and mainland (18.75 ± 1.17) coastal grasslands (GLM test: Z = 2.345; df = 1; p = 0.128). No significant differences were found in the inverse Simpson's index (H_2) between coastal grasslands of arthropod communities of the Azores (10.71 ± 0.63) and mainland (12.86 ± 0.82) (GLM test: Z = 3.803; df = 1; p = 0.054). When the inverse of the Berger–Parker index (H_3) was analysed between the Azores (5.07 ± 0.29) and mainland (5.74 ± 0.34) coastal grasslands, no significant differences were observed either (GLM test: Z = 8.018; df = 1; p = 0.153).

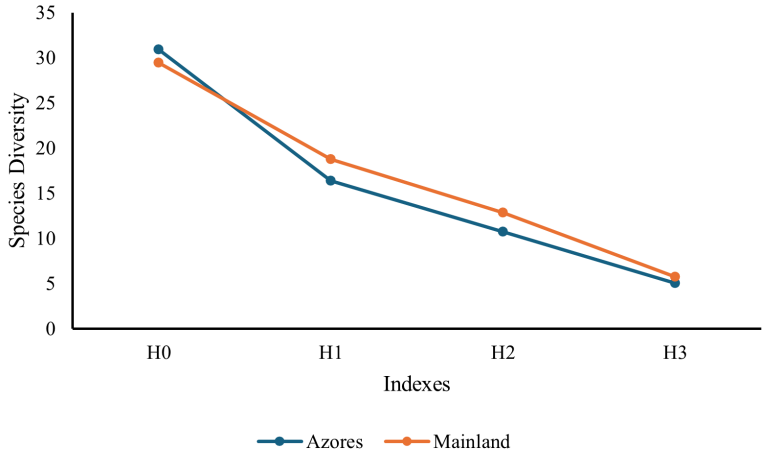

Figure 5. Differences between mean Specific Richness (H_0), mean Shannon–Wiener exponent (H_1), mean Simpson's inverse (H_2), and mean Berger–Parker's inverse (H_3) in the Azores and mainland coastal grasslands communities.

When the Evenness was analysed, significant differences were observed between the Azores (0.82 ± 0.010) and mainland (0.88 ± 0.011) coastal grasslands (Kruskal–Wallis test: K-W = 18.080; df = 1; $p \leq 0.001$) (Figure 6).

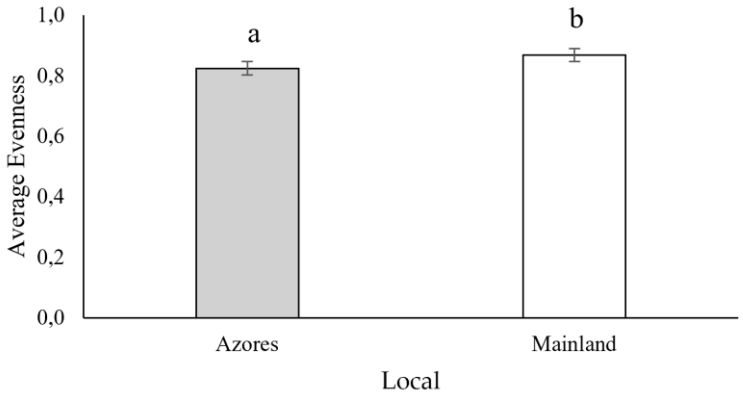

Figure 6. Evenness means for Azores and mainland coastal grasslands. Different letters indicate significant differences (Kruskal–Wallis test; $p < 0.05$).

When the Fisher's Alpha index in each region was analysed, we found significant differences between the Azores (13.98 ± 0.71) and mainland (24.07 ± 1.78) coastal grasslands (Kruskal–Wallis-test: K-W= 20.783; df = 1; $p \leq 0.001$) (Figure 7).

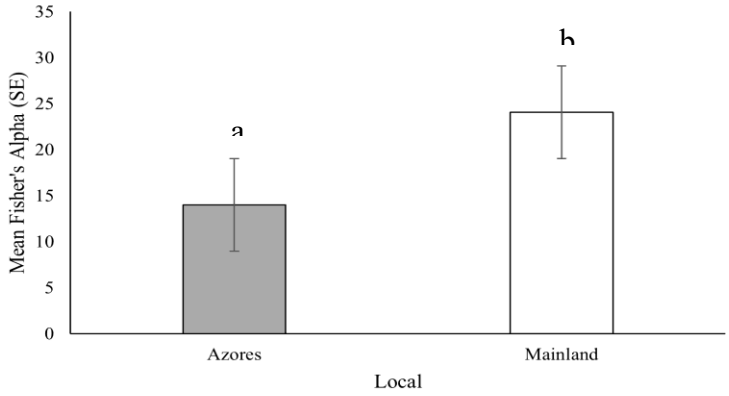

Figure 7. Fisher's Alpha means for Azores and mainland coastal grasslands. Different letters indicate significant differences (Kruskal–Wallis test; $p < 0.05$).

3.3.3. Dissimilarity Index (Jaccard)

Analysing the beta partition between sites in each region with the Jaccard index for the global beta diversity, we found significant dissimilarity between the Azores (0.897 ± 0.06) and mainland (0.923 ± 0.06) coastal grasslands (GLM test: Z = 38.615; df = 1; $p \leq 0.001$). We also observed differences for the Beta Replacement between Azores (0.41 ± 0.26) and mainland (0.36 ± 0.23 (GLM test: Z = 8.794; df = 1; p= 0.003)), and for Beta Richness in both locals: Azores (0.49 ± 0.24) and mainland (0.56 ± 0.22) (GLM test: Z = 21.587; df = 1; $p \leq 0.001$) (Figure 8).

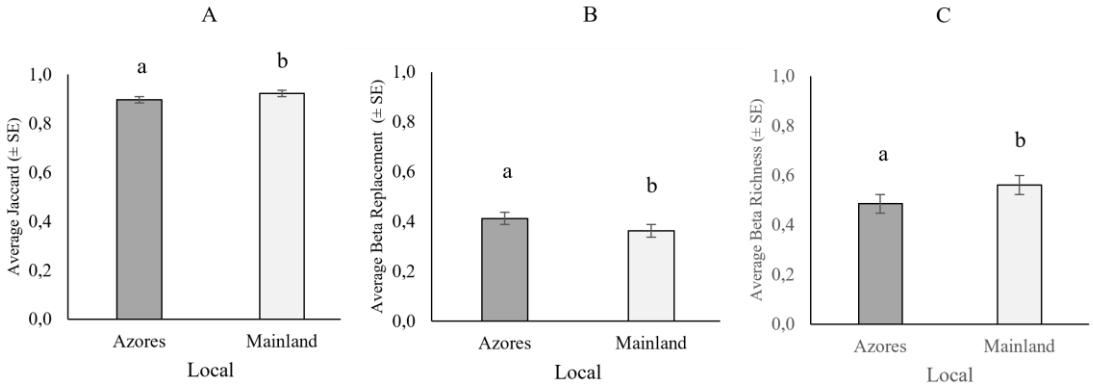

Figure 8. Comparison between Azores and mainland coastal grasslands of the between sites mean Jaccard dissimilarity index (**A**), mean Beta Replacement (**B**), and mean Beta Richness (**C**) indexes between sites. Different letters indicate significant differences (GLM test; $p < 0.05$).

3.4. Discussion

Our results indicate that there is a high difference in arthropod regional species richness (gamma diversity, sensu Magurran, 2004) between the Azores and Portugal mainland coastal grasslands. Indeed, the total number of species and morphospecies in the Azorean coastal grasslands is almost half the number of the collected species in the mainland's coastal grasslands (cf. Table 1). In certain taxonomic groups, this difference is particularly noteworthy; for instance, the proportion of beetles (Coleoptera) compared to other insect groups is particularly higher on the mainland than in the Azores. Other examples are the species richness of the Arachnida and Hemiptera Orders, with almost twice as many morphospecies in mainland coastal grasslands at the regional level. Nevertheless, other groups have very similar numbers of morphospecies collected in both areas (e.g., Diptera and Lepidoptera). This result partially confirms our first prediction that lower diversity would be expected on the island-modified coastal grassland when compared to the mainland grassland since insular systems tend to be species poor and disharmonic (Warren et al., 2015; Whittaker et al., 2017).

However, when we analyse the alpha diversity (local diversity), the results are mixed. On the one hand, there is no statistical difference in the diversity profiles measured by the Hill numbers (mean species richness, rarity, and dominance), but such differences were observed when computing Fisher's alpha (Figure 7). Higher Fisher's alpha values on the mainland indicate greater specific richness. The results also suggest that we are in the presence of a stable ecosystem. Those values also corroborate the evenness results (higher in the mainland coastal grasslands). Conversely, the low values in the Azores might suggest some environmental degradation, habitat loss, or other stressors that lead to ecosystem homogenization (e.g., similar resource availability, habitat types, or levels of competition), affecting biodiversity. Despite a large regional difference in species richness, both communities support similar effective species numbers at a local scale as measured by the Hill numbers. This is against our initial prediction in terms of diversity profiles in both grassland ecosystems. In a recent critique of the Hill numbers approach, Ricotta and Feoli (Ricotta and Feoli, 2024) suggested that in some situations in which there is a non-linear response of diversity measures, the conversion of classical diversity measures to Hill numbers is not useful. At this stage, we have no evidence that our two investigated communities differ in the rate of uncertainty associated with species

additions, and consequently, we assume that the patterns observed are similar in the two communities.

Nevertheless, despite this apparent similarity of local diversity profiles in both regions, when analysing the results obtained through the beta diversity partition using the Jaccard dissimilarity index, we observe significant differences in arthropod community structure between the mainland and the Azorean coastal grasslands. In the Azores, sample sites are more similar in species composition when compared to the mainland (Figure 7A). In both cases, arthropod species compositional differences are mostly due to beta richness differences between sites within each region (Figure 7B, C). The anthropogenic replacement of specialist native species by generalist non-native ones can lead to "biotic homogenization" (McKinney and Lockwood, 1999), which can cause a similarity in the composition of the various communities over time (Olden, 2006; Baeten et al., 2012). In the Azores, human action during the last five centuries has likely contributed to this process since most of the islands' coastal areas are visibly altered in relation to their original ecosystems (Cardoso et al., 2009). In contrast, some of the areas remain relatively little disturbed, which could further contribute to this differentiation.

We know that species spatial replacement refers to the well-known fact that species tend to replace each other along ecological gradients that are sufficiently long (i.e., turnover) (Whittaker, 1952; Legendre, 2014). Interestingly, species spatial replacement is higher across the Azorean sites than across mainland sites, and beta richness differences are higher on the mainland than in the Azores. One factor that may be responsible for these differences is the type of surrounding landscape. For example, the island of São Miguel is characterized by naturalized vegetation and semi-natural pastures with relatively high human activity, which increases habitat patchiness and might contribute to the observed higher turnover (Leo et al., 2024). At the same time, many adjacent areas to the coastal grasslands in the Azores are heavily used for agriculture and pasture, particularly in spring, which may further contribute to the observed differences across locations. On the mainland, on the other hand, there might be greater regional stability on niche availability, allowing plant species to maintain their populations (Soininen, 2010). Some work on islands demonstrates that turnover decreases when naturalized vegetation, together with existing native forests, forms a layer of continuous vegetation (Leo et al., 2024).

However, when we observed the gamma richness in both regions, we observed a significant difference. That difference could be explained by the geographic distance between some collection sites, such as, for example, Sines and Setúbal, whose distances between both locations exceeded a few tens of kilometres. This distance may also have contributed to the increase in the collection area, which became bigger than in the Azores. Despite being in similar conditions (maritime influence, type of substrate, altitude), environmental conditions (type of vegetation) and/or climatic conditions (temperature, wind, or exposure to the sun) may contribute to the difference in species fixed in some locations, generating the high total beta diversity (Figure 7A).

Concerning the abundance, we found a significant difference between the two coastal grassland systems, with a significantly higher abundance in the Azores compared to the mainland. Indeed, most of the commonly identified species are more abundant in the insular than in the mainland coastal grasslands. The species *Lasius grandis*, *Mecinus pascuorum,* or *Taylorilygus apicalis*, for example, showed a great difference in their abundance. Other Hemiptera, like *Nabis capsiformis*, *Kleidocerys ericae,* or *Sogatella nigeriensis,* also show a high difference in their abundance in the Azores coastal grasslands when compared to the mainland. This discrepancy could be explained by an apparent abundance compensation in some arthropods (Stadler et al., 2022). These results are in line with our initial prediction that some abundance compensation could occur in the Azores' coastal grasslands.

Lastly, when we analysed the species composition of both areas, we found that many arthropod species in the Azorean coastal grassland are common to those found in the mainland, which suggests that the Portuguese mainland may have been an important source of arthropods for the colonization of the islands, what was expected for both geographic (proximity) and political reasons. Although the islands' biodiversity depends on several well-known factors (e.g., migration and extinction rate, habitat diversity, and others (Walter, 2004; Warren et al., 2015; Portillo et al., 2019), anthropogenic factors, like commerce and tourism, could contribute to the species' introduction and are thus an important determinant of biodiversity. Indeed, exotic species are continuously introduced in the Azores and found mostly in coastal areas (Borges et al., 2013; Borges et al., 2022b).

3.5. Conclusions

This comparison of the coastal grasslands of the Azores and mainland Portugal allowed us to gain a deeper understanding of the composition and diversity profiles of the arthropod communities in both regions and the main differences between island and continental environments. As arthropod communities belong to numerous types of ecosystem services, the loss of many of these organisms could have devastating consequences. For example, as the Azores is an agricultural region, many organisms could play an important role in adjacent agricultural areas, whether through pollination, recycling of materials, or pest control (e.g., Sodhi and Ehrlich, 2010; Cock et al., 2012). Even on the mainland, in some coastal areas, this could also occur, considering that some of the areas are also located in rural regions. Thus, losses in arthropod communities could greatly affect the productivity of these agricultural regions. Furthermore, some of these organisms may also be closely linked to the host plants they share. Although situations may occur in which some organisms can functionally replace others in some of the ecological services provided, they may not be able to achieve the same performance as the former (Aslan et al., 2014; Heleno et al., 2022). Moreover, as these coastal communities host many exotic species, they could be the reservoirs of potential agricultural pests or invasive species.

Lastly, comparative studies are important tools for conservation and restoration programs, and thus, they should be continued and monitored over longer time scales (Patiño et al., 2017). This knowledge will allow us to develop better strategies to mitigate the anthropogenic changes suffered over the years in these areas, trying, if possible, to reverse their effects. Work carried out in the Azores and elsewhere shows that it is possible to restore part of some of these lost ecosystems, as well as some of the characteristics they had, through the repopulation of native species (Heleno et al., 2010; Luong et al., 2019; Sexton and Emery, 2020). More work must be done to understand which factors could influence the arthropod communities in the Azores and mainland coastal grasslands.

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Appendix A

Table A1. Location, coordinates, and verbatim locality of plots in São Miguel Island, Setúbal Peninsula, and Sines.

Location ID	Coordinates		Locality
AZ_01	37°44′48″ N	25°42′46″ W	Relva
AZ_02	37°51′40″ N	25°51′12″ W	Ferraria
AZ_03	37°53′57″ N	25°49′04″ W	Mosteiros
AZ_04	37°49′53″ N	25°39′30″ W	São Vicente
AZ_05	37°49′26″ N	25°36′15″ W	Calhetas
AZ_06	37°50′05″ N	25°30′40″ W	Ribeira Grande
AZ_07	37°50′31″ N	25°30′01″ W	Ribeirinha
AZ_08	37°46′43″ N	25°37′25″ W	Ponta Delgada
AZ_09	37°45′34″ N	25°39′31″ W	Ponta Delgada
AZ_10	37°45′00″ N	25°37′17″ W	Ponta Delgada
AZ_11	37°45′05″ N	25°34′58″ W	Lagoa
AZ_12	37°43′07″ N	25°27′04″ W	Vila Franca do Campo
AZ_13	37°47′37″ N	25°11′34″ W	Fajã do Araújo
ML_01	38°25′01″ N	9°12′43″ W	Cabo Espichel
ML_02	38°25′11″ N	9°12′42″ W	Cabo Espichel
ML_03	38°25′12″ N	9°12′04″ W	Cabo Espichel
ML_04	38°25′56″ N	9°10′25″ W	Azoia
ML_05	38°26′32″ N	9°08′42″ W	Azoia
ML_06	38°26′47″ N	9°09′17″ W	Azoia
ML_07	38°26′58″ N	9°12′01″ W	Meco
ML_08	38°27′16″ N	9°11′51″ W	Meco
ML_09	38°27′43″ N	9°11′34″ W	Meco
ML_10	37°50′59″ N	8°47′41″ W	Porto Covo
ML_11	37°51′42″ N	8°47′36″ W	Porto Covo
ML_12	37°53′27″ N	8°47′45″ W	Porto Covo
ML_13	37°53′57″ N	8°47′52″ W	Sines
ML_14	37°54′30″ N	8°47′58″ W	Sines
ML_15	37°54′57″ N	8°48′08″ W	Sines
ML_16	38°27′08″ N	9°11′27″ W	Meco
ML_17	38°26′13″ N	9°11′52″ W	Azoia
ML_18	38°26′38″ N	9°11′50″ W	Azoia

Table A2. List of morphospecies of arthropods identified for the Azores and Mainland. Legend: MS ID—morphospecies identification; E—endemic from the Azores; N—native non-endemic; I—introduced; NA—not attributed.

MS ID	Class	Order	Family	Azores	Mainland	Establishment Mean
73	Arachnida	Araneae	Araneidae	42	66	I
102	Arachnida	Araneae	Araneidae	16	117	NA
138	Arachnida	Araneae	Araneidae	8	1	I
279	Arachnida	Araneae	Araneidae	0	5	NA
282	Arachnida	Araneae	Araneidae	0	13	NA
284	Arachnida	Araneae	Araneidae	0	22	NA
306	Arachnida	Araneae	Araneidae	0	13	NA
307	Arachnida	Araneae	Araneidae	0	11	NA
308	Arachnida	Araneae	Araneidae	0	6	NA
316	Arachnida	Araneae	Araneidae	0	12	NA
318	Arachnida	Araneae	Araneidae	0	3	NA
347	Arachnida	Araneae	Araneidae	0	8	NA
447	Arachnida	Araneae	Araneidae	0	1	NA
477	Arachnida	Araneae	Araneidae	0	2	NA
519	Arachnida	Araneae	Araneidae	0	2	NA
530	Arachnida	Araneae	Araneidae	0	4	NA
722	Arachnida	Araneae	Araneidae	1	0	NA

723	Arachnida	Araneae	Araneidae	1	0	NA
725	Arachnida	Araneae	Araneidae	8	0	NA
728	Arachnida	Araneae	Araneidae	1	0	NA
374	Arachnida	Araneae	Cheiracanthiidae	0	6	NA
446	Arachnida	Araneae	Dictynidae	0	1	NA
349	Arachnida	Araneae	Gnaphosidae	0	5	NA
375	Arachnida	Araneae	Gnaphosidae	0	1	NA
605	Arachnida	Araneae	Gnaphosidae	0	1	NA
32	Arachnida	Araneae	Linyphiidae	25	0	I
33	Arachnida	Araneae	Linyphiidae	52	15	I
130	Arachnida	Araneae	Linyphiidae	18	0	N
131	Arachnida	Araneae	Linyphiidae	11	4	I
312	Arachnida	Araneae	Linyphiidae	0	13	NA
350	Arachnida	Araneae	Linyphiidae	0	29	NA
370	Arachnida	Araneae	Linyphiidae	0	41	NA
371	Arachnida	Araneae	Linyphiidae	0	7	NA
596	Arachnida	Araneae	Linyphiidae	1	0	NA
597	Arachnida	Araneae	Linyphiidae	0	16	NA
310	Arachnida	Araneae	Lycosidae	0	1	NA
407	Arachnida	Araneae	Lycosidae	0	2	NA
529	Arachnida	Araneae	Lycosidae	0	8	NA
317	Arachnida	Araneae	Philodromidae	0	12	NA
329	Arachnida	Araneae	Philodromidae	0	23	NA
445	Arachnida	Araneae	Philodromidae	0	9	NA
553	Arachnida	Araneae	Pisauridae	0	1	NA
18	Arachnida	Araneae	Salticidae	73	13	I
45	Arachnida	Araneae	Salticidae	31	28	I
85	Arachnida	Araneae	Salticidae	61	7	I
104	Arachnida	Araneae	Salticidae	16	6	N
313	Arachnida	Araneae	Salticidae	0	5	NA
551	Arachnida	Araneae	Salticidae	0	1	NA
552	Arachnida	Araneae	Salticidae	0	2	NA
563	Arachnida	Araneae	Salticidae	3	0	NA
724	Arachnida	Araneae	Salticidae	1	0	NA
729	Arachnida	Araneae	Salticidae	0	1	NA
265	Arachnida	Araneae	Tetragnathidae	0	52	NA
437	Arachnida	Araneae	Tetragnathidae	52	0	NA
726	Arachnida	Araneae	Tetragnathidae	0	3	NA
278	Arachnida	Araneae	Theridiidae	0	3	NA
311	Arachnida	Araneae	Theridiidae	0	18	NA
368	Arachnida	Araneae	Theridiidae	0	11	NA
518	Arachnida	Araneae	Theridiidae	0	3	NA
606	Arachnida	Araneae	Theridiidae	0	1	NA
17	Arachnida	Araneae	Thomisidae	90	97	I
315	Arachnida	Araneae	Thomisidae	0	32	NA
373	Arachnida	Araneae	Thomisidae	0	13	NA
440	Arachnida	Araneae	Thomisidae	0	59	NA
727	Arachnida	Araneae	Thomisidae	4	0	NA
76	Arachnida	Opiliones	Leiobunidae	32	0	N
548	Arachnida	Opiliones	Phalangiidae	0	2	NA
143	Diplopoda	Julida	Julidae	1	0	I
61	Insecta	Coleoptera	Apionidae	72	3	I
478	Insecta	Coleoptera	Cantharidae	0	1	NA
488	Insecta	Coleoptera	Cantharidae	0	6	NA
354	Insecta	Coleoptera	Carabidae	0	65	NA
539	Insecta	Coleoptera	Carabidae	0	2	NA
542	Insecta	Coleoptera	Carabidae	0	1	NA
591	Insecta	Coleoptera	Carabidae	0	2	NA
421	Insecta	Coleoptera	Cerambycidae	0	49	NA
429	Insecta	Coleoptera	Cerambycidae	0	5	NA
23	Insecta	Coleoptera	Chrysomelidae	11	49	N

