In-situ assessment of the impact of climate change on pasture quality and associated arthropod communities in Terceira Island.

Tese de Doutoramento

Sophie Wallon

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Orientadores

Professor Rui Bento Elias

Professor Paulo A.V. Borges

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Summary

Climate change represents one of the most pressing global challenges of our time, with profound implications for ecosystems and biodiversity across the planet. Alterations in temperature and precipitation patterns driven by mostly anthropogenic activities threaten the delicate balance of ecological communities, particularly in isolated environments such as the Azorean Archipelago. This study investigates the effects of climate change on arthropod diversity within intensively managed pastures in the Terceira Island (Azores), with a focus on understanding how local scale rising temperatures influence these vital components of agroecosystems.

Utilizing Open Top Chambers (OTCs) to simulate *in situ* warming, this thesis employs a multifaceted approach, combining taxonomic and functional trait modelling to assess the responses of arthropod communities to increased temperature over time. Our findings reveal distinct patterns in how various arthropod taxa respond to increased temperatures. Notably, while beetle richness declines under warmer conditions, spider diversity showed a significant increase, underscoring the complexity of ecological responses to climate stressors. Additionally, changes regarding diversity indices between two years suggests a dynamic of arthropod communities to changing environmental conditions, highlighting the potential for resilience within these ecosystems.

The study further explores the influence of elevational gradients on arthropod assemblages, revealing that microhabitat variations significantly affect community composition and functional traits. Traits such as body size and iridescence emerge as relevant factors in the adaptive capacity of arthropods to elevated temperatures, with implications for their ecological roles in pastures. Interestingly, our analysis indicates a weak significance between grass biomass and arthropod diversity, suggesting that habitat structure and microclimate variability may play pivotal roles in shaping community dynamics.

This research contributes to a growing body of knowledge on the impacts of climate change on biodiversity, particularly in the context of agricultural systems under increased temperatures. By addressing the nuanced relationships between temperature, elevation, grass biomass, and arthropod diversity, this thesis not only improves our understanding of ecological interactions in the face of climate change in the Azores, but also provides valuable insights for future sustainable pasture management.

Resumo

As alterações climáticas representam um dos desafios globais mais prementes do nosso tempo, com profundas implicações para os ecossistemas e a biodiversidade em todo o planeta. As alterações nos padrões de temperatura e precipitação provocadas por actividades em grande parte de origem antropogénica ameaçam o delicado equilíbrio das comunidades ecológicas, particularmente em ambientes isolados como o arquipélago dos Açores. Este estudo investiga os efeitos das alterações climáticas na diversidade de artrópodes em pastagens geridas de forma intensiva nos Açores, com o objetivo de compreender como o aumento da temperatura influencia a estrutura das comunidades dos agroecossistemas.

Utilizando câmaras de topo aberto (OTCs) para simular o aquecimento *in situ*, esta tese emprega uma abordagem multifacetada, combinando modelação de dados taxonómicos e das caraterísticas funcionais das espécies para avaliar as respostas das comunidades de artrópodes ao aumento da temperatura ao longo do tempo. Os nossos resultados revelam padrões distintos na forma como os vários taxa de artrópodes respondem ao aumento da temperatura. Nomeadamente, enquanto a riqueza de escaravelhos diminui sob condições mais quentes, a diversidade de aranhas mostra um aumento significativo, sublinhando a complexidade das respostas ecológicas aos factores de stress climático. Além disso, as alterações relativas aos índices de diversidade entre dois anos sugerem uma dinâmica das comunidades de artrópodes face às alterações das condições ambientais, salientando o potencial de resiliência destes ecossistemas.

O estudo explora ainda a influência dos gradientes de elevação nas comunidades de artrópodes, revelando que as variações de micro-habitat afectam significativamente a composição da comunidade e os traços funcionais. Caraterísticas como o tamanho do corpo e a iridescência surgem como factores relevantes na capacidade de adaptação dos artrópodes a temperaturas elevadas, com implicações para o seu papel ecológico nas pastagens. Curiosamente, a nossa análise indica uma fraca significância estatística entre a biomassa de gramíneas e a diversidade de artrópodes, sugerindo que a estructura do habitat e a variabilidade microclimática podem desempenhar um papel fundamental na formação da dinâmica da comunidade de artrópodes.

Esta investigação contribui para um conjunto crescente de conhecimentos sobre os impactos das alterações climáticas na biodiversidade, particularmente no contexto de sistemas agrícolas sujeitos a temperaturas mais elevadas. Ao abordar as relações matizadas entre temperatura, elevação, biomassa de gramíneas e diversidade de artrópodes, esta tese não só melhora a nossa compreensão das interações ecológicas face às alterações climáticas nos Açores, como também fornece informações valiosas para uma futura gestão sustentável das pastagens.

List of chapters, publications and author contributions

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.

This thesis includes a version of three original papers published in indexed peer reviewed journals and one in preparation for publication. The inclusion of co-authors reflects the fact that the work came from active collaboration between researchers and acknowledges input into team-based research. All work presented was carried out in the School of Agricultural and Environmental Sciences (FCAA) at the University of the Azores, Angra do Heroísmo *campus*, Portugal.

Chapter 1: introduction – S. Wallon wrote the text, which was revised by the supervisors.

Chapter 2: A version of Chapter 2 has been published [**Wallon, S., Melo, C., Tsafack, N., Elias, R.B. & Borges, P.A.V. (2023) Assessing the effects of climate change on arthropod abundance in Azorean pastures: PASTURCLIM project's baseline monitoring data.** ***Biodiversity Data Journal*****, 11, e103723**]. S. Wallon was responsible for all areas of data collection and analysis, as well as for writing the entire draft version of the paper and revising it according to co-authors' comments. P.A.V. Borges and N. Tsafack contributed to dataset preparation and data analysis. P.A.V. Borges imported the dataset in GBIF. R.B. Elias and C. Melo helped with the data sampling. R.B. Elias is the PASTURCLIM project leader and was involved in the early stages of concept formation. P.A.V. Borges was the supervisory author on this study and was involved throughout it in species identification, concept formation. All co-authors contributed to manuscript reviewing.

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Discussion – S. Wallon wrote the text, which was revised by the supervisors.

Chapter 1 - Introduction

1.1. Climate Change and Its Global Impacts

Climate change is a global phenomenon with far-reaching consequences for ecosystems worldwide (Abhijeet et al., 2023; Hartmann et al., 2022; Portner et al., 2022). Alterations in temperature and precipitation patterns can significantly impact the composition and distribution of plant and animal communities across diverse landscapes (Arnell et al., 2019; Ohba et al., 2019; Ordonez et al., 2016; Papalexiou et al., 2019). Anthropogenic activities, particularly the emission of greenhouse gases, have driven this rapid change, resulting in significant consequences for biodiversity and ecosystem functioning (Yoro et al., 2020).

Across the globe, ecosystems are responding to these climate-induced stressors, from terrestrial forests to marine environments. Biodiversity patterns are being altered, with some species experiencing population declines, habitat shifts, or even extinction, while others thrive under new conditions (Habibullah et al., 2022; Pecl et al., 2017). The rate of climate change poses challenges for species with limited dispersal capabilities or specific habitat requirements, as their ability to adapt is often constrained by the rapid pace of environmental shifts (Pörtner et al., 2021).

1.2. Climate Change and Agriculture

Agriculture is one of the sectors most vulnerable to climate change. Its dependence on stable climatic conditions makes it highly sensitive to alterations in temperature, precipitation, and the occurrence of extreme weather events (Malhi et al., 2020). These changes not only influence the overall productivity of agricultural systems but can also affect the quality of key resources like pastures, which are vital for livestock production and the livelihoods of farming communities (M. Cheng et al., 2022; Scarlett, 2010).

Pastures, as foundational components of many agricultural systems, are especially susceptible to the effects of global warming (Tubiello et al., 2007). Increased temperatures and altered precipitation regimes can disrupt the growth cycles of forage plants, leading to changes in pasture composition and quality (Berauer et al., 2020; Melo et al., 2022). This, in turn, affects the availability of nutritious feed for grazing animals, potentially lowering livestock yields. Additionally, altered climatic conditions can promote the spread of invasive plant species, further altering pasture ecosystems and making sustainable pasture management more challenging (Ordonez et al., 2016).

1.3. Arthropods and Climate Change

Arthropods are present in all types of habitats and represent the most abundant taxon in the world (E. O. Wilson, 1987). They are also highly responsive to modifications in their environment and easy to sample, making them excellent candidates for studying the impacts of climate change (Boggs, 2016; Johnson et al., 2016; Marta et al., 2021). Species under climatic changes may react differently regarding their physiological and ecological requirements.

Therefore, abundances within species may vary positively or negatively depending on whether adequate abiotic (e.g., temperature, relative humidity) and biotic (e.g., food source) conditions are encountered (Sohlström et al., 2022). For instance, one of the principal impacts of global warming in agriculture is the shift in plant phenology (Ekholm et al., 2020). This shift can accelerate the growth and development rates of certain species, especially crop pests, posing challenges for agriculture in the future (Skendžić et al., 2021)

In agricultural systems, these ecological changes are particularly concerning. Arthropods play essential roles as pollinators, decomposers, and predators, integral to the health of these ecosystems (M. Ferrante et al., 2023; Verma et al., 2023). However, their sensitivity to changes in temperature, humidity, and food availability means they are highly vulnerable to climate change impacts (Boggs, 2016; Høye, 2020). Warming temperatures can shorten developmental times for certain crop pests, leading to rapid population growth and subsequent pest outbreaks that threaten agricultural productivity (Skendžić et al., 2021). At the same time, beneficial arthropods, such as pollinators, may experience declines in regions where climatic conditions exceed their physiological tolerances, posing a threat to ecosystems reliant on these species for pollination and other ecosystem services (Goulson et al., 2015; Willmer, 2012).

Changing climatic conditions can disturb the balance between pests and their natural predators (Harvey, Heinen, Gols, et al., 2020). Arthropods with limited dispersal capacities, unable to move to more favorable climates, may face increased risks of local extinction (Jeremy T. Kerr, 2020). This disruption in arthropod communities can alter ecosystem dynamics, posing significant challenges for sustainable agriculture and ecosystem management (Jankielsohn, 2018; Schowalter, 2022). Therefore, understanding how arthropod populations respond to climate change is critical for predicting the future impacts of global warming on both natural and managed ecosystems (Harvey, Heinen, Armbrecht, et al., 2020).

As global temperatures rise, ground-dwelling arthropod species are likely to respond in various ways depending on their physiological tolerance, dispersal capacity, and ecological interactions (Beckers et al., 2020; Brusse et al., 2024; González-Tokman et al., 2020; Harvey, Tougeron, et al., 2023; Solascasas et al., 2022). Some studies suggest that warming may accelerate the development and reproduction of certain species, particularly those that thrive in warmer climates, including various pest species (Skendžić et al., 2021; Van Klink et al., 2020). Conversely, other species may experience declines if the new climatic conditions exceed their physiological limits. For instance, changes in temperature and humidity could negatively impact ground-dwelling species that rely on cooler, more stable environments, potentially leading to shifts in community structure and ecosystem functioning (Hickling et al., 2006; Sharma et al., 2018). Furthermore, broader trends indicate that terrestrial arthropods are experiencing declines, which may have cascading effects on ecosystem dynamics (Fraser et al., 2015).

Changes in precipitation patterns are also expected to affect arthropod communities (Barnett et al., 2016). For species that rely on stable moisture levels for survival, prolonged droughts or changes in humidity could disrupt their life cycles, leading to declines in abundance or shifts in species composition. In the case of the Azores, where precipitation is projected to become more irregular, with wetter winters and drier summers (Santos et al., 2004), arthropod communities may experience significant changes in distribution and abundance.

Various specific effects of climate change on insect populations have been documented, including:

- Direct Impacts of Temperature

Changes in average temperatures and extreme weather events have a significant impact on insect populations. In different climatic regions, these temperature changes can increase survival rates, alter growth and mortality patterns, trigger earlier life cycle events and increase reproductive rates (Harvey, Tougeron, et al., 2023). For example, the western and southern United States have experienced a surge in pine beetle outbreaks that have severely affected large areas of forest (Creeden et al., 2014; Negrón et al., 2020). This increase in beetle populations over the past decade has been linked to milder winters, allowing multiple generations to thrive within a year and ultimately increasing population density (Kurz et al., 2008; Mitton et al., 2012). However, predicting the diverse effects of climate warming on insects remains complex, as these effects depend on several factors, including the biology of specific species (Deutsch et al., 2008a) and temperature-dependent interactions with host plants. Furthermore, these temperature effects are often exacerbated by other climatic variables, such as changes in precipitation patterns (Jamieson et al., 2012).

- Changes in Insect Distributions

Insect distributions are shifting in response to climate change (Parmesan, 2006). Species adapted to cold or alpine environments, such as certain bumblebees, are experiencing habitat loss and range contraction (Kerr et al., 2015). In contrast, less specialized species in the northern hemisphere are expanding their ranges northwards as warming creates new suitable habitats. One notable study found that three out of four butterfly species recorded have experienced northward range expansions (Parmesan, 2006). These range shifts in agricultural pests, disease vectors (e.g. mosquitoes and ticks; (Ogden et al., 2014), invasive species and other arthropods are likely to have significant impacts on human populations. Given the variability of range shifts among species, comprehensive ecological studies of insect diversity are essential to understand future outcomes.

- Biodiversity and Biomass Loss

The ongoing decline in insect diversity and abundance is a major concern in the context of climate change (Bellard et al., 2014; Hallmann et al., 2017). Studies in Europe have reported a decline in flying insect biomass of more than 75% over a 27-year period (Mhamdi et al., 2016). Long-term records spanning over a century in Europe and North America show climate-driven declines in bumblebee populations (Kerr et al., 2015). Because of their high sensitivity to climate change and critical ecological roles, insects serve as important indicators or 'canaries' that signal the wider impacts of climate change on other organisms, including plants that rely on them for pollination and larger animals that depend on them for food.

- Changes in Food Web Interactions

Climate change also has indirect effects on insect food sources, predators, parasites and associated microbes (Laws, 2017; Tougeron et al., 2020). For example, the synchronization between pollinating insects and their host plants can be disrupted by fluctuations in temperature and precipitation, leading to mismatched timing of pollination activities (Pyke et al., 2016; Schaeffer et al., 2014; Solga et al., 2014). Such disruptions pose significant challenges for insects that depend on specific plants for their survival.

1.4. Climate Change in Oceanic Archipelagos

Oceanic archipelagos, due to their isolation and unique environmental conditions, are especially sensitive to the impacts of climate change (Harter et al., 2015; Taylor et al., 2016). The combination of geographical isolation, limited land area, and a high degree of endemism makes island ecosystems particularly vulnerable to environmental shifts (Duvat et al., 2017; Petzold et al., 2019). Changes in temperature and precipitation patterns can have profound effects on island biodiversity, especially for species already living in specialized or restricted habitats (Whittaker et al., 2007).

Islands are also highly exposed to sea-level rise, more frequent and intense storms, and shifting ocean currents, all of which can amplify the direct effects of climate change on terrestrial ecosystems (Harter et al., 2015). These climatic changes threaten not only the persistence of native species but also the ecological processes that sustain these fragile ecosystems (Harter et al., 2015; Fernández-Palacios et al., 2021). Altered rainfall patterns can impact freshwater availability and soil moisture, critical factors for plant growth and the overall health of island ecosystems (Fernández-Palacios et al., 2021).

Additionally, the small size and isolation of island populations make them particularly susceptible to species invasions, often exacerbated by climate change (Fernández-Palacios et al., 2021; Harter et al., 2015). Warmer temperatures and altered precipitation regimes may facilitate the spread of invasive species, which can outcompete native species for resources and disrupt island food webs. Thus, oceanic archipelagos serve as natural laboratories for studying the complex interactions between climate change, species dynamics, and ecosystem functioning (Kier et al., 2009).

1.5. Climate Change in the Azores

In the Azores, the single greatest estimated impact of global change may be the alteration in annual precipitation distribution, with wetter winters while the other seasons become drier (Santos et al., 2004).

This shift could significantly affect the islands' water resources, increasing severe precipitation events in winter and imposing water deficit stresses during summer (Santos et al., 2004). Projections indicate that the average temperature for the Azores is expected to increase between +1.2 and +2.3º C by the 2070-2099 period, along with an average decrease in precipitation of 7.25 mm per year (Azevedo et al., 1999; Azevedo et al., 1998). The PRAC (PRAC, 2017) highlights the most important impacts associated with climatic factors in the Azores, including stress-induced reductions in production during drought conditions, decreased pasture quality, and the expansion of pest species.

Arthropods are crucial to the ecological integrity of these islands, and their response to climate change remains an area requiring further research. Although there are already studies investigating arthropod communities in grasslands under climate change around the world (Barnett et al., 2016; Brusse et al., 2024; Buchholz et al., 2013; Cheng et al., 2021; Joern et al., 2013; Sohlström et al., 2022), there are also few studies on the impact of climate change on Azorean arthropods (Aparício et al., 2018; Ferreira et al., 2016, 2019). However, research focused on arthropod communities in Azorean pastures is limited (Borges, 1997; Borges, 1999a; Borges, 1999b; Borges, 2008; Rigal et al., 2018).

1.6. Agriculture in the Azores and Climate Change Impacts

The Azores archipelago, characterized by its volcanic origin and remote location, faces unique environmental challenges that make it particularly susceptible to the impacts of climate change. Agriculture forms a significant part of the region’s economy, with over 56% of the land dedicated to pastures or other agricultural activities (PRAC, 2017). Historically, land use in the Azores has evolved, with a shift toward increased reliance on forage crops and pasture-based livestock systems. In Terceira Island, more than 60% of the land is used for agriculture and pastures. The latter, alone account for 41.51% of the total land area, underlining their importance in both economic and ecological terms (Cruz et al., 2007).

However, the region’s agricultural systems are now under increasing pressure from the changing climate. According to regional projections, by 2100, the Azores could experience an increase in temperature of 1.2 to 2.3°C and a decrease in annual precipitation, with significant implications for water availability, pasture productivity, and overall agricultural sustainability (Azevedo et al., 1998; Santos et al., 2004). These changes are likely to affect not only the quantity but also the quality of pastureland, which forms the foundation of the dairy and beef industries on the island.

Increased temperatures, prolonged droughts, and shifts in seasonal precipitation patterns may lead to reduced pasture growth and lower-quality forage. This could impose water stress during the summer months, while more intense rainfall during the winter could cause soil erosion and nutrient loss, further reducing pasture productivity. The economic impacts of such changes on local agriculture are difficult to quantify due to market dynamics and technological advancements in farming practices, yet the wider vulnerability of the sector is evident (Lavalle et al., 2009).

1.7. The Role of Arthropods in Pastures and Ecosystem Functioning

Arthropods are the most diverse group of animals on Earth and play critical roles in both natural and agricultural ecosystems (Zhang, 2013). In pastures, they contribute to essential ecological processes such as pollination, decomposition, and the biological control of pests (Nagy et al., 2020; Solascasas et al., 2022; Teixeira et al., 2023; Verma et al., 2023). However, they are also highly sensitive to environmental changes, making them excellent bioindicators for studying the effects of climate change (Gerlach et al., 2013). The arthropod communities in grassland ecosystems are particularly vulnerable to shifts in temperature, humidity, and food availability—factors that can influence their population dynamics and interactions with other species (García-Robledo et al., 2016; González-Tokman et al., 2020; Harvey, Tougeron, et al., 2023; Sharma, 2014; Solascasas et al., 2022).

In the Azores, research on arthropod communities in pasture ecosystems is limited, despite their critical ecological role. Some studies have been conducted on arthropod diversity in natural and semi-natural habitats in the region (Borges, 1999a; Borges, 1999b b; Rigal et al., 2018), but there has been little investigation into the impacts of climate change on these communities. Given the projected climatic changes for the Azores, understanding how arthropods respond to climatic changes (e.g. temperature increases) is essential for predicting future ecological dynamics in pasture ecosystems.