71	Insecta	Coleoptera	Chrysomelidae	12	0	I
106	Insecta	Coleoptera	Chrysomelidae	30	0	I
208	Insecta	Coleoptera	Chrysomelidae	2	0	I
215	Insecta	Coleoptera	Chrysomelidae	8	0	N
239	Insecta	Coleoptera	Chrysomelidae	20	0	I
280	Insecta	Coleoptera	Chrysomelidae	0	20	NA
289	Insecta	Coleoptera	Chrysomelidae	0	15	NA
327	Insecta	Coleoptera	Chrysomelidae	0	32	NA
366	Insecta	Coleoptera	Chrysomelidae	0	7	NA
367	Insecta	Coleoptera	Chrysomelidae	0	72	NA
381	Insecta	Coleoptera	Chrysomelidae	0	24	NA
401	Insecta	Coleoptera	Chrysomelidae	0	16	NA
417	Insecta	Coleoptera	Chrysomelidae	0	18	NA
435	Insecta	Coleoptera	Chrysomelidae	0	10	NA
450	Insecta	Coleoptera	Chrysomelidae	0	25	NA
455	Insecta	Coleoptera	Chrysomelidae	0	51	NA
459	Insecta	Coleoptera	Chrysomelidae	0	15	NA
462	Insecta	Coleoptera	Chrysomelidae	0	1	NA
469	Insecta	Coleoptera	Chrysomelidae	0	3	NA
476	Insecta	Coleoptera	Chrysomelidae	0	5	NA
480	Insecta	Coleoptera	Chrysomelidae	0	4	NA
491	Insecta	Coleoptera	Chrysomelidae	0	44	NA
525	Insecta	Coleoptera	Chrysomelidae	0	62	NA
544	Insecta	Coleoptera	Chrysomelidae	0	1	NA
545	Insecta	Coleoptera	Chrysomelidae	0	2	NA
547	Insecta	Coleoptera	Chrysomelidae	0	2	NA
574	Insecta	Coleoptera	Chrysomelidae	0	1	NA
585	Insecta	Coleoptera	Chrysomelidae	0	1	NA
587	Insecta	Coleoptera	Chrysomelidae	0	2	NA
592	Insecta	Coleoptera	Chrysomelidae	0	1	NA
598	Insecta	Coleoptera	Chrysomelidae	0	28	NA
600	Insecta	Coleoptera	Chrysomelidae	0	13	NA
602	Insecta	Coleoptera	Chrysomelidae	0	9	NA
604	Insecta	Coleoptera	Chrysomelidae	0	14	NA
40	Insecta	Coleoptera	Coccinellidae	37	0	I
111	Insecta	Coleoptera	Coccinellidae	129	2	I
135	Insecta	Coleoptera	Coccinellidae	38	5	N
154	Insecta	Coleoptera	Coccinellidae	22	0	I
155	Insecta	Coleoptera	Coccinellidae	2	0	N
156	Insecta	Coleoptera	Coccinellidae	2	1	I
231	Insecta	Coleoptera	Coccinellidae	0	24	NA
233	Insecta	Coleoptera	Coccinellidae	1	0	NA
361	Insecta	Coleoptera	Coccinellidae	0	3	NA
426	Insecta	Coleoptera	Coccinellidae	0	16	NA
466	Insecta	Coleoptera	Coccinellidae	0	5	NA
573	Insecta	Coleoptera	Coccinellidae	0	1	NA
603	Insecta	Coleoptera	Coccinellidae	0	11	NA
67	Insecta	Coleoptera	Cryptophagidae	1	0	I
599	Insecta	Coleoptera	Cryptophagidae	0	8	NA
81	Insecta	Coleoptera	Curculionidae	10	0	I
101	Insecta	Coleoptera	Curculionidae	6	0	I
136	Insecta	Coleoptera	Curculionidae	286	18	I
243	Insecta	Coleoptera	Curculionidae	0	2	I
274	Insecta	Coleoptera	Curculionidae	0	4	NA
277	Insecta	Coleoptera	Curculionidae	0	5	NA
299	Insecta	Coleoptera	Curculionidae	0	9	NA
321	Insecta	Coleoptera	Curculionidae	0	15	NA
332	Insecta	Coleoptera	Curculionidae	0	5	NA
357	Insecta	Coleoptera	Curculionidae	0	6	NA
358	Insecta	Coleoptera	Curculionidae	0	6	NA
359	Insecta	Coleoptera	Curculionidae	0	5	NA

360	Insecta	Coleoptera	Curculionidae	0	12	NA
427	Insecta	Coleoptera	Curculionidae	0	2	NA
448	Insecta	Coleoptera	Curculionidae	0	2	NA
473	Insecta	Coleoptera	Curculionidae	0	3	NA
486	Insecta	Coleoptera	Curculionidae	0	1	NA
508	Insecta	Coleoptera	Curculionidae	0	11	NA
579	Insecta	Coleoptera	Curculionidae	0	1	NA
580	Insecta	Coleoptera	Curculionidae	0	1	NA
581	Insecta	Coleoptera	Curculionidae	0	1	NA
594	Insecta	Coleoptera	Curculionidae	0	1	NA
336	Insecta	Coleoptera	Dasytidae	0	202	NA
495	Insecta	Coleoptera	Dermestidae	0	107	NA
496	Insecta	Coleoptera	Dryophthoridae	0	1	NA
234	Insecta	Coleoptera	Elateridae	2	0	E
353	Insecta	Coleoptera	Elateridae	0	4	NA
414	Insecta	Coleoptera	Elateridae	0	1	NA
556	Insecta	Coleoptera	Elateridae	0	6	NA
576	Insecta	Coleoptera	Elateridae	0	2	NA
339	Insecta	Coleoptera	Malachiidae	0	21	NA
419	Insecta	Coleoptera	Malachiidae	0	3	NA
513	Insecta	Coleoptera	Malachiidae	0	42	NA
422	Insecta	Coleoptera	Melyridae	0	14	NA
460	Insecta	Coleoptera	Melyridae	0	25	NA
528	Insecta	Coleoptera	Melyridae	0	4	NA
451	Insecta	Coleoptera	Mordellidae	0	130	NA
52	Insecta	Coleoptera	Nitidulidae	54	8	I
75	Insecta	Coleoptera	Nitidulidae	26	0	I
192	Insecta	Coleoptera	Nitidulidae	10	0	NA
301	Insecta	Coleoptera	Nitidulidae	0	47	NA
356	Insecta	Coleoptera	Nitidulidae	0	9	NA
402	Insecta	Coleoptera	Nitidulidae	0	4	NA
601	Insecta	Coleoptera	Nitidulidae	0	2	NA
720	Insecta	Coleoptera	Nitidulidae	0	1	NA
461	Insecta	Coleoptera	Oedemeridae	0	20	NA
489	Insecta	Coleoptera	Oedemeridae	0	7	NA
41	Insecta	Coleoptera	Phalacridae	14	10	N
340	Insecta	Coleoptera	Phalacridae	0	10	NA
501	Insecta	Coleoptera	Phalacridae	0	1	NA
566	Insecta	Coleoptera	Phalacridae	0	2	NA
567	Insecta	Coleoptera	Phalacridae	0	8	NA
535	Insecta	Coleoptera	Rutelidae	0	4	NA
540	Insecta	Coleoptera	Rutelidae	0	7	NA
394	Insecta	Coleoptera	Scarabaeidae	0	17	NA
22	Insecta	Coleoptera	Staphylinidae	1	0	NA
115	Insecta	Coleoptera	Staphylinidae	1	1	NA
134	Insecta	Coleoptera	Staphylinidae	8	0	I
213	Insecta	Coleoptera	Staphylinidae	0	1	NA
291	Insecta	Coleoptera	Staphylinidae	0	1	NA
351	Insecta	Coleoptera	Staphylinidae	0	1	NA
352	Insecta	Coleoptera	Staphylinidae	0	1	NA
543	Insecta	Coleoptera	Staphylinidae	0	3	NA
487	Insecta	Coleoptera	Tenebrionidae	0	1	NA
507	Insecta	Coleoptera	Tenebrionidae	0	24	NA
520	Insecta	Coleoptera	Tenebrionidae	0	13	NA
593	Insecta	Coleoptera	Tenebrionidae	0	2	NA
26	Insecta	Diptera	Agromyzidae	64	0	NA
126	Insecta	Diptera	Agromyzidae	10	1	NA
616	Insecta	Diptera	Agromyzidae	0	26	NA
53	Insecta	Diptera	Calliphoridae	16	3	NA
194	Insecta	Diptera	Calliphoridae	1	0	NA
560	Insecta	Diptera	Calliphoridae	0	1	NA

453	Insecta	Diptera	Carnidae	0	7	NA
7	Insecta	Diptera	Cecidomyiidae	44	0	NA
624	Insecta	Diptera	Cecidomyiidae	0	20	NA
8	Insecta	Diptera	Chloropidae	32	35	NA
150	Insecta	Diptera	Chloropidae	4	0	NA
15	Insecta	Diptera	Drosophilidae	102	0	NA
27	Insecta	Diptera	Drosophilidae	79	0	NA
615	Insecta	Diptera	Drosophilidae	0	6	NA
617	Insecta	Diptera	Drosophilidae	0	4	NA
43	Insecta	Diptera	Hybotidae	5	0	NA
159	Insecta	Diptera	Hybotidae	1	0	NA
619	Insecta	Diptera	Hybotidae	0	7	NA
622	Insecta	Diptera	Hybotidae	0	2	NA
34	Insecta	Diptera	Lauxaniidae	7	0	NA
618	Insecta	Diptera	Lauxaniidae	0	7	NA
46	Insecta	Diptera	Lonchopteridae	67	69	NA
3	Insecta	Diptera	Muscidae	123	71	NA
14	Insecta	Diptera	Muscidae	69	0	NA
30	Insecta	Diptera	Muscidae	65	8	NA
142	Insecta	Diptera	Muscidae	70	6	NA
151	Insecta	Diptera	Muscidae	4	0	NA
166	Insecta	Diptera	Muscidae	5	0	NA
177	Insecta	Diptera	Muscidae	4	0	NA
214	Insecta	Diptera	Muscidae	1	0	NA
225	Insecta	Diptera	Muscidae	95	0	NA
230	Insecta	Diptera	Muscidae	1	0	NA
263	Insecta	Diptera	Muscidae	0	13	NA
614	Insecta	Diptera	Muscidae	0	57	NA
621	Insecta	Diptera	Muscidae	0	1	NA
623	Insecta	Diptera	Muscidae	0	112	NA
625	Insecta	Diptera	Muscidae	0	1	NA
626	Insecta	Diptera	Muscidae	0	7	NA
721	Insecta	Diptera	Muscidae	0	4	NA
127	Insecta	Diptera	Opomyzidae	4	3	NA
28	Insecta	Diptera	Rhinophoridae	82	15	NA
2	Insecta	Diptera	Scathophagidae	52	0	NA
181	Insecta	Diptera	Sciaridae	23	0	NA
627	Insecta	Diptera	Sciaridae	0	1	NA
10	Insecta	Diptera	Sepsidae	352	0	NA
144	Insecta	Diptera	Sepsidae	82	0	NA
161	Insecta	Diptera	Sepsidae	59	0	NA
193	Insecta	Diptera	Sepsidae	6	0	NA
613	Insecta	Diptera	Sepsidae	0	2	NA
575	Insecta	Diptera	Stratiomyidae	0	7	NA
4	Insecta	Diptera	Syrphidae	15	7	NA
5	Insecta	Diptera	Syrphidae	34	12	NA
56	Insecta	Diptera	Syrphidae	4	3	NA
205	Insecta	Diptera	Syrphidae	2	0	NA
254	Insecta	Diptera	Syrphidae	1	0	NA
258	Insecta	Diptera	Syrphidae	1	0	NA
288	Insecta	Diptera	Syrphidae	3	0	NA
294	Insecta	Diptera	Syrphidae	0	2	NA
383	Insecta	Diptera	Syrphidae	0	9	NA
550	Insecta	Diptera	Syrphidae	0	2	NA
628	Insecta	Diptera	Syrphidae	0	15	NA
629	Insecta	Diptera	Syrphidae	0	1	NA
55	Insecta	Diptera	Tephritidae	77	0	NA
210	Insecta	Diptera	Tephritidae	220	1	NA
335	Insecta	Diptera	Tephritidae	0	4	NA
386	Insecta	Diptera	Tephritidae	0	2	NA
514	Insecta	Diptera	Tephritidae	0	2	NA

620	Insecta	Diptera	Tephritidae	0	31	NA
29	Insecta	Diptera	Tipulidae	2	0	NA
204	Insecta	Diptera	Tipulidae	1	0	NA
490	Insecta	Diptera	Ulidiidae	0	1	NA
433	Insecta	Hemiptera	Alydidae	0	6	NA
125	Insecta	Hemiptera	Anthocoridae	44	3	I
140	Insecta	Hemiptera	Anthocoridae	16	0	NA
203	Insecta	Hemiptera	Anthocoridae	2	0	NA
293	Insecta	Hemiptera	Anthocoridae	0	5	NA
314	Insecta	Hemiptera	Anthocoridae	1	0	NA
380	Insecta	Hemiptera	Anthocoridae	0	4	NA
410	Insecta	Hemiptera	Anthocoridae	0	1	NA
523	Insecta	Hemiptera	Anthocoridae	0	1	NA
6	Insecta	Hemiptera	Aphididae	257	48	N
16	Insecta	Hemiptera	Aphididae	42	2	NA
24	Insecta	Hemiptera	Aphididae	58	2	NA
88	Insecta	Hemiptera	Aphididae	127	45	N
89	Insecta	Hemiptera	Aphididae	31	0	N
108	Insecta	Hemiptera	Aphididae	13	0	N
112	Insecta	Hemiptera	Aphididae	1	0	N
124	Insecta	Hemiptera	Aphididae	19	10	N
376	Insecta	Hemiptera	Aphididae	13	0	NA
474	Insecta	Hemiptera	Aphididae	0	1	NA
50	Insecta	Hemiptera	Aphrophoridae	285	241	I
319	Insecta	Hemiptera	Aphrophoridae	0	2	NA
387	Insecta	Hemiptera	Aphrophoridae	0	3	NA
467	Insecta	Hemiptera	Aphrophoridae	0	1	NA
465	Insecta	Hemiptera	Blissidae	0	43	NA
31	Insecta	Hemiptera	Cicadellidae	185	0	NA
113	Insecta	Hemiptera	Cicadellidae	57	0	I
133	Insecta	Hemiptera	Cicadellidae	301	14	NA
189	Insecta	Hemiptera	Cicadellidae	35	0	N
236	Insecta	Hemiptera	Cicadellidae	8	0	NA
244	Insecta	Hemiptera	Cicadellidae	1	0	I
245	Insecta	Hemiptera	Cicadellidae	17	0	N
253	Insecta	Hemiptera	Cicadellidae	1	0	N
257	Insecta	Hemiptera	Cicadellidae	3	0	NA
342	Insecta	Hemiptera	Cicadellidae	1	0	N
369	Insecta	Hemiptera	Cicadellidae	0	1	NA
378	Insecta	Hemiptera	Cicadellidae	0	25	NA
393	Insecta	Hemiptera	Cicadellidae	0	4	NA
470	Insecta	Hemiptera	Cicadellidae	0	3	NA
483	Insecta	Hemiptera	Cicadellidae	0	1	NA
522	Insecta	Hemiptera	Cicadellidae	0	3	NA
48	Insecta	Hemiptera	Cixiidae	0	13	NA
272	Insecta	Hemiptera	Cixiidae	0	14	NA
409	Insecta	Hemiptera	Cixiidae	0	8	NA
423	Insecta	Hemiptera	Cixiidae	0	15	NA
418	Insecta	Hemiptera	Coreidae	0	13	NA
479	Insecta	Hemiptera	Coreidae	0	4	NA
412	Insecta	Hemiptera	Cydnidae	0	2	NA
12	Insecta	Hemiptera	Delphacidae	243	0	N
49	Insecta	Hemiptera	Delphacidae	252	45	N
77	Insecta	Hemiptera	Delphacidae	44	3	N
271	Insecta	Hemiptera	Delphacidae	0	5	NA
331	Insecta	Hemiptera	Delphacidae	0	5	NA
428	Insecta	Hemiptera	Delphacidae	0	3	NA
557	Insecta	Hemiptera	Delphacidae	0	20	NA
153	Insecta	Hemiptera	Flatidae	3	0	N
328	Insecta	Hemiptera	Flatidae	0	1	NA
114	Insecta	Hemiptera	Liviidae	1	0	E

20	Insecta	Hemiptera	Lygaeidae	49	6	N
51	Insecta	Hemiptera	Lygaeidae	40	0	NA
141	Insecta	Hemiptera	Lygaeidae	14	15	N
338	Insecta	Hemiptera	Lygaeidae	0	19	NA
341	Insecta	Hemiptera	Lygaeidae	0	12	NA
355	Insecta	Hemiptera	Lygaeidae	0	4	NA
87	Insecta	Hemiptera	Miridae	433	26	N
195	Insecta	Hemiptera	Miridae	3	0	N
211	Insecta	Hemiptera	Miridae	74	0	NA
413	Insecta	Hemiptera	Miridae	0	1	NA
438	Insecta	Hemiptera	Miridae	1	0	NA
569	Insecta	Hemiptera	Miridae	0	8	NA
571	Insecta	Hemiptera	Miridae	0	1	NA
58	Insecta	Hemiptera	Nabidae	27	0	N
72	Insecta	Hemiptera	Nabidae	180	3	N
377	Insecta	Hemiptera	Nabidae	0	100	NA
439	Insecta	Hemiptera	Oxycarenidae	1	0	I
117	Insecta	Hemiptera	Pentatomidae	53	13	I
408	Insecta	Hemiptera	Pentatomidae	0	1	NA
430	Insecta	Hemiptera	Pentatomidae	0	8	NA
463	Insecta	Hemiptera	Pentatomidae	0	9	NA
500	Insecta	Hemiptera	Pentatomidae	0	12	NA
68	Insecta	Hemiptera	Psyllidae	15	21	I
546	Insecta	Hemiptera	Psyllidae	0	2	NA
379	Insecta	Hemiptera	Reduviidae	0	2	NA
396	Insecta	Hemiptera	Reduviidae	0	6	NA
406	Insecta	Hemiptera	Reduviidae	0	1	NA
524	Insecta	Hemiptera	Reduviidae	0	2	NA
531	Insecta	Hemiptera	Reduviidae	0	1	NA
554	Insecta	Hemiptera	Reduviidae	0	1	NA
443	Insecta	Hemiptera	Rhopalidae	0	1	NA
504	Insecta	Hemiptera	Rhopalidae	0	10	NA
532	Insecta	Hemiptera	Rhopalidae	0	1	NA
198	Insecta	Hemiptera	Rhyparochromidae	2	0	N
218	Insecta	Hemiptera	Rhyparochromidae	1	9	N
588	Insecta	Hemiptera	Rhyparochromidae	0	1	NA
19	Insecta	Hemiptera	Saldidae	4	1	N
589	Insecta	Hemiptera	Saldidae	0	1	NA
475	Insecta	Hemiptera	Scutelleridae	0	22	NA
568	Insecta	Hemiptera	Tettigometridae	0	1	NA
411	Insecta	Hemiptera	Tingidae	0	4	NA
492	Insecta	Hemiptera	Tingidae	0	10	NA
9	Insecta	Hymenoptera	Aphelinidae	96	0	NA
93	Insecta	Hymenoptera	Aphelinidae	10	0	NA
128	Insecta	Hymenoptera	Aphelinidae	9	2	NA
561	Insecta	Hymenoptera	Aphelinidae	0	13	NA
661	Insecta	Hymenoptera	Aphelinidae	0	587	NA
35	Insecta	Hymenoptera	Apidae	19	6	I
36	Insecta	Hymenoptera	Apidae	16	3	NA
345	Insecta	Hymenoptera	Apidae	0	11	NA
390	Insecta	Hymenoptera	Apidae	0	7	NA
399	Insecta	Hymenoptera	Apidae	0	3	NA
549	Insecta	Hymenoptera	Apidae	0	2	NA
559	Insecta	Hymenoptera	Apidae	0	1	NA
572	Insecta	Hymenoptera	Apidae	0	3	NA
578	Insecta	Hymenoptera	Apidae	0	1	NA
13	Insecta	Hymenoptera	Braconidae	16	0	NA
25	Insecta	Hymenoptera	Braconidae	55	0	NA
109	Insecta	Hymenoptera	Braconidae	3	0	NA
207	Insecta	Hymenoptera	Braconidae	3	0	NA
251	Insecta	Hymenoptera	Braconidae	0	2	NA

276	Insecta	Hymenoptera	Braconidae	0	6	NA
645	Insecta	Hymenoptera	Braconidae	0	12	NA
653	Insecta	Hymenoptera	Braconidae	0	1	NA
660	Insecta	Hymenoptera	Braconidae	1	0	NA
662	Insecta	Hymenoptera	Braconidae	0	6	NA
663	Insecta	Hymenoptera	Braconidae	0	22	NA
485	Insecta	Hymenoptera	Chalcididae	0	3	NA
389	Insecta	Hymenoptera	Colletidae	0	8	NA
502	Insecta	Hymenoptera	Colletidae	3	0	NA
674	Insecta	Hymenoptera	Colletidae	0	3	NA
47	Insecta	Hymenoptera	Encyrtidae	5	0	NA
91	Insecta	Hymenoptera	Encyrtidae	13	2	NA
121	Insecta	Hymenoptera	Encyrtidae	3	0	NA
123	Insecta	Hymenoptera	Encyrtidae	3	0	NA
646	Insecta	Hymenoptera	Encyrtidae	0	4	NA
665	Insecta	Hymenoptera	Encyrtidae	0	4	NA
100	Insecta	Hymenoptera	Eulophidae	6	4	NA
122	Insecta	Hymenoptera	Eulophidae	69	86	NA
536	Insecta	Hymenoptera	Eumenidae	0	3	NA
42	Insecta	Hymenoptera	Figitidae	7	0	NA
97	Insecta	Hymenoptera	Figitidae	2	0	NA
157	Insecta	Hymenoptera	Figitidae	7	0	NA
343	Insecta	Hymenoptera	Figitidae	0	2	NA
595	Insecta	Hymenoptera	Figitidae	0	2	NA
643	Insecta	Hymenoptera	Figitidae	0	1	NA
644	Insecta	Hymenoptera	Figitidae	0	1	NA
648	Insecta	Hymenoptera	Figitidae	0	3	NA
21	Insecta	Hymenoptera	Formicidae	593	6	N
44	Insecta	Hymenoptera	Formicidae	5	5	N
137	Insecta	Hymenoptera	Formicidae	20	4	N
139	Insecta	Hymenoptera	Formicidae	30	0	N
219	Insecta	Hymenoptera	Formicidae	12	0	I
220	Insecta	Hymenoptera	Formicidae	2	0	N
241	Insecta	Hymenoptera	Formicidae	9	0	N
262	Insecta	Hymenoptera	Formicidae	0	177	NA
268	Insecta	Hymenoptera	Formicidae	0	50	NA
292	Insecta	Hymenoptera	Formicidae	0	18	NA
320	Insecta	Hymenoptera	Formicidae	0	13	NA
322	Insecta	Hymenoptera	Formicidae	0	20	NA
425	Insecta	Hymenoptera	Formicidae	0	3	NA
436	Insecta	Hymenoptera	Formicidae	0	1	NA
449	Insecta	Hymenoptera	Formicidae	0	9	NA
464	Insecta	Hymenoptera	Formicidae	0	8	NA
482	Insecta	Hymenoptera	Formicidae	0	5	NA
654	Insecta	Hymenoptera	Formicidae	0	2	NA
657	Insecta	Hymenoptera	Formicidae	0	5	NA
669	Insecta	Hymenoptera	Formicidae	0	6	NA
672	Insecta	Hymenoptera	Formicidae	0	4	NA
37	Insecta	Hymenoptera	Halictidae	113	0	NA
145	Insecta	Hymenoptera	Halictidae	30	0	NA
190	Insecta	Hymenoptera	Halictidae	5	0	NA
362	Insecta	Hymenoptera	Halictidae	0	11	NA
388	Insecta	Hymenoptera	Halictidae	0	1	NA
441	Insecta	Hymenoptera	Halictidae	0	9	NA
456	Insecta	Hymenoptera	Halictidae	0	6	NA
512	Insecta	Hymenoptera	Halictidae	0	2	NA
652	Insecta	Hymenoptera	Halictidae	0	2	NA
664	Insecta	Hymenoptera	Halictidae	0	19	NA
670	Insecta	Hymenoptera	Halictidae	0	15	NA
38	Insecta	Hymenoptera	Ichneumonidae	32	4	NA
148	Insecta	Hymenoptera	Ichneumonidae	20	0	NA

160	Insecta	Hymenoptera	Ichneumonidae	2	0	NA
175	Insecta	Hymenoptera	Ichneumonidae	8	0	NA
209	Insecta	Hymenoptera	Ichneumonidae	1	1	NA
235	Insecta	Hymenoptera	Ichneumonidae	2	0	NA
237	Insecta	Hymenoptera	Ichneumonidae	7	0	NA
249	Insecta	Hymenoptera	Ichneumonidae	1	0	NA
296	Insecta	Hymenoptera	Ichneumonidae	0	5	NA
326	Insecta	Hymenoptera	Ichneumonidae	0	3	NA
337	Insecta	Hymenoptera	Ichneumonidae	0	2	NA
363	Insecta	Hymenoptera	Ichneumonidae	0	3	NA
420	Insecta	Hymenoptera	Ichneumonidae	0	4	NA
472	Insecta	Hymenoptera	Ichneumonidae	0	3	NA
484	Insecta	Hymenoptera	Ichneumonidae	0	1	NA
647	Insecta	Hymenoptera	Ichneumonidae	0	3	NA
649	Insecta	Hymenoptera	Ichneumonidae	0	1	NA
650	Insecta	Hymenoptera	Ichneumonidae	0	3	NA
655	Insecta	Hymenoptera	Ichneumonidae	0	9	NA
656	Insecta	Hymenoptera	Ichneumonidae	0	1	NA
658	Insecta	Hymenoptera	Ichneumonidae	0	2	NA
442	Insecta	Hymenoptera	Megachilidae	1	0	NA
673	Insecta	Hymenoptera	Megachilidae	0	2	NA
92	Insecta	Hymenoptera	Mymaridae	6	2	NA
252	Insecta	Hymenoptera	Mymaridae	6	0	NA
659	Insecta	Hymenoptera	Mymaridae	0	9	NA
516	Insecta	Hymenoptera	Pelecinidae	0	2	NA
65	Insecta	Hymenoptera	Pteromalidae	13	0	NA
96	Insecta	Hymenoptera	Pteromalidae	24	0	NA
212	Insecta	Hymenoptera	Pteromalidae	8	7	NA
666	Insecta	Hymenoptera	Pteromalidae	0	7	NA
667	Insecta	Hymenoptera	Pteromalidae	0	13	NA
199	Insecta	Hymenoptera	Sphecidae	4	0	NA
671	Insecta	Hymenoptera	Sphecidae	0	4	NA
11	Insecta	Hymenoptera	Tenthredinidae	12	0	NA
39	Insecta	Hymenoptera	Tenthredinidae	4	0	NA
165	Insecta	Hymenoptera	Tenthredinidae	0	5	NA
176	Insecta	Hymenoptera	Tenthredinidae	9	0	NA
642	Insecta	Hymenoptera	Tenthredinidae	0	1	NA
651	Insecta	Hymenoptera	Tenthredinidae	0	32	NA
98	Insecta	Hymenoptera	Trichogrammatidae	10	0	NA
668	Insecta	Hymenoptera	Trichogrammatidae	0	1	NA
191	Insecta	Hymenoptera	Vespidae	1	0	NA
333	Insecta	Hymenoptera	Vespidae	0	11	NA
404	Insecta	Hymenoptera	Vespidae	0	1	NA
458	Insecta	Hymenoptera	Vespidae	1	0	NA
184	Insecta	Lepidoptera	Choreutidae	20	0	N
692	Insecta	Lepidoptera	Choreutidae	0	8	NA
129	Insecta	Lepidoptera	Crambidae	19	0	NA
687	Insecta	Lepidoptera	Crambidae	0	9	NA
74	Insecta	Lepidoptera	Geometridae	8	0	NA
107	Insecta	Lepidoptera	Geometridae	2	0	E
186	Insecta	Lepidoptera	Geometridae	3	0	NA
686	Insecta	Lepidoptera	Geometridae	0	4	NA
689	Insecta	Lepidoptera	Geometridae	0	1	NA
232	Insecta	Lepidoptera	Lycaenidae	3	0	NA
690	Insecta	Lepidoptera	Lycaenidae	0	3	NA
1	Insecta	Lepidoptera	Noctuidae	24	0	NA
183	Insecta	Lepidoptera	Noctuidae	11	0	NA
185	Insecta	Lepidoptera	Noctuidae	2	0	NA
509	Insecta	Lepidoptera	Noctuidae	0	7	NA
685	Insecta	Lepidoptera	Noctuidae	0	4	NA
688	Insecta	Lepidoptera	Noctuidae	0	1	NA

171	Insecta	Lepidoptera	Pieridae	1	0	E
415	Insecta	Lepidoptera	Pieridae	4	1	N
691	Insecta	Lepidoptera	Pieridae	0	4	NA
382	Insecta	Lepidoptera	Pyralidae	0	27	NA
217	Insecta	Lepidoptera	Tortricidae	9	0	I
693	Insecta	Lepidoptera	Tortricidae	0	8	NA
444	Insecta	Mantodea	Empusidae	0	1	NA
240	Insecta	Neuroptera	Hemerobiidae	2	0	NA
255	Insecta	Orthoptera	Acrididae	3	1	N
267	Insecta	Orthoptera	Acrididae	0	42	NA
270	Insecta	Orthoptera	Acrididae	0	16	NA
493	Insecta	Orthoptera	Acrididae	0	5	NA
503	Insecta	Orthoptera	Acrididae	0	99	NA
511	Insecta	Orthoptera	Acrididae	0	10	NA
468	Insecta	Orthoptera	Prophalangopsidae	0	1	NA
63	Insecta	Orthoptera	Tetrigidae	7	0	NA
64	Insecta	Orthoptera	Tetrigidae	4	0	NA
682	Insecta	Orthoptera	Tetrigidae	0	10	NA
202	Insecta	Orthoptera	Tettigoniidae	9	0	NA
229	Insecta	Orthoptera	Tettigoniidae	44	0	NA
309	Insecta	Orthoptera	Tettigoniidae	0	6	NA
416	Insecta	Orthoptera	Tettigoniidae	3	0	NA
683	Insecta	Orthoptera	Tettigoniidae	0	7	NA
82	Insecta	Orthoptera	Trigonidiidae	69	3	I
196	Insecta	Phasmida	Phasmatidae	1	0	I
94	Insecta	Psocodea	Caeciliusidae	48	3	N
120	Insecta	Psocodea	Ectopsocidae	21	0	I
206	Insecta	Psocodea	Trichopsocidae	7	0	N
200	Insecta	Thysanoptera	Thripidae	0	1	N
		Total		**7861**	**5654**	

Chapter 4. Coastal grassland vegetation records from São Miguel Island (Azores) and the south-western coast of mainland Portugal

Abstract

Background

The present work provides an inventory of the plant species recorded in two distinct coastal grassland vegetations: the Azores Archipelago (São Miguel Island) and the southwestern coast of mainland Portugal (Sesimbra and Sines regions – Setúbal District). Sites were selected in both regions to have a similar general substrate (rocky), latitude, and elevation. Thirty-one sites were selected in the coastal grasslands: thirteen were located on São Miguel Island and eighteen on the mainland, distributed across Sesimbra (12) and Sines (6). All sites were visited once during the spring of 2022. In each site, 30 photos were taken at 5-meter intervals, for a total of 930 photos.

The Sesimbra and Sines regions were chosen because they represent well-preserved examples of coastal grassland vegetation on the southwestern coast of mainland Portugal, sharing similar environmental characteristics with the coastal grasslands of São Miguel Island, such as rocky substrate, Atlantic exposure, and comparable latitude. This design allows a meaningful comparison between insular and continental vegetation under similar abiotic conditions, providing a standardized framework for documenting coastal plant diversity across contrasting geographic contexts.

New information

Most records correspond to previously known occurrences documented in national databases, but this dataset standardizes and updates those records through direct, georeferenced field observations. A few taxa represent distributional updates within the sampled plots. Several introduced and invasive species, such as *Carpobrotus edulis* and *Oxalis pes-caprae*, were also documented. The most represented families include Asteraceae, Poaceae, Fabaceae, and Brassicaceae, which are characteristic of coastal grassland vegetation in the region.

Keywords: Sampling event; Occurrence; Plants; Azores; Mainland Portugal; Coastal grasslands; Photographic sampling

4.1. Introduction

Grasslands, including coastal variants, have been widely studied in terms of plant and faunal composition (Jones and Donnelly, 2004); (Feher et al., 2021). These ecosystems are of particular importance because they serve as habitats for numerous organisms that provide crucial ecosystem services for humans, such as nutrient cycling, carbon sequestration, and pollination (Peters et al., 2016). Nevertheless, studies focusing specifically on coastal grassland vegetation remain comparatively scarce, leaving much to be explored (Calado et al., 2024).

Vegetation cover plays a key role in the structuring of ecosystems, with certain organisms being closely linked to the type of vegetation present, without which they cannot establish themselves. Examples include the monarch butterfly (*Danaus plexippus* (Linnaeus, 1758)) and plants of the genus *Asclepias* spp.(Greenstein et al., 2022), as well as the "Lundy cabbage flea beetle" (*Psylliodes luridipennis*, Chrysomelidae), which depends on the plant *Coincya wrightii*, endemic to Lundy Island, England (Compton et al., 2007). The decline of these plant populations would certainly lead to a reduction of the respective arthropod communities.

Anthropogenic activities and climate change significantly affect the structure of natural ecosystems (Wick et al., 2016; Lister and Garcia, 2018; Bardgett et al., 2021; Dai et al., 2022). Oceanic islands are particularly sensitive to such pressures, as their restricted area and isolation make them vulnerable to trade, tourism, and biological invasions (Delgado and Riera, 2020; Borges et al., 2022; Boieiro et al., 2024; Calado et al., 2025). Understanding the composition of coastal vegetation is therefore essential to assess how such factors influence ecosystem structure and biodiversity.

Coastal grassland vegetation represents a valuable component of Atlantic ecosystems, combining Euro-Atlantic, Mediterranean, and Macaronesian floristic elements.

Understanding its composition across island and mainland contexts provides insights into biogeographical patterns, habitat specificity, and potential drivers of species turnover.

This data paper aims to document and make publicly available a standardised inventory of plant species recorded in coastal grasslands of São Miguel Island (Azores) and the Sesimbra and Sines regions (Setúbal District, south-western coast of mainland Portugal). The dataset constitutes a baseline for future ecological and biogeographical studies, biodiversity monitoring, and conservation planning.

4.2. General Description

Purpose: The primary objective of this study is to provide a comprehensive inventory of plants in the coastal grasslands across São Miguel Island (Azores Archipelago), Sesimbra and Sines regions (Setúbal District in south-western coast of mainland Portugal).

Additional information: The dataset includes information on the diversity and composition of plants communities, recorded through the project's monitoring surveys.

4.3. Project Description

Title: Phenotypic Plasticity of Pest and Biological Control Agents: Contrasting Mainland and Insular Coastal Ecosystems

Personnel: Paulo A.V. Borges, Hugo Calado, Ruben Heleno, António O. Soares, Lurdes Borges.

Study area description: The study was conducted in the coastal grasslands of São Miguel Island (Azores Archipelago, North Atlantic) and south-western coast of mainland Portugal (Setúbal District – Sesimbra and Sines regions) (Figure 1).

The Azores Archipelago is located in the centre of the North Atlantic, approximately 1,600 km from mainland Portugal, extending about 600 km between Santa Maria and

Corvo (37°–40° N; 25°–31° W). The archipelago has regular and abundant rainfall, an oceanic climate with relatively stable temperatures, high humidity throughout the year, and persistent winds, especially during autumn and winter (Santos et al., 2004); (Borges et al., 2019; IPMA, 2020).

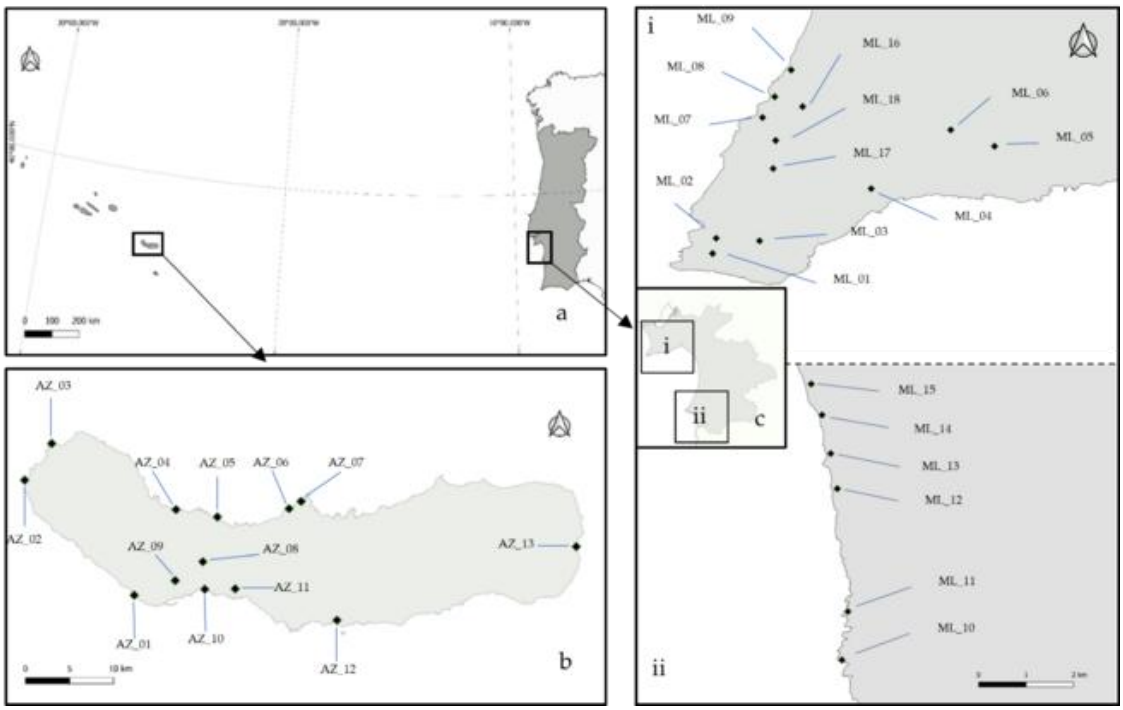

Figure 1. Sampling areas with the plots indicated: **a** Azores Archipelago and Portugal mainland; **b** São Miguel's Island; **c** Setúbal District; (**i**) Sesimbra; (**ii**) Sines (source: Calado et al., 2024).

Mainland Portugal is located in south-western Europe (33°–43° N; 9°–6° W), with a total land area of approximately 89,015 km². The Setúbal District lies on the south-western coast of mainland Portugal, south of Lisbon, and encompasses the regions of Sesimbra and Sines. The mainland has a Mediterranean climate, characterised by warm, dry summers and cool, wet winters (Carvalho et al., 2014); (De Lima et al., 2015).

Design description: Thirty-one sampling sites were selected in coastal grassland vegetation across both regions, chosen to share similar environmental characteristics such as rocky substrate, latitude, and elevation. Thirteen sites were located on São Miguel Island, and eighteen on the mainland (twelve in the Sesimbra region and six in the Sines region).