1.8. General aims and objectives

This thesis aims to investigate the effects of climate change on arthropod communities in grasslands of the Azorean archipelago, a topic that has not been extensively studied in the region. More specifically, the work aims to test the impact of increased temperature on arthropod communities in grasslands within the island of Terceira (Azores). By focusing on how rising temperatures affect the distribution, abundance and ecological interactions of ground-dwelling arthropods in these unique volcanic landscapes, this research aims to provide new insights into ecosystem dynamics in response to climate change. The results will contribute to the understanding of the impacts of climate change on biodiversity, particularly in isolated environments such as the Azores, where few studies have addressed these critical ecological relationships. Ultimately, this work aims to highlight the essential role of arthropods in pasture ecosystems and inform future conservation and management strategies in the face of ongoing climate change.

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 "**Assessing the effects of climate change on arthropod abundance in Azorean pastures: PASTURCLIM project's baseline monitoring data"**, aims to present the experimental setup with the use of Open Top Chambers (OTCs) developed to simulate a temperature increase *in situ*, within the PASTURCLIM project. It also aims to present the main arthropod dataset used to carry out this investigation.

The third Chapter is entitled "**Effects of a short-term temperature increase on arthropod communities associated with pastures**". Here, we address a first analysis at a taxonomic level considering each experimental field separately. The objectives are to assess whether an increase in temperature within the Open Top Chambers (i) changes the species composition; (ii) affects the overall abundance of arthropods; and (iii) if it impacts the relative abundances of species.

Chapter 4, entitled "**Unveiling Arthropod Responses to Climate Change: A Functional Trait Analysis in Intensive Pastures**", we take a different approach to assess the impact of increased temperatures, by focusing on the functional traits of arthropods and integrating the elevational factor. The objectives are: (i) to study the response of different arthropod guilds to temperature increases. This is done within the pasture communities and along the altitudinal gradient. More specifically, we want to assess whether predator-prey dynamics and herbivore abundance were affected by increasing temperatures; (ii) to test if there is a specific pattern in the distribution of arthropod species body sizes as temperatures increase in grassland ecosystems; (iii) to examine whether increased temperatures influence two specific traits of beetles—their coloration and the presence or absence of iridescence—as these characteristics may play a role in their thermoregulation and ability to withstand elevated temperatures.

Chapter 5, entitled "**Assessing Temperature-Induced Changes in Arthropod Communities Over One Year Using Open Top Chambers: A Comparative Analysis**", aims to compare arthropods communities after one year experiment using taxonomic approach and introducing the grass biomass as an explanatory variable. The objectives are to assess after one year experiment: (i) if the presence of OTCs induced changes in the species composition; (ii) which variable most influences arthropod communities?

1.9. References

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Chapter 2. Assessing the effects of climate change on arthropod abundance in Azorean pastures: PASTURCLIM project's baseline monitoring data

Abstract

Background

The data we present are part of the project PASTURCLIM (Impact of climate change on pasture's productivity and nutritional composition in the Azores). The project aims to assess the consequences of climate change (e.g. temperature increase) on the grass production and its quality for forage, as well as to assess changes in the arthropod communities associated with the Azorean intensive pastures. An *in situ* experiment was set up using Open Top Chambers (OTCs), in order to simulate an increasing of temperature (average of +1.2ºC) on pastures. In this contribution, we present the data relative to the arthropod sampling.

New information

We provide an inventory of all arthropods recorded inside OTCs and in control plots in three intensively managed pastures dominated by grasses in Terceira Island (Azores): two of them dominated by ryegrass, *Lolium multiflorum* Lam. (Poaceae), located respectively at 186 m and 301 m above sea level; and one field dominated by common velvetgrass, *Holcus lanatus* L. (Poaceae), located at an altitude of 385 m.

A total of 41351 specimens were collected. Organisms collected belong to four classes, 15 orders, 60 families and 171 species/morphospecies (including 34 taxa identified only at order, family or genus level). Therefore, for only 137 taxa, we have a scientific name associated (n = 38918). A total of 75% of the species (n = 129 species) are considered introduced (including all the species with indeterminate colonisation status that are possibly also exotic species (n = 7622)), representing 71% of the total abundance (n = 29664 specimens). A total of 19% of the species (n = 33 species) are considered native nonendemic representing 28% of the total abundance (n = 11608 specimens). Only one endemic species was sampled, the wolf spider *Pardosa acorensis* Simon, 1883 (1% of the species), representing 0.2% of the total abundance (n = 79 specimens). Spiders (5056 specimens) and beetles (18310 specimens) were the dominant taxa representing, respectively, 20 and 78 morphospecies. Since the main aim of this study was to have a better knowledge on arthropod communities present in Azorean pastures under a simulated temperature increase, the principal novelty of this paper is the contribution with distribution and abundance data to a baseline knowledge on the future consequences of climate changes on arthropod communities in Azorean pastures.

Keywords: Arthropods, Climate change, Grasses, Open Top Chamber, Pasture, Pitfall traps.

2.1. Introduction

Climatic changes occurring on Earth imply mainly changes in temperature (Arnell et al., 2019; Portner et al., 2022) and in rainfall patterns (Ohba et al., 2019; Papalexiou et al., 2019), which affect ecosystems as well as their biodiversity (Habibullah et al., 2022; Sharma et al., 2018). Grasslands used as forage crops are affected at different levels by the increase of temperature: i) Increased growth rate, in which higher temperatures can stimulate the growth rate of forage crops. As a result, grasslands can produce more forage, which can be beneficial for livestock. However, changes in seasonal precipitation would reduce these benefits, particularly in areas with low summer rainfall (Hopkins et al., 2007); ii) Drought stress, in which higher temperatures comes with the higher risk of drought, which can be detrimental to the growth of forage crops. Drought stress can reduce the yield of grasslands and result in poor-quality forage; iii) Changes in plant composition (Feeley et al., 2020), in which some species may become less abundant, while others may thrive, which can alter the nutritional value of the forage, decreasing protein and mineral nutrient concentrations, as well as altering lipid composition (DaMatta et al., 2010); iv) Changes in plant phenology, in which some grasses are affected as well as their functional traits and chemical composition (Ekholm et al., 2020; Lee et al., 2013; Melo et al., 2022; Piao et al., 2019). All these factors can lead to cascading effects on biodiversity and on ecosystem services (Banerjee et al., 2018; García et al., 2018; Mirás-Avalos et al., 2018; Moss et al., 2022a; Selvaraj et al., 2013).

Adaptation to climate change for agriculture will be definitively a crucial point to overpass in order to avoid an economic crisis in the coming years (Aguiar et al., 2018; Rivera et al., 2018; Vizinho et al., 2021). Regarding wildlife, there has been great concern for many years concerning the decline of arthropods (Brantley et al., 2012; Halsch et al., 2021; Seibold et al., 2019; E. O. Wilson, 1987). In anthropised ecosystems such as for crops or pastures, they are responsible for many ecosystem services (e.g. pollination, decomposition of organic matter, pest control and predation), but can also be responsible for ecosystem disservices (e.g. pest, parasitism, herbivory, seed predation, crop damage) (Cardenas et al., 2022; Marco Ferrante, Lamelas-López, et al., 2022). Climate changes may also affect this balance of services and disservices by inducing shifts in species composition (Harter et al., 2015). Climate changes may influence species presence/absence, fluctuation of abundances and can even favour the dominance of some species in the ecosystem with the threat of creating a boom of pest species (Buchholz et al., 2013; Sohlström et al., 2022). The risk is higher on island ecosystems because of the limited area available and the usually lower altitudinal range. Therefore, climate changes represent a real threat for island biodiversity (Borges et al., 2019; Harter et al., 2015; Portner et al., 2022; Veron et al., 2019).

Predictions for the Azores suggest a temperature increase between 1.6 and 2.72°C till the end of the century (respectively following the two scenarios from the PRAC: RCP4.5 and RCP 8.5). Changes in the rainfall pattern are also expected due to the increase in heavy rains and storms in the winter and prolonged droughts during the summer (PRAC, 2017).

Nowadays, the main activity in the Azores is dairy and meat production. Thus, most of the land between the sea level and middle altitude (500 m) is used for agriculture (e.g. intensive pasture and forage crops) representing 56% of the territory (PRAC, 2017). The impact of temperature increase on the arthropod communities of Azorean pastures is unknown.

Therefore, an *in-situ* experiment was established to collect baseline data in order to help understand how the increase of the temperature affects the arthropod communities associated with intensive pastures in the Azores.

2.2. General description

Purpose: To provide baseline data on arthropod species richness and abundance from intensively managed pasture in Terceira Island (Azores) under natural and modified climatic conditions (e.g. increase in temperature via Open Top Chambers - OTCs). These data will allow us to assess the effects of climate change on arthropod's communities in Azorean pastures.

Additional information: Open Top Chambers (OTCs) are raised from the floor (around 5 cm) and allow free movement of all crawling arthropods around the pasture. Instead, for flying arthropods, OTCs represent an artificial barrier and data collected would present a bias due to this obstacle. Therefore, we focused on the collection of crawling arthropods using pitfall traps filled with ethylene glycol.

2.3. Project description

Title: PASTURCLIM - Impact of climate change on pasture's productivity and nutritional composition in the Azores

Personnel: Project leaders: Rui B. Elias
Team members: Paulo A.V. Borges, Sophie Wallon, Catarina D. Melo.
External Consultants : Teresa M. Ferreira.
Parataxonomists: Sophie Wallon; Mauro Matos.

Taxonomist: Paulo A.V. Borges.
Darwin Core Database management: Paulo A. V. Borges, Sophie Wallon.
Fieldwork: Sophie Wallon, Catarina D. Melo, Rui B. Elias.

Study area description: The study was conducted on the Archipelago of the Azores (North Atlantic), on Terceira Island (decimal coordinates 38.712925, -27.234912) which is the third largest island of the Archipelago with 400.2 km and a maximum altitude above sea level of 1021 m. The Azores are from volcanic origin and have a temperate oceanic climate, relatively wet with mild temperature at low altitude, all year long.

Design description: The study areas were intensive pastures located at different elevations (Table 1). All pastures were dominated by grasses. The two fields at lower elevations (A and B) were covered by the annual ryegrass, *Lolium multiflorum* Lam. (Poaceae) and the field at higher elevation (C) was covered by the perennial common velvetgrass, *Holcus lanatus* L. (Poaceae).

Table 1. Description of the locality, habitat, elevation and coordinates (in decimal degrees) of the three fields sampled in Terceira island, Azores.

Locality	**Site Code**	**Habitat**	**Grass cover species**	**Elevation (m)**	**Longitude**	**Latitude**
Santa Bárbara-Field_A	A	Pasture	*Lolium multiflorum*	186	-27.35381	38.70351
Santa Bárbara-Field_B	B	Pasture	*Lolium multiflorum*	301	-27.32578	38.70164
Granja da Universidade-Field_C	C	Pasture	*Holcus lanatus*	385	-27.17008	38.69777

Funding: Core funding was obtained from the Project PASTURCLIM (ACORES-01-0145- FEDER-000082) financed by FEDER at 85% and by Azorean Public funds at 15% through the Operational Programme Azores 2020.

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Darwin-Core and GBIF management were funded by the project Portal da Biodiversidade dos Açores (2022-2023) - PO Azores Project - M1.1.A/INFRAEST CIENT/001/2022.

2.4. Sampling methods

Description: The study was conducted in three intensive pastures on Terceira Island (Azores) (Fig. 1). In each field, 20 plots (1 x 1 m) were set up in an area of 100m where cattle were not allowed. Amongst those 20 plots, 10 were randomly chosen to be surrounded by an OTCs (in order to simulate an increase of +1.2ºC average), while the other 10 were considered as control plots. OTCs were built including a 1 m plot and a margin of 25 cm all around. The aim of this margin was to allow the same set-up of the pitfall traps as in the control plots (e.g. with one pitfall trap at each corner); it also allows free space for scientists to enter inside the OTCs without stepping on the plot. Temperature and relative humidity were recorded through data loggers (Easy Log: EL-USB-2) in control plots and inside OTCs.

Sampling description: The focus of the study were the arthropods associated with pasture for foraging production. As OTCs represent a physical barrier for flying insects, our focus was made on crawling arthropods. OTCs were raised about 5 cm above the ground and allowed arthropod movement around the experimental area. Pitfall traps were then used for the sampling.

Grasses inside each plot were seasonally and manually harvested to evaluate the biomass. Therefore, pitfall traps were set up and collected before harvesting grasses.

Pitfalls were set up for 14 days, in each field, in the winter of 2020. During the summer of 2020, in the fields A and C, pitfall traps were set up for 14 days, while they were set up for 13 days in Field B.

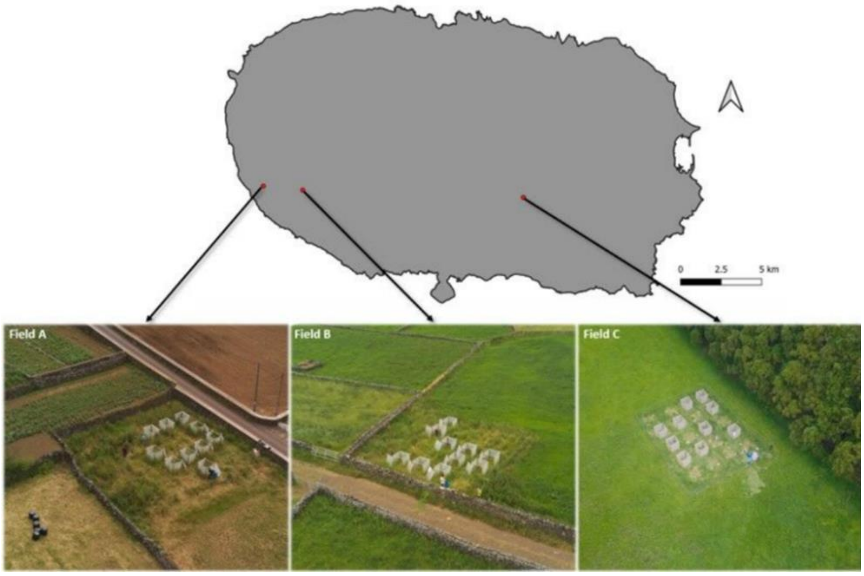

Figure 1. Picture and localisation of each field on the island of Terceira. Each experimental area is covered with 10 control plots and 10 plots surrounded by an OTC (Photo credits: Sebeyes Production).

Pitfall traps consisted in a 330 ml plastic cups, about 12 cm deep and 8 cm of diameter at the top (Fig. 2). Traps were filled with ethylene glycol. We used car's cooling liquid at 20% ethylene glycol and added few drops of soap to break the water tension. Specimens collected were then stored into ethanol (96%).

For each season (winter and summer), four pitfall traps were set up on each corner of each plot resulting in four traps per plot (Fig. 3). All traps were active for 14 days, except during the summer, in field B, where the traps were active for 13 days.

In the winter (March 2020) and before sorting arthropods, the four traps of each plot were merged into one sample corresponding to the plot. For this reason, for the winter 2020 period, only the pitfall number 1 (PTF_1) appears in the column "eventID" that corresponds to four pitfall traps merged into one single sample. Then in the summer (September 2020), each pitfall trap was kept separately before sorting, resulting in four pitfalls for each plot (PTF_1; PTF_2; PTF_3; PTF_4).

In the Event table, the location ID name includes the following information:

Code Site (A, B or C), Control (C) or Treatment with OTCs (T), Plot Number (1 to 10)_ Year of collection - Month of collection_ Pitfall trap (PTF)_ Pitfall number (1 to 4).

For example, the location ID "AC7_2020-09_PTF_3" corresponds to the "Field A Control Plot number 7_ collected in September 2020_ Pitfall trap _ Number 3"

Quality control: After collection, specimens were stored in ethanol (96%) before sorting. Specimens, adults and juveniles, were identified in the laboratory by a trained parataxonomist (Sophie Wallon) and organised following a system of morphospecies (Oliver et al., 1996). Final identification was done by the senior author (Paulo A.V. Borges).

Figure 2. A pitfall trap. The trap was then covered with a plastic dish raised from the ground to avoid overflow of the trap due to eventual rainfall (Photo credit: Sophie Wallon).

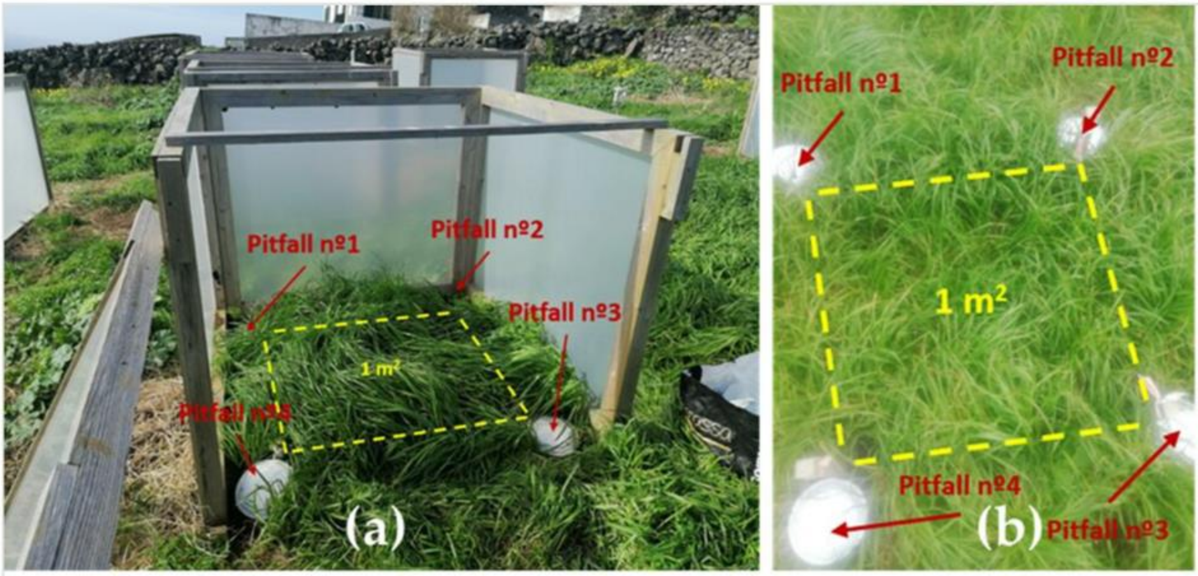

Figure 3. Set-up of an OTC plot (a) and a control plot (b) (Photo credits: Sophie Wallon)

For each species identified, a colonisation status (Endemic, Native (non-endemic), Introduced, Indeterminate) named as "establishmentMeans" in the Occurrence table, was attributed following Borges et al. (2022).

Step description: Specimens were identified, based on the Azorean arthropods collection "Dalberto Teixeira Pombo Insect Collection (DTP), University of Azores" created and maintained by Professor Paulo A.V. Borges. A new collection reference was created, in the framework of the project PASTURCLIM, referencing each species occurring in the present dataset. If the specimen observed did not correspond to species/morphospecies recorded in any specimen already recorded in the Azorean arthropods collection or if its identification was not possible, then a new morphospecies number was attributed to that specimen (identificationRemarks in Occurrence table).

2.5. Geographic coverage

Description: Terceira Island, Azores, Portugal.
Coordinates: -27.394 and -27.0150 Latitude; 38.814 and 38.638 Longitude.

2.6. Taxonomic coverage

Description: The following classes and orders of arthropods are covered:
Arachnida: Araneae, Opiliones, Pseudoscorpiones; Chilopoda: Lithobiomorpha, Scutigeromorpha; Diplopoda: Julida, Polydesmida; and Insecta: Coleoptera, Dermaptera, Hemiptera, Hymenoptera, Lepidoptera, Neuroptera, Orthoptera, Psocoptera.