Each site comprised a 2,500 m² (0.25 ha) plot, corresponding to a standardised sampling unit of coastal grassland vegetation.

Funding: H.R.M.G.C. was funded by the Regional FRCT Ph.D. Grant M3.1.a/F/012/2021: Phenotypic Plasticity of Pest and Biological Control Agents: Contrasting Mainland and Insular Coastal Ecosystems. AOS and PAVB were also funded by FCT through national and European funds by UID/00329/2023 - Centre for Ecology, Evolution and Environmental Changes (CE3C), and by the Regional Directorate for Science, Innovation and Development [Regional Government of the Azores] through the PROSCIENTIA Incentive System M1.1.A/FUNC.UI&D/021/2025 [UI&D/GBA/2025].

4.4. Sampling Methods

4.4.1. Sampling description

All 31 sites were visited once during the spring of 2022 (March–May), resulting in 31 sampling events. At each site, a 45-minute survey was carried out to record vegetation composition: 30 minutes were dedicated to photographic sampling and 15 minutes to direct visual observation and preliminary species identification. Each site covered an area of approximately 2 500 m², defined for methodological consistency rather than by minimum area calculation, to ensure adequate spatial coverage and logistical feasibility across all sampling locations.

Thirty photographs were taken per site, at 5-metre intervals and 1.2 metres above ground level, totalling 930 photographs. Photographs were taken using a Sony HD Movie 720p camera. No vegetation cover-abundance scale (e.g. Braun–Blanquet) was applied, as the study focused exclusively on documenting species occurrences rather than quantitative vegetation analysis.

4.4.2. Quality control

All photographs were later examined individually on a computer to verify and confirm species identifications (Figure 2). Photographs were then organised into a digital archive to facilitate taxonomic validation.

When necessary, field observations and photographs were cross-checked against online resources such as the Azorean Biodiversity Portal and the Flora-On database to ensure taxonomic consistency.

Figure 2. Examples of ground photos from different plots in the Azores (A) and mainland Portugal (B), showing some of the plant species and morphospecies: 1 – *Dimorphotheca fruticosa*; 2 – *Trifolium* sp.; 3 – *Carpobrotus edulis*; 4 – *Oxalis pes-caprae*.

4.4.3. Step description

In the laboratory, all photographs were organised and used for taxonomic identification. Plant taxa were identified to the species level whenever possible, using the Azorean Biodiversity Portal and the Flora-On database as references. When reproductive structures were absent, morphologically distinct plant entities were classified as morphospecies, following the same operational criteria applied in previous arthropod studies (Calado et al., 2024). Each morphospecies represents a unique morphological unit and is treated as an Operational Taxonomic Unit (OTU).

Photographic data were obtained using a Sony HD Movie 720p camera, with 30 photographs taken per site at 5-metre intervals and 1.2 metres above ground level, totalling 930 images. This equipment provided sufficient image resolution for accurate post-field identification of plant taxa and morphospecies.

4.5. Geographical coverage

Description: The study was conducted in the coastal grasslands of São Miguel Island (Azores Archipelago, North Atlantic) and south-western coast of mainland Portugal (Setúbal District – Sesimbra and Sines regions).

General spatial coverage: The study was conducted in the coastal grasslands of São Miguel Island (Azores Archipelago, North Atlantic) and south-western coast of mainland Portugal (Setúbal District – Sesimbra and Sines regions).

Coordinates: 37°43'7"N and 38°27'43"N Latitude; 25°51'12"W and 8°47'36"W Longitu de.

4.6. Taxonomic coverage

Description: Taxonomic ranks

Kingdom: Plantae

Phylum: Magnoliophyta, Pinophyta, Pteridophyta.

Class: Genopsida, Liliopsida, Magnoliopsida, Pinopsida, Polypodiopsida.

Order: Alismatales, Apiales, Asparagales, Asterales, Boraginales, Brassicales, Caryophyllales, Dipsacales, Ephedrales, Ericales, Fabales, Fagales, Gentianales, Geraniales, Lamiales, Malpighiales, Malvales, Myrtales, Oxalidales, Pinales, Poales, Polypodiales, Proteales, Ranunculales, Rosales, Sapindales, Saxifragales, Solanales, Vitales, Zingiberales.

Family: Acanthaceae, Agavaceae, Aizoaceae, Amaranthaceae, Amaryllidaceae, Anacardiaceae, Apiaceae, Apocynaceae, Araceae, Asparagaceae, Asphodelaceae, Aspleniaceae, Asteraceae, Boraginaceae, Brassicaceae, Cactaceae, Campanulaceae, Caryophyllaceae, Crassulaceae, Cupressaceae, Dennstaedtiaceae, Dryopteridaceae, Ephedraceae, Ericaceae, Euphorbiaceae, Fabaceae, Fagaceae, Geraniaceae, Juncaceae, Lamiaceae, Linaceae, Malvaceae, Myrtaceae, Oleaceae, Onagraceae, Orchidaceae, Orobanchaceae, Oxalidaceae, Papaveraceae, Pinaceae, Pittosporaceae, Plantaginaceae,

Plumbaginaceae, Poaceae, Polygonaceae, Primulaceae, Proteaceae, Rhamnaceae, Rosaceae, Rubiaceae, Scrophulariaceae, Solanaceae, Tamaricaceae, Thymelaeaceae, Tropaeolaceae, Urticaceae, Valerianaceae, Verbenaceae, Vitaceae, Zingiberaceae.

4.7. Temporal coverage

Notes: 3 March 2022 – 17 May 2022.

4.8. Collection Data

Collection name: Renato_PhD

Collection identifier: PHEPLA

Specimen preservation method: Photo Record

4.9. Usage licence

Creative Commons Public Domain Waiver (CC-Zero)

4.10. Data Resources

Data package title: Coastal Grassland Vegetation Records from São Miguel Island (Azores) and Mainland Portugal

Resource link: https://ipt.gbif.pt/ipt/resource?r=coastal_plants

Alternative identifiers: https://www.gbif.org/dataset/2265c6e2-4ab7-4af2-93af-ba377a7d4e43

Number of data sets: 2

Data set name: Event Table

Character set: UTF-8

Download URL: http://ipt.gbif.pt/ipt/resource?r=coastal_plants

Data format: Darwin Core Archive

Data format version: 1.2

Description: The dataset was published in the Global Biodiversity Information Facility platform, GBIF (Calado et al., 2025a). The following data-table includes all the records for which a taxonomic identification of the species was possible. The dataset submitted to GBIF is structured as a sample occurrence dataset that has been published as a Darwin Core Archive (DwCA), which is a standardised format for sharing biodiversity data as a set of one or more data tables. The core data file contains 31 records (eventID). This GBIF IPT (Integrated Publishing Toolkit, Version 2.5.6) archives the data and, thus, serves as the data repository. The data and resource metadata are available for download in the Portuguese GBIF Portal IPT.

Column label	Column description
eventID	Identifier of the events, unique for the dataset.
locationID	Identifier of the locations, unique for the dataset.
country	The name of the country or major administrative unit in which the Location occurs (Portugal).
countryCode	The standard code for the country in which the Location occurs (PT).
stateProvince	The name of the next smaller administrative region than country (state, province, canton, department, region, etc.) in which the Location occurs.
county	The full, unabbreviated name of the next smaller administrative region than stateProvince (county, shire, department, etc.) in which the Location occurs.
municipality	The full, unabbreviated name of the next smaller administrative region than county (city, municipality etc.) in which the Location occurs.
locality	The specific description of the place.
verbatimLocality	The original textual description of the place.
locationRemarks	Comments or notes about the Location.
habitat	The habitat for an Event (coastal grasslands).
minimumElevationInMeters	The lower limit of the range of elevation (altitude, usually above sea level), in meters.
decimalLatitude	Approximate centre point decimal latitude of the field site in GPS coordinates.
decimalLongitude	Approximate centre point decimal longitude of the field site in GPS coordinates.
geodeticDatum	Standard Global Positioning System coordinate reference for the location of the sample collection points.
coordinateUncertaintyinMeters	Uncertain value of coordinate metrics.
coordinatePrecision	Value in decimal degrees to a precision of six decimal places.

georeferenceSources	Navigation system used to record the location of sample collections.
samplingProtocol	The sampling protocol used to capture the species (45 minutes at an area of 2 500 m^2; 30 minutes taking photos, 15 minutes identifying plants).
sampleSizeValue	A numeric value for a measurement of the size (time duration, length, area, or volume) of a sample in a sampling Event.
sampleSizeUnit	The unit of measurement of the size (time duration, length, area, or volume) of a sample in a sampling Event.
samplingEffort	The amount of effort expended during an Event (1 person)
year	Year the sample was collected (2022).
month	The integer month in which the Event occurred.
day	The integer day of the month on which the Event occurred.
eventDate	The date-time or interval during which an Event occurred.

Data set name: Occurrence Table

Character set: UTF-8

Download URL: http://ipt.gbif.pt/ipt/resource?r=coastal_plants

Data format: Darwin Core Archive

Data format version: 1.2

Description: The dataset was published in the Global Biodiversity Information Facility platform, GBIF (Calado et al., 2025a). The following data table includes all the records for which a taxonomic identification of the species was possible. The dataset submitted to GBIF is structured as an occurrence table that has been published as a Darwin Core Archive (DwCA), which is a standardised format for sharing biodiversity data as a set of one or more data tables. The core data file contains 742 records (occurrenceID). This GBIF IPT (Integrated Publishing Toolkit, Version 2.5.6) archives the data and, thus, serves as the data repository. The data and resource metadata are available for download in the Portuguese GBIF Portal IPT.

Column label	Column description
eventID	Identifier of the events, unique for the dataset.
type	Type of the record, as defined by the Dublin Core Standard.
license	Reference to the licence under which the record is published.
institutionID	The identity of the institution publishing the data.

collectionID	The identity of the collection publishing the data.
institutionCode	The code of the institution publishing the data (UAc)
collectionCode	The code of the collection where the specimens are conserved (PHEPLA)
datasetName	Name of the dataset (Renato_PhD)
basisOfRecord	The nature of the data record.
recordedBy	A list (concatenated and separated) of names of people, groups or organisations who performed the sampling in the field.
occurrenceID	Identifier of the record, coded as a global unique identifier.
kingdom	Kingdom name.
phylum	Phylum name.
class	Class name.
order	Order name.
family	Family name.
genus	Genus name.
specificEpithet	Specific epithet name.
infraspecificEpithet	Infraspecific epithet name.
scientificNameAuthorship	The authorship information for the scientificName formatted according to the conventions of the applicable nomenclaturalCode.
identificationRemarks	Comments or notes about the Identification (Morphospecie's number in Renato PhD Collection).
identifiedBy	A list (concatenated and separated) of names of people, groups or organisations who assigned the Taxon to the subject.
dateIdentified	The date on which the subject was determined as representing the Taxon.
scientificName	The full scientific name, with authorship and date information if known.
taxonRank	Lowest taxonomic rank of the record.

4.11. Additional information

A total of 213 plant species and morphospecies were recorded across the two coastal grassland regions (Azores = 98; mainland = 132).

In the Azores, 98 taxa belonging to three classes were identified: *Liliopsida*, *Magnoliopsida*, and *Polypodiopsida*.

In mainland Portugal, 132 taxa were recorded, belonging to four classes: *Genopsida*, *Liliopsida*, *Magnoliopsida*, and *Pinopsida*.

In total, 17 species were common to both regions (Figure 3; Table 1).

Table 1. Common species in the Azores and mainland coastal grasslands.

Class	Order	Family	Species
Liliopsida	Poales	Poaceae	*Arundo donax* L.
Magnoliopsida	Caryophyllales	Aizoaceae	*Carpobrotus edulis* (L.) N.E.Br.
	Apiales	Apiaceae	*Foeniculum vulgare* Mill.
			Daucus carota L.
	Asterales	Asteraceae	*Galactites tomentosus* Moench
			Coleostephus myconis (L.) Rchb.f.
			Sonchus tenerrimus L.
	Brassicales	Brassicaceae	*Lobularia maritima* (L.) Desv.
	Fabales	Fabaceae	*Ornithopus compressus* L.
	Oxalidales	Oxalidaceae	*Oxalis pes-caprae* Schreb.
	Lamiales	Plantaginaceae	*Plantago lanceolata* L.
			Plantago coronopus L.
			Veronica persica Poir.
	Ericales	Primulaceae	*Lysimachia arvensis* (L.) U.Manns & Anderb.
	Gentianales	Rubiaceae	*Sherardia arvensis* L.
	Solanales	Solanaceae	*Solanum mauritianum* Scop.
	Rosales	Urticaceae	*Parietaria judaica* L.

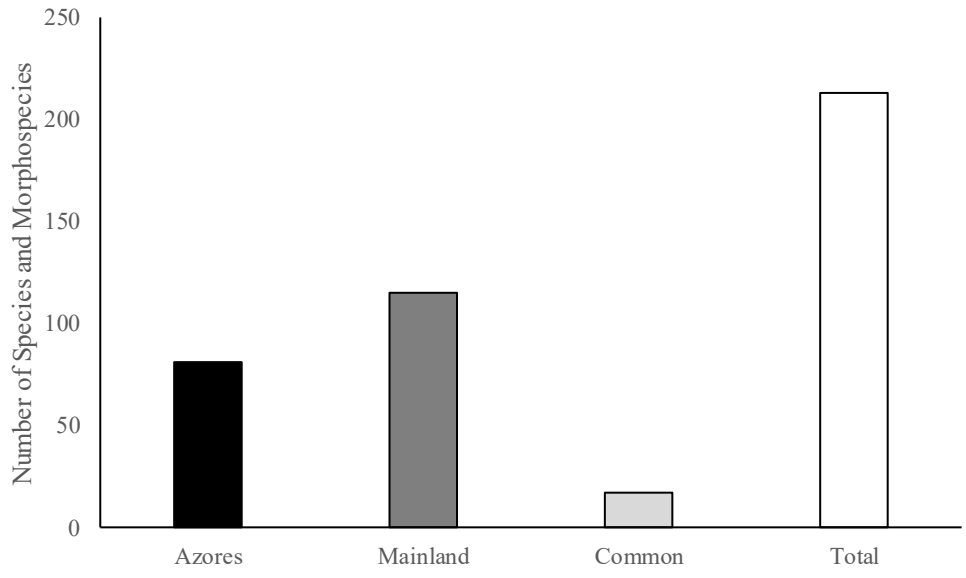

Figure 3. Number of species collected in the Azores and in the Portugal mainland.

4.12. Conclusions

This data paper provides a standardised, georeferenced inventory of plant species recorded in coastal grasslands of São Miguel Island (Azores Archipelago) and in the Sesimbra and Sines regions (Setúbal District, south-western coast of mainland Portugal).

A total of 213 taxa were recorded, including 17 species common to both regions. The dataset reveals higher species richness in mainland coastal grasslands compared with those of São Miguel Island.

Two invasive species, *Carpobrotus edulis* and *Oxalis pes-caprae*, were documented in both regions. No new endemic or threatened species were identified, although the dataset updates and validates existing distributional records.

The dataset, already accessible through GBIF (Calado et al., 2025b), is presented here in a validated and standardised format to ensure transparency, interoperability, and long-term usability. By providing detailed methodological, taxonomic, and metadata documentation, this data paper supports future ecological and biogeographical research on Atlantic coastal ecosystems (Boieiro et al., 2024; Calado et al., 2025b), as well as biodiversity monitoring and conservation planning across these habitats.

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Chapter 5. Contrasting structure of trophic networks from the Azores and mainland Portugal

Abstract

The colonization of oceanic islands and the evolution of insular species interactions remain central topics in ecology. Ecological network analysis helps reveal how evolution and community structure may unfold given the organisms present, yet coastal grassland systems are still understudied. Here we compare bipartite trophic networks (plant–aphid, aphid–ladybird, and aphid–ant) from coastal grasslands in two regions: the Azores and mainland Portugal. Our aim was to assess differences in network composition and structure, thereby improving understanding of ecological dynamics and potential evolutionary implications in island versus mainland communities. Over four months, we recorded interactions among plants, aphids, ladybirds, and ants on São Miguel Island (Azores) and in the Setúbal Peninsula/Sines region (mainland). For each network we computed degree, normalized degree, species strength, and specialization (d′). We also tested whether the number of biotic interactions per region was associated with temperature, humidity, and elevation. Azorean networks (plant–aphid, aphid–ladybird, aphid–ant) contained, on average, more interactions than mainland networks. However, most structural metrics did not differ significantly between regions, except in the plant–aphid network, where plants showed higher specialization and species strength on the mainland. We found no strong correlations between humidity, temperature, or elevation and the number of interactions per network.

Keywords: Aphids, coastal grasslands, ladybirds, specialization, trophic networks.

5.1. Introduction

How oceanic islands were colonised and how they shape ecology and evolution of insular species has long challenged the curiosity of ecologists (Thornton and New 2007; Warren et al. 2015; Borregaard et al. 2017; Alhmedi et al. 2018). The "theory of island biogeography" predicts that biodiversity of oceanic islands – those that have never been connected to a continent – is related to their distance from continents, as well as to the colonization and extinction rates of the species that reach these locations (MacArthur and

Wilson 1963; Warren et al. 2015; Whittaker et al. 2017). At the same time, it is also well established that species diversity on islands is closely linked to habitat diversity (Lack, 1973), where the successful establishment of new species depends on the availability of vacant niches, including those constrained by the presence of competitors, mutualists, prey, and predators (i.e., their Eltonian niche: Larson et al., 2010; Petalas et al., 2024).

The biological poverty of insular environments – largely resulting from the colonization filter imposed by geographic isolation – constrains species' potential resources, and likely their trophic interactions and derived evolutionary constraints ((MacArthur and Wilson, 1963; Warren et al., 2015; Whittaker et al., 2023; Whittaker et al. 2023). One way to evaluate species ecological function and to predict potential evolutionary constraints in the communities they integrate is to evaluate their trophic niche (Soberon and Peterson, 2005; Lavergne et al., 2013; FitzGerald et al., 2018). The emergent properties of such interactions can be characterised by compiling information between the species and the links that hold those species together within a network approach (Heleno et al., 2014; Delmas et al., 2019). Networks provide a broader understanding of a species' role within its broader biological context, thus simultaneously focusing of the trees without missing the forest (Odum and Barrett, 2005; Heleno et al., 2020; Hou et al., 2023). In this context, bipartite network analysis offers a valuable framework for addressing research and biodiversity management questions (Llopis-Belenguer et al., 2023).

Trophic networks provide a framework to understand the relationship between community composition (i.e., the species present at a given site), and ecosystem functioning (the flow of energy and matter) by analysing the underlying structure of biotic interactions (i.e. species interdependencies) (McCann, 2007; Delmas et al., 2019). Therefore, exploring the structure of ecological networks can provide insights about their functioning and degree resilience, for example in the context of agriculture intensification (Morrison et al., 2020), or habitat loss (Kaiser-Bunbury et al., 2010; Evans et al., 2013). In this study, we focus on three types of trophic associations: plant–aphid, aphid–ladybird, and aphid–ant. By analysing interactions between these groups of species in different locations, we can gain insights into how these organisms have adapted to their specific environments.

The biological context set by oceanic islands and continents has been very informative to explore community assembly rules (Losos and Ricklefs 2009; Whittaker et al. 2017). In

this regard, the comparison between European and Azorean communities - colonised largely by European propagules – can yield particularly informative insights (Heleno and Vargas, 2015). It is known that some interactions among species (whether antagonistic or mutualistic) can act as filters for the entry of new species and, consequently, influence the structure and dynamics of communities (Post and Palkovacs, 2009; Ponisio et al., 2019). Thus, by contrasting bipartite networks from the coastal grasslands of the Azores and from mainland Portugal, we can explore whether biogeographic contexts affect community structure and functioning.

Coastal grasslands, due to the marked differences they exhibit compared to their inland counterparts, not only differ from the original vegetation but also show substantial differences abiotic factors, such as temperature and humidity (Diamond and Smeins, 1988; Holstein, 2011; Calado et al., 2024). At the same time, coastal grasslands in the Azores exhibit lower arthropod diversity compared to their continental counterparts, although there appears to be an apparent abundance compensation in the islands (Calado et al., 2024).

Understanding to what extent these differences determine changes in regional trophic networks through a bottom-up effect, mediated by resource availability, particularly in plant cover diversity, can be tested using ladybirds (Coleoptera: Coccinellidae). Ladybirds comprise nearly 6000 species (see Vanderberg 2002) distributed worldwide, and present a high diversity with regards to their life history, development, distribution, habitat, and trophic relationships (see Hodek et al. 2012). Most species of this family are top predators recognized as useful natural enemies of pests, including aphids (Aphidoidea), scale insects (Coccoidea), whiteflies (Aleyrodoidea) or mites (Acari). Although evolutionary responses in predator-prey systems are generally ‘‘top-down’’, the resource availability both in time and space appears to play a major role in life history evolution of predaceous coccinellids (Dixon, 2000; Borges et al., 2011).

Abiotic resistance represented by the climate of colonizable regions could hinder the establishment of insects. For instance, the climatic conditions of southern Europe, including Portugal and the Azores could have influenced the establishment and spread of *Harmonia axyridis* (Soares et al., 2017; Ameixa et al., 2019; Alaniz et al., 2021). However, the lack of success of *H. axyridis* as an invader species in those regions can also be explained by a combination of biotic factors, first on resource availability and

second when most direct competitors for limited resources are absent or are uncommon (Soares et al., 2017; 2018). Environmental conditions can in turn determine the structure and composition of biotic communities, where composition refers to the identity and relative abundance of species, and structure to how those species interact within trophic networks. Some studies have shown that temperature or soil composition can affect plant distribution and abundance (Austin, 2002). In contrast to northern temperate regions, Mediterranean regions and the Azores support a high abundance of species from the genus *Scymnus*, which are typically small and, in the Azores, may represent more than 90% of the total Coccinellidae abundance (Soares et al. 2017; 2021). The scarcity of studies contrasting the trophic structure of coccinellid communities prevents testing hypotheses aimed at better understanding their biology, ecology and evolution.

Here, we aim to contrast the structure of bipartite networks (both antagonistic and mutualistic) of the aphidophagous coccinellid guilds from coastal grasslands of the Azores and mainland Portugal. Given that plants form the base of terrestrial food webs, constraining herbivorous interactions and in turn higher trophic levels (Halaj and Wise, 2001; Van Veen and Sanders, 2013), we quantified plant-aphid, aphid-ladybird, and aphid-ant networks in both locations. Based on previous theoretical and empirical evidence, we hypothesize that insular trophic networks are less diverse and more generalized than their continental counterparts.

5.2. Materials and Methods

To explore the differences on the structure of trophic networks between plants, aphids, predators and ants, 24 sites were selected for sampling in both regions (12 in the Azores and 12 in mainland Portugal). Sites were selected based on similar substrates (rocky), latitude, and elevation (See Supplementary Table S1) and for more details (Calado et al., 2024).

5.2.1. Study Area

The Azores archipelago lies in the centre of the North Atlantic, approximately 1600 km from mainland Portugal, with an extension of about 600 km between Santa Maria and Corvo (37°–40° N; 25°–31° W), (Elias et al., 2016; Borges et al., 2019) (Figure 1a). The archipelago's climate is temperate oceanic, with regular and abundant rainfall, high levels

of relative humidity and persistent winds, mainly during the winter and autumn seasons (Borges et al., 2019; Neto et al., 2020; Pavão et al., 2023).

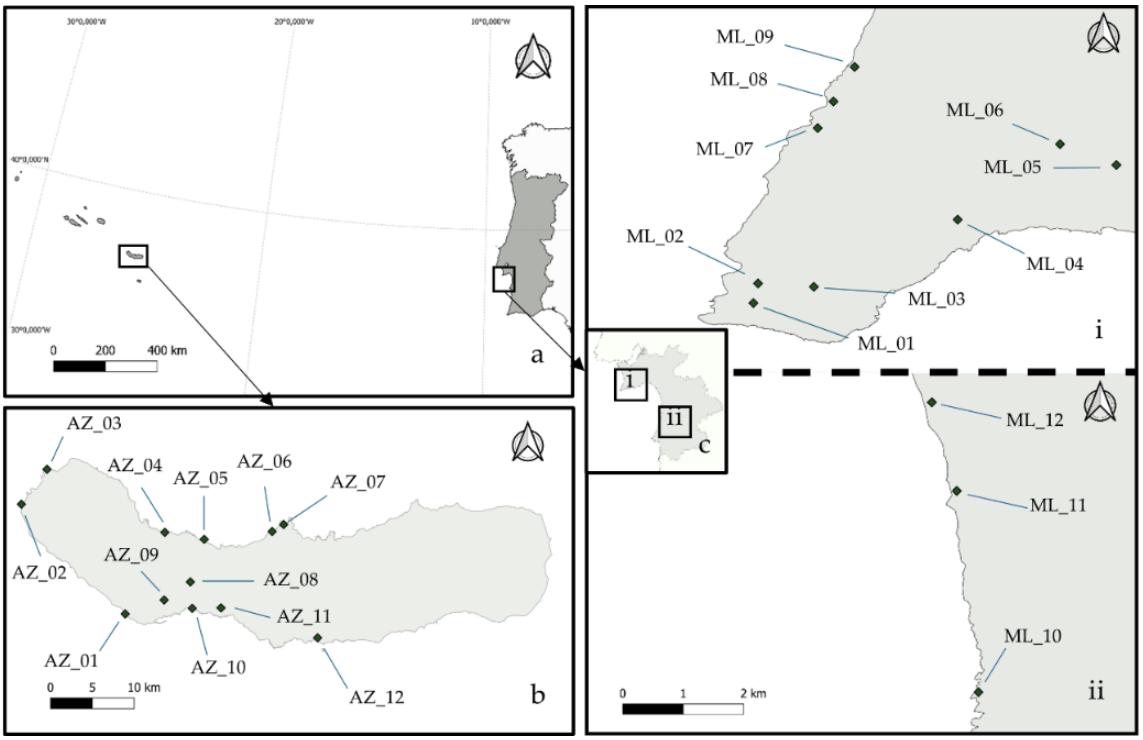

Figure 1. Location of the sampling sites in insular and mainland areas included in this study: (a) Azores Archipelago and mainland Portugal; (b) São Miguel Island; (c) Setúbal district; (i) Sesimbra; (ii) Sines (adapted from Calado et al. (2024)).

Mainland Portugal is in the southwest of Europe (33° - 43° N; 9° 6° W), with a total land area of approximately 89,015 km2 (Mileu et al., 2022). The Setúbal district is in the southern west coast of mainland Portugal, south of Lisbon, and encompasses the regions of Sesimbra and Sines. Mainland Portugal has a Mediterranean climate characterised by warm and dry summers and cool and wet winters (Carvalho et al., 2014; Santos et al., 2019).

5.2.2. Trophic interactions

Each site corresponded to an area of approximately 2500 m^2 (0.25 ha). All selected sites were sampled four times between March and July 2022. Since the climate conditions that occur in spring in the Azores normally begin one month later than in the mainland, the samplings on the mainland occurred between March – June and in the Azores between April – July. All insect samples were collected between 10:00 and 16:00 to capture the period of highest insect activity at all sites.

Due to the reduced number of sampled interactions on most sites and visits, the data from each type of interaction was pooled to create three insular and three continental networks.

On each visit, a 30 min. period was spent in each site walking randomly to observe the presence of networks between aphids and host plants, aphids and ladybirds, or aphids and ants. For each network, the species of host plants, aphids, lady beetles, and ants were recorded, as well as the number of aphid individuals and the presence or absence of ants. Photographs of the plant species that hosted colonies of aphids or ladybirds were also taken for later identification. For each site and visit temperature and humidity were recorded using a data logger Testo 174 H (see Supplementary Table S2) and altitude and coordinates were also recorded with a hand-held GPS.

For more accurate identification, some individuals were taken to the laboratory. All collected organisms were placed in 100 ml plastic flasks containing 99% absolute alcohol for later sorting and identification. The senior authors (PAVB and AOS) identified all morphospecies of the Azorean samples to the species level when possible. All species collected in the Azores were categorized into four colonization categories according to Borges et al. 2022 (see Supplementary Table S3). A database for events and occurrences was created using the Darwin Core criteria. Voucher specimens are retained in PHEPLA collection, at Azores University.

Networks were compiled into bipartite matrices quantifying respectively the interactions between plants and aphids, aphids and ladybirds, and ladybirds and ants, each of them for the insular and mainland regions. These matrices were used to characterise bipartite network structure by calculating the following species-level descriptors: linkage level or degree (i.e., the number of species with which a species directly interacts); normalized degree (i.e., the degree divided by the potential number of interactions a species could have with species from the other trophic level); species strength (measures the total influence of a species on all species from the other trophic level by summing species dependencies, sensu Bascompte et al., (2006), and specialization (d') (measures the selectivity of a species' interactions as the departure of the observed distribution of interactions from the expected distribution under a null model, where $d'=0$ indicates no selectivity and $d'=1$ indicates maximum selectivity) (Blüthgen et al., 2006). Species topological descriptors were calculated with package bipartite v 2.18 for R (R Core Team, 2025).

5.2.3. Data Analysis

The Kolmogorov–Smirnov test was performed to assess data normality. When the data did not meet normality assumptions, the Mann–Whitney U test was applied to compare the values of degree, normalised degree, species strength, and specialisation (d') between the mainland and Azorean networks. Additionally, the effects of altitude, humidity, and temperature on the number of interactions within each bipartite network (plant–aphid, aphid–ladybird, and aphid–ant) were analysed for both regions (the Azores and mainland Portugal). Since the variables describing environmental conditions and the number of interactions within each bipartite network did not meet the assumptions of normality and homoscedasticity, Spearman's rank correlation was used as a non-parametric alternative.

Because networks derived from individual plots and months were too small to yield meaningful network-level descriptors, we pooled all interactions of each type (plant–aphid, aphid–ladybird, and aphid–ant) across all plots, sites, and months within each bioregion. This resulted in one composite network per bioregion (Azores and mainland). Consequently, replication at the network level was insufficient to statistically compare overall network structure across treatments. We therefore used these two networks to test whether, and how, species-level metrics differed between bioregions. Statistical significance was set at $p < 0.05$. All statistical analyses were conducted using SPSS v. 29.0.1 (IBM Corporation, 2023).

5.3. Results

5.3.1. Trophic networks

A total of 651 interactions were recorded over the four months of observation, encompassing the three different trophic networks at each bioregion (plant-aphid: 292 in the Azores and 65 on the mainland; aphid-ladybird: 34 in the Azores and 9 on the mainland; aphid-ant: 197 in the Azores and 54 on the mainland) (Figure 2).

Similarly, we identified 25 plant species, 13 aphid species, 6 ladybird species, and 4 ant species. Eleven species were unique to the mainland, thirty to the Azores, with seven species shared between both regions (see Supplementary Table S3). Regarding the life cycle of the plants observed interacting with aphids, 56.0% were perennial and 20.0%

were annual or biennial, while 24.0% had an indeterminate life cycle (Royal Botanic Gardens, Kew, 2025). Plants identified on the mainland were mostly perennial (71.4%), with 28.6% unclassified. In the Azores, 52.4% of the plants were perennial, 23.8% annual or biennial, and 23.8% indeterminate (Figure 3) (see Supplementary Table S4).

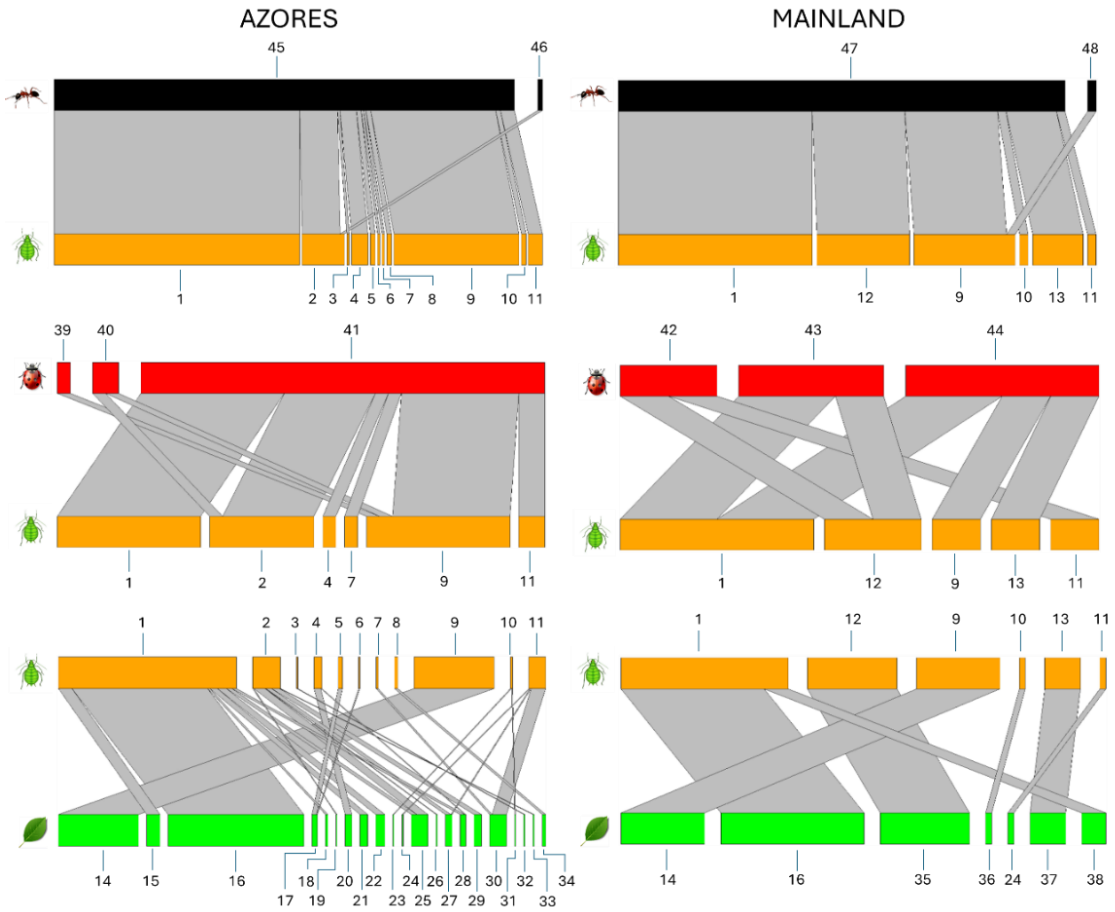

Figure 2. Bipartite trophic networks plots illustrating the trophic interactions, and their frequency between host plants, aphids, ladybirds and ants in the Azores and on mainland Portugal. Species codes: aphids, 1 – *Aphis fabae*, 2 – *Aphis gossypii*, 3 – *Aphis* sp., 4 – *Aphis spiraecola*, 5 – *Cavariella aegopodii*, 6 – *Dysaphis foeniculus*, 7 – *Hyperomyzus lactucae*, 8 – *Megoura viciae*, 9 – *Melanaphis donacis*, 10 – *Myzus persicae*, 11 – *Uroleucon sonchi*, 12 – *Capitophorus* sp., 13 - *Therioaphis* sp.; plants, 14 – *Arundo donax*, 15 – *Banksia integrifolia*, 16 – *Carpobrotus edulis*, 17 – *Daucus carota*, 18 – *Delairea odorata*, 19 – *Echium creticum*, 20 – *Erigeron annuus*, 21 – *Foeniculum vulgare*, 22 – *Galactites tomentosus*, 23 – *Holcus lanatus*, 24 – *Leontodon* sp., 25 – *Lotus* sp., 26 – *Oenothera indecora*, 27 – *Plantago lanceolata*, 28 – *Rumex* sp., 29 – *Solanum mauritianum*, 30 – *Sonchus tenerrimus*, 31 – *Symphytum officinale*, 32 – *Thymus vulgaris*, 33 – *Verbena bonariensis*, 34 – *Vicia* sp., 35 – *Dittrichia viscosa*, 36 – *Hypericum perforatum*, 37 – *Ononis ramosissima*, 38 – *Scolymus hispanicus*; ladybirds, 39 – *Oenopia doublieri*, 40 – *Scymnus interruptus*, 41 – *Scymnus nubilus*, 42 – *Coccinella septempunctata*, 43 - *Hyperaspis pseudopustulata*, 44 – *Scymnus* sp.; ants, 45 – *Lasius grandis*, 46 - *Tetramorium* sp., 47– *Camponotus* sp., 48 – *Tapinoma* sp..

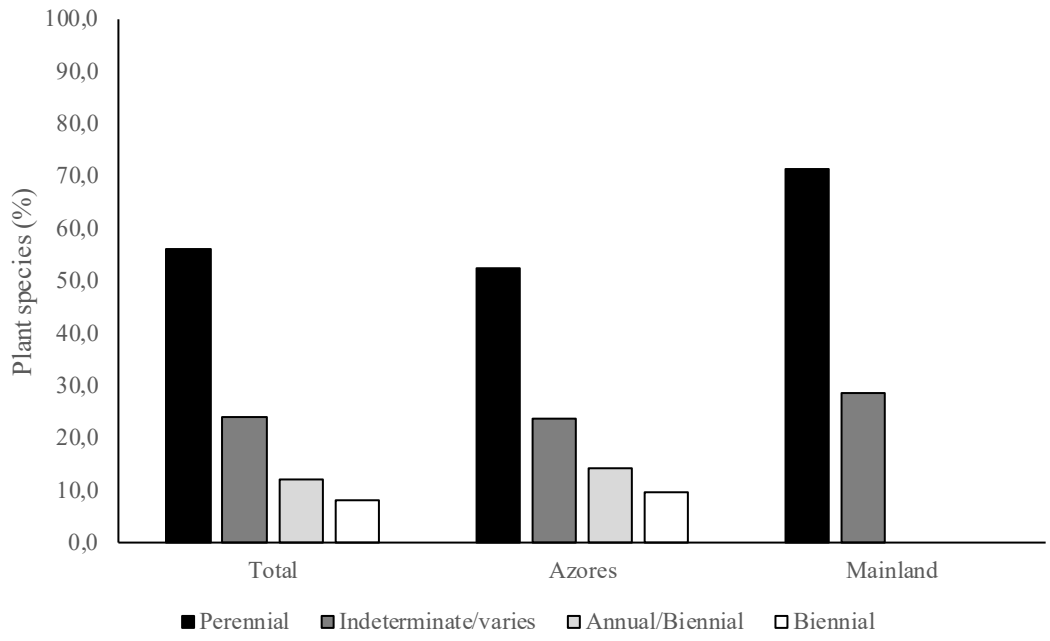

Figure 3. Proportion of plant species by life cycle and region (the Azores and mainland Portugal).

5.3.2. Environmental drivers and trophic networks

We found distinct patterns in the correlations between environmental variables (humidity, temperature, and elevation) and the number of interactions within each bipartite network (plant–aphid, aphid–ladybird, and aphid–ant) across both regions (Table 1).

Table 1 – Comparison of metric values (degree, normalized degree, species strength and specialization) across different trophic network (plants-aphids, aphids-ladybirds, and aphids-ants), between the Azores and mainland Portugal (Mann-Whitney U test; $p < 0.05$).

Network		**degree**		**normalized degree**		**species strength**		**specialization (d')**	
	N	*U*	*p*	*U*	*p*	*U*	*p*	*U*	*p*
Ants (with aphids)	4	1.5	0.667	2.5	1.000	1.0	0.667	1.0	0.667
Aphids (with ants)	17	35.5	0.808	35.5	0.808	48.0	0.149	35.0	0.884
Aphids (with ladybirds)	11	15.0	1.000	15.0	1.000	20.0	0.429	22.0	0.247
Ladybirds (with aphids)	6	5.0	1.000	6.0	0.700	6.0	0.700	6.5	0.400
Aphids (with plants)	17	22.0	0.301	52.0	0.062	30.0	0.808	54.0	0.037
Plants (with aphids)	28	56.0	0.376	112.0	0.042	111.0	0.048	113.0	0.036

In the Azores, there was no significant correlation between humidity and the number of interactions in plants-aphids network ($\rho = 0.25$; $p = 0.09$), nor in aphids-ants' network ($\rho = 0.22$; $p = 0.14$). The correlation between humidity and the number of interactions in the aphid-ladybird network was negligible ($\rho = 0.03$; $p = 0.85$). Regarding temperature, a

moderate positive correlation was found with the number of interactions in the aphid-ladybird network (ρ = 0.35; p = 0.02), while the plant-aphid (ρ = 0.13; p = 0.38) and aphid-ant (ρ = 0.19; p = 0.21) network showed non-significant correlations. As for elevation, no correlations were found in the number of interactions in the plant-aphid (ρ = -0.05; p = 0.76), aphid-ladybird (ρ = -0.14; p = 0.34), and aphid-ant (ρ = 0.05; p = 0.73).

In mainland Portugal, the number of interactions in all trophic networks was positively associated with humidity, particularly in the plant-aphid (ρ = 0.39; p = 0.01) and aphid-ant (ρ = 0.38; p = 0.01) network. However, there was no significant correlation between humidity and number of interactions in aphid-ladybird network (ρ = 0.28; p = 0.06). Temperature showed significant moderate positive correlations with the number of all interactions: plant-aphid (ρ = 0.47; p < 0.001), aphid-ladybird (ρ = 0.36; p = 0.01), and aphid-ant (ρ = 0.55; p < 0.001). In contrast, elevation showed no significant correlations with the number of interactions in the observed networks: plant-aphid (ρ = -0.15; p = 0.32), aphid-ladybirds (ρ = 0.02; p = 0.89), and aphid-ant (ρ = -0.20; p = 0.17).