Taxa included:

Rank	Scientific Name	Common Name
class	Arachnida	Arachnids
order	Araneae	Spiders
order	Opiliones	Harvestmen
order	Pseudoscorpiones	Pseudoscorpions
class	Chilopoda	Centipedes
order	Lithobiomorpha	Centipedes
order	Scutigeromorpha	Centipedes
class	Diplopoda	Millipedes
order	Julida	Millipedes
order	Polydesmida	Millipedes
class	Insecta	Insects
order	Coleoptera	Beetles
order	Dermaptera	Earwigs
order	Hemiptera	Bugs
order	Hymenoptera	Ants
order	Lepidoptera	Moths
order	Neuroptera	Lacewings
order	Orthoptera	Crickets, Grasshoppers
order	Psocodea	Psocids, Barklice, Booklice

2.7. Temporal coverage

Notes: Winter 2020 (03-2020):
Field A: 20 February 2020 till 5 March 2020 (14 days)
Field B: 26 February 2020 till 11 March 2020 (14 days)
Field C: 24 February 2020 till 9 March 2020 (14 days)

Summer 2020 (09-2020):
Field A: 24 August 2020 till 7 September 2020 (14 days)
Field B: 25 August 2020 till 7 September 2020 (13 days)
Field C: 27 August 2020 till 10 September 2020 (14 days)

2.8. Collection data

Collection name: Entomoteca Dalberto Teixeira Pombo at University of Azores
Collection identifier: DTP
Specimen preservation method: All specimens were preserved in 96% ethanol.
Curatorial unit: Dalberto Teixeira Pombo insect collection at the University of the Azores
(Curator: Paulo A. V. Borges)

Usage licence: Creative Commons Public Domain Waiver (CC-Zero)

2.9. Data resources

Data package title: Monitoring grassland's arthropods in an in situ climate change experimentation (Terceira, Azores, Portugal)
Resource link: http://ipt.gbif.pt/ipt/resource?r=pasturclim_otc
Alternative identifiers: https://www.gbif.org/dataset/2276a616-3da6-4528-89c4-bcefd34a4f6e

Number of data sets: 2

Data set name: Event Table
Character set: UTF-8
Download URL: http://ipt.gbif.pt/ipt/resource?r=pasturclim_otc
Data format: Darwin Core Archive
Data format version: Version 1.4
Description: The dataset is available on the Global Biodiversity Information Facility platform, GBIF (Wallon et al. 2023). The event table dataset is organied following the Darwin Core Archive (DwCA) format and contains 297 records (eventID).

Column label	**Column description**
eventID	An identifier for every single event and specific to the dataset.
samplingProtocol	The methods or protocols used during an Event.
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.
eventDate	Date or date range the record was collected.
year	Year of the event.
month	Month of the event.
verbatimEventDate	The verbatim original representation of the date and time information.
habitat	Description of the habitat in which the Event occurred.
fieldNotes	Note to facilitate the characterisation of the plot treatment: Control plot or plot surrounded by an Open Top Chamber.
locationID	An identifier for the set of location information (specific to the dataset).
islandGroup	Name of the archipelago of the sampling site.
island	Name of the island of the sampling site (Terceira Island).
country	Name of the country of the sampling site.
countryCode	The standard code for the country in which the Location occurs.
stateProvince	An identifier for every single event and specific to the dataset.
municipality	Municipality of the sampling site.
locality	Name of the locality.
minimumElevationInMetres	The lower limit of the range of elevation (altitude, usually above sea level), in metres.
maximumElevationInMetres	The highest limit of the range of elevation (altitude, usually above sea level), in metres.
decimalLatitude	Geographic coordinate (Decimal degrees): sampling location Latitude.
decimalLongitude	Geographic coordinate (Decimal degrees): sampling location Longitude.

geodeticDatum	Spatial reference system (SRS) upon which the geographic coordinates given in decimalLatitude and decimalLongitude are based.
coordinateUncertaintyInMetres	Coordinates' uncertainty in metres to the site of the true sampling area.
coordinatePrecision	A decimal representation of the precision of the coordinates given in the decimalLatitude and decimalLongitude.
georeferenceSources	A map, gazetteer or other resource used to georeference the Location.

Data set name: Occurrences table
Character set: UTF-8
Download URL: http://ipt.gbif.pt/ipt/resource?r=pasturclim_otc
Data format: Darwin Core Archive
Data format version: version 1.4
Description: The dataset is available on the Global Biodiversity Information Facility platform, GBIF (Wallon et al. 2023). The occurrence table dataset is organised following the Darwin Core Archive (DwCA) format and contains 6051 records (occurrenceID).

Column label	Column description
Event ID	An identifier for every single event and specific to the dataset.
type	The type of the related resource.
licence	Information about rights held in and over the resource.
institutionID	An identifier for the institution having custody of the object(s) or information referred to in the record.
collectionID	An identifier for the collection or dataset from which the record was derived.
institutionCode	The name in use by the institution having custody of the object(s) or information referred to in the record.
collectionCode	The acronym identifying the collection or dataset from which the record was derived.
datasetName	The name identifying the dataset from which the record was derived.
basisOfRecord	The specific nature of the data record.
occurrenceID	An identifier built as a "Globally Unique IDentifier".
recordesBy	Names of people responsible for recording the original occurrence.
organismQuantity	A number for the quantity of organisms.
organismQuantityType	The type of quantification system used for the quantity of organisms.
sex	The sex of the biological individual(s) represented in the occurrence.
lifeStage	The age class or life stage of the Organism(s) at the time the Occurrence was recorded.
establishmentMeans	The process of establishment of the species in the location, using a controlled vocabulary: 'native', 'introduced', 'indeterminate'.
occurrenceRemarks	Comments or notes about the Occurrence mentioning the 'endemic' species.
identifiedBy	Names of people who assigned the Taxon to the subject.
dateIdentified	The date on which the subject was determined as representing the Taxon.
identificationRemarks	Dalberto Teixeira Pombo (DTP) collection's morphospecies number attributed to specimens identified.
scientificName	Full scientific name, with authorship and date information, if known. When identification to species level was not possible, then it is the name in the lowest level taxonomic rank that can be determined.
kingdom	Scientific name of the kingdom in which the taxon is classified.

phylum	Scientific name of the phylum in which the taxon is classified.
class	Scientific name of the class in which the taxon is classified.
order	Scientific name of the order in which the taxon is classified.
family	Scientific name of the family in which the taxon is classified.
genus	Scientific name of the genus in which the taxon is classified.
subgenus	Scientific name of the sub genus in which the taxon is classified.
specificEpithet	The species epithet of the scientific name.
infraspecificEpithet	Name of the lowest or terminal infraspecific epithet of the scientific name.
taxonRank	The taxonomic rank of the most specific name in the scientific name.
scientificNameAuthorship	The authorship information related to the scientific name.

2.10. Additional information

We collected a total 41,351 specimens belonging to four classes, 15 orders, 60 families and 171 morphospecies (including 34 taxa identified only at order, family or genus level). Therefore, 137 taxa have a scientific name associated (n = 38918) (from now on "species")

Table 2. Inventory of arthropods collected in three pastures (Fields A, B and C) in Terceira Island (Azores, Portugal) in control plots (C) and plots surrounded by an OTC (T).
AC - Field A control plot; AT - Field A plot OTC; BC - Field B control plot; BT - Field B plot OTC; CC - Field C control plot; CT - Field C plot OTC.
The list includes only the specimens identified at species-level. Class, order, family and scientific name follow alphabetical sequence. Colonisation statuses, based on Borges et al. (2022) and abundance per field and treatment, are provided. Colonisation status (Origin): END - Endemic; NAT - native non-endemic; INTR - introduced; IND - indeterminate.

Family	Scientific Name	Origin	AC	AT	BC	BT	CC	T	Total
Arachnida	**Araneae**								
Dysderidae	*Dysdera crocata* C. L. Koch, 1838	INTR	3	3	1	11	2	12	32
Gnaphosidae	*Marinarozelotes lyonneti* (Audouin, 1826)	INTR		1					1
Gnaphosidae	*Zelotes aeneus* (Simon, 1878)	INTR			2	2			4
Linyphiidae	*Agyneta fuscipalpa* (C. L. Koch, 1836)	INTR	98	58		1	1	1	159
Linyphiidae	*Erigone atra* Blackwall, 1833	INTR	3		4	1	182	67	257
Linyphiidae	*Erigone autumnalis* Emerton, 1882	INTR	148	88	79	67	54	9	445
Linyphiidae	*Erigone dentipalpis* (Wider, 1834)	INTR	109	52	87	95	569	248	1160
Linyphiidae	*Mermessus bryantae* (Ivie & Barrows, 1935)	INTR	10	8	4	5	25	42	94
Linyphiidae	*Mermessus fradeorum* (Berland, 1932)	INTR	5	8	20	24	99	102	258
Linyphiidae	*Neriene clathrata* (Sundevall, 1830)	INTR		1		1			2
Linyphiidae	*Oedothorax fuscus* (Blackwall, 1834)	INTR	170	151	72	65	975	473	1906
Linyphiidae	*Ostearius melanopygius* (O. Pickard-Cambridge, 1880)	INTR	23	43	12	44		3	125
Linyphiidae	*Prinerigone vagans* (Audouin, 1826)	INTR	13	9	2	5	13	4	46
Linyphiidae	*Tenuiphantes tenuis* (Blackwall, 1852)	INTR	43	69	30	80	41	71	334
Lycosidae	*Pardosa acorensis* Simon, 1883	END				1	50	28	79
Mimetidae	*Ero furcata* (Villers, 1789)	INTR						1	1
Oecobiidae	*Oecobius navus* Blackwall, 1859	INTR	1						1
Tetragnathidae	*Pachygnatha degeeri* Sundevall, 1830	INTR			33	67	7	34	141
Theridiidae	*Cryptachaea blattea* (Urquhart, 1886)	INTR				3			3
Zodariidae	*Zodarion atlanticum* Pekár & Cardoso, 2005	INTR	3	3		1			7
Arachnida	**Opiliones**								
Leiobunidae	*Leiobunum blackwalli* Meade, 1861	NAT					2621	1313	3934

Family	Scientific Name	Origin	AC	AT	BC	BT	CC	T	Total
Sclerosomatidae	*Homalenotus coriaceus* (Simon, 1879)	NAT	1	5	73	283	71	68	501
Arachnida	**Pseudoscorpiones**								
Chthoniidae	*Chthonius ischnocheles* (Hermann, 1804)	INTR		1					1
Neobisiidae	*Neobisium maroccanum* Beier, 1930	INTR		1				1	2
Chilopoda	**Lithobiomorpha**								
Lithobiidae	*Lithobius pilicornis pilicornis* Newport, 1844	NAT	2	5	7	15	25	13	67
Chilopoda	**Scutigeromorpha**								
Scutigeridae	*Scutigera coleoptrata* (Linnaeus, 1758)	INTR	13	39	1				53
Diplopoda	**Julida**								
Blaniulidae	*Blaniulus guttulatus* (Fabricius, 1798)	INTR	1					5	6
Blaniulidae	*Nopoiulus kochii* (Gervais, 1847)	INTR					2	1	3
Blaniulidae	*Proteroiulus fuscus* (Am Stein, 1857)	INTR	2	4				4	10
Julidae	*Cylindroiulus propinquus* (Porat, 1870)	INTR	1	1	1		19	15	37
Julidae	*Ommatoiulus moreleti* (Lucas, 1860)	INTR	504	278	21	25	60	186	1074
Diplopoda	**Polydesmida**								
Paradoxosomatidae	*Oxidus gracilis* (C.L. Koch, 1847)	INTR			2		7	10	19
Polydesmidae	*Polydesmus coriaceus* Porat, 1870	INTR	107	72	108	164	215	276	942
Insecta	**Coleoptera**								
Anthicidae	*Hirticollis quadriguttatus* (Rossi, 1792)	NAT	3	2					5
Aphodiidae	*Calamosternus granarius* (Linnaeus, 1767)	INTR	5	1		1			7
Apionidae	*Aspidapion radiolus* (Marsham, 1802)	NAT	1	13		1	6	11	32
Carabidae	*Agonum muelleri muelleri* (Herbst)	INTR			3				3
Carabidae	*Amara aenea* (De Geer, 1774)	INTR			6		1		7
Carabidae	*Anisodactylus binotatus* (Fabricius, 1787)	INTR	3	3	87	33	190	88	404
Carabidae	*Bembidion ambiguum* Dejean, 1831	INTR	1	3	1	3	1		9
Carabidae	*Calosoma olivieri* Dejean, 1831	NAT	2	2	16	30	1	1	52
Carabidae	*Harpalus distinguendus distinguendus* (Duftschmidt, 1812)	INTR	139	198	23	13			373
Carabidae	*Laemostenus complanatus* (Dejean, 1828)	INTR	1	5					6
Carabidae	*Notiophilus quadripunctatus* Dejean, 1826	NAT	287	191	44	48			570
Carabidae	*Ophonus ardosiacus* (Lutshnik, 1922)	INTR		1					1
Carabidae	*Paranchus albipes* (Fabricius, 1796)	INTR					28	170	198
Carabidae	*Pseudoophonus rufipes* (De Geer, 1774)	INTR	247	127	3343	2480	285	466	6948
Carabidae	*Pterostichus vernalis* (Panzer, 1796)	INTR	3		19	6	567	709	1304
Carabidae	*Stenolophus teutonus* (Schrank, 1781)	NAT			1		30	5	36
Chrysomelidae	*Epitrix cucumeris* (Harris, 1851)	INTR	1						1
Chrysomelidae	*Epitrix hirtipennis* (Melsheimer, 1847)	INTR		1					1
Coccinellidae	*Rhyzobius lophanthae* (Blaisdell, 1892)	INTR		1					1
Coccinellidae	*Scymnus interruptus* (Goeze, 1777)	NAT	3			1			4
Coccinellidae	*Scymnus nubilus* Mulsant, 1850	NAT	3			1			4
Corylophidae	*Sericoderus lateralis* (Gyllenhal, 1827)	INTR	6	18		2	1	1	28
Curculionidae	*Coccotrypes carpophagus* (Hornung, 1842)	INTR		1	1			4	6

Family	Scientific Name	Origin	AC	AT	BC	BT	CC	T	Total
Curculionidae	*Mecinus pascuorum* (Gyllenhal, 1813)	INTR		1					1
Curculionidae	*Orthochaetes insignis* (Aubé, 1863)	NAT		1					1
Curculionidae	*Sitona discoideus* Gyllenhal, 1834	INTR	49	16	8	24	10	2	109
Curculionidae	*Tychius picirostris* (Fabricius, 1787)	INTR						2	2
Dryophthoridae	*Sitophilus oryzae* (Linnaeus, 1763)	INTR			1				1
Dryophthoridae	*Sphenophorus abbreviatus* (Fabricius, 1787)	INTR	31	10	8	7	5	3	64
Dryopidae	*Dryops luridus* (Erichson, 1847)	NAT	1				14	11	26
Elateridae	*Aeolus melliculus moreleti* Tarnier, 1860	INTR	52	12	12	5	5		86
Elateridae	*Melanotus dichrous* (Erichson, 1841)	INTR	3	1			16	13	33
Hydrophilidae	*Cercyon haemorrhoidalis* (Fabricius, 1775)	INTR	39	3	13	6	13	1	75
Hydrophilidae	*Sphaeridium bipustulatum* Fabricius, 1781	INTR					1		1
Latridiidae	*Cartodere nodifer* (Westwood, 1839)	INTR						4	4
Mycetophagidae	*Litargus balteatus* Le Conte, 1856	INTR	1						1
Mycetophagidae	*Typhaea stercorea* (Linnaeus, 1758)	INTR	15	11	3				29
Nitidulidae	*Carpophilus fumatus* Boheman, 1851	INTR					2	1	3
Nitidulidae	*Epuraea biguttata* (Thunberg, 1784)	INTR	3				1		4
Nitidulidae	*Phenolia limbata tibialis* (Boheman, 1851)	INTR	1						1
Nitidulidae	*Stelidota geminata* (Say, 1825)	INTR	4	1	8	1	2		16
Phalacridae	*Stilbus testaceus* (Panzer, 1797)	NAT	1		1				2
Ptiliidae	*Ptenidium pusillum* (Gyllenhal, 1808)	INTR	2	1	3	3	1	1	11
Scarabaeidae	*Onthophagus taurus* (Schreber, 1759)	INTR	1	1	11	13	5		31
Scarabaeidae	*Onthophagus vacca* (Linnaeus, 1767)	INTR		2	1	1			4
Staphylinidae	*Aleochara bipustulata* (Linnaeus, 1760)	IND	8	2	2		31	3	46
Staphylinidae	*Aleochara verna* Say, 1833	IND					1		1
Staphylinidae	*Aloconota sulcifrons* (Stephens, 1832)	IND	13			1	6		20
Staphylinidae	*Amischa analis* (Gravenhorst, 1802)	IND	36	21	39	68	408	110	682
Staphylinidae	*Amischa forcipata* Mulsant & Rey, 1873	IND	3				24	4	31
Staphylinidae	*Anotylus nitidifrons* (Wollaston, 1871)	IND	1429	621	125	33	284	47	2539
Staphylinidae	*Anotylus nitidulus* (Gravenhorst, 1802)	IND	9	3			3	3	18
Staphylinidae	*Astenus lyonessius* (Joy, 1908)	IND	1						1
Staphylinidae	*Atheta aeneicollis* (Sharp, 1869)	IND	1				3	12	16
Staphylinidae	*Atheta fungi* (Gravenhorst, 1806)	IND	42	1					43
Staphylinidae	*Atheta palustris* (Kiesenwetter, 1844)	IND	2				2	5	9
Staphylinidae	*Atheta pasadenae* Bernhauer, 1806	IND	3				5	3	11
Staphylinidae	*Carpelimus corticinus* (Gravenhorst, 1806)	IND	1						1
Staphylinidae	*Carpelimus zealandicus* (Sharp, 1900)	INTR				6			6
Staphylinidae	*Coproporus pulchellus* (Erichson, 1839)	IND						1	1
Staphylinidae	*Cordalia obscura* (Gravenhorst, 1802)	IND	265	61	80	50	152	75	683
Staphylinidae	*Gabrius nigritulus* (Gravenhorst, 1802)	IND	1				6	1	8
Staphylinidae	*Gyrohypnus fracticornis* (Müller, 1776)	IND	10	4	29	32	26	17	118
Staphylinidae	*Ocypus olens* (Müller, 1764)	IND	97	108	303	484	6	23	1021

Family	Scientific Name	Origin	AC	AT	BC	BT	CC	T	Total
Staphylinidae	*Oligota pumilio* Kiesenwetter, 1858	IND	18	57	2	16	12	24	129
Staphylinidae	*Oligota pusillima* (Gravenhorst, 1806)	IND	2	5		4			11
Staphylinidae	*Philonthus longicornis* Stephens, 1832	IND					3		3
Staphylinidae	*Philonthus quisquiliarius quisquiliarius* (Gyllenhal, 1810)	IND						1	1
Staphylinidae	*Pseudoplectus perplexus* (Jacquelin du Val, 1854)	IND					2	1	3
Staphylinidae	*Quedius simplicifrons* Fairmaire, 1862	IND				2	13	14	29
Staphylinidae	*Rugilus orbiculatus* (Paykull, 1789)	IND	802	214	159	148	108	41	1472
Staphylinidae	*Sepedophilus lusitanicus* Hammond, 1973	IND	4	3			1		8
Staphylinidae	*Stenomastax madeirae* Assing, 2003	IND	12		1		54	11	78
Staphylinidae	*Sunius propinquus* (Brisout de Barneville, 1867)	IND		3					3
Staphylinidae	*Tachyporus chrysomelinus* (Linnaeus, 1758)	IND	3					2	5
Staphylinidae	*Tachyporus nitidulus* (Fabricius, 1781)	IND	13	38	8	26	6	7	98
Staphylinidae	*Xantholinus longiventris* Heer, 1839	IND	1	1	3	18	9	6	38
Tenebrionidae	*Blaps lethifera* Marsham, 1802	INTR		1					1
Anisolabididae	*Euborellia annulipes* (Lucas, 1847)	INTR	1	5	20	185	2	20	233
Forficulidae	*Forficula auricularia* Linnaeus, 1758	INTR	1802	1482	75	69	8	30	3466
Anthocoridae	*Anthocoris nemoralis* (Fabricius, 1794)	NAT		2				1	3
Aphididae	*Rhopalosiphoninus latysiphon* (Davidson, 1912)	INTR	4	17	1	1		1	24
Cicadellidae	*Anoscopus albifrons* (Linnaeus, 1758)	NAT	24	15	16	45	22	6	128
Cicadellidae	*Euscelidius variegatus* (Kirschbaum, 1858)	NAT	1	3			4	2	10
Cydnidae	*Geotomus punctulatus* (A. Costa, 1847)	NAT	245	60	22	6			333
Delphacidae	*Kelisia ribauti* Wagner, 1938	NAT			2	1	23	2	28
Delphacidae	*Megamelodes quadrimaculatus* (Signoret, 1865)	NAT					19	3	22
Lygaeidae	*Kleidocerys ericae* (Horváth)	NAT			1				1
Nabidae	*Nabis pseudoferus ibericus* Remane, 1962	NAT	7	1	2	3	1		14
Rhyparochromidae	*Beosus maritimus* (Scopoli, 1763)	NAT	18	4		1		1	24
Rhyparochromidae	*Scolopostethus decoratus* (Hahn, 1833)	NAT	35	18	1	1			55
Saldidae	*Saldula palustris* (Douglas)	NAT				1			1
Insecta	**Hymenoptera**								
Apidae	*Bombus ruderatus* (Fabricius, 1775)	INTR				1			1
Formicidae	*Hypoponera eduardi* (Forel, 1894)	NAT	89	91	308	161		2	651
Formicidae	*Lasius grandis* Forel, 1909	NAT	230	310	192	305	89	67	1193
Formicidae	*Linepithema humile* (Mayr, 1868)	INTR	2	36	25	1		2	66
Formicidae	*Monomorium carbonarium* (F. Smith, 1858)	NAT	3	10					13
Formicidae	*Tetramorium caespitum* (Linnaeus, 1758)	NAT	1470	1296	204	89			3059
Insecta	**Lepidoptera**								
Noctuidae	*Mythimna unipuncta* (Haworth, 1809)	NAT			5	1			6
Insecta	**Neuroptera**								

Family	Scientific Name	Origin	AC	AT	BC	BT	CC	T	Total
Chrysopidae	*Chrysoperla agilis* Henry et al., 2003	NAT	1	1				7	9
Chrysopidae	*Chrysoperla lucasina* (Lacroix, 1912)	NAT	1	1				7	9
Insecta	**Orthoptera**								
Gryllidae	*Eumodicogryllus bordigalensis* (Latreille, 1804)	INTR	23	8	56	13	80	20	200
Gryllidae	*Gryllus bimaculatus* De Geer, 1773	INTR	9	9	5	2			25
Insecta	**Psocodea**								
Ectopsocidae	*Ectopsocus briggsi McLachlan, 1899*	INTR						1	1
	TOTAL		8909	6039	5859	5412	7636	5063	38918

Regarding the colonisation status, introduced species (also those with an "indeterminate" colonisation status that are most probably exotic species (n = 7622)) represented 71% (n = 29664 specimens) of the total abundance and 75% (129 species) of the total richness; 28% (n = 11608 specimens) of the total abundance and 19% (33 species) of the total richness were represented by native non-endemic species; finally, endemic species represented 0.2% (n = 79 specimens) of the total abundance and 1% (one species) of the total richness.