5.3.3. Degree, normalized degree, specialization and species strength.

No significant differences were found in the mean degree between the Azores and the mainland for any trophic level on any network (Table 1; Figure 4).

Regarding the normalized degree, results were also mostly non-significant (Table 1). However, we observed a significant difference for plants in the plant-aphid network between the Azores and the mainland (U = 112.0; p = 0.042) (Table 1; Figure 4).

When examining the species strength results, no significant differences were found between most networks from both regions, except for plants in the plant–aphid network, which showed a significant difference between locations (Azores and mainland) (U = 111.0; p = 0.048) (Table 1; Figure 4), with values being more pronounced on the mainland than in the Azores.

Finally, the results for specialization closely mirrored those of normalized degree, with both plants and aphids being less specialized in the Azores than on the mainland (plant-aphid network), showing a significant difference between the two regions (aphids: U = 54.0; p = 0.037; plants: U = 113.0; p = 0.036) (Table 1; Figure 4), with higher values on the mainland than in the Azores.

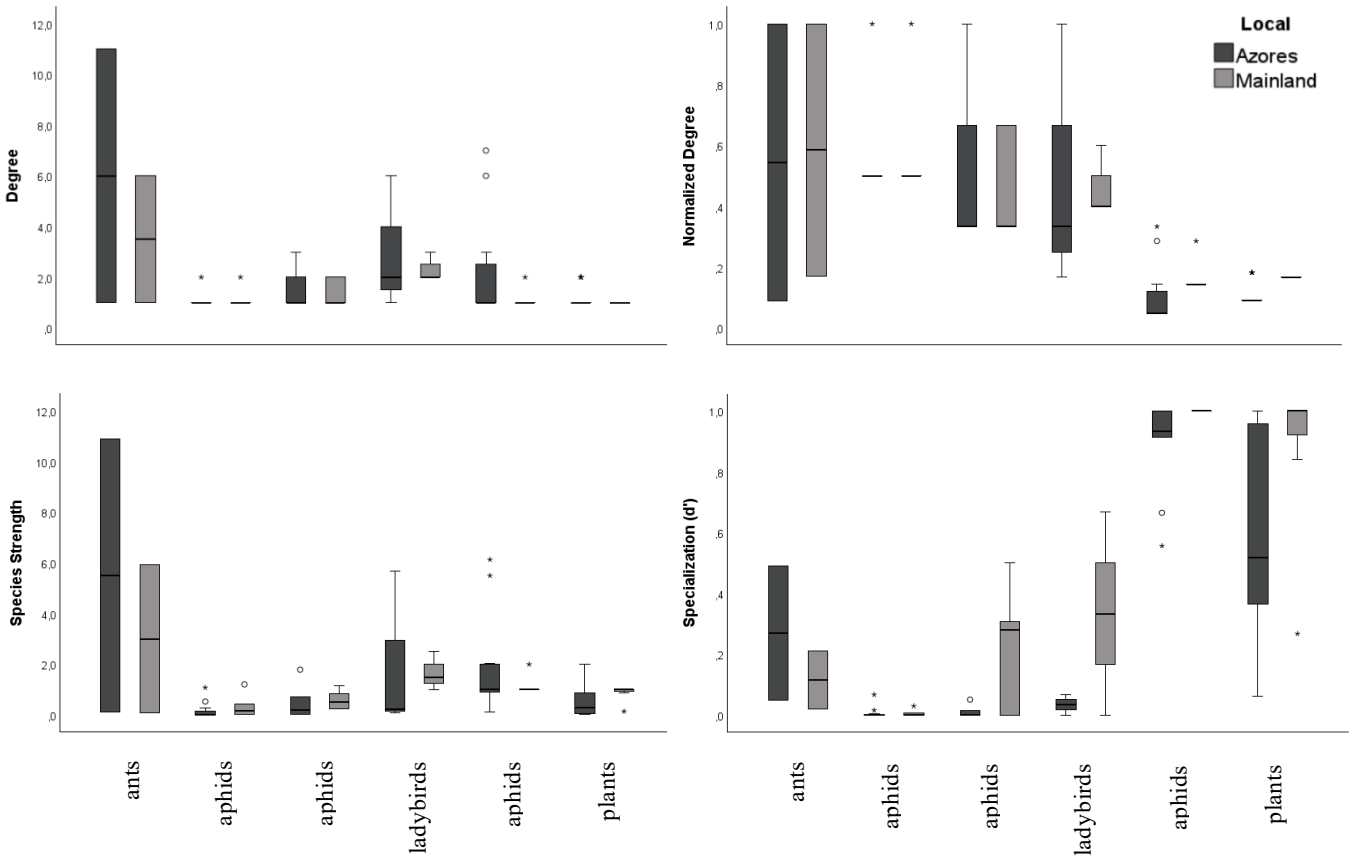

Figure 4. Comparison between mean species roles (degree, normalized degree, species strength and specialization *d*') for each trophic level between the Azores and mainland Portugal networks.

5.4. Discussion

Contrary to our hypothesis, our results indicate greater interaction diversity in the trophic networks of coastal grasslands in the Azores than in mainland Portugal. A higher number of plant species hosting aphids was observed in the coastal grasslands of the Azores (21 species) compared with those on the mainland (6 species) (Table S3). At the same time, more aphid species were found in the Azores (11) than on the mainland (6). The number of ladybirds and ants was consistently low, with three species of ladybirds and two of ants in both regions.

Despite the low number of recorded species, the data provides valuable insights into how trophic networks are structured in both regions. In the Azores, the networks were dominated by introduced plant species such as *Carpobrotus edulis*, *Foeniculum vulgare*, and *Arundo donax* (Campoy et al., 2018), which are known to host various aphid species,

including *Aphis gossypii* and *Melanaphis donacis* Holman 2009). In contrast, on the mainland, native species such as *Dittrichia viscosa* and *Ononis ramosissima* showed the highest number of aphid occurrences (Kavallieratos et al., 2002). Although quantitative data on aphid colony abundance were recorded, they were not integrated into the present analysis due to differences in sampling frequency and standardisation. However, our field observations suggest that *Carpobrotus edulis*, *Arundo donax*, and *Dittrichia viscosa* exhibited high aphid densities. These differences may indicate that the type and composition of vegetation influence the structure and composition of local trophic networks, determining the occurrence of particular species according to host-plant availability and characteristics (Lu et al., 2022; Schuldt et al., 2018).

The ladybird species recorded in this study are generalist aphidophagous predators typically found in low herbage of coastal habitats, including dunes, grasslands, heathlands and scrub. *Hyperaspis pseudopustulata* Mulsant, 1853, and *Oenopia doublieri* (Mulsant, 1846) have a very local distribution and are often found on low vegetation such as reed and reedmace in coastal wetlands (Roy and Brown, 2018; Nedvěd, 2020). *Coccinella septempunctata* Linnaeus, 1758, in turn, is an ubiquitous species also recorded from coniferous, deciduous, and mixed woodlands and agroecosystems on both cereals and broad-leaved crops such as field beans, and also gardens (Hodek et al., 2012, Crowley et al., 2021). Despite the importance of *Scymnus* spp., with more than 600 described species (Rosagro et al., 2020), the distribution status is not well known. The *Scymnus* spp. distribution might include grasslands of coastal areas from Mediterranean area and surrounded crop as corn fields in the Azores (e.g., Borges et al*.,* 2018; Roy and Brown, 2018, Nedvěd 2020; Soares et al. 2021).. Although all ladybird individuals observed on host plants were recorded during sampling, only those showing clear predation behaviour were included in the trophic network analyses. This criterion ensured that only confirmed feeding interactions were considered, avoiding potential overestimation of links based solely on species co-occurrence. Although no direct measurement of floral traits was conducted, Including these variables in future studies could contribute to a better understanding of the trophic dynamics associated with specific vegetation covers.

Despite differences in biodiversity, no significant differences were found in the roles of species within the bipartite aphid-ant and aphid-ladybird networks. In addition, regarding specialization in the same bipartite network, we observed lower specialization among aphids in the Azores compared to the mainland Portugal. In continental environments,

organisms tend to exhibit greater specialization, often associating with fewer plant species than their counterparts in the Azores (Figure 3).

According to the theory of island biogeography, islands are expected to harbour lower biodiversity than continents (MacArthur and Wilson, 1963; Lack, 1973; Whittaker et al., 2017). Therefore, our findings do not conform to the theoretical expectations, which could be caused by several reasons. One factor that may have played a role are the climatic differences between the two regions: the Azores have a more subtropical and humid climate, which supports the growth of mesophytic vegetation more suitable for aphid populations (Rego et al., 2024), while the mainland Portugal has a temperate climate where xerophytic species dominate (Chozas et al., 2017). Indeed, our results appears to support that idea, once we found a positive correlation between the humidity and number of aphids in the Azores and in mainland (Figure 4). In this way, temperature and humidity appears to influence the number of interactions within each trophic web, where more humidity and more temperature are associated with more interactions. By general consensus, predator-prey associations are usually determined by habitat characteristics, phenology, prey size or abundance, or by the presence of natural enemies (Dixon 2000). Therefore, increased resource availability, associate with abundance compensation observed on islands (Calado et al., 2024) could result in reduced specialization. It means that insular ladybird predators may be better adapted to exploit unpalatable prey. If so, palatability and diet breadth may be dynamic traits subject to evolutionary change (Rana et al., 2002).

Another important factor could be differences in the anthropogenic pressure, with Azorean coastal ecosystems likely having experienced greater disturbances than the sampling region on the mainland, leading to shifts in biodiversity. Tourism and commerce could play an important role in this, by introducing more invasive species to the region (Anderson et al., 2015). For example, most plants found interacting with aphids in the Azores were introduced, with some of them considered invasive (Supplementary Table S3). A likely explanation for this pattern is that in insular communities, anthropogenic disturbance has led to changes in the composition and structure of vegetation, favouring the occurrence of annual and opportunistic species (Elias et al. 2019; Silva and Smith, 2006; Rego et al., 2024). Such environments, being more prone to disturbance, show a higher likelihood of harbouring species with ruderal strategies, adapted to unstable conditions and rapid colonisation (Grime, 1977; Wingler, 2023). In contrast, continental

environments, characterised by greater ecological stability, tend to be dominated by perennial species exhibiting competitive or stress-tolerant strategies (Wingler, 2023).

Lastly, because our study lacked sufficient replication of independent networks to statistically compare differences in emergent network structure, we focused instead on comparing species-level descriptors between the Azorean and mainland networks. This approach still provides valuable insights into the drivers of biotic interactions in the Azores and on the mainland, how trophic networks are structured, which organisms play key roles within them, and the potential consequences of their decline or extinction. It is known that certain organisms play a disproportionately important role in ecological networks, and their loss can lead to the collapse of entire systems through cascading effects (Van Veen and Sanders, 2013). Others, in contrast, may be lost with minimal structural impact, as their ecological roles can be more easily replaced by existing species. Arthropod communities contribute to numerous ecosystem services, and the loss of many of these organisms could have devastating ecological consequences (Isaacs et al., 2009, Noriega et al., 2018).

Finally, this type of study may prove useful for the development of conservation and ecosystem monitoring programs, as well as for the creation of biocontrol strategies aiming to mitigate anthropogenic impacts on a given ecosystem. For instance, given the agricultural landscape of the Azores, many arthropod species may play vital roles in adjacent farmlands through pollination, nutrient recycling, or biological pest control (e.g., Sodhi and Ehrlich, 2010; Ferrante et al., 2022). Further research is needed to clarify if the patterns shown here, namely that of greater diversity of plant-herbivore diversity in the Azores than in mainland Portugal, are indeed a general rule or a particular sampling artefact.

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Appendix A

Supplementary Table S1. Location, coordinates, and verbatim locality of the sampled plots in São Miguel Island (AZ – Azores), Setubal Peninsula, and Sines (ML – mainland Portugal).

Location ID	Coordinates	Locality
AZ_01	37°44′48″ N 25°42′46″ W	Relva
AZ_02	37°51′40″ N 25°51′12″ W	Ferraria
AZ_03	37°53′57″ N 25°49′04″ W	Mosteiros
AZ_04	37°49′53″ N 25°39′30″ W	São Vicente
AZ_05	37°49′26″ N 25°36′15″ W	Calhetas
AZ_06	37°50′05″ N 25°30′40″ W	Ribeira Grande
AZ_07	37°50′31″ N 25°30′01″ W	Ribeirinha
AZ_08	37°46′43″ N 25°37′25″ W	Ponta Delgada
AZ_09	37°45′34″ N 25°39′31″ W	Ponta Delgada
AZ_10	37°45′00″ N 25°37′17″ W	Ponta Delgada
AZ_11	37°45′05″ N 25°34′58″ W	Lagoa
AZ_12	37°43′07″ N 25°27′04″ W	Vila Franca do Campo
ML_01	38°25′01″ N 9°12′43″ W	Cabo Espichel
ML_02	38°25′11″ N 9°12′42″ W	Cabo Espichel
ML_03	38°25′12″ N 9°12′04″ W	Cabo Espichel
ML_04	38°25′56″ N 9°10′25″ W	Azoia
ML_05	38°26′32″ N 9°08′42″ W	Azoia
ML_06	38°26′47″ N 9°09′17″ W	Azoia
ML_07	38°26′58″ N 9°12′01″ W	Meco
ML_08	38°27′16″ N 9°11′51″ W	Meco
ML_09	38°27′43″ N 9°11′34″ W	Meco
ML_10	37°51′42″ N 8°47′36″ W	Porto Covo
ML_11	37°53′57″ N 8°47′52″ W	Sines
ML_12	37°54′57″ N 8°48′08″ W	Sines

Supplementary Table S2. Humidity, temperature, altitude, and number of interactions by spot and by months in each location (Azores and mainland). Legend: Hum. – humidity; Temp. – temperature; Alt. – altitude; N. Int – number of interactions.

	Azores						Mainland					
Month 1				**N. Int.**			**Month 1**				**N. Int.**	
Spot	**Hum. (%)**	**Temp. (ºC)**	**Alt (m)**	**Hos/Aph**	**Aph/Lad**	**Aph/Ant**	**Spot**	**Hum. (%)**	**Temp. (ºC)**	**Alt (m)**	**Hos/Aph**	**Aph/Lad**	**Aph/Ant**
1	58,6	19,8	53	2	0	0	1	53	17,2	125	0	0	0
2	78,1	20,8	8	0	0	0	2	54,9	15,6	131	0	0	0
3	61	22,7	5	3	0	2	3	46	20,5	146	0	0	0
4	55,7	21,1	15	0	0	0	4	49,8	16,7	172	0	0	0
5	56,1	20,4	7	0	0	0	5	49,9	14,7	195	0	0	0
6	77,8	15,2	23	0	0	0	6	38,4	13,3	195	0	0	0
7	78,2	14,7	35	1	0	0	7	58,7	17,1	46	0	0	0
8	83,9	18,6	189	1	0	0	8	44,6	19,2	42	0	0	0
9	47,5	22,7	100	0	0	0	9	49,6	20,4	40	0	0	0
10	42,8	23,1	8	0	0	0	10	45,3	20,8	12	2	0	1
11	60,8	24,5	50	0	0	0	11	61,1	18,5	11	0	0	0
12	75	26,5	65	0	0	0	12	52,3	22,3	6	0	0	0
Mean	**64,63**	**20,84**	**46,50**	**0,58**	**0,00**	**0,17**	**Mean**	**50,30**	**18,03**	**93,42**	**0,17**	**0,00**	**0,08**
Month 2				**N. Int.**			**Month 2**						
Spot	**Hum. (%)**	**Temp. (ºC)**	**Alt (m)**	**Hos/Aph**	**Aph/Lad**	**Aph/Ant**	**Spot**	**Hum. (%)**	**Temp. (ºC)**	**Alt (m)**	**Hos/Aph**	**Aph/Lad**	**Aph/Ant**
1	62,7	22,5	53	17	8	8	1	36	20,2	125	0	0	0
2	51,5	26,3	8	0	0	0	2	37,4	21,8	131	0	0	0
3	69,7	21,1	5	37	1	5	3	34,3	20,4	146	0	0	0
4	72,4	19,6	15	6	0	3	4	31,5	15,1	172	0	0	0
5	69,3	23	7	2	0	2	5	42,9	13,6	195	1	1	0
6	61,1	24,7	23	8	0	1	6	38,7	14,4	195	0	0	0
7	58,2	26	35	8	1	3	7	42	17	46	0	0	0
8	66,4	20,2	189	4	0	3	8	44,8	22,4	42	0	0	0
9	63,5	24,5	100	2	1	1	9	42	22,3	40	0	0	0
10	60	26,7	8	2	0	0	11	57,1	16	12	0	0	0
11	58,8	27,1	50	1	1	1	13	53,1	20,5	11	0	0	0
12	47	26,1	65	5	0	4	15	41,9	19,2	6	3	0	3
Mean	**61,72**	**23,98**	**46,50**	**7,67**	**1,00**	**2,58**	**Mean**	**41,81**	**18,58**	**93,42**	**0,33**	**0,08**	**0,25**
Month 3				**N. Int.**			**Month 3**				**N. Int.**		
Spot	**Hum. (%)**	**Temp. (ºC)**	**Alt (m)**	**Hos/Aph**	**Aph/Lad**	**Aph/Ant**	**Spot**	**Hum. (%)**	**Temp. (ºC)**	**Alt (m)**	**Hos/Aph**	**Aph/Lad**	**Aph/Ant**
1	66	22,5	53	7	0	7	1	51,4	24,9	125	1	1	1
2	63,4	24,1	8	7	0	5	2	58,1	24,1	131	0	0	0
3	54,2	26	5	29	4	21	3	65,8	21,2	146	0	0	0
4	69,6	23,3	15	16	1	15	4	61,9	23,3	172	0	0	0
5	60,9	24,6	7	3	1	2	5	58,8	21,8	195	0	1	0
6	61,6	23,1	23	15	2	11	6	57,4	21,9	195	0	0	0
7	52,1	27,6	35	6	4	5	7	59,2	22,6	46	0	0	0

8	58,4	23,2	189	1	0	1	8	48,9	28,2	42	0	0	0
9	69,2	22,8	100	10	0	10	9	61,9	21,8	40	4	0	3
10	58,9	24,8	8	1	0	0	11	78,4	19,2	12	0	0	0
11	53,8	24,4	50	2	0	1	13	49,9	28,3	11	0	0	0
12	70,1	22,8	65	14	0	14	15	76,5	18,8	6	0	0	0
Mean	**61,52**	**24,10**	**46,50**	**9,25**	**1,00**	**7,67**	**Mean**	**60,68**	**23,01**	**93,42**	**0,42**	**0,17**	**0,33**

Month 4				**N. Int.**			**Month 4**				**N. Int.**		
Spot	**Hum. (%)**	**Temp. (°C)**	**Alt (m)**	**Hos/Aph**	**Aph/Lad**	**Aph/Ant**	**Spot**	**Hum. (%)**	**Temp. (°C)**	**Alt (m)**	**Hos/Aph**	**Aph/Lad**	**Aph/Ant**
1	77,1	25,9	53	20	3	18	1	74,2	21,3	125	7	0	6
2	63,1	28,2	8	5	1	3	2	77,7	20	131	1	0	0
3	68,8	26,6	5	16	1	15	3	65,5	23,6	146	4	1	4
4	59,6	27	15	10	0	10	4	60,6	24,8	172	2	0	1
5	58,9	29,4	7	2	2	1	5	65,5	23,1	195	3	1	3
6	50,7	29,2	23	2	0	2	6	64,8	23,5	195	2	0	2
7	65	25,1	35	7	0	7	7	53,1	28,5	46	1	0	1
8	70	26,3	189	6	1	6	8	52,6	28,1	42	2	0	2
9	65,4	27,5	100	5	1	5	9	58,6	28,8	40	5	1	4
10	62,3	27,6	8	3	1	0	11	66	24,4	12	13	2	10
11	54,5	29,6	50	1	0	1	13	58	26,5	11	9	1	8
12	65,1	27,7	65	5	0	4	15	65,1	24,8	6	5	1	5
Mean	**63,38**	**27,51**	**46,50**	**6,83**	**0,83**	**6,00**	**Mean**	**63,48**	**24,78**	**93,42**	**4,50**	**0,58**	**3,83**

Supplementary Table S3. List of species identified with interactions for the Azores and mainland. Legend: N – native non-endemic; I – introduced; Inv – invasive; NA – not attributed according to (Borges et al., 2022).

Plant species with aphids	Azores	Mainland	Establishment mean
Arundo donax	X	X	Inv
Banksia integrifolia	X		I
Carpobrotus edulis	X	X	Inv
Daucus carota	X		NA
Delairea odorata	X		I
Dittrichia viscosa		X	N
Echium creticum subsp. creticum	X		NA
Erigeron annuus	X		NA
Foeniculum vulgare	X		I
Galactites tomentosa	X		I
Holcus lanatus	X		Inv
Hypericum perforatum		X	N
Leontodon sp.	X	X	N
Lotus sp.	X		I
Oenothera indecora	X		I
Ononis ramosissima		X	N
Plantago lanceolata	X		I

Rumex sp.	X		Inv
Scolymus hispanicus		X	N
Solanum mauritianum	X		Inv
Sonchus tenerrimus	X		I
Symphytum officinale	X		I
Thymus vulgaris	X		I
Verbena bonariensis	X		I
Vicia sp.	X		I
Aphid species			
Aphis fabae	X	X	I
Aphis gossypii	X		N
Aphis sp.	X		NA
Aphis spiraecola	X		I
Capitophorus sp.		X	NA
Cavariella aegopodii	X		I
Dysaphis foeniculus	X		N
Hyperomyzus lactucae	X		I
Megoura viciae	X		NA
Melanaphis donacis	X	X	I
Myzus persicae	X	X	I
Therioaphis sp.		X	NA
Uroleucon sonchi	X	X	NA
Ladybird species			
Oenopia doublieri	X		I
Scymnus interruptus	X		N
Scymnus nubilus	X		N
Scymnus sp.		X	NA
Coccinella septempunctata		X	NA
Hyperaspis pseudopustulata		X	NA
Ant species			
Camponotus sp.		X	NA
Tapinoma sp.		X	NA
Lasius grandis	X		N
Tetramorium sp.	X		NA

Supplementary Table S4. List of plant species identified, sites where was observed interactions (Azores and mainland), and life cycle (Royal Botanic Gardens, Kew, 2025). Legend: N. Sit. Az. – Number of sites in the Azores; N. Sit. Ml. – Number of sites in mainland.

Plant species	N. Sit. Az.	N. Sit. Ml.	Life cycle
Arundo donax	9	2	Perennial
Banksia integrifólia	1		Perennial
Carpobrotus edulis	5	5	Perennial
Daucus carota	4		Biennial
Delairea odorata	2		Perennial
Dittrichia viscosa		8	Perennial
Echium creticum subsp. creticum	1		Biennial
Erigeron annuus	2		Annual/Biennial
Foeniculum vulgare	1		Perennial
Galactites tomentosa	3		Annual/Biennial
Holcus lanatus	1		Perennial
Hypericum perforatum		1	Perennial
Leontodon sp.	1	1	Indeterminate/varies
Lotus sp.	9		Indeterminate/varies
Oenothera indecora	1		Annual/Biennial
Ononis ramosissima		2	Perennial
Plantago lanceolata	3		Perennial
Rumex sp.	3		Indeterminate/varies
Scolymus hispanicus		2	Indeterminate/varies
Solanum mauritianum	3		Perennial
Sonchus tenerrimus	7		Indeterminate/varies
Symphytum officinale	1		Perennial
Thymus vulgaris	1		Perennial
Verbena bonariensis	1		Perennial
Vicia sp.	2		Indeterminate/varies

Chapter 6. Consequences of slow and fast development in *Scymnus nubilus*: effect of prey type

Abstract

Understanding how prey type influences development and reproductive performance in predatory insects is essential for predicting their adaptive potential and effectiveness as biological control agents. This study examined the effect of two aphid species with different eco-physiological suitability – *Aphis fabae* Scopoli and *Myzus persicae* (Sulzer) – on the developmental rate and reproductive traits of the ladybird *Scymnus nubilus* Mulsant. Individuals fed on *A. fabae* developed significantly faster, achieved higher body weights, and produced more eggs than those reared on *M. persicae*. Two distinct developmental patterns, fast and slow, were identified. Fast-developing individuals exhibited shorter pre-oviposition periods and higher fecundity, indicating superior fitness. These results highlight the presence of phenotypic plasticity within *S. nubilus* populations, suggesting that developmental flexibility may facilitate adaptation to varying prey environments. Such intraspecific variation has important implications for understanding adaptive potential in insular ecosystems and for optimising the use of *S. nubilus* as a biological control agent under changing environmental conditions.

Keywords: life-history traits; phenotypic plasticity; *Scymnus nubilus*; prey suitability; biological control; island adaptation

6.1. Introduction

The processes of speciation and adaptive radiation on islands have long captivated evolutionary biologists, as these isolated systems serve as natural laboratories where the mechanisms driving diversification, endemism, and extinction can be directly studied and compared across taxa (Warren et al., 2015; Borregaard et al., 2017; Alhmedi et al., 2018). The way in which many organisms evolve and adapt to specific environments, as well as the mechanisms that lead to isolation and the formation of new species, continues to raise questions and generate controversy (Thornton and New, 2007). Several factors are pointed out as drivers of evolution in isolated environments, including climate, geographical distance, area, absence of predators, genetic drift, and the founder effect (MacArthur and Wilson, 1963; Larson et al., 2010; Petalas et al., 2024). Terrestrial

arthropods, and insects in particular, stand out as one of the most successful groups in colonizing new habitats, being widely used in evolutionary studies and models (Borges et al., 2011; Hembry et al., 2021).

Life histories can be defined as the age-specific probabilities of survival and reproduction throughout the lifespan (Partridge and Harvey, 1988). In addition to mortality and fecundity, other traits, such as development rate, maturation and females body weight, also affects life history . The evolution of life history traits by natural selection depends upon genetic variation on which selection can act to produce adaptations in response to environmental heterogeneity. High genetic variation, however, does not mean high heritability of life history traits due to high phenotypic variation engendered by the environment (i.e., phenotypic plasticity, genotype by environment interactions) (Fabian and Flatt, 2012).This means that, although life history traits are under strong selection, which should erode genetic variance, several factors can maintain genetic and phenotypic variation for these traits, including environmental heterogeneity (Stearns, 1992; Roff, 1993); Houle, 2001; Gibert et al., 2019). Given the characteristics of island ecosystems, with relatively simple architectures compared to mainland counterparts (Graham et al., 2017), we should expect that the erosion of genetic and phenotypic variance could be higher in these ecosystems. However, such erosion may not occur under the environmental conditions of the Azores, given the higher arthropod species richness and diversity of the coastal grasslands of São Miguel Island (Azores) (Calado et al., 2024), including the species richness and diversity of aphid resources for aphidophagous predators (Calado et al., 2025).

Due to the role of ladybirds (Coleoptera: Coccinellidae) as biological control agents, its food relationships, an important component of its ecology, have attracted the attention of applied and evolutionary ecologists (e.g., Rana et al., 2002; Soares et al., 2004; Borges et al., 2011). Many studies have documented the effects of different prey on life-history traits, including development rate, adult body weight and fecundity, which have been used to assign prey to different categories of suitability (e.g. Michaud, 2005; Hodek et al., 2012). Despite their stenophagy (Hodek et al., 2012), laboratory experiments seem to confirm the general view that ladybird predators have broad diets (e.g. Bristow, 1988; Albuquerque et al., 1997; Evans, 2003), and development rate can be a surrogate in the identification of optimal abiotic and biotic conditions. Although abiotic conditions are the main factors that directly influence the presence of a given organism. Biotic factors

also play an important role, influencing a species' ability to establish itself even when it exhibits a high level of invasiveness. (Soares et al., 2018, 2017). It is well established that intra- and interspecific interactions largely depend on fluctuations in these two sets of factors (abiotic and biotic), which directly influence development rates (Singh et al., 2024).

Within ladybird species, development rate appear to exhibit plasticity (Jalali et al., 2014; Singh et al., 2016; Singh et al., 2024), being faster under favourable abiotic and biotic conditions and slower under adverse ones (Hodek et al., 2012), which, in turn, may determine females' fecundity. However, field observations indicate that ladybirds exhibit specific habitat preferences, narrowing their prey range (e.g., (Honěk, 2012). Moreover, laboratory experiments reveal that ladybirds previously selected for better performance on an aphid species performed significantly worse when reared to a different aphis species. That is, specialization on one species of aphid resulted in a poorer performance on another (Rana et al., 2002). Food resource diversity may trigger eco-physiological responses in terms of development rate and fitness, where a better-adapted organism will develop more rapidly and present higher fitness, which may, ultimately, determine the adaptative success and the maintenance of phenotypic plasticity. However, there have been very few studies directly addressing phenotypic plasticity which could determine habitat preference and dietary shifts in ladybirds.

The genus *Scymnus*, the most diverse within the Coccinellidae family, includes more than 800 species (Chen et al., 2015). Many of species are generalist predators presenting a high potential as biological control agents against different major agroforestry pests (Borges et al., 2013; Çelebi and Kaplan, 2025; Rosagro et al., 2020). The present study aims to explore the: i) existence of slow and fast developing immature stages of *Scymnnus nubilus* Mulsant when fed on two different aphid species, with different levels of suitability [(*Aphis fabae* Scopoli and *Myzus persicae* (Sulzer), the most and least suitable, respectively (Borges et al., 2024, p. 202)] and ii) consequences of slow and fast development rates on sex-ratio, adult body weight and reproductive attributes. Considering the availability of food resources in the coastal grasslands of the Azores (high environmental heterogeneity in terms of species richness and abundance of aphids), the most suitable habitat for *S. nubilus* (Soares et al., 2017; Calado et al., 2025), we hypothesis the existence of slow and fast developers in the immature stages of *S. nubilus*, but a better performance when predators fed on *A. fabae*, which in turns will translate into

a reduction in the length of sexual maturation, increase in adult body weight and greater fitness.

6.2. Methodology

6.2.1. Parental generation

Adults of *S. nubilus* were collected in coastal grasslands of the Santa Clara area, São Miguel Island, Azores, Portugal (37°44′17.65″ N, 25°42′1.14″ W), using an entomological sweep net (40 cm diameter, 50 cm length, 0.25 mm mesh). Specimens were transported to the laboratory, paired and placed in plastic boxes (10 cm diameter × 2.5 cm height) with lids with a 0.25 mm metal mesh. Pairs were divided into two populations (n = 10 pairs each) and fed daily *ad libitum* with aphids. One population was supplied with *A. fabae*, reared on *Vicia faba* (L.) under controlled conditions (15 ± 1 °C; 65 ± 5% RH; 16L:8D). The second population was fed *M. persicae*, reared on *Vicia faba* under controlled conditions (20 ± 1 °C; 65 ± 5% RH; 16L:8D). All pairs also received a supplementary food source consisting of honeydew on a moistened cotton, replaced every day. Both populations were maintained for 4 weeks under controlled conditions (20 ± 1 °C; 65 ± 5% RH; 16L:8D). Eggs laid during this period were collected for subsequent experiments.

6.2.2. Assessment of the occurrence of slow and fast development rates

From each laboratory population, 120 eggs were collected (total = 240) and individually placed inside a 2.5 cm diameter plastic boxes with mesh-covered lids. Two cohorts were set: i) larvae fed under single diets of *A. fabae* (N = 120) or *M. persicae* (N = 120). Eggs and larvae were maintained under controlled conditions (20 ± 1 °C; 65 ± 5% RH; 16L:8D) and monitored twice daily until adult emergence. Food was replaced every day. The sex and the body weight of the adults obtained were recorded.

6.2.3. Effects of immature slow and fast development rates on sex-ratio, adult body weight and reproduction.

Adults obtained in each cohort were classified in two groups: fast-developing and slow-developing individuals.

Four experimental groups were established, each consisting of 10 pairs (n = 40 pairs): Fast Development *A. fabae* (FDAf), Slow Development *A. fabae* (SDAf), Fast Development *M. persicae* (FDMp), and Slow Development *M. persicae* (SDMp). Groups were maintained under the same controlled conditions and provided daily *ad libitum* with the same aphid species and honeydew as supplement. A piece of cotton was placed inside the petri dish to stimulate oviposition and facilitate egg collection (Soares et al., 2025). For each pair, pre-oviposition period, fertility, and fecundity were recorded over 15 days from the first oviposition.

Eggs laid were collected daily by transferring the cotton substrate to 5 cm diameter Petri dishes (1 cm height), labelled, and maintained under the same conditions. Eggs were monitored once daily for 10 days, and the number of eggs that hatched was recorded.

6.2.4. Data Analysis

Data normalities were assessed using the Shapiro–Wilk test, applied to each dataset representing the four development rates of *S. nubilus* (FDAf, SDAf, FDMp, and SDMp). The results indicated no significant deviation from normal distribution ($p > 0.05$). To visually evaluate the goodness of fit to normal distribution, fitted normal probability density curves were generated for each dataset using the observed mean (μ) and standard deviation (σ). These curves were computed in Microsoft Excel using the normal probability density function, which describes the expected theoretical distribution under normality (Zar, 2010):

$$f(x) = \frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{(x-\mu)^2}{2\sigma^2}}$$

Development time of immature stages, pre-oviposition period of females, females' fecundity, and body weight of both females and males of fast and slow developing *S. nubilus* fed on *A. fabae* or *M. persicae* were statistically analysed using a Generalized Linear Model (GZLM). GZLM analyses considered the normal error distribution and the identity link function. When data did not meet the assumption of normality, a Poisson error distribution with a log link function was applied. Pairwise multiple comparisons were carried out, and *p*-values were corrected using the Bonferroni test.

The statistical significance of sex ratios in adults originating from fast or slow developing larvae, fed on *A. fabae* or *M. persicae*, was assessed by comparing the observed sex proportions against an expected 1:1 ratio. Mean values were considered significantly different when $p < 0.05$. All statistical analyses were conducted using SPSS v.29.0.1 (IBM Corporation, 2025).

6.3. Results

6.3.1. Fast and slow patterns

According to the results, the data followed a normal distribution, showing no significant deviations ($p > 0.05$; Shapiro–Wilk test) (Table 1).

Table 1. Results of the Shapiro–Wilk test assessing the normality of immature development time distributions for *S. nubilus* under different cohort.

Cohort	Shapiro–Wilk W	df	p-value	Normality
FDAf	0.971	32	0.523	Normal ($p > 0.05$)
SDAf	0.944	30	0.116	Normal ($p > 0.05$)
FDMp	0.962	44	0.151	Normal ($p > 0.05$)
SDMp	0.944	39	0.052	Normal ($p > 0.05$)

For both cohorts, a similar normal distribution patterns in immature development were observed: Fast and Slow (Figure 1). The fitted normal density curves (blue lines in Figure 1) depict the ideal Gaussian distributions based on the observed parameters.

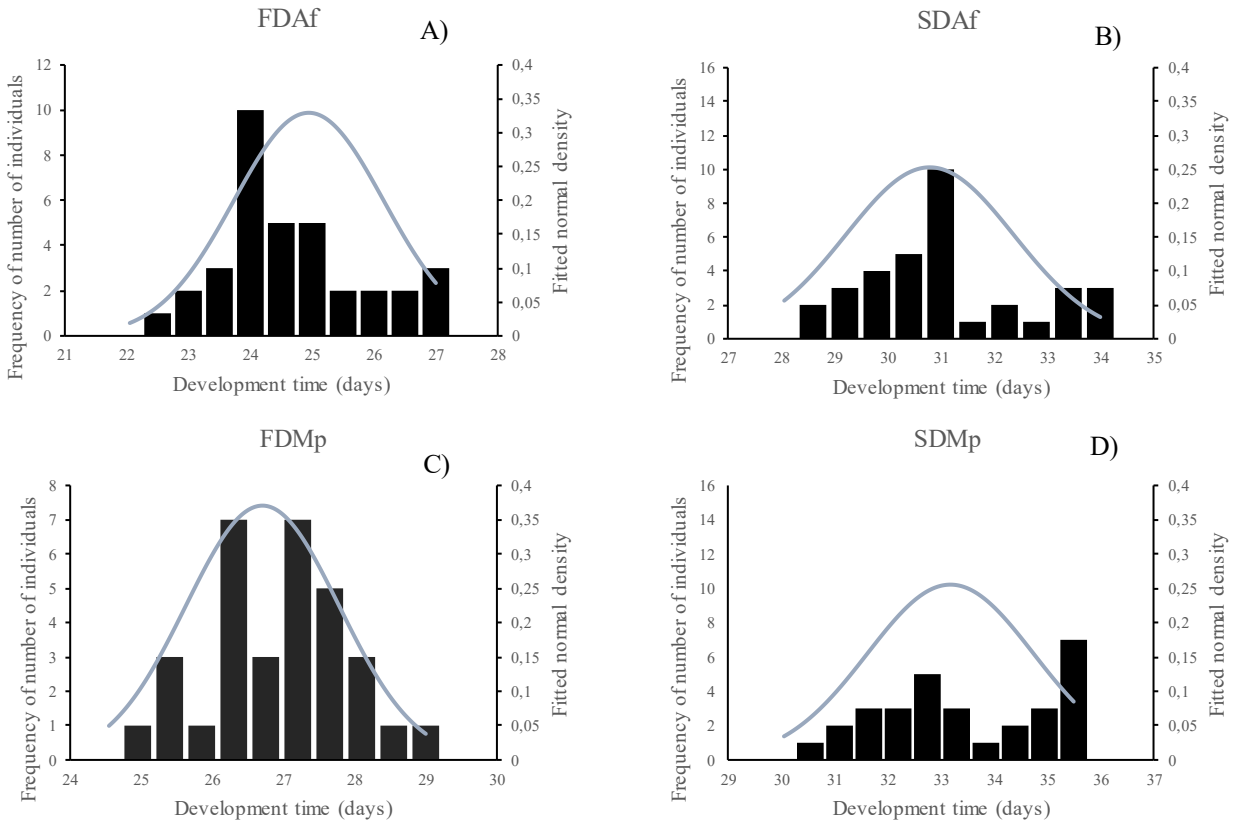

Figure 1. Frequency distribution of total development time and fitted normal density (blue line) of *S. nubilus* under two treatments: A) Fast development with A. fabae (FDAf); B) Slow development with *A. fabae* (SDAf); C) Fast development with *M. persicae* (FDMp); D) Slow development with *M. persicae* (SDMp).

6.3.2. Assessment of the occurrence of slow and fast development rates

No significant interaction was found between the factors immature developmental time (fast or slow developers) and the prey species (*A. fabae* or *M. persicae*) ($\chi^2 = 2.591$, df = 1, p = 0.107). Developmental time (days ± SE) of fast developers (25.69 ± 0.15 days) was significantly lower (31.80 ± 0.15 days) than slow developers ($\chi^2 = 755.84$, df = 1, $p \leq 0.0001$) and immature stages of *S. nubilus* develop faster when fed with *A. fabae* (27.56 ± 0.14 days) than those fed with *M. persicae* (29.93 ± 0.16 days) ($\chi^2 = 111.89$, df = 1, $p \leq 0.001$; Table 2).

Table 2. Development time of the fast and slow developering larvae of *S. nubilus* fed on *A. fabae* or *M. persicae*.

	A. fabae		***M. persicae***	
Immature life-history trait	**Fast Developing**	**Slow Developing**	**Fast Developing**	**Slow Developing**
Development time (days ± SE)	24.69 ± 0.20a	30.44 ± 0.20c	26.70 ± 0.23b	33.16 ± 0.24d

Effects of immature slow and fast development rates on sex-ratio, adult body weight and reproduction Sex ratio of adults originating from fast or slow developing larva, fed on *A. fabae* did not significantly differ (Total: $\chi^2 = 0.3205$, df = 1, p = 0.571). No significant difference was found for fast ($\chi2 = 0.9848$, df = 1, p = 321) and slow developing larva ($\chi2 = 0.08$, df = 1, p = 0.777) (Figure 2). Sex ratio of adults originating from fast or slow developing larva, fed on *M. persicae* did not significantly differ (Total: $\chi2 = 1.2882$, df = 1, p = 0.256). No significant difference was found for fast ($\chi2 = 0.1802$, df = 1, p = 0.671), but it was significant for slow developing larva ($\chi2 = 8.333$, df = 1, p = 0.0038) (Figure 2).

Concerning pre-oviposition length of females (days ± SE), no significant interaction was found between the factors immature developmental time (fast or slow developers) and the prey species (*A. fabae* or *M. persicae*) ($\chi^2 = 2.314$, df = 1, p = 0.128). Pre-oviposition period length of females from fast developers (4.22 ± 0.46 days) were significantly lower (6.56 ± 0.57 days) than females from slow developers ($\chi^2 = 9.904$, df = 1, p = 0.002) and pre-oviposition period length of females fed with *A. fabae* (5.26 ± 0.52 days) than those fed with *M. persicae* (5.26.93 ± 0.51 days) ($\chi^2 = 0.$, df = 1, *p* = 0.999; Table 3).