Spiders (Arachnida, Araneae) and beetles (Insecta, Coleoptera) were the two most diversified and abundant groups.

Altogether, *Pseudoophonus rufipes* (De Geer, 1774) (Coleoptera, Carabidae), an omnivorous ground beetle, dominated the samples and represented 17% of the total arthropod abundance. This ground beetle dominated summer samples, while the predator rove beetle *Ocypus olens* (Müller, 1764) (Coleoptera, Staphylinidae) dominated winter samples.

The dominant spider was *Oedothorax fuscus* (Blackwall, 1834) (Araneae, Linyphiidae) representing 5% of overall arthropod abundance. It was also the most dominant spider species in summer samples, while winter samples were dominated by the spider *Erigone dentipalpis* (Wider, 1834) (Araneae, Linyphiidae).

Some species distributions varied with elevation and consequently with the type of field. The ground-beetle *Notiophilus quadripunctatus* Dejean, 1826 (Coleoptera, Carabidae) dominated winter samples (n = 464, 14%) at the low altitude field (field A) and the European earwig *Forficula auricularia* Linnaeus, 1758 (Dermaptera) was the most abundant arthropod in the summer samples (n = 3177, 24%) of the same field; at the intermediate altitude field (field B), the rove beetle *Ocypus olens* (Müller, 1764) (Coleoptera, Staphylinidae) (n = 579, 25%) dominated winter samples and the ground beetle *Pseudoophonus rufipes* (De Geer, 1774) (Coleoptera, Carabidae) (n = 5822, 61%) summer samples; finally, the rove beetle *Amischa analis* (Gravenhorst, 1802) (Coleoptera, Staphylinidae) was the most abundant species during the winter (n = 211, 14%) in the upper altitude field (field C), while the harvestman *Leiobunum blackwalli* (Arachnida, Opiliones) (n = 3882, 33%) was the dominant species in summer.

Our study is responding to the need to have baseline data to understand long-term insect decline patterns (Seibold et al., 2019). Setting monitoring programmes using arthropods is important for understanding and managing pest populations, detecting environmental changes, assessing the impact of management practices and identifying potential threats to biodiversity (P. A. V. Borges et al., 2019).

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Chapter 3. Effects of a short-term temperature increase on arthropod communities associated with pastures

Abstract

The impact of climate change on islands is expected to cause dramatic consequences on native biodiversity. However, little data is available for arthropod communities in island agroecosystems. In this study we simulate a small-scale climatic change (average of +1.2◦C), using Open Top Chambers (OTCs) in forage crops in the Azores archipelago (Portugal) and test the responses of arthropod communities associated with intensively managed pastures. In three sites, twenty 1x1 m plots were established: 10 treatment plots with OTCs and 10 control plots. Arthropods were sampled with pitfall traps on two sampling events (winter and summer in 2020). When considering all species collected, arthropods abundance was lower in OTCs. Specific taxa, as spiders and beetle showed a fast response to the OTCs presence. The assemblage of non-indigenous spiders well adapted pastures showed a significant difference in diversity with a slightly greater richness but lower abundance inside the warmer plots. However, the presence of OTCs resulted in a decrease in beetle richness and abundance. This decline may be attributed to the multiple effects of warming. Therefore, it is imperative to conduct further investigations to elucidate the ecological processes that underlie the observed patterns.

Keywords: Invertebrates; Azores; climate changes; grasses; islands, species diversity

3.1. Introduction

Climate change is happening at a fast pace, and the results are the increase of temperature (Arnell et al., 2019; Portner et al., 2022), change in precipitation patterns (Ohba et al., 2019; Papalexiou et al., 2019), and the increase of the frequency and severity of extreme natural events (Banerjee et al., 2018; Hettiarachchi et al., 2018; Myhre et al., 2019; Yin et al., 2018). Those changes are altering ecosystems and affecting biodiversity (Habibullah et al., 2022; Sharma et al., 2018). Agroecosystems which support food production, are no exceptions and they also can be impacted in several ways: climate change can cause heat stress on crops and reduce yields, altered precipitation regimes jeopardize available water in the critical growth periods, and natural disasters can cause direct damages (Cook et al., 2018; Craig et al., 2019; Elahi et al., 2022; Schoene et al., 2012).

In particular, island environments are especially sensitive to climate change and have been identified among the most vulnerable ecosystems to climate shifts and extremes (Nurse et al., 2014). On islands, the vulnerability is defined by the system's capacity to respond to modifications in the abiotic environment and their adaptation to climate change can be challenging (Harter et al., 2015; Santos et al., 2004; Taylor et al., 2016; Vogiatzakis et al., 2016). For instance, in the Azorean Islands (nine islands located in the North Atlantic), the main consequence of climate change is the increase of temperature and the decrease of rain (Azevedo et al., 1999; Azevedo et al., 1998). The two respective scenarios, RCP4.5 and RCP 8.5 (PRAC, 2017), predicted an increase of temperature between 0.78 °C and 0.90 °C until 2039 and a further increase to between 1.5 °C and 2.8 °C until the end of the century is also expected. Those changes in climate may also result in shifts in cloud layer altitudes, which, in turn, may alter altitudinal zonation of the vegetation and different species assemblages, mostly promoting species losses (Harter et al., 2015). According to projection models, the distribution of the unique biota of the Azores will be affected (Ferreira et al., 2016; Patiño et al., 2016) by the loss of suitable climatic space due to climate change and should be taken into account for the design of protected areas (Ferreira et al., 2019). Following the "Programa Regional para as Alterações Climáticas" (Regional Program for Climate Change) (PRAC, 2017), the most important impacts associated with climatic factors in the Azores are the stress induced on ecosystems and natural resources which causes the reduction of agriculture production in situations of drought, the reduction of quality of the pasture and fodder, and the expansion of some insect pests.

In the Azores archipelago, around 56% of the land is dedicated to agroecosystems of which 46% are permanent pastures (Barnett et al., 2016), representing 88% of usable agricultural area (Governo dos Açores, 2020). The grasslands and pastures cover about 41.5% of Terceira (Cruz et al., 2007; Reis et al., 2015), the third largest island in the archipelago. They support semi-extensive dairy and beef cattle farming, both by fodder production and direct grazing (Massot, 2015). Although the impacts of global change on grasses in pastures is already widely studied, and relationships between nutritive parameters and environmental factors that can alter grass digestibility for cattle and grass quality are confirmed (Berauer et al., 2020; Hart et al., 2022; Melo et al., 2022), there is still limited data available related to the impact of climate change on Azorean agroecosystems. It is, however, likely that, similarly to native ecosystems, these are also threatened by climate change. Since arthropods provide a wide range of ecosystem services (e.g. pollination, biological control) and also cause ecosystem disservices (e.g. crop damages, pest outbreaks), how their diversity is changing with the changing climate should be of utmost importance in agroecosystems (Allan et al., 2015; Borges et al., 2021; Ferrante et al., 2022; Zhang et al., 2007).

In the last years, a plethora of studies have shown the impact of global change on arthropods in grasslands, pinpointing how climate change can affect arthropod communities and alter their diversity and/or composition (Barnett et al., 2016; Buchholz et al., 2013; Gobbi et al., 2006; Pitta et al., 2019). Fully controlled, short-term experiments (less than two years) already indicate an impact of increased temperature on arthropod abundances and richness(Buchholz et al., 2013; Hågvar et al., 2009; Molina-Montenegro et al., 2009; Sohlström et al., 2022)

Despite the fact that experiments have already highlighted changes occuring in arthropod communities in different grassland and pasture in the world under climate change, and that the arthropod communities of Azorean pastures have been investigated in detail (Borges, 2008; Borges & Brown, 1999, 2004; Cardoso et al., 2009; Rigal et al., 2018), no study has yet scrutinized the impact of climate change (e.g. increase of temperature) on those communities in the Azores.

In this short-term, *in situ* experiment we aim to test the impacts of increasing temperature on arthropod communities in pastures on Terceira, the third largest island of the Azores archipelago, using Open Top Chambers (OTCs).

We hypothesize that warming will affect arthropod communities and we aim to identify which groups or species of arthropods are more likely to respond positively or negatively to an increase in temperature.

We address the following research questions:

i) Does the increase in temperature within OTCs change the species composition? Due to the small-scale and the short-term of the experiment we predict little or no changes in the species composition and consequently, that communities will remain highly similar between the two treatments.

ii) Does the increase in temperature in OTCs change the total abundance of arthropods? Based on previous studies, we expect higher total arthropods abundance in OTCs than in the control plots with ambient temperature.

iii) Does the increase in temperature impact the relative abundances of species? We expect shifts in the ratio of common, rare and dominant species, especially an increasing dominance of a few, thermophilus, species.

3.2. Materials and Methods

3.2.1. Study Area

The study was conducted in three experimental intensively managed pasture fields on Terceira Island (area 402 km^2 and maximum elevation of 1023 m), located in the Azores archipelago in Portugal (38°37′ N–38°48′ N, 27°02′ W–27°23′ W). The three fields (marked as A, B, and C) were located at three different altitudes: 186 m a.s.l. (latitude: 38.703596°N; longitude: -27.353805°W), 301 m a.s.l. (latitude: 38.701639°N; longitude: - 27.325783°W) and 386 m a.s.l. (latitude: 38.697770°N; longitude: -27.170075°W), respectively (Figure 1). All fields are considered as intensive pasture, dominated by the Italian ryegrass, *Lolium multiflorum* Lam. (Poaceae) in fields A and B, and dominated by the common velvet grass, *Holcus lanatus* L. (Poaceae) in field C.

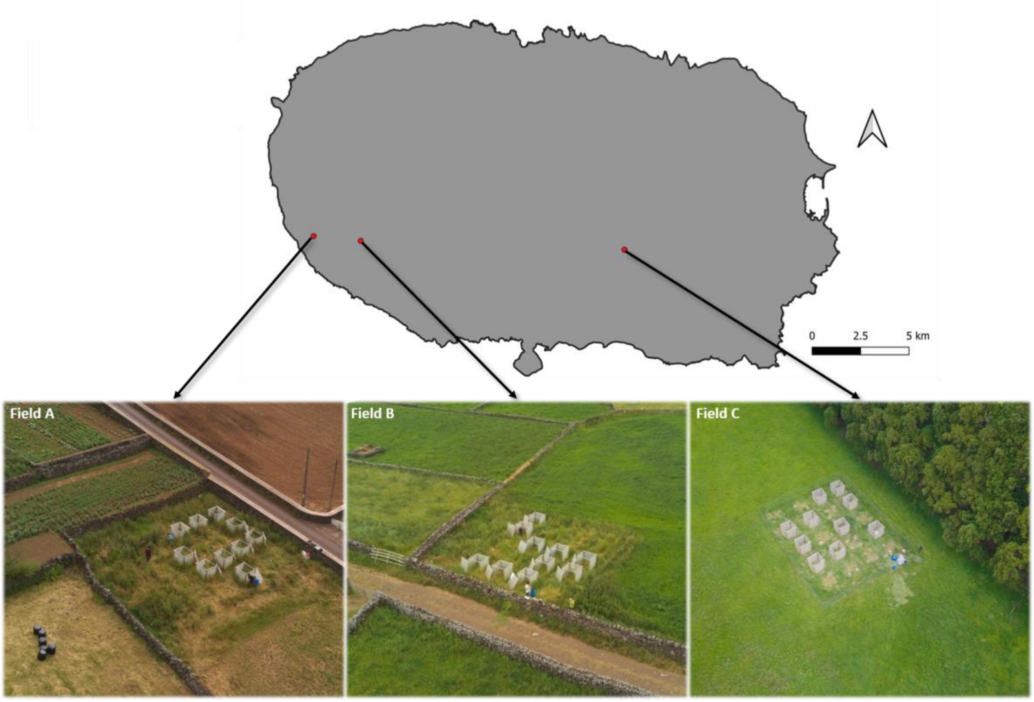


Figure 1. Aerial photos and locations of each field on the island of Terceira. Field A, B and C are located respectively at 186 m, 301 m and 386 m a.s.l. Each experimental area is covered with 10 control plots and 10 plots surrounded with an OTC. (Photo credits: Sebeyes production).

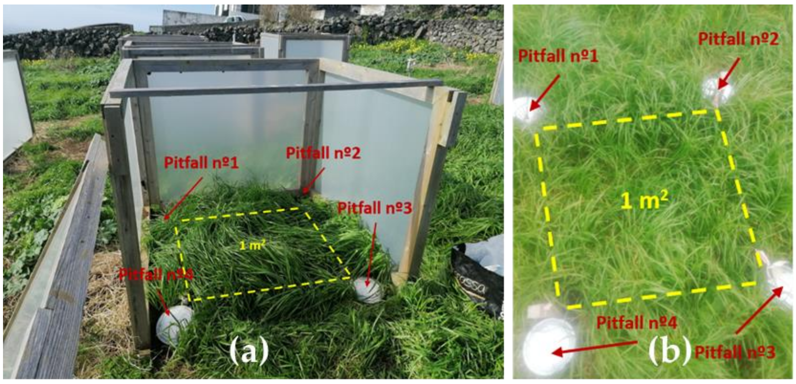


Figure 2. Setup of an OTC plot (a) and a control plot (b) (Photo credits: Sophie Wallon).

3.2.2. Experimental Design

An *in situ* experimental was set up using Open Top Chambers (OTCs). OTCs are widely used on climate change investigation in order to modify abiotic conditions *in situ* and simulate an increase of temperature (Aronson et al., 2009). The OTC panels act as a wind shield, minimizing the amount of heat lost through convection, and the open top allows rainfalls as well as air circulation, creating small eddies (Hollister et al., 2022).

In each field, twenty (1x1 m) plots were set up on a grid pattern with 1.5 m space between each plot (Figure 2). Of the twenty plots, ten were randomly chosen as control and the other ten were surrounded by OTCs. Data loggers (Easy Log: EL-USB-2) were set up to collect the temperature data inside the OTCs as well as in the control plots. The temperature inside the OTCs was in average 1-1.4 °C higher than in the control plots. OTCs were set up in order to include the 1x1m plot as well as a margin of 25 cm all around the plot. This allowed scientists to circulate around the plot without damaging it, as well as to set up the pitfall traps on each outside corner of the plot but still inside the OTCs. The OTCs were also slightly lifted up from the ground (with around 5 cm) in order to allow crawling arthropods to disperse freely around the whole sampling area. Indeed, it is due to the short-term of the experiment, to the plot's proximity to each other in each field, and due to the good dispersal capacities of crawling arthropods, that our first prediction (i), is that there will be minimal to no alterations in the species composition, which implies that the communities will remain considerably similar between both treatments.

In both seasons, the sampling was done before mowing the grass. No cattle were allowed inside the sampling area. It is important to note that the experimental set up (control and OTCs) was mounted the whole year around. Thus, the OTCs and control plots were not moved between the two sampling seasons.

3.2.3. Arthropod Sampling and Identification

For this study, we focused on arthropod communities associated with an intensive pasture management. As OTCs represent a physical barrier for flying insects and can induce bias into the results, the present study focuses on crawling arthropods. As pitfall traps target crawling arthropods, they were used for sampling. Four pitfall traps were set on each outside corner of each plot giving a total of 80 pitfall traps per field. Pitfall traps set up inside the OTCs were located on the 25 cm margin around the plot (see also in Experimental design). Pitfall traps consisted in a 330 ml plastic cup, about 12 cm deep and 8 cm of diameter at the top, filled with car's cooling liquid at 20% ethylene glycol at which we added few drops of soap to break water tension. Pitfall traps were covered, using small iron sticks, with a plastic dish lifted up from the opening of the trap and letting it free of access. The dish protects the trap from eventual rain and avoid its over flow. Specimen collected were stored in ethanol (96%). For the analyses, the data from the four pitfalls of each plot were merged in one single sample giving a total of 10 replicates per treatment: 10 controls and 10 OTCs per fields. Arthropod sampling was performed during the winter and the summer 2020 using pitfall traps set for 14 days, with a single exception of Field B in summer for which traps were available 13 days. In this case the 14th day capture was extrapolated from the other days.

All arthropods sampled were sorted and identified to species level, when possible, for the following target groups: Arachnida (Araneae, Opiliones, Pseudoscorpiones), Diplopoda, Chilopoda and Insecta (excluding Diptera, Hymenoptera - but including Formicidae - and Lepidoptera). Unidentified specimens were assigned to a morphospecies code. Initial sorting and identification were performed by the first author (SW) and students acting as parataxonomists (see list in Acknowledgments) and then by an expert taxonomist (PAVB). The nomenclature and colonization status of the species follows the recent checklist of the Azorean arthropods (Borges et al., 2022). The analyses were conducted using the abundance of adult individuals identified to morpho(species) level. Despite de fact that in previous studies on Azorean arthropods juvenile spiders were commonly used (e.g. Cardoso *et al.* 2009), in our study the dominance of Erigoninae linyphiid spiders made this approach more difficult. All specimens are stored in Dalberto Teixeira Pombo (DTP) Collection in University of Azores (Terceira Island). Data are available in Wallon *et al.* (2023) - (direct data access at: http://ipt.gbif.pt/ipt/resource?r=pasturclim_otc).

In intensive pastures on Terceira, exotic arthropods are usually predominant and the abundance of native and/or endemic species are reduced due to the high level of disturbance of the land (Cardoso et al., 2009; Rigal et al., 2018). Thus, as most of the species involved in our study are considered introduced for the Azores, no importance was given to the biogeographical origin of species in the analysis.

3.2.4. Data Analysis

We combined catch data from the four traps present in each plot. In cases where a trap became damaged (no more than one per sampling event) and data was consequently lost, the missing information was estimated by extrapolating from the data gathered from the other three traps. Additionally, when the traps were operational for only 13 days, we extended the sampling period to 14 days through extrapolation.

Given the relatively low distances between experimental plots, we could not rule out the possibility of spatial autocorrelation among samples. As the precise coordinates of the experimental units were unknown, we established an artificial grid system at each site, using the measured distances between plots and the site coordinate (see above) serving as the reference point for the centre of the initial plot located in the top left corner of the grid. These calculated coordinates for the centre of each plot were then utilized to calculate the Moran's I values as a means of testing for spatial autocorrelation. Since our samples were, indeed, found to be spatially autocorrelated and they were also obtained through a repeated sampling protocol of the same sites, we incorporated both temporal and spatial autocorrelation into our model-building process and employed generalized linear mixed models (GLMMs) with multivariate normal random effects with Penalized Quasi-Likelihood, using the glmmPQL() function from the MASS package ((Venables et al., 2002).

As response variables, we calculated the total activity-densities for each sampling event (i.e. the pooled number of arthropods from the four traps in summer or winter) as well as the first four Hill numbers ($q = 0\text{-}3$). Hill numbers (Chao et al., 2014; Gotelli et al., 2013) are diversity measures that summarize the number and relative abundance of different species in a community into a single value. The degree of importance given to the more or less dominant species increases with the q parameter. Hill number 0 represents the number of species in the community whilst Hill numbers 1, 2, and 3 equal to the exponential of the Shannon entropy index, the inverse Simpson index, and the inverse Berger-Parker index, respectively.

We included treatment as a fixed variable, sampling season as a random variable and generated a correlation structure from the coordinates of the sampling plots to account for spatial autocorrelation. Count data were analyzed using a quasipoisson distribution whilst for the Hill numbers a Gaussian distribution (with a log link) was used. The same modelling approach was used for all captured arthropods, and spiders and beetles separately.

Partial distance-based redundancy analysis (db-RDA, (Legendre et al., 1999)) was used to investigate the effect of the treatment on arthropod community structure. Similarly to the GLMM approach, sampling season and the exact location of the plots (as x and y coordinates) were considered as random effects, and were partialled out using the “Condition” term in the capscale() function from the vegan (version 2.6-4, Oksanen, 2022) package. Jaccard distances were used to compare communities and the significance of the model and the treatment effects were tested using a permutational ANOVA, with 999 iterations. Similarity percentage (SIMPER) analysis was used to identify the arthropod taxa that contributed the most to the observed difference between the treatments (Clarke, 1993).

We also calculated beta diversity using Jaccard Index, also known as the “dissimilarity’s distances” to test the homogeneity in species composition.

3.3. Results

3.3.1. General Patterns on Species Abundance

Overall, we collected 41,351 specimens belonging to four classes, 15 orders, 60 families and 171 morphospecies. Of these, 34 taxa were only identified at order, family or genus level, resulting in 137 taxa with scientific species names associated (n = 38,918) (from now on "species") (see complete data in Wallon et al. 2023).

Introduced species (including those with indeterminate colonization status but still likely being exotic species (n = 7622)) represented 71% (n = 29664 specimens) of the total abundance and 75% (129 species) of the total richness; native non-endemic species represented 28% (n = 11608 specimens) of the total abundance and 19% (33 species) of the total richness; endemic species represented 0.2% (n = 79 specimens) of the total abundance and 1% (one species) of the total richness..

The two most diverse and abundant groups were the spiders (Arachnida, Araneae) and the beetles (Insecta, Coleoptera).

Overall, the omnivorous ground beetle *Pseudoophonus rufipes* (De Geer, 1774) (Coleoptera, Carabidae) dominated the samples and accounted for 17% of the total arthropod abundance. Besides the overall dominance, this species also dominated the summer samples, but the *Ocypus olens* (Müller, 1764) (Coleoptera, Staphylinidae) predatory rove beetle became dominant in the winter samples.

Oedothorax fuscus (Blackwall, 1834) (Araneae, Linyphiidae) was the dominant spider, representing 5% of the overall arthropod abundance. It was also the most abundant spider species in summer samples whilst the winter samples were dominated by the *Erigone dentipalpis* (Wider, 1834) (Araneae, Linyphiidae) spider.

Of the 20 most common species, four are considered native (*Leiobunum blackwalli, Tetramorium caespitum, Hypoponera eduardi*, *Homalenotus coriaceus*), one of undetermined origin (*Lithobius* sp.) and the other fifteen as introduced at the level of the Azores.

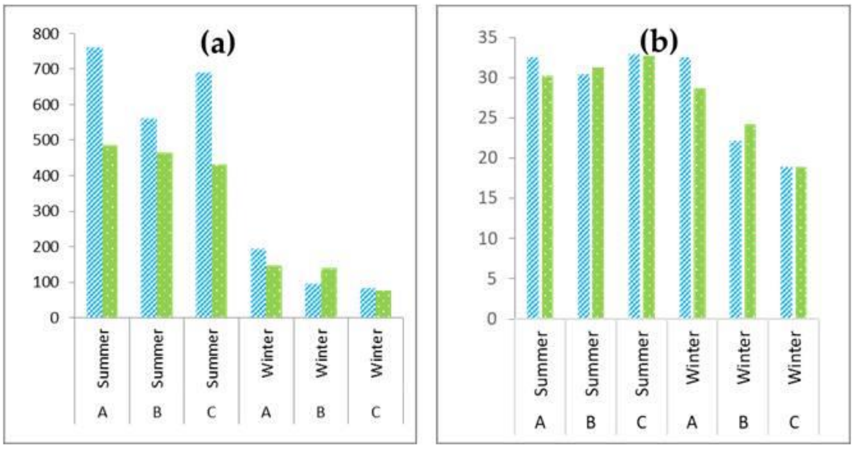


Figure 3: (a) Mean abundance and (b) mean number of species of arthropods collected in the two treatments (OTC in green dots, Control in blue stripes) for the three fields (A, B and C).

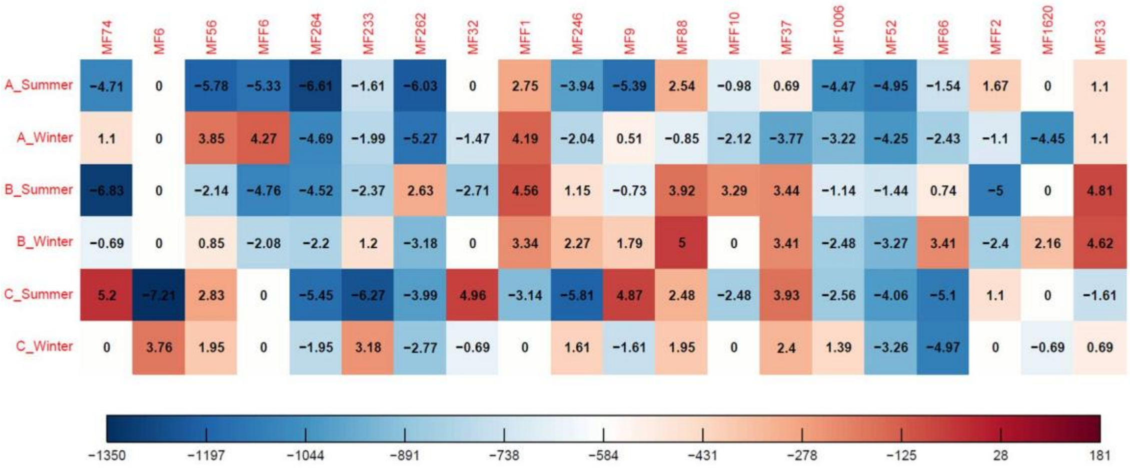
Although not significantly, the dominance structure varied slightly with elevation and therefore with the type of field. In the low altitude field (field A) the ground-beetle *Notiophilus quadripunctatus* Dejean, 1826 (Coleoptera, Carabidae) dominated the winter samples (n = 464, 14%), and the European earwig *Forficula auricularia* Linnaeus, 1758 (Dermaptera) the summer samples (n = 3177, 24%); at the intermediate altitude field (field B), the rove beetle *Ocypus olens* (Müller, 1764) (Coleoptera, Staphylinidae) (n = 579, 25%) dominated the winter samples and the ground beetle *Pseudoophonus rufipes* (De Geer, 1774) (Coleoptera, Carabidae) (n = 5822, 61%) the summer samples; and in the upper altitude field (field C), the rove beetle *Amischa analis* (Gravenhorst, 1802) (Coleoptera, Staphylinidae) was the most abundant species during winter (n = 211, 14%) while the harvestman *Leiobunum blackwalli*

(Arachnida, Opiliones) (n = 3882, 33%) was dominant in summer. Mean abundance and richness in OTC and Control plots in all fields are presented (Figure 3).

3.3.2. Effects of OTC treatment on Species Composition and Abundances Patterns

According to the fitted GLMMs, the effect of OTCs treatment on arthropods abundance was significant ($t = -4.88$, $p < 0.001$), with a decrease in abundance in the OTC treatment compared to the control plots. The variance of the random intercepts was 0.62 (SD = 0.78) for season, and 43.90 (SD = 6.63) for the residual. However, the effect of OTCs treatment on arthropod richness (which also correspond to the Hill number, q0) was not significant ($t = 0.34$, $p = 0.73$). The variance of the random intercepts was 0.02 (SD = 0.15) for season, and 44.79 (SD = 6.69) for the residual. Figure 4 visualizes the abundance differences of the twenty most abundant species between sampling sites and seasons.

Dissimilarities between plots showed a seasonal variation, with greater dissimilarities (high β-diversity values) between winter plots than between summer ones (Figure 5).

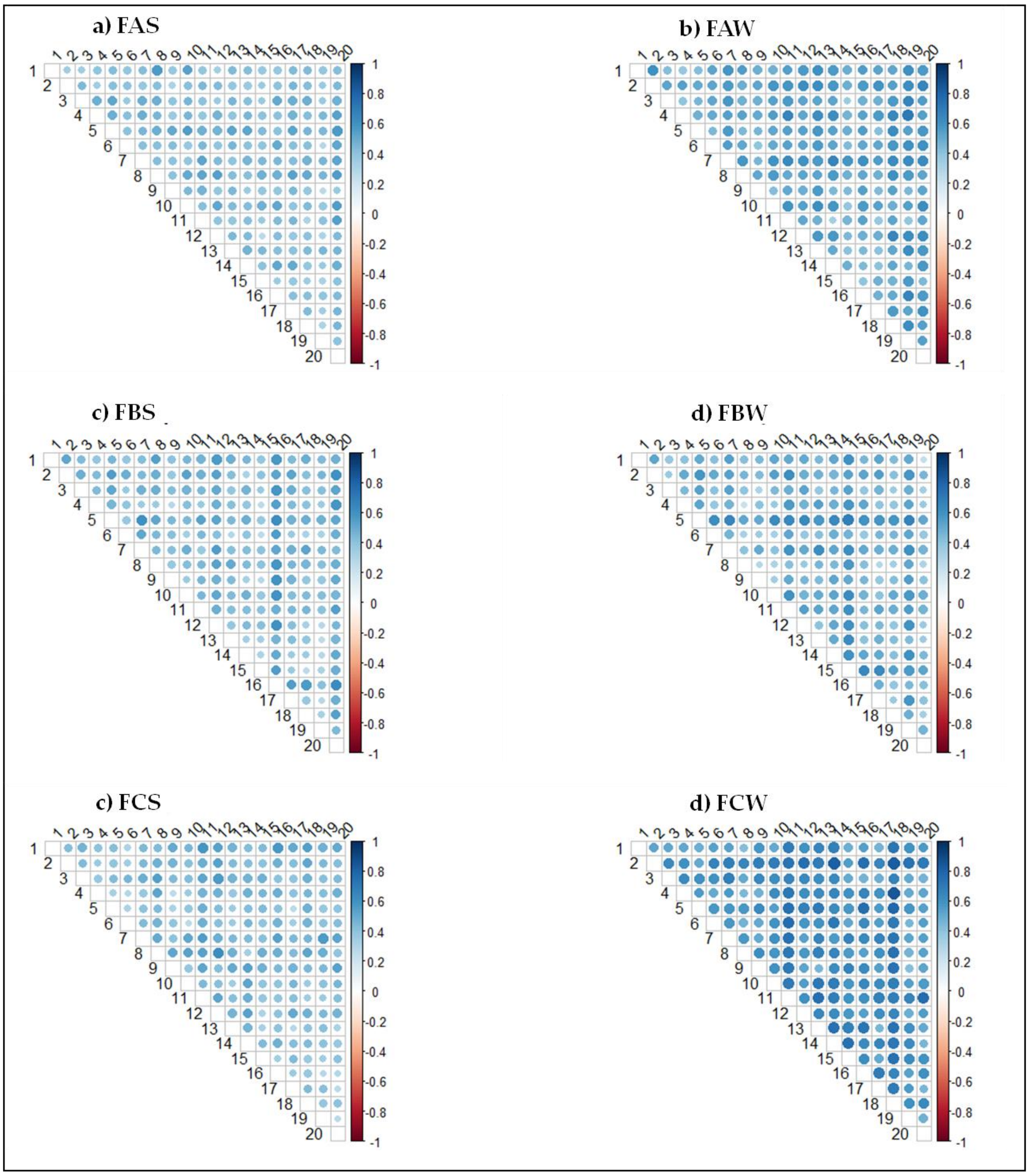


	MF74	MF6	MF56	MFF6	MF264	MF233	MF262	MF32	MFF1	MF246	MF9	MF88	MFF10	MF37	MF1006	MF52	MF66	MFF2	MF1620	MF33
A_Summer	−4.71	0	−5.78	−5.33	−6.61	−1.61	−6.03	0	2.75	−3.94	−5.39	2.54	−0.98	0.69	−4.47	−4.95	−1.54	1.67	0	1.1
A_Winter	1.1	0	3.85	4.27	−4.69	−1.99	−5.27	−1.47	4.19	−2.04	0.51	−0.85	−2.12	−3.77	−3.22	−4.25	−2.43	−1.1	−4.45	1.1
B_Summer	−6.83	0	−2.14	−4.76	−4.52	−2.37	2.63	−2.71	4.56	1.15	−0.73	3.92	3.29	3.44	−1.14	−1.44	0.74	−5	0	4.81
B_Winter	−0.69	0	0.85	−2.08	−2.2	1.2	−3.18	0	3.34	2.27	1.79	5	0	3.41	−2.48	−3.27	3.41	−2.4	2.16	4.62
C_Summer	5.2	−7.21	2.83	0	−5.45	−6.27	−3.99	4.96	−3.14	−5.81	4.87	2.48	−2.48	3.93	−2.56	−4.06	−5.1	1.1	0	−1.61
C_Winter	0	3.76	1.95	0	−1.95	3.18	−2.77	−0.69	0	1.61	−1.61	1.95	0	2.4	1.39	−3.26	−4.97	0	−0.69	0.69

Figure 4. Heatmap showing the correlation between abundances and samples of the twenty most common species in all sites for different seasons. The colors and the corresponding values of the heatmap are logarithmic numbers of the relative species abundance. The colored bar in the legend has been converted back to species abundance counts. The species abundance counts indicate the abundance differences between the control plots and the OTCs. Blue colors tend to indicate at a lower abundance inside the OTCs, while reddish colors indicate higher abundances inside the OTCs. A, B and C correspond to the three pastures followed by the sampling season. On the heatmap, species appear as morphospecies (MF). From the left to the right, the correspondence are the following ones: MF74 *Pseudoophonus rufipes* (Coleoptera); MF6 *Leiobunum blackwalli* (Opiliones); MF56 *Forficula auricularia* (Dermaptera); MF F6 *Tetramorium caespitum* (Hymenoptera); MF 264 *Anotylus nitididfrons* (Coleoptera); MF 233 *Oedothorax fuscus* (Araneae); MF 262 *Rugilus orbiculatus* (Coleoptera); MF 32 *Pterostichus vernalis* (Coleoptera); MF F11 *Solenopsis* sp. (Hymenoptera); MF 246 *Erigone dentipalpis* (Araneae); MF 9 *Ommatoiulus moreleti* (Julida); MF 88 *Ocypus olens* (Coleoptera); MF F10 *Hypoponera* sp. (Hymenoptera); MF 37 *Polydesmus coriaceus* (Polydesmida); MF 1006 *Lithobius* sp. (Lithobiomorpha); MF 52 *Cordalia obscura* (Coleoptera); MF 66 *Amischa anali*s (Coleoptera); MF F2 *Hypoponera eduardi* (Hymenoptera); MF 1620 *Notiophilus quadripunctatus* (Coleoptera); MF 33 *Homalenotus coriaceus* (Opiliones).

Those results were confirmed by the db-RDA (Figure 6) that showed a significant difference in species composition between the arthropod communities sampled in OTCs versus those sampled in control plots ($F = 3.2096$, $p < 0.001$). The SIMPER analysis identified the harvestman, *Homalenotus coriaceus* (Simon, 1879) (MF33), and the beetles *Paranchus albipes* (Fabricius, 1796) (MF51), *Cordalia obscura* (Gravenhorst, 1802) (MF52), *Amischa analis* (Gravenhorst, 1802) (MF66), *Rugilus orbiculatus* (Paykull, 1789) (MF262), and *Anotylus nitididfrons* (Wollaston, 1871) (MF264) which contributed the most to the observed difference between the two treatments.

When GLMMs were applied to a subset of the data containing beetles only, the results indicated a significant negative effect of OTC treatment on both the beetles' abundance (estimate = -0.36, SE=0.07, t = -5.39, $p < 0.001$) and species richness (estimate = -0.102, SE = 0.039, t = -2.619, p = 0.01). The variance components showed that the effect of the season accounted for a small but significant proportion of the beetle abundance variance (0.35, SE = 0.12) while variance components of the beetle species richness GLMM highlighted significant beetle' species richness seasonal variations (variance < 0.001, SD < 0.001). This indicates that there was a significant seasonal variability in the beetles' richness and abundance.
For spiders, the abundance was significantly lower in OTC treatments (estimate = -0.23, SE = 0.11, t = -2.10, $p < 0.001$). On the other hand, OTCs had a significantly positive effect on spider richness (estimate = 0,11, SE=0.04, t = 3,03, $p < 0.001$).


a) FAS

b) FAW

c) FBS

d) FBW

c) FCS

d) FCW

Figure 5. Heatmaps of the dissimilarities from the pairwise beta diversity analyses with using a Jaccard index a) FAS, field A in summer, b) FAW, field A in winter, c) FBS, field B in summer, d) FBW, field B in winter, e), FCS, field C in summer, f) FCW, field C in winter. Numbers 1 to 10 correspond to the 10 Control plots and 11 to 20 correspond to the 10 OTCs. Color scale ranging from light to dark blue indicates increasing levels of dissimilarity. In the right side of the heatmap, the legend color shows the dissimilarity values and the corresponding color.