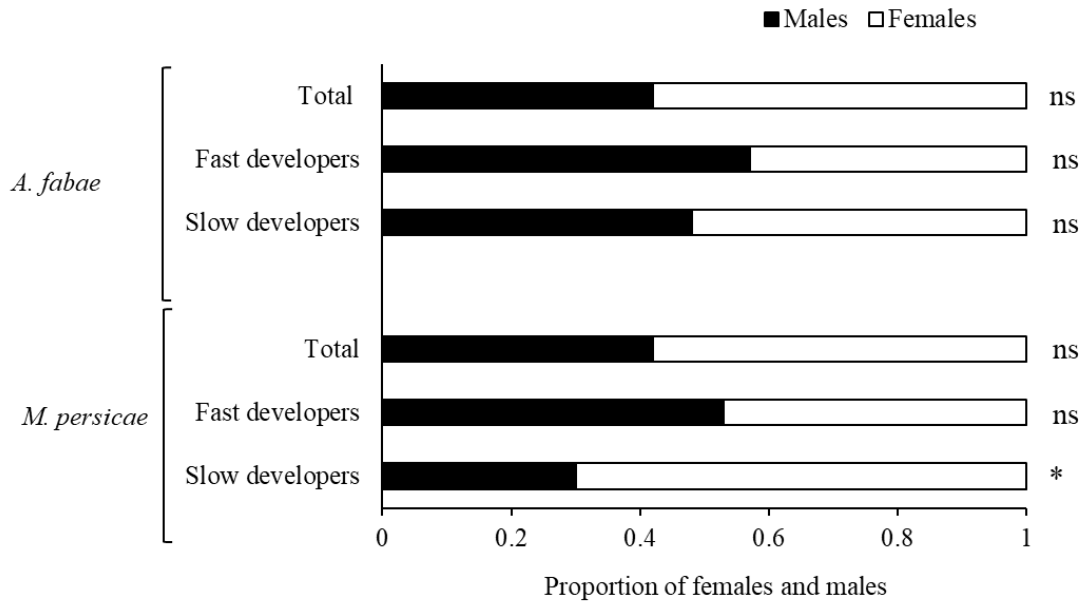

Figure 2. Sex ratios by adults originating from fast or slow developing larva, fed on *A. fabae* or *M. persicae*. Legend: asterisk means significant differences (p < 0.05).

In terms of females' fecundity (total number of eggs laid for 15 days ± SE), there was a significant interaction between the factors immature developmental time (fast or slow developers) and the prey species (*A. fabae* or *M. persicae*) ($\chi^2 = 54.155$, df = 1, p = 0.001). Fecundity of females originating from fast developing larva (140.4 ± 2.7 eggs), was significantly lower (42.6 ± 1.6 eggs) than females fecundity originating from slow developing larva ($\chi^2 = 792.5$, df = 1, $p \leq 0.001$) and fecundity of females fed with *A. fabae* (125.0 ± 2.6 eggs) than those fed with *M. persicae* (47.9 ± 1.7 eggs) ($\chi^2 = 513.1$, df = 1, $p \leq 0.001$; Table 3).

Table 3. Life-history traits of the fast and slow developers of immature stages of *S. nubilus* fed on *A. fabae* or *M. persicae*.

	A. fabae		***M. persicae***	
Adult life-history traits	**Fast developers**	**Slow developers**	**Fast developers**	**Slow developers**
Pre-oviposition length (days ± SE)	3.8 ± 0.61a	7.3 ± 0.85b	4.7 ± 0.68a	5.9 ± 0.76a
Fecundity (eggs laid 15 days ± SE)	194.1 ± 4.4a	80.5 ± 2.8c	101.6 ± 8.0b	22.6 ± 1.5d
Adult body weight (mg ± SE)				
Males	1.18 ± 0.02a	1.08 ± 0.03ab	0.96 ± 0.02b	1.00 ± 0.04b
Females	1.55 ± 0.02a	1.58 ± 0.03a	1.09 ± 0.03c	1.27 ± 0.02b

Concerning males body weight (mg ± SE), there was a significant interaction between the factors immature developmental time (fast or slow developers) and the prey species (*A. fabae* or *M. persicae*) ($\chi^2 = 4.532$ df = 1, p = 0.033). In general, males body weight originating from fast developing larva (1.07 ± 0.02 mg) did not significantly differ from males body weight originating from slow developing larva (1.04 ± 0.02 mg) ($\chi^2 = 1.213$, df = 1, p = 0.271) but body weight of males previously fed with *A. fabae* (1.13 ± 0.02 mg) are significantly higher than males body weight previously fed with *M. persicae* (0.98 ± 0.02 mg) ($\chi^2 = 21.83$, df = 1, $p < 0.001$; Table 3). Overall, pairwise comparison reveals that body weight of males originating from fast developing larva and previously fed with *A. fabae* are significantly heavier (Table 3).

Concerning females body weight (mg ± SE), there was a significant interaction between the factors immature developmental time (fast or slow developers) and the prey species (*A. fabae* or *M. persicae*) ($\chi^2 = 6.09$ df = 1, p = 0.014). In general, females body weight originating from fast developing larva (1.32 ± 0.02 mg) significantly differ from females body weight originating from slow developing larva (1.42 ± 0.02 mg) ($\chi^2 = 13.342$, df = 1, $p < 0.001$) and body weight of females previously fed with *A. fabae* (1.57 ± 0.02 mg) are significantly higher than females body weight previously fed with *M. persicae* (1.18

± 0.01 mg) ($\chi^2 = 182.52$, df = 1, $p \leq 0.001$; Table3). Overall, pairwise comparison reveals that body weight of females previously fed with *A. fabae* are significantly heavier (Table 3).

6.4. Discussion

For predatory ladybirds, different aphid species represent food resources with different levels of suitability. Despite their polyphagy as to accepted food, coccinellids are very specific as far as essential food is concerned (Soares et al., 2004). Different prey may lead to significant changes in immature survival rates, development times and body weights of emerging adults. The rate of sexual maturation, as well as fecundity and fertility, are also altered depending on prey quality (Michaud, 2005; Hodek et al., 2012). In this study, we predicted a better performance of *S. nubilus* fed on *A. fabae*. Indeed, our results reveal a better performance for immature developmental time, fecundity, and pre-oviposition length when *A. fabae* was provided. The results agree with previous findings in which *A. fabae* has been shown to be a more suitable prey for *S. nubilus*(Borges et al., 2024).

We can ask to what extent food specialization results strictly from selection driven by prey limitation or, alternatively, from selection driven by habitat preferences. The answer to that question is, however, unclear. Ferrer et al. (2016) carried out a study to disentangle the role of the habitat or prey quality on prey specialization of two closely related predatory ladybird beetles, the arboreal *Adalia decempunctata* (L.) and the habitat generalist *A. bipunctata* (L.). The authors predicted that *A. decempunctata* females would be adversely affected by consuming an aphid that they are unlikely to regularly feed on in the field (*Acyrtosiphon pisum* (Harris)). However, average body mass of *A. bipunctata* and *A. decempunctata* were similar independently of the trees from which prey was collected and did not significantly differ from that of laboratory females reared on unusual prey for *A. decempunctata*. Moreover, the difference between the larval growth rates when fed on *Eucallipterus tiliae tiliae* (L.) and *A. pisum* was larger for *A. decempunctata* larvae than for *A. bipunctata*. In terms of reproductive performance, again, *A. decempunctata* laid more eggs and did not change the condition of the gonads when fed on the unusual *Rhopalosiphum padi* (L.) compared to aphids they usually fed on in the field. Overall, this study failed to demonstrate a better efficiency of the specialist when fed its usual prey and a detrimental effect when fed on prey that it is unlikely to encounter

in the field. Therefore, the authors claimed that the narrow diet of the specialist ladybird is most likely a consequence of it occupying a narrow habitat rather than the quality of the prey. In the coastal grasslands of the Azores, *M. persicae* are not found but *A. fabae* is one of the most abundant aphid species (Calado et al., 2024). Considering that *S. nubilus* is mostly found in coastal grasslands of the archipelago, our results seem to support Ferrer et al. (2016) claim, that is, the better performance of the *S. nubilus* fed on *A. fabae* may result from occupying a narrow habitat rather than from the quality of the prey.

We hypothesised the existence of slow and fast developing larvae of *S. nubilus*. Similar to a previous study (Pandey et al., 2013), our results revealed the existence of two significantly different developmental rates in a cohort of *S. nubilus*, regardless of the aphid provided as a food source (Figure 1). Furthermore, the rate of development of the immature stages of *S. nubilus* translated into a reduction in the length of sexual maturation, increase in adult body weight and greater fitness. Such patterns have previously been reported in few other studies, including the phytophagous beetle *Zygogramma bicolorata* Pallister (Coleoptera: Chrysomelidae) (Pandey et al., 2013) and the ladybird predators *Propylea dissecta* (Mulsant) and *Cheilomenes sexmaculata* Fabricius (Mishra and Omkar, 2012).

In general, our results revealed that sex ratio did not vary as a function of prey species. In coccinellids, sex ratio is typically close to 50:50 (Nedvěd and Honěk, 2012). However, a significant female bias (60%) was observed in slow-developing larvae fed on *M. persicae*. To the best of our knowledge, except for sex-ratio bias due to infection by a male-killing agent, an increased proportion of males was found at high temperatures (30 °C) in *Harmonia axyridis* Pallas (Lombaert et al., 2008) and in *P. dissecta* at 35 °C (Omkar and Pervez, 2004). It is not possible to explain to what extent such bias may result from a trade-off resulting from the fact that slow-developing larvae give rise to females with low fitness or, on the other hand, from a higher mortality of larvae that would result in males.

A more detailed analysis of the cohorts (FDAf, SDAf, FDMp, and SDMp) revealed that fast-developing individuals in both populations exhibited higher fecundity and shorter pre-oviposition periods than slow-developing individuals. Consequently, faster-developing individuals appear better adapted to their respective food sources than slower-

developing individuals. This suggests the occurrence of phenotypic plasticity within cohorts, influencing adaptation to specific food sources, as reflected in fitness traits. Phenotypic plasticity is the ability of a single genotype to express different phenotypes (behaviour, physiology, or other environmentally sensitive traits) in response to different environments (Gibert et al., 2019). The ability of a species to adapt to new conditions demonstrates its adaptive plasticity, which will be greater or less depending on how well it adapts to the new existing conditions.

In many organisms, particularly insects, such developmental variability may reflect different evolutionary strategies related to habitat conditions. Fast-developing individuals typically produce more eggs and develop more quickly, prioritising quantity in environments where prey or predators are abundant, whereas slower-developing individuals adopt a more conservative strategy Pandey et al., 2013; Kindsvater et al., 2016; Ward-Fear et al., 2024). According to many authors (Miller et al., 1988; Ortiz, 2023; Mauritsson, 2024), faster-developing organisms tend to achieve larger body size as a strategy to reduce predation risk. In contrast, our study observed that fast-developing immatures produced smaller eggs than slow-developing individuals, while newly hatched larvae from the slow group were slightly larger than fast larvae. Further studies are needed to validate these findings.

Overall, many organisms maintain distinct developmental trajectories within a single population, reflecting genetic variability as an adaptive strategy. *Scymnus nubilus* appears to follow a similar pattern, likely influenced by adaptation to specific food sources, with better-adapted individuals developing faster and exhibiting higher fitness than their slower counterparts. These traits are particularly relevant for species considered as potential biological control agents, as variability in developmental and reproductive traits could affect their effectiveness against specific pests. Similarly, adaptation to novel habitats may be constrained if resource availability does not match the species' life-history requirements. Some studies have already addressed how different food sources may affect the development of *Scymnus* species (Borges et al., 2024), but the long-term effects, particularly across future generations, remain poorly understood.

Altogether, these findings provide new insights into the adaptive strategies of *S. nubilus*, highlighting the ecological relevance of developmental polymorphism in island predator populations.

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Chapter 7. General Discussion

The present study contributes to a better understanding of coastal grassland ecosystems in the Azores and mainland Portugal, particularly regarding the structure of their biological communities. This work also provides insight into how species interact with each other and allows us to assess differences in trophic network structure in each of the studied regions. At the same time, through laboratory experiments, it was possible to observe the phenotypic plasticity of a given organism in response to food variability, as well as the direct consequences on its fitness over time.

7.1. Phenotypic and Community Differences Between Insular and Mainland Ecosystems

To assess the ecological and phenotypic differences between insular and mainland ecosystems, several collections of arthropod communities were carried out across two distinct regions — the Azores and mainland Portugal. This process followed previously defined and standardised protocols, ensuring data robustness and the creation of structured metadata, which were subsequently used throughout this thesis and prepared for future sharing and reproducibility. The datasets have been published on the GBIF platform following the Darwin Core standard, and were also used in the analyses of species abundance and richness across the two bioregions, as described in Chapters 2 and 3 (see Calado et al., 2024; 2025).

In Chapter 2, a more detailed analysis of the data revealed significant differences between the coastal grasslands of the Azores and those of mainland Portugal, with the latter exhibiting greater arthropod richness and higher abundance of generalist species. In contrast, insular coastal grasslands showed lower diversity, associated with the dominance of a few species. This analysis was carried out using the Hill series (Chapter 3) and the Fisher's α diversity index. The results obtained support the hypothesis that insular systems tend to exhibit lower diversity compared with their continental counterparts (Whittaker et al., 2017).

Although the Hill series analyses did not reveal significant differences in terms of alpha diversity (considering dominant and rare species, as well as evenness), beta diversity indices differed between regions, being higher on the mainland. This indicates that species turnover among mainland sites was greater than that observed in the Azores. Simultaneously, the Fisher's α values indicated higher species richness in the mainland communities.

These differences may suggest that insular coastal grassland systems are indeed structurally simpler, although such simplicity is not solely the result of geographic isolation but may also stem from greater anthropogenic and/or climatic pressures exerted on these ecosystems, leading to community homogenisation.

Regarding the differences in gamma richness between the two regions, the results followed the expected pattern, being higher in the mainland than in the Azores. However, this differentiation may also be related to the geographical distance between some of the continental sampling sites, even though they exhibit similar environmental characteristics (see Chapters 2 and 3).

From an evolutionary perspective, the differences between insular and continental communities may reflect both resource availability and the adaptability of organisms (Losos and Ricklefs, 2009; Whittaker et al., 2017). The reduced genetic variability observed in insular populations, associated with geographical isolation, may have led to genetic erosion and, consequently, limited capacity to exploit new habitats. (Gillespie and Roderick, 2002). This situation could result in lower phenotypic plasticity and reduced adaptive ability under changing environmental conditions.

The implementation of these studies allows for a clearer analysis of the potential differences between insular and mainland arthropod communities, largely confirming the greater structural simplicity of ecological networks in island systems. Such comparisons therefore enable the evaluation of potential limitations in resource availability and contribute to understanding how these differences are reflected in trophic structures and interactions — aspects that are explored further in Chapters 4 and 5.

7.2. Trophic Structure and Functional Interactions

The investigation of trophic network structures and interactions within arthropod communities from the Azores and mainland Portugal was addressed in Chapters 4 and 5 (Calado et al., 2025a). Following the analysis of the variations in abundance and diversity obtained for both regions (Chapters 2 and 3), the respective ecosystems were characterised, with a particular focus on vegetation cover and trophic interactions among specific groups of organisms.

To this end, data were collected on the floristic composition of both regions, recording the plant species observed in each sampling site. The information was gathered using previously defined and standardised protocols, ensuring consistent and comparable sampling between locations. This approach provided sufficient data to evaluate the similarities and differences between insular and mainland plant communities. The resulting dataset was subsequently structured according to Darwin Core standards to enable publication and sharing through the GBIF platform, where it is available as Calado et al., (2025a)

At the same time, trophic interactions between plants–aphids, aphids–ladybirds, and aphids–ants were recorded for both the Azorean and mainland sites.

These observations aimed to test the hypothesis that insular trophic networks would be simpler than those of the mainland. However, the results did not confirm this expectation, revealing that insular networks exhibited greater richness than their continental counterparts (Chapter 5).

These differences can be explained by the type of vegetation predominant in each region, which is strongly influenced by local climatic conditions. In mainland areas, the drier and more temperate climate favours the development of xerophytic vegetation (Chozas et al., 2017) whereas the humid subtropical climate of the Azores allows for the growth of annual and biennial plant species, that supports a higher diversity of aphids in the Azores compared to the mainland (Rego et al., 2024).

Although a greater diversity of prey may suggest an increased availability of resources, this does not necessarily imply a higher genetic variability in predators that would allow for more efficient exploitation of those resources.

In other words, predatory organisms may present adaptive limitations in exploiting these prey species, resulting in evolutionary costs associated with adaptation. Accordingly, Chapter 6 was conducted with the objective of analysing the genetic variability of an aphidophagous predator, *Scymnus nubilus*, in response to the use of different food resources.

7.3. Phenotypic Variability on Life-History Traits of *Scymnus nubilus*

Building upon the results obtained at the comparative analysis of island vs. mainland arthropod and plant communities in coastal grasslands of São Miguel Island (Azores) and Mainland Portugal and structure of trophic networks, an investigation was conducted to understand how arthropod variability at the community scale may drive the adaptive potential of*a* predators. Based on the assumption that insular networks tend to be less complex than their continental counterparts, it was hypothesised that phenotypic variability of predators–would also be lower on islands compared with mainland regions.

In Chapter 6, this hypothesis was tested by conducting an experiment specifically on a native ladybeetle predator recorded on coastal grasslands of Azores, using *Scymnus nubilus* as the model organism. This species, belonging to the family Coccinellidae, is recognised for its potential as a biological control agent due to its ability to feed on various agricultural pests, including aphids, whiteflies and mites.

To evaluate phenotypic variability, a controlled feeding experiment was conducted to examine whether developmental trajectories and reproductive traits diverged when individuals were exposed to prey of contrasting nutritional quality. This approach allowed the assessment, through phenotypic expression, of whether genetic variability existed within a given population in response to the food provided. Similar developmental rates among individuals fed on the same prey type would indicate low genetic variability,

whereas marked variation — where some individuals develop faster than others — would suggest higher pre-existing genetic diversity (Hodek et al., 2012).

The results indicated that for two cohorts of *S. nubilus*, each exposed to different aphid species (*Aphis fabae* and *Myzus persicae*), there were significant differences in both developmental rate and adult characteristics, both within and between feeding treatments.

These results reveal a marked phenotypic plasticity, where, within the same population, some individuals developed more rapidly than others, producing a bimodal developmental pattern. A better adaptation of *S. nubilus* to *A. fabae* was also observed, confirming preliminary findings from previous studies (Borges et al., 2024). Indeed, our data reflect this trend in immature developmental rates, adult body size and fecundity levels.

These alternative developmental modes suggest flexible strategies of resource allocation, adjusted according to prey quality – a pattern consistent with the ecological differences documented between continental and insular environments (Roff, 1993; Evans, 2003). The occurrence of both fast- and slow-developing individuals within a population may have direct implications for population maintenance, depending on resource availability fluctuations. Fast-developing individuals may be more capable of exploiting resources efficiently throughout their life cycle, although potentially at a cost to their overall fitness (Stearns, 1992).

Thus, controlled laboratory studies that simulate simplified trophic networks — such as bipartite aphid–ladybird systems — when combined with field observations, constitute an essential tool for understanding how these networks operate in nature and the ecological implications associated with them. This integrated approach allows for a deeper understanding of how a species' phenotypic plasticity influences trophic interactions between organisms, both in insular and mainland ecosystems.

7.4. Final Conclusion and Future Perspectives

Although this study provides relevant data that contribute to a better understanding of how insular and mainland coastal grassland communities are structured and the ecological implications associated with their disturbances, several aspects warrant further and continuous investigation.

The time available for a more detailed analysis was relatively limited, considering the scope and diversity of the data collected. The work involved the acquisition of a significant amount of information, part of which still requires additional processing and analysis. With these data, it will be possible to conduct more detailed assessments of the relative abundance of plant species by region, to understand the variation in species richness within each bioregion, and to investigate the interrelationships between vegetation cover and arthropod abundance and richness in each of the ecosystems studied.

This information may prove essential for a deeper understanding of the processes underlying the formation and maintenance of trophic networks in coastal grasslands.

At the same time, adverse climatic conditions delayed the collection of some organisms required for the continuation of laboratory experiments that would have been valuable for testing the influence of different prey types on the phenotypic plasticity of *Scymnus nubilus* across multiple generations, thereby allowing a more robust evaluation of the trade-off hypothesis.

Future work could explore these data further and expand knowledge on the capacity of certain species to adapt to new environments. A more detailed analysis of the biotic and abiotic factors at each location will contribute to a broader understanding of these ecosystems.

Such knowledge will make it possible to define more effective ecological management strategies, particularly in the control of agricultural pests and/or invasive species that may interfere with trophic networks, thereby mitigating negative environmental and economic impacts.

Thus, from a multifaceted perspective, this work contributes to the preservation and enhancement of existing ecosystems, substantially improving the environmental conditions and ecosystem services derived from them — elements that are fundamental to the sustainability of numerous species, including humankind.

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Phenotypic Plasticity of Pest and Biological Control Agents

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