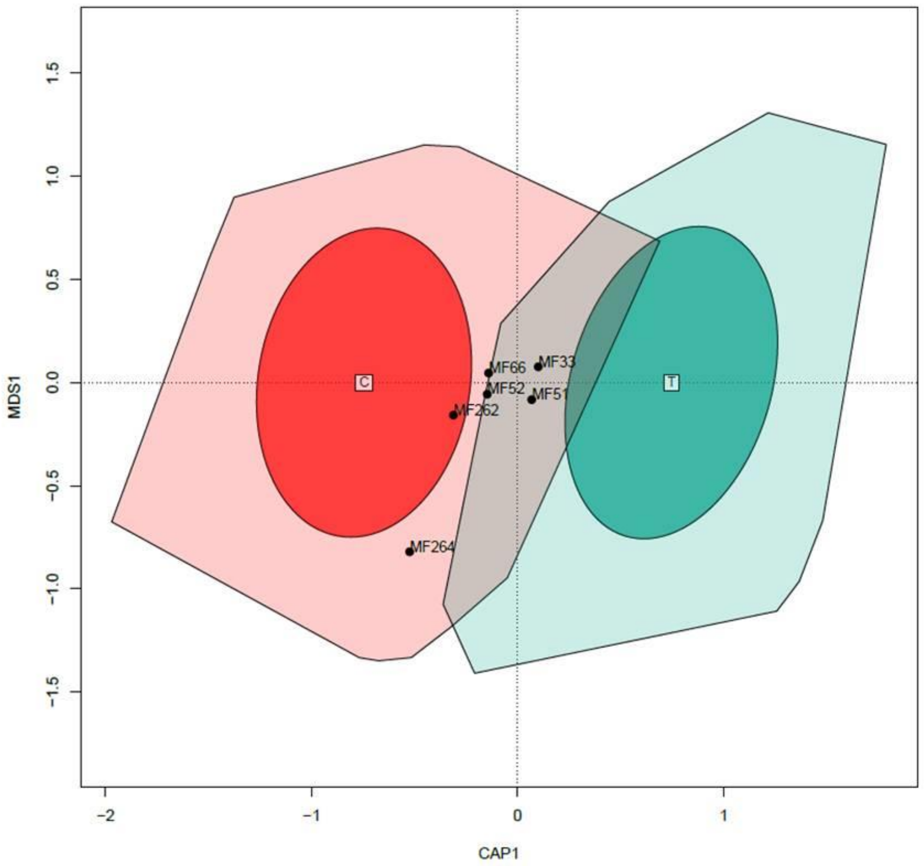


Figure 6. Partial distance-based redundancy analysis. Colored hulls represent the ordination space in which all samples are included and ellipses represent areas in which 75% of the samples are included. Red color (C) corresponds to control and green color (T) corresponds to the OTC treatment. Species most responsible for differences between treatments are marked: MF33 *Homalenotus coriaceus* (Simon, 1879); MF51 *Paranchus albipes* (Fabricius, 1796); MF52 *Cordalia obscura* (Gravenhorst, 1802); MF66 *Amischa analis* (Gravenhorst, 1802); MF262 *Rugilus orbiculatus* (Paykull, 1789); MF264 *Anotylus nitidifrons* (Wollaston, 1871).

3. 3.3. Effects of OTC treatment on Species Relative Abundance Patterns

Table 1. Results of the t-value extracted from the glmmPQL in order to compare Hill Number values considering all arthropods, beetles and spiders. Hill number q1 represents the exponential of the Shannon entropy index whilst q2, and q3 correspond to the, the inverse Simpson index, and the inverse Berger-Parker index, respectively. t-value indicate the trend inside the OTCs. Significance: p<0.001 "***"; p<0.01 "**" p<0.05 "*".

	All arthropods			**Beetles**			**Spiders**		
	t-value	**p-value**	**Sign.**	**t-value**	**p-value**	**Sign.**	**t-value**	**p-value**	**Sign.**
q1	-0.069	0.945		-1.893	0.061		3.226	0.002	**
q2	-0.345	0.731		-1.818	0.072		2.330	0.021	*
q3	0.096	0.923		-1.801	0.074		1.862	0.065	

The analysis of the Hill number series (Table 1) found no significant difference in the exponential of the Shannon entropy (q=1) between the control and OTC plots either for all arthropods or for beetles. This value, however, showed a highly significant difference for spiders (p = 0.002). Diversity curves (Gotelli et al., 2013) (Figure S1; S2; S3) highlighted a trend for a higher evenness inside the spider communities in OTCs.

For q=2, which represents the inverse of the Simpson index, there was a significant difference between the control and OTC plots for spiders (p = 0.021). However, there was no significant difference between the control and OTC plots for beetles and when considering all arthropods.

For q=3, which represents the inverse of the Berger-Parker index, there was no significant difference between the control and OTC plots for all arthropods, beetles, or spiders.

3.4. Discussion

Disentangling the impact of temperature increase on biodiversity patterns in agroecosystems constitutes a fundamental research challenge. During this short-term experiment, we simulated an increase of temperature using OTCs and tested the impacts on arthropods occurring on intensively grazed Azorean pastures.

Most of the species we caught were introduced ones, commonly distributed in agroecosystems. Indeed, since highly disturbed habitats, such as Azorean intensive pastures, mainly select for species with high dispersal capacities which can rapidly colonize ecosystems and respond to disturbances, less flexible indigenous species often have a competitive disadvantage, and the presence of one or few dominant exotic species is common (Cardoso et al., 2009; Meijer et al., 2011; Rigal et al., 2018).

The OTCs had a significant negative effect on both the abundance and diversity of arthropods, suggesting that increased-temperature environments are less favorable for most arthropods in these pastures. Additionally, the study found that treatment effect was not uniform for all arthropods but differed between taxa, with beetles and spiders showing different trends under the OTC treatment. Consequently, some taxa may be more vulnerable to global warming than others, which, in turn may influence the ecosystem services they deliver or the disservices they cause. Indeed, Thakur *et al.* (2017) found that warming can increase predation effects and reduce the co-existence of prey, while Moss & Evans (2022) demonstrate how it can negatively impact arable farming systems, potentially harming wildflowers and insects that rely on them. In addition, Skendžić et al. (2021) suggest that warming can also lead to an increase in pest abundance and promote the spread of invasive species.

3.4.1 Effects of OTCs on Species Composition on Arthropods and Abundances Patterns

Our results indicate that the composition of the entire arthropods community was impacted by the OTC treatment. Although the richness of the overall community was not affected, in the case of particular taxa we noticed signs of changes that should be confirmed over much needed long-term experiments.

Indeed, some common agroecosystems species, such as *Paranchus albipes*, *Cordalia obscura*, *Amischa analis*, *Rugilus orbiculatus*, *Anotylus nitidifrons*, and *Homalenotus coriaceus*, contributed disproportionately more to the observed differences than other species.

Beetles’ richness (mostly composed of carabids and rove beetles) was lower inside the OTCs and they were found to be more diverse in control plots. Although Thiele (1977) identified temperature and humidity among the most influential abiotic factors for carabids populations, a direct avoidance of warmer sites was not reported. Several carabid species, however, have been reported to decline with warming (Müller-Kroehling et al., 2014), and since most ground beetle species inhabiting agricultural fields are mostly eurytopic and present a considerable dispersal ability (Holland, 2002), they likely can avoid unsuitably hot areas. Rove beetles, similarly to carabids, have good dispersal abilities (Halder, 2011) and the capacity to avoid unsuitably areas. They, on the other hand, are often thermophilous and tend to develop faster in higher temperatures than in cold conditions (Irmler et al., 2018).

In contrast to beetles, spiders’ richness (which belong mostly to the linyphiids) was higher inside the OTCs. This could be explained by a higher plant biomass and vegetations structural complexity inside the OTCs in our experiment (Melo et al., 2022) which favors a higher predator, and thus spider, diversity. Indeed, Borges & Brown (Borges & Brown, 2004; Borges & Brown, 2001) found that, in Azorean pastures, linyphiids spiders, that build their web close to the ground, tend to occur more in dense and structurally diverse grass that provide more structure for shelters and web attachments. In our experiment, the main linyphiids species sampled were *Odeothorax fuscus* (Blackwall, 1834), *Erigone dentipalpis* (Wider, 1834), *Erigone atra* Blackwall, 1833, *Erigone autumnalis* Emerton, 1882 and *Tenuiphantes tenuis* (Blackwall, 1852) which are agrobiont species very common in cultivated areas, agroecosystems and disturbed areas (Blandenier, 2009; Downie et al., 2000; Harper, 2020; Thorbek et al., 2003). On the other hand, no effect of the vegetation was observed in other taxa in our experiment. This might be due to the fact that pitfalls traps catch ground-dwelling taxa whereas other species live in higher strata of the vegetation and were not the target of our experiment. If sampling had been conducted in the upper layers of vegetation, with greater plant biomass higher arthropod abundances could also have been expected (Prather et al., 2020, 2019).

The overall abundance, as well as that of beetles and spiders, were negatively impacted by the OTCs. Yet, the responses of different arthropod groups cannot be easily generalized. Indeed, in our study, the diversity of spider increased inside the OTCs, whilst that of beetles decreased. Thus, in Azorean pastures, spiders and beetles appear to respond differently to an increase of temperature.
Our study agrees with Kwon et al. (2015) who showed that more beetle species will decrease rather than increase as climate warms. Although, in their paper, Kwon et al. (2015) report a decrease of the rove beetle species *Ocypus coreanus* with warming climate, this contradicts with our results where *O. olens*, a species from the same genus, was found in higher abundances in treated plots. Therefore, the two species react seemingly differently to abiotic changes.

Besides taxa responding differently to the heating treatment, the community composition also showed seasonal difference: we observed higher beta diversity values in winter when all species were considered in the community. This pattern might be explained by the fact that most arthropods in the Azores have a reduced abundance during the winter and tend to peak during the summer (Borges, 1995; Borges et al., 2017) and the fewer individuals in samples allow a greater influence of stochastic processes in community assembly, which, in turn, might create more disparities between plots.

3.4.2. Effects of OTCs on Species' Relative Abundances Patterns

Species diversity is influenced not only by the number of species present in a community and their overall abundances, but also by the way individuals are distributed among those species. Although other studies, in which similar taxa were monitored as our experiment, found that certain species of ground beetles, spiders and Hemiptera became superabundant and the evenness declined with the rise of temperature (Buchholz et al., 2013; Høye et al., 2021; Skendžić et al., 2021), our results did not show this pattern. In our study, the Berger-Parker indexes did not reveal a clear dominance pattern, and our results agree with those of Tsafack et al. (2020), who observed a negative effect of temperature on dominant arthropods in Northern Chinese grasslands. Furthermore, OTCs had a significantly positive impact on spider evenness, suggesting that the treatment is promoting the survival and persistence of a wide range of spider species, rather than just a few dominant species. This may be caused by either the changes in microclimatic conditions or vegetation structure caused by the OTC (e.g. higher plant biomass, (Borges & Brown, 2004; Borges & Brown, 2001) which could provide more favorable conditions for some species.
Yet, this reduction in dominance, and the increase of evenness, was statistically significant for spiders only. Indeed, even though a decrease in beetle abundance was observed with the GLMMs, Hill number analysis surprisingly did not reveal statistical differences and neither did when all arthropods were considered. Other taxa not analyzed here separately, or differences between species' ecology could also play in masking the trends.

Indeed, as our results showed, responses to increased temperature can be variable from one taxonomic group to the other and from one species to the other. Undoubtedly, species balance between their responses to higher temperature in the altered environment, their optimum thermal conditions, and resource (e.g. food or habitat) availability, and this balance highly depends on species' traits. Paler et al. (2021) found variations in beetle diversity with OTCs treatment when looking at their feeding behavior, body size and color. Moreover, as arthropods are ectotherms, changes in their physiology and metabolism under heat stress can depend on their developmental stages or locomotion capacities (Garcia et al., 2019). Diel activity may also have an impact on the arthropod responses to increased temperature and nocturnal species can be less prone to daylight heat effects than diurnal ones because they remain hidden from the direct solar exposition and extreme temperatures (Thiele, 1977). Altogether, considering species' ecology (i.e. traits) is key for a mechanistic understanding of the processes driving community-wise adaptations to warming. Thus, to disentangle the impacts of OTCs on the arthropod community, future investigation focusing on functional traits are necessary.

This can be particularly important with species of great economic importance (e.g. pests or natural enemies). For example, in a context of increased temperature, Hannigan et al. (2022) observed that the pest *Sitona gressorius* (Fabricius, 1792) has its activity (dispersal and feeding rate) increased. With climate change, this represents a risk of pest spreading in agroecosystems (Tubiello et al., 2007). A similar species in our study, *Sitona discoideus* Gyllenhal, 1834, that is also considered a plant pest in different part of the world (Goldson et al., 1984; Kean et al., 2001), however did not show a positively correlating abundance trend with the increasing temperature.

Additionally, since significant changes in species composition over a prolonged period can increase the probability of altered ecosystem functions (Cardinale et al., 2012), to monitor these changes, and to clarify effects of temperature on arthropod communities on a larger temporal scale, longer-term experiments are increasingly needed.

Although our experiment was successful to predict some impacts of climate change on Azorean arthropods communities, some limitations may apply. The OTCs seems to have an indirect effect on the arthropod communities: they had an effect on the vegetation structure, particularly by increasing plant biomass (unpublished data), which may affect our results. These effects, however, need to be confirmed with further investigations. Moreover, Nash et al. (2013) warn that OTCs can reach extreme temperatures during the day that do not reflect the average increased temperature commonly used in climate change investigations. The two climate scenarios we used (RCP4.5 e RCP 8.5 (PRAC, 2017)) are the intermediate and worst-case scenarios. Although these are widely used in climate change research, Pielke & Ritchie (2021) highlighted that overly emphasizing the worst-case scenarios may potentially overestimate the impacts, thus their assessment requires careful consideration and critical evaluation in climate research.

3.5. Conclusions

Our results suggest that the simulated warming had a significant impact on arthropod communities in the study area, by affecting their species richness, evenness, and dominance structure. However, the impact varies depending on the arthropod group, or even from species to species.

Although our study provides some important insights on the impact of increased temperature on Azorean pasture arthropods, more research is needed to allow a deeper insight. For instance, the comparison of this result with a simulated increase of temperature along an altitudinal gradient as well as a long-term study could help to untangle the impacts of increased temperatures in varying environments and on species with different cold adaptations. In addition, more studies on the ecology and functional traits of selected key species in Azorean pastures could help to predict general arthropod population trends for the future.

Supplementary Materials: The following supporting information can be downloaded at: www.mdpi.com/xxx/s1, Figure S1: Diversity curves using Hill numbers for arthropod assemblages in the Fields A, B and C for both seasons, winter and summer; Figure S2: Diversity curves using Hill numbers for beetle assemblages in the Field A, B and C for both seasons, winter and summer; Figure S3: Diversity curves using Hill numbers for spider assemblages in the Field A, B and C for both seasons, winter and summer.

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Chapter 4. Unveiling Arthropod Responses to Climate Change: A Functional Trait Analysis in Intensive Pastures

Abstract: This study investigates the impact of elevated temperatures on arthropod communities in intensively managed pastures on the volcanic island of Terceira, Azores (Portugal), using a functional trait approach. Open Top Chambers (OTCs) were employed to simulate increased temperatures, and the functional traits of ground dwelling arthropods were analyzed along a small elevation gradient (180–400 m) during winter and summer. Key findings include lower abundances of herbivores, coprophagous organisms, detritivores, and fungivores at high elevations in summer, with predators showing a peak at middle elevations. Larger-bodied arthropods were more prevalent at higher elevations during winter, while beetles exhibited distinct ecological traits, with larger species peaking at middle elevations. The OTCs significantly affected the arthropod communities, increasing the abundance of herbivores, predators, coprophagous organisms, and fungivores during winter by alleviating environmental stressors. Notably, iridescent beetles decreased with elevation and were more common inside OTCs at lower elevations, suggesting a thermoregulatory advantage. The study underscores the importance of considering functional traits in assessing the impacts of climate change on arthropod communities and highlights the complex, species-specific nature of their responses to environmental changes.

Keywords: functional traits; arthropods; grassland; Azores; increased temperature; open top chambers; altitudinal gradient

4.1. Introduction

Climate change has emerged as a defining challenge on a global scale, reshaping ecosystems and challenging the ability of different species to adapt (Pecl et al., 2017; Pörtner et al., 2021). In the context of these changes, arthropods as a taxonomic group are emerging as particularly sensitive indicators of environmental change (Boggs, 2016; Marta et al., 2021). These tiny but ecologically important organisms play a key role in maintaining ecosystem balance and are highly sensitive to changes in temperature, precipitation, and other environmental variables (Johnson et al., 2016; Samways et al., 2020). Thus, arthropods play a crucial role in ecosystem dynamics, reflecting the complex interplay between climate change and biological responses (Brose et al., 2016).

As temperature patterns shift and precipitation becomes more erratic (Pfahl et al., 2017; Spinoni et al., 2017), arthropods in different habitats are subject to disruptions in their abundance, distribution, and life cycles (Montgomery et al., 2020). Understanding the impact of climate change on these arthropods is crucial not only for biodiversity conservation, but also for disentangling wider ecological consequences.

The global dimension of this issue enhances its importance. As indicators of environmental health, arthropods provide valuable insights into the wider effects of climate change (Basset et al., 2019). Studying their responses to these changes can reveal patterns that transcend geographical boundaries, contributing to a more comprehensive understanding of the ecological consequences of climate change on a global scale (Barua et al., 2012; Wilson et al., 2021).

Within this global panorama, however, our study focuses on a more specific investigation—the realm of pastureland arthropods in the volcanic archipelago of the Azores. Intensive managed pastures represent more than 56% of the land occupation in this region (PRAC, 2017). These islands host a unique diversity of arthropods, with most endemic species being currently restricted to mid-to-high-elevation native forests (Barua et al., 2012; Wilson et al., 2021). By narrowing our focus to a particular ecological niche (e.g., pastureland), we aim to unravel the nuances of climate change impacts on a specific group of arthropods associated with intensively managed pasture, providing insights that can be extrapolated to similar ecosystems worldwide.

The pastures in the Azores serve as habitats for various arthropod species from different origins (indigenous and non-indigenous) (Borges, 1999; Borges & Brown, 1999; Rego et al., 2015; Wallon, Elias, et al., 2023; Wallon, Melo, et al., 2023). The interdependence between these arthropods and the grassland ecosystem is important for the good health of the pastures (Joern et al., 2013; Prather et al., 2020; Solascasas et al., 2022). As climate change affects the Azores with temperature increases and changes in precipitation patterns (stronger events during the winter and longer periods of drought through the summer) (Cresswell-Clay et al., 2022; Santos et al., 2004), it poses unprecedented challenges for agriculture. In accordance with the findings presented in (PRAC, 2017), the primary impacts linked to climatic factors in the Azores revolve around induced stress and diminished agricultural production during drought conditions. Additionally, there is notable evidence of reduced pasture and fodder quality, accompanied by the expansion of certain insect pests.

In the context of the Azores, temperatures are expected to increase by a value between 0.78 °C and 0.90 °C by 2039. Looking further ahead, to the end of the century, temperature projections indicate an increase of between 1.5 °C and 2.8 °C, corresponding to the two different scenarios, RCP4.5 and RCP8.5 (PRAC, 2017).

The Azores, with their isolated and distinct ecological context (Borges et al., 2011; Schaefer et al., 2011), face both challenges and opportunities because of climate change. Shifts in temperature and precipitation pose a threat to the stability of arthropod communities (Ferreira et al., 2016), while, at the same time, opening avenues for understanding their resilience and adaptive strategies.

To unravel the specific impacts of climate change on arthropods in the Azores, our study used Open Top Chambers (OTCs) as a controlled experimental tool along an altitudinal gradient. OTCs provide a unique opportunity to simulate temperature increases, allowing us to mimic expected climate scenarios (Aronson et al., 2009). First, this controlled environment allows for a focused study of how the arthropod communities within the pastures respond to elevated temperatures (Buchholz et al., 2013a; Sophie Wallon, Tsafack, et al., 2023), a key facet of climate change. The use of OTCs aims to bridge the gap between observational studies and experimental manipulations (Hanson et al., 2020; Hollister et al., 2023), which should provide a more nuanced understanding of the direct effects of temperature change on arthropod functional traits in the Azores. Secondly, the inclusion of a small elevation gradient (180–400 m) in experiments on the effects of climate change on arthropod communities is crucial, as it provides natural variations in temperature and environmental conditions, allowing researchers to study species and community responses to these changes in a controlled setting (Hodkinson, 2005; Körner, 2007). The combination of OTCs and an elevation gradient is essential for understanding how climate change might alter biodiversity patterns and ecological interactions across treatments and elevations.

Traditionally, species community monitoring has relied on the application of diversity indices based on taxonomic classifications (Chiarucci et al., 2011). These indices, such as the Shannon Diversity Index and species richness, provide valuable metrics for assessing the diversity and evenness of species within an ecosystem (Chao et al., 2014). However, while taxonomic approaches provide a snapshot of community composition, they may miss subtle shifts in functional dynamics and ecological interactions (Villéger et al., 2010). Our previous study acknowledged the utility of these traditional metrics (Sophie Wallon, Tsafack, et al., 2023), but recognized the need for a more comprehensive approach to capture the nuanced responses of arthropod communities to climate change. By incorporating functional traits into our analysis, we aim to overcome the limitations of taxonomy-based assessments and provide a more holistic understanding of how arthropods are responding to changing environmental conditions in Azores pastures. This shift in methodology allows us to uncover functional nuances that may be obscured by traditional taxonomy-based alpha diversity measures (e.g., species richness, the Shannon Index), ultimately enriching our understanding of the ecological impacts of increased temperature on arthropod communities.

Functional traits, which include morphological and behavioral characteristics, provide a more dynamic lens through which to examine species' responses to changing climate or disturbances (Brousseau et al., 2018; Mouillot et al., 2013; Rigal et al., 2018). The importance of this different approach lies in its ability to unravel how arthropod communities function within the ecological framework of Azores pastures under climate change. By focusing on functional traits, we can decipher not only which species are present, but also how they interact with their environment, providing a more nuanced understanding of the ecological consequences of temperature increase.

We aim to determine how increasing temperatures (simulating climate-induced changes) along a short elevation gradient manifest themselves in a functional trait approach to arthropod communities within intensively managed pastureland. To this end, we seek to identify key functional traits that serve as indicators of adaptation or vulnerability in the context of temperature increase.

We posit that different guilds of arthropods within pastureland communities will display varying responses to temperature changes. Specifically, we anticipate that predator-and-prey relationships, as well as the presence of herbivores, will be reshaped under increased temperatures due to grass biomass availability. Arthropod guilds may respond differently to temperature shifts along the elevational gradient and between treatments due to their distinct ecological roles and specific traits. Predators, for instance, may experience changes in prey availability or altered hunting efficiencies (decreases in predators in the warmest sites: OTCs and lower altitudes), while herbivores may face shifts in plant suitability along the gradient, the treatment, and seasons (Barton et al., 2009).

We hypothesize that as temperatures increase in pastureland ecosystems, there will be a specific pattern in the distribution of arthropod species' body sizes, with smaller species in the warmest sites (OTCs and lower altitudes) (Kingsolver et al., 2008).

Beetles' color and iridescence may influence their thermoregulation and capacity to support increased temperatures. Darker beetles should prevail in cooler sites, while iridescent beetles may be more abundant in warmer sites (Alves et al., 2018; Ospina-Rozo et al., 2022).

4.2. Materials and Methods

4.2.1. Study Area

The research was carried out on three experimental intensively managed pastures on the island of Terceira, part of the Azores archipelago in Portugal. The island of Terceira covers an area of 402 square kilometers and reaches a maximum altitude of 1023 m. Its geographical coordinates are between 38°37′ N and 38°48′ N latitude and 27°02′ W and 27°23′ W longitude. The sites, designated A, B and C, which are of low, middle, and high elevation, are located at different heights above sea level: site A at 186 m, site B at 301 m, and site C at 386 m. Their specific latitudes and longitudes are 38.703596° N, −27.353805° W for Site A, 38.701639° N, −27.325783° W for Site B, and 38.697770° N, −27.170075° W for Site C (Figure 1.). Each of these sites is classified as intensive pasture land. The primary vegetation consists of Italian ryegrass, *Lolium multiflorum* Lam. (Poaceae), in Sites A and B, and common velvet grass, *Holcus lanatus* L. (Poaceae), in Site C.

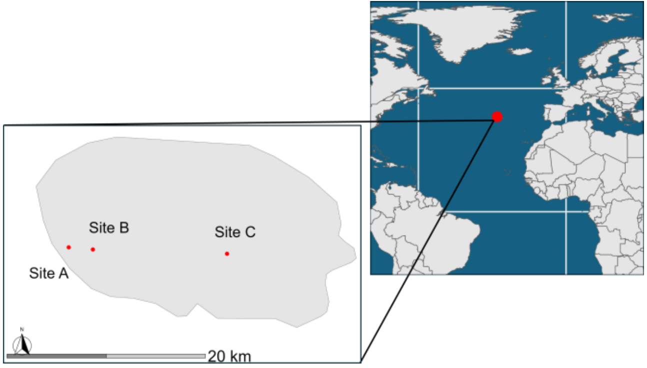

Figure 1. Localization of the island of Terceira and experimental sites.

4.2.2. Experimental Design

A field experiment was established using Open Top Chambers (OTCs). OTCs are common tools used in climate change research to manipulate abiotic environmental conditions directly in the field to mimic an increase in temperature (Aronson et al., 2009). The structure of OTCs includes panels that act as wind barriers, effectively reducing heat loss by convection. In addition, their open-top design allows rain to enter and air to circulate freely, resulting in the creation of small air vortices or eddies (Hollister et al., 2023).

Within each field, twenty plots measuring 1 × 1 m were arranged in a grid layout, while maintaining a distance of 1.5 m between them. Half of these plots, selected at random, served as a control group, while the remaining ten were enclosed by OTCs. To monitor temperature variations, data loggers (Easy Log: EL-USB-2) were installed both inside the OTCs and within the control plots. On average, temperatures within the OTC-enclosed plots were found to be 1.2 °C higher than those in the control plots. The OTCs were designed to encompass the 1 × 1 m plots, as well as an additional 25 cm border around each plot. This buffer area allowed for easy access to the plots for maintenance and monitoring without causing damage and facilitated the placement of pitfall traps at each outer corner of the plot, still within the boundaries of the OTCs. Additionally, the OTCs were elevated approximately 5 cm off the ground to permit the unimpeded movement of crawling arthropods throughout the entire sampling area.

Sampling took place in two different seasons, winter and summer 2020, and was carried out before any mowing of the grass. Cattle access to the sampling plots was not possible, since fences were implemented. Most importantly, the experimental design, which included both control plots and plots enclosed by OTCs, was maintained throughout the year. Consequently, there was no relocation of the OTCs and control plots between the two sampling periods.

4.2.3. Arthropod Sampling and Identification

In this research, we concentrated on the impact of intensive pasture management on arthropod communities, with a specific focus on crawling arthropods. This focus was necessitated by the fact that OTCs act as barriers to flying insects, potentially skewing results towards these ground-dwelling species. To facilitate sampling, pitfall traps were employed, specifically targeting epigean arthropods. Across each plot, four pitfall traps were positioned at every corner, resulting in a total of 80 traps per field. These traps, consisting of a 330 mL plastic cup with dimensions of approximately 12 cm in depth and 8 cm in diameter at the opening, were filled with a 20% solution of ethylene glycol from car cooling liquid and a few drops of soap to reduce water surface tension. To protect the traps from rain and prevent overflow, they were covered with a plastic dish secured by small iron sticks, allowing unobstructed access to the traps. The collected specimens were preserved in 96% ethanol.

For analysis purposes, the data from the four traps at each plot were combined into a single sample, yielding 10 replicates for each treatment type across the fields: ten for control and ten for OTCs. Arthropod collection was executed in the winter and summer of 2020, with the traps set for 14 days, except for one instance, in Field B, during summer, where the traps were set for 13 days—here, data for the 14th day were extrapolated based on the other days' findings. However, species richness estimates were not extrapolated.

All collected arthropods were sorted and identified to the species level when feasible, covering target groups such as Arachnida (Araneae, Opiliones, Pseudoscorpiones), Diplopoda, Chilopoda, and most Insecta groups, including Formicidae and Lepidoptera, but excluding Diptera and Hymenoptera. Unidentified specimens were given a morphospecies code. The initial sorting and identification tasks were carried out by the lead author (SW) and assisting students (acknowledged as parataxonomists), followed by verification by an expert taxonomist (PAVB). Species nomenclature and colonization status followed the latest checklist of Azorean arthropods (Borges et al., 2022).

It is noteworthy that, in Terceira's intensive pastures, exotic arthropods typically dominate, with native and/or endemic species' presence diminished due to significant land disturbance (Cardoso et al., 2009b; Rigal, Cardoso, Lobo, Triantis, Whittaker, Amorim, Alexandre, et al., 2018). Consequently, no distinction was made regarding the biogeographical origin of species in our analyses. Despite previous Azorean arthropod studies often including juvenile spiders (e.g. Cardoso et al., 2009), the prevalence of Erigoninae linyphiid spiders in this study posed challenges to adopting such an approach. All specimens are stored in the Dalberto Teixeira Pombo (DTP) Collection at the University of the Azores (Terceira Island), with data accessible in (Sophie Wallon, Melo, et al., 2023) through a specified URL.

4.2.4. Functional Traits

We gathered data on body size and dispersal ability for each arthropod species studied. We also compiled a collection of functional traits related to resource use. Finally, for beetles, specific traits were gathered regarding their color and presence or absence of iridescence (Table 1).

Information on traits was gathered through a thorough review of the literature, encompassing original species descriptions, initial records of species in the Azores, short communications, and ecological research. Additionally, information was obtained from experts who identified the specimens, or specialists (P.A.V. Borges, Pedro Cardoso, Sofia Terzopoulou) in the relevant taxonomic group, in cases where specific species information was unavailable.

Functional traits for each species were determined based on the characteristics of the adult stage. For morphospecies that could not be identified to species level, we assumed functional traits based on the closest taxonomic classification available, such as genus or family. Details of these trait assignments for each species can be found in Tables S1 and S2.

Table 1. Selection, definition, and ecological relevance of the functional traits used in the study.

Traits Category	Traits	Data Type	Attributes (Abbreviations)	Definition	Ecological Relevance
Guild	Type of food	Multi-choice nominal	Plants (FoodPl); animals (FoodAni); fungi (FoodFg); detritus (FoodDet); coprophagous organisms (FoodCopro)	Each guild is categorized according to the primary food consumed by the species during their adult stages, except for Lepidoptera, for which the classification is based on the feeding habits of the larvae.	Under different climatic conditions, the natural resources available for arthropod feeding may vary. This can affect arthropod feeding guilds and lead to different arthropod communities.
Feeding behavior	Mode of ingestion	Nominal	Chewing and cutting (IngCC); piercing and sucking (IngPS); external digestion and sucking (IngEDS)	Depends on the type of mouthpart and, thus, on the way in which arthropods feed. For Lepidoptera, the classification is based on the mouthparts of the larvae.	Determines feeding strategies and diet specialization, influencing nutrient cycling and energy flow within ecosystems.
Ecological	Body size	Continuous	Standardized body size (bodysizeStand); body size (bodysize)	Defined as species mean body length.	Species' body size is linked to their metabolism, which influences their adaptability and ecological niches.
Ecological	Dispersal ability	Nominal	Low dispersal ability (Ldisp); High dispersal ability (Hdisp)	Dispersal ability (high or low) is attributed based on physical characteristics of the animal. Presence or absence of wings and ballooning capacity for spiders.	Animals with high dispersal ability will tend to respond more quickly to unsuitable abiotic conditions in order to find a more suitable environment. In contrast, animals with low dispersal ability will have more difficulty in migrating to better conditions.
Ecological	Diel activity	Multi-choice nominal	Day (ActDay); Night (ActNig); Twilight (ActTw)	Refers to the main period of activity of the species during the day.	Diel activity shapes how species interact with their environment and each other, and also impacts how arthropods respond to heat. Nocturnal species are less affected by daytime temperatures, as they avoid direct sunlight and extreme heat by remaining hidden.
Coloration	Color of beetle cuticle	Nominal	Black (Color_Black); blackish (Color_Blackish); reddish-brown (Color_ReddishBrown)	Refers to the main nuance observed on the cuticle. Black refers to a black cuticle. Blackish refers to a main black tendency with a reddish/orange color. Reddish-brown refers to a main tendency orange/brown.	Color can serve several functions, including signaling, mating, camouflage, and thermoregulation. For this reason, beetle color should provide information about the heat tolerance of the species.
Coloration	Presence of iridescence on beetle cuticle	Nominal	Iridescence (IridescentColor)	Refers to the presence or absence of iridescence on the beetle cuticle.	The presence of iridescence helps thermoregulation by reducing solar absorption and limiting risks of overheating.

4.2.5. Data Analysis

Data from the four traps in each plot were grouped into a single value for analysis. During the winter, in four sampling events, one of the four traps was damaged due to flooding or earth filling. In these cases, we estimated the theoretical abundance of four traps by extrapolating from the data collected by the remaining three traps. Similarly, in cases in which traps were only operated for 13 days instead of the planned 14, we adjusted the sampling period by extrapolating arthropod abundances to cover the full 14 days. In situations in which either trap was damaged or the sampling period was reduced by one day, we assumed that species richness remained unchanged; only arthropod abundances were extrapolated.

Each trap was assigned a habitat, Field A, B or C, at low, middle, and high elevation, respectively, a treatment (control or OTCs), and a location (plot located on the edges or in the center of the field). All analysis were performed with R software (4.2.3) (R Core Team, 2023).

The analyses were carried out for winter and summer separately, considering all arthropods collected and only the most diverse taxon, namely the beetles (Insecta, Coleoptera).

For all arthropods, the traits analyzed were the following: the trophic guild (herbivorous, predators, fungivores, detritivores, and coprophagous organisms), how arthropods ingest food, e.g., feeding behaviors (piercing/sucking, chewing/cutting, and external digestion and sucking), some ecological traits, such as the daily activity (diurnal, nocturnal or active during twilight), the dispersal abilities (high or low dispersal abilities), and the standardized body size.

Body size standardization was applied for each order present in our samples for analyses, considering all arthropods as follows:

> Standardized body size of Species x = (body size of Species × Order average body size)/Order Standard Deviation body size

For beetles, the traits analyzed were the following: the trophic level (herbivorous, predators, fungivores, and detritivores), the beetle's coloration, the presence or absence of iridescence and some ecological traits, such as the daily activity (diurnal, nocturnal or active during twilight), high dispersal abilities, and the real body size. Feeding behaviors were not analyzed, as all beetles feed by chewing and cutting, and it was thus not a relevant functional trait to incorporate. Additionally, coprophagous trophic level and low dispersal abilities were not analyzed for beetles due to the lack of sufficient data to perform the analysis (only 3 species sharing those traits).

For each trait, we calculated the community weighted means (CWM) using the "functcomp" function from the FD package (Laliberté et al., 2010). The CWMs express the mean attribute value between species occurring at a site, weighted by the relative abundance of each species (Violle et al., 2007), and were calculated as follows:

$$\mathrm{CWM}_j = \sum_{i=1}^{S} p_i x_{ij}$$

where CWMj is the community-weighted mean value of trait attribute j, p_i is the relative abundance of species i (i = 1, 2, ..., S), and x_{ij} is the value of trait attribute j for species i. Prior to the CWM computation, abundance data were square-root-transformed to reduce the influence of highly dominant species. Nominal traits were dummy-transformed to as many binary variables as there were trait attributes. All binary traits were then treated as continuous variables using the "bin.num" parameter in the function "functcomp".

The resulting CWM values for both seasons were combined with habitat, location, and treatment information to form a comprehensive data frame. The relationships were visualized using boxplots created with the ggplot2 package, highlighting differences by field, location, and treatment conditions. A series of analyses of variance (ANOVA) was conducted to investigate the effects of elevation, location, and treatment on each trait, including the interaction terms on each CWM variable and for each season. When the overall ANOVA model was statistically significant, post hoc pairwise comparisons were performed using the "lsmeans" package to determine differences between levels of significative factors and/or interaction.

Preliminary tests indicated only four traits for all arthropods and four traits for beetles responding with low significances for the effect of the plot location (edges or center) with ANOVA, and, according to post hoc pairwise comparison, of the few traits responding to the effect of plot location, most were not significant. Thus, we restricted our ANOVA to the fundamental effects of our design, i.e., field, treatment, and interaction between the two.

Because several tests were performed for each season, we decided to correct the P-values using the False Discovery Rate method (FDR, (Benjaminit et al., 1995)) to guard against inflation of Type-I errors.

4.3. Results

In total, over the three fields and two seasons (winter and summer), we collected 41,351 specimens. For the current analysis involving functional traits, only adult specimens were considered, giving a total of 35,735 arthropods from four classes, 15 orders, 60 families, and 171 morphospecies. From these, 34 taxa were identified only at the order, family, or genus level, resulting in 137 taxa with associated scientific species names (n = 32,821), which will be referred to as 'species' from here on (see full data in (Sophie Wallon, Melo, et al., 2023)).

Our CWM analyses (Figure 2) show that the most important and strongest effect on all the functional traits studied is the factor field (e.g., elevation gradient) during both seasons for all arthropods and beetles. The second most important factor influencing functional traits is the treatment (control and OTC), i.e., elevated temperature. For all the arthropods, increased temperature had a greater effect during winter, especially on the ecological traits and guilds. Feeding behavior was not affected by the presence of OTCs. For the beetles, increased temperature had an effect on all the functional traits in both seasons. However, the effect was stronger in winter than in summer.

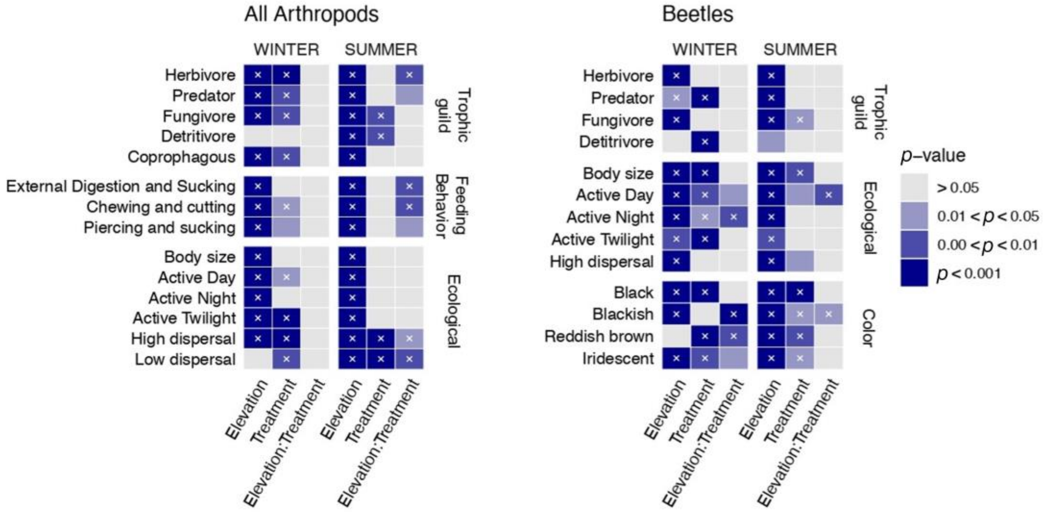

Figure 2. Heatmap for winter and summer season, highlighting the results of the analysis of variance (ANOVA), considering all arthropods and only beetles, which was conducted to investigate the effects of elevation, treatment, and their interaction (Elevation:Treatment) on each trait community weighted means (CWM) variables. On the (**left**) *y*-axis are the different traits analyzed. IngEDS: external digestion and sucking; IngCC: chewing and cutting; IngPS: piercing and sucking; Hdisp: high dispersal ability; Ldisp: low dispersal ability; ActDay: diurnal; ActNig: nocturnal; ActTw: active during twilight. On the (**right**) *y*-axis are the different categories of traits analyzed. The *x*-axis presents the different factors analyzed: elevation, treatment, and their interaction (Elevation:Treatment). The colors indicate the level of significance (dark blue, $p < 0.001$; medium blue, $0.00 < p < 0.01$; light blue, $0.01 < p < 0.05$, and gray, $p > 0.05$). Cells marked with a "x" mean that the effect remained significant after the FDR correction for multiple testing. Results of the ANOVA are detailed in Tables A1 and A3.

Finally, the interaction between field and treatment was the third main effect, and it showed that the effect of climate change varied according to the elevation. For all the arthropods, the interaction "field/treatment" showed an effect only in summer, mainly on feeding behavior and dispersal ability.

For the beetles, the interaction between field and treatment had a very small effect on diurnal activity, and for blackish beetles, this occurred in summer. In winter, color traits and diurnal and nocturnal activity were the most responsive traits. The results with the adjusted p-values were very similar, with only a few decreases with some significance. However, this did not change the main pattern of the results, confirming what was previously established.
With this context in mind, let us delve into the details.

4.3.1. Winter and Summer Traits Analysis for All Arthropods

4.3.1.1. Guilds

Considering all the arthropods during the summer, all the guilds (Figure 3) showed significantly lower abundances at high altitude than at middle and low altitude. There is an exception for predators, for which the highest abundance was found at mid-altitude for both seasons, showing a hump shape along the altitudinal gradient. During winter, the herbivores, coprophagous organisms, and fungivores also showed lower abundances at high altitude than at low altitude. However, the altitude gradient was less pronounced than in summer. Nevertheless, during winter, there was a treatment response for all trophic levels, with higher abundances in the OTCs, except for the detritivores, which showed no significant differences between altitude and treatment.

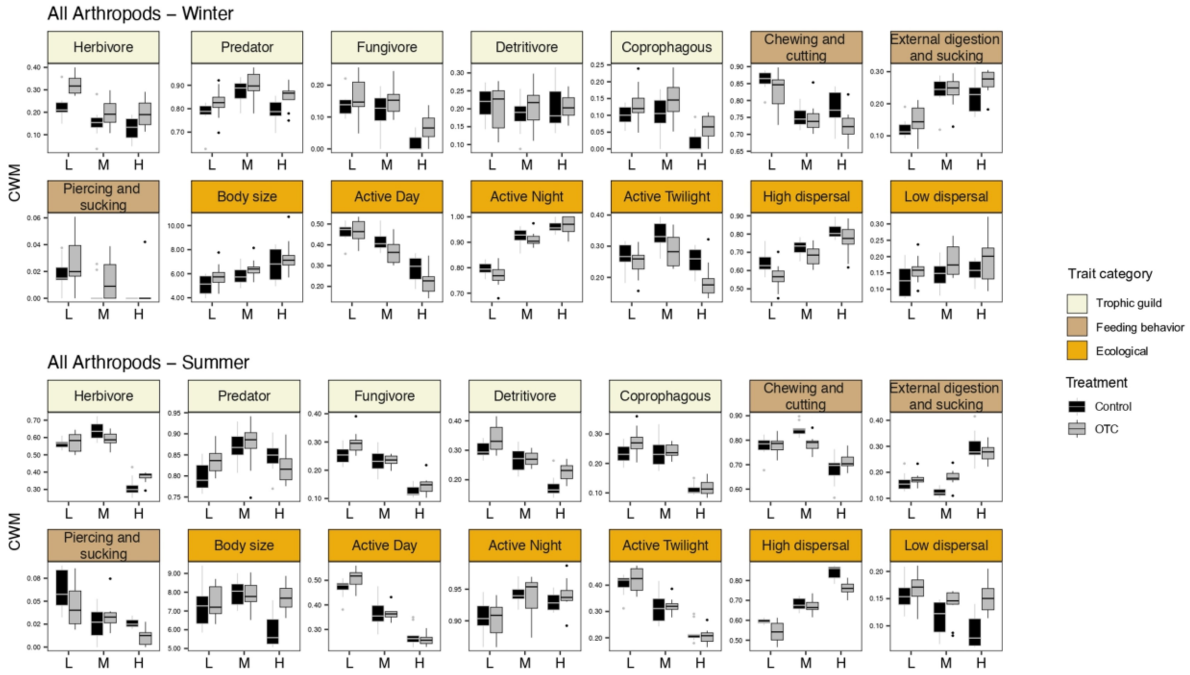

Figure 3. Boxplots highlighting the effect of the treatment (control vs. OTCs) on different traits along the elevation gradient considering all arthropods during the winter and the summer. On y-axis are the values of the community weighted means (CWM) and on x-axis is the elevation factor: low (L), middle (M), and high (H) elevation. Black box plots indicate the control plots, while gray box plots represent the OTCs. ANOVA and post hoc pairwise comparisons results are available in Tables A1 and A2.

4.3.1.2. Ecological Traits

With respect to ecological traits, during summer, low and high dispersers follow opposite trends, with a certain decrease along the altitudinal gradient for low dispersers and, inversely, an increase towards higher altitudes for high dispersers. During winter, high-dispersing arthropods also increase with altitude, but low-dispersing arthropods show no differences between fields. For both seasons, the OTCs showed a higher number of low-dispersal arthropods, while for the high-dispersal arthropods, the OTCs showed a lower number of individuals than the control plots.
During the summer, the low-elevation field had the smallest body size community, while the medium-elevation field had the largest body size community. During winter, the arthropod body size increased

with altitude, with larger arthropods at the highest altitude. Although there appears to have been a difference in body size between treatments in the high-altitude field during the summer, no significant differences were found (Figure 3 and Table A1).

In summer and winter, the diurnal arthropods decreased with altitude, while the nocturnal arthropods followed the opposite trend. In summer, the twilight arthropods decreased with altitude and in winter, they showed a hump shape along the altitude gradient with higher abundances at middle elevation. There were also fewer twilight and diurnal arthropods in the OTCs in winter.

4.3.1.3. Feeding Behaviors

In terms of feeding behavior (Figure 3), chewing/cutting and piercing/sucking arthropods are less abundant at high altitude and show a slight decrease along the altitudinal gradient for both seasons. However, arthropods feeding by external digestion and sucking (e.g., spiders) are more abundant at the highest altitudes (Tables A1 and A2).

4.3.2. Winter and Summer Beetle Trait Analysis

4.3.2.1. Guilds

In terms of guilds, there was no clear pattern across all the guilds. Herbivores follow a hump shape along the altitudinal gradient in summer and a U shape in winter. Thus, the middle altitude field showed a large seasonal variation in herbivore beetles (Figure 4).

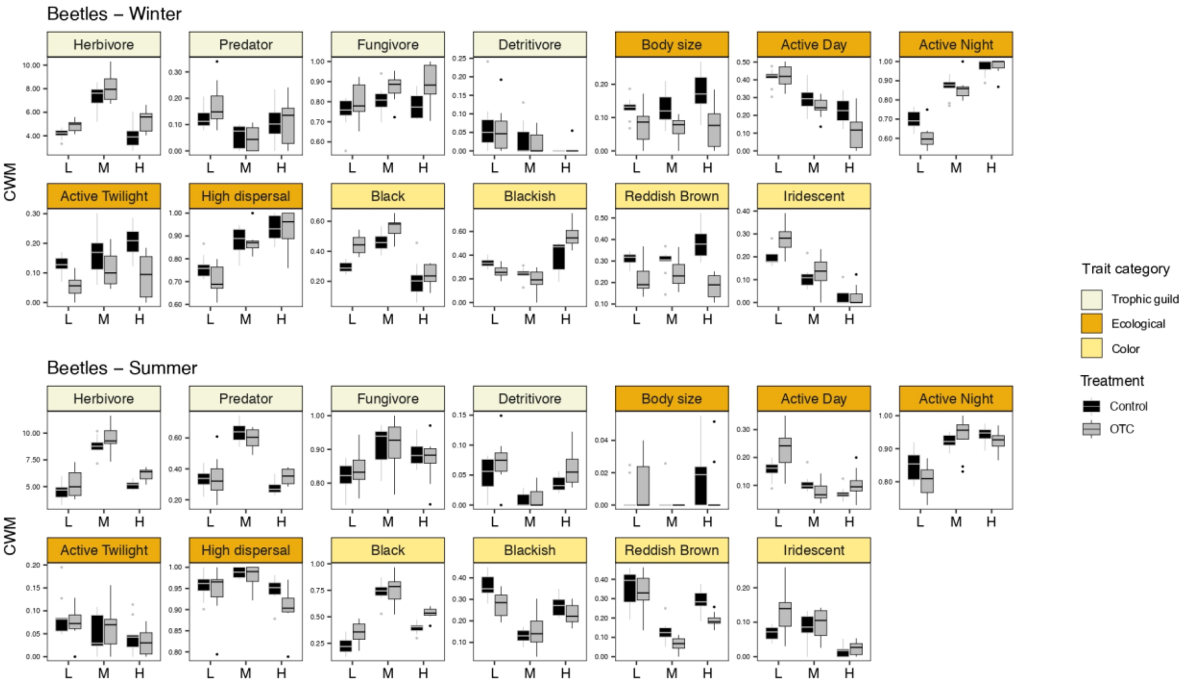

Figure 4. Boxplots highlighting the effect of the treatment (control vs. OTCs) on different traits along the elevation gradient considering only beetles during the winter and the summer. On y-axis are the value of the community weighted means (CWM) and on x-axis is the elevation factor: low (L), middle (M), and high (H) elevation. Black box plots indicate the control plots, while gray box plots represent the OTCs. ANOVA and post hoc pairwise comparisons results are available in Tables A3 and A4.

The predators appeared to be homogeneous at different altitudes, with no major changes along the altitudinal gradient. However, in winter, more predators were observed inside the OTCs.

Fungivores do not show major changes between different altitudes and seasons.

The detritivores were more abundant during the winter, perhaps due to the higher humidity and availability of decaying matter. In addition, fewer detritivores were observed inside the OTCs during winter.

4.3.2.2. Ecological Traits

The beetle body sizes showed a hump shape along the altitudinal gradient, with larger species at middle altitude in both seasons. Larger beetles were also found in the OTCs during summer (Figure 4).
The number of diurnal beetles decreased along the altitudinal gradient in both seasons. In winter, fewer diurnal beetles were observed inside the OTCs.
The number of nocturnal beetles tended to increase with altitude, in addition to the fact that fewer nocturnal beetles were present inside the OTCs during winter.
The crepuscular beetles showed an opposite pattern between winter and summer. They decreased along the altitudinal gradient in summer and increased in winter.
Finally, the high-dispersal beetles showed a hump shape along the altitudinal gradient in summer, but a clear increase with altitude in winter.

4.3.2.3. Color and Iridescence

During the summer, the beetles with orange and red shades (blackish and reddish brown) appeared to be less abundant at middle altitude and showed a U-shape along the altitudinal gradient. The highest abundance was found at low elevation (Figure 4).
Contrastingly, the black beetles were significantly more abundant at mid-altitude in both seasons, showing a hump shape along the altitudinal gradient. The lowest abundances of black beetles were observed at low altitudes.
Differences between treatments were observed for the black and reddish-brown beetles in both seasons. More black beetles were observed in the OTCs, while more reddish-brown beetles were observed in control plots.
Finally, the iridescent beetles showed a clear and significant gradient along the altitudes and during both winter and summer. More iridescent beetles were observed at low altitudes, while the lowest number of iridescent beetles was found at high altitudes. During winter, differences between treatments were observed, with more iridescent beetles inside the OTCs, especially at low elevation.

4.4. Discussion

The analysis of the functional traits across the three elevations and temperature treatments provides valuable insights into the effects of climate and environmental change on arthropod communities. The results of this study also highlight the complex and diverse responses of arthropods to short-term climate change, with distinct patterns emerging across different functional traits and seasonal conditions.

4.4.1. Influence of Elevational Gradient and Seasonality

4.4.1.1. Guilds

The elevational gradient significantly influenced the arthropod and beetle communities, with noticeable variations between seasons. For all the arthropods, during the summer, guilds such as herbivores, coprophagous organisms, detritivores, and fungivores showed lower abundances at high elevations. This supports previous findings that arthropod diversity and abundance tend to decrease with elevation (González-Reyes et al., 2017; Röder et al., 2010), potentially due to the optimal balance between temperature, precipitation, and other environmental conditions (Pilar et al., 2020; Röder et al., 2017). However, the patterns were not uniform across all the guilds, with the predators showing more homogeneous distributions along the gradient, albeit still with a peak at middle elevation. This confirms the finding in previous studies that different trends in the response of arthropod abundance along the elevational gradient depended on the level of taxonomic and functional resolution (Röder et al., 2017). In a recent elevational study on Terceira Island native forest habitats, mixed results were also obtained, with the total species richness of all arthropods, Coleoptera, and Psocodea showing a monotonic decrease with elevation, but peaking at mid-high elevation for Araneae and endemic species (Reinier de Vries et al., 2021).

During the winter, the guild analyzed with all the arthropods showed mostly differences between treatments, which will be discussed in the following section.

The beetles during the summer, herbivores, and predators also showed a peak at middle elevation, agreeing with Pilar et al. (2020) and Röder et al. (2017). The numbers of fungivores and detritivore beetles were very low during summer, probably due to the fact that their distribution is closely linked to the availability of organic matter and litter quality. However, litter quality depends mostly on water availability and temperature (Wu et al., 2021). The lack of litter quality in summer explains the low abundances of those guilds. Detritivore arthropods play a crucial role in the decomposition of dead organic matter, including plant material and animal remains (Mancinelli et al., 2013). In our experiment, most of the detritivores were not strictly decomposers of the organic matter of either animal or plant origin, but of both. Thus, during the summer, the drop in their abundance was mainly due to the quasi-absence of litter, which represented a considerable part of the diet of our detritivores. During the winter, these organisms often exhibit increased abundance, potentially due to the higher humidity and availability of decaying matter (Haitao et al., 2009). Indeed, detritivore beetles were more abundant during the winter, which aligns with findings that cooler temperatures often slow down decomposition rates, leading to a prolonged availability of decaying matter (Aerts, 1997; Davidson et al., 2006). The higher humidity during winter months may further support the activity and abundance of detritivores, as moisture plays a crucial role in maintaining their physiological functions (Moorhead et al., 2006).

4.4.1.2. Ecological Traits

Another particularly interesting finding was the varying responses of arthropods with different dispersal abilities along the elevation gradient. During the summer, low-dispersal arthropods tended to decrease in abundance at higher elevations, while high-dispersal arthropods showed the opposite trend, becoming more abundant at higher elevations. This trend suggests that the ability to move more widely provides an advantage for some arthropods and beetles, as they track shifting climate conditions, a pattern observed in various ecosystems for arthropods and other taxa (Matheson et al., 2023; Sahlean et al., 2014). These findings highlight the critical need to consider dispersal capabilities when examining the ecological impacts of climate change on arthropod communities.

One more key result was the shift in the body size distribution of the arthropod community along the elevation gradient, with larger-bodied species becoming more prevalent at higher elevations, particularly during the winter season. This finding aligns with previous research demonstrating that larger-bodied arthropods often succeed in colder, higher-elevation environments, probably due to metabolic and thermoregulatory adaptations (Horne et al., 2018; Kingsolver et al., 2008; Wardhaugh et al., 2018). The prevalence of larger-bodied species at higher elevations during winter may reflect their ability to better withstand harsher conditions, while smaller species may struggle to maintain their energetic requirements

However, the beetles exhibited distinct ecological traits along the elevation gradient. Our data show that two of the largest beetle species were more abundant at the middle elevation than at the low or high elevations, e.g., the staphylinid, *Ocypus olens* (Müller, 1764), and the ground Beetle, *Calosoma olivieri* Dejean, 1831. Therefore, contrary to expectations, our results showed that larger beetle species tend to peak at middle elevations. This is likely to be due to the favorable conditions for growth and development found at these levels for grassland arthropods, where resource availability and environmental conditions are well-balanced. Arthropod abundance generally peaks at higher elevations on gradients with a very dry base and a sharp increase in precipitation with elevation (Supriya et al., 2019). However, the prolonged developmental time required by larger insects can be disadvantageous at higher elevations due to shorter active seasons (Ouisse et al., 2020). Therefore, climatic conditions pose a significant obstacle to their optimal development and may limit their distribution along elevational gradients (Sota, 1996). However, these patterns can vary, since some of the most iconic large Azorean endemic forest-adapted ground-beetles are restricted to high-elevation, hyper-humid forests (Gaston et al., 2006).

The daily activity patterns of all the arthropods and beetles showed that the crepuscular and diurnal arthropods decreased with elevation, while the nocturnal arthropods increased, a trend that was consistent across both seasons. The altered patterns of activity across the diurnal, nocturnal and crepuscular arthropods along the elevational gradient and between seasons suggests that climate change could disrupt important temporal niche partitioning within arthropod communities. Furthermore, diel activity may influence arthropod responses to increased temperatures, with nocturnal species potentially being less affected by daylight heat compared to diurnal species. This is because nocturnal arthropods remain hidden from direct solar exposure and extreme temperatures (Thiele, 1977). However, our experiment showed opposite results to these findings, with more diurnal activity at lower elevations and more nocturnal activity at higher elevations. Species-specific responses and the complex interplay of environmental factors, including food availability and predation pressure, also influence diel activity (Ockendon et al., 2014), and could explain the results of our experiment.

This shift in activity patterns may also be due to the thermal constraints imposed by elevation (harsher conditions and colder periods), which can influence the temporal niche partitioning within arthropod communities. As Lobo (2024) states, "hotter is not better", and some species of beetle with specific metabolic mechanisms are able to maintain their nocturnal activity under cold temperatures. Different metabolic mechanisms can make it difficult for diurnal beetles to remain active at cooler temperatures. The crepuscular beetles exhibited opposite patterns between winter and summer, decreasing in summer and increasing in winter, possibly due to shifts in temperature and resource availability that influenced their activity periods.

This highlights the complex ways in which climate change can impact the structure and dynamics of arthropod communities, with cascading effects on ecosystem function.

4.4.1.3. Feeding Behaviors

The feeding behaviors were notably influenced by elevation, with the chewing/cutting and piercing/sucking arthropods decreasing at higher elevations, while those utilizing external digestion (e.g., spiders) increased. This may reflect adaptations to resource availability and climatic conditions at different elevations. Conversely, predators and scavengers that rely on external digestion, such as spiders (mostly linyphiids in the current study), may have found a higher and more consistent grass cover throughout the year at the high elevation in our experiment, providing a more favorable ecosystem, as shown by Borges & Brown (2004 & 2001). Our data also revealed a high number of harvestmen from the Leiobunidae family, which also rely on external digestion, at high elevation. Their high number could have been due to the higher moisture levels that they tend to prefer (Punzo et al., 2007), which naturally occurs at this elevation. These adaptations highlight the complex interplay between environmental conditions and arthropod feeding strategies across altitudinal gradients.

4.4.1.4. Beetle Color and Iridescence

The results indicate the significant presence of iridescent beetles along the altitudinal gradient, with more iridescent beetles observed at lower elevations compared to higher elevations. This pattern suggests that iridescence may be an adaptation to cope with the higher temperatures typically found at lower elevations and emphasizes the role of iridescence in thermoregulation. Indeed, iridescence in beetles can serve various ecological functions, including camouflage, signaling, and thermoregulation (Allahverdyan et al., 2013; Seago et al., 2009; Vukusic, 2003). In fact, iridescent surfaces reflect a significant portion of incident light, which can help regulate body temperature by reducing heat absorption. Conversely, at higher elevations, where temperatures are generally cooler, the advantage of iridescence in thermoregulation might be less pronounced, resulting in fewer iridescent beetles (Davis et al., 2008). It is noteworthy that all Azorean endemic beetles found in high-elevation, hyper-humid forests (at approximately 500 m to 1000 m above sea level), although not part of this study, are typically non-iridescent and mostly blackish. In our study, we did not collect endemic Azorean beetles, since their habitat is at higher elevation and the Azorean intensive pastures are mostly composed of introduced species and very few native ones. Therefore, it would be interesting in the future to study the coloration of native and endemic beetles in more detail to see whether their response follows the same trend as that of introduced beetles. The observed coloration trends along the elevational gradient in our experiment reveal significant ecological and adaptive patterns in beetle populations. During the summer, the beetles with orange and red nuances, such as blackish and reddish-brown beetles, exhibited a U-shaped distribution, with the highest abundances at low elevations. This pattern suggests that these colorations may be more effective for thermoregulation and camouflage in the warmer environments found at lower elevations (Badejo et al., 2020; Lindstedt et al., 2009; Young, 1960). Conversely, the black beetles displayed a hump-shaped distribution, being more abundant at middle elevations during both seasons. The adaptive significance of melanism in black beetles, particularly for absorbing heat in cooler environments, might explain their success in these mid-altitudinal zones (Trullas et al., 2007).

4.4.2. Effects of Increased Temperature (OTC Experiment)

4.4.2.1. Guilds

The increased temperature of the OTCs played a crucial role in the arthropod and beetle traits observed, especially during winter. The higher abundances of herbivores, predators, coprophagous organisms, and fungivores within the OTCs during winter suggest that increased temperatures may alleviate some environmental stressors, leading to increased activity and survival. Vasseur et al. (2014) agree that an increase in temperature has these effects on ectotherms. However, they caution that it is important to consider the effect of the temperature mean and variance, as their model predicts that mid-latitude species will be most susceptible to large declines in performance under a future climate scenario when these two factors are considered. Furthermore, higher temperatures in OTCs during winter may reduce the energy costs associated with thermoregulation (for warming), allowing more resources to be allocated to foraging, mating, and development (Lahondère, 2023; Sears et al., 2015). Such effects are known to be particularly pronounced in winter for insects, when thermal stress is typically higher, and the relative benefits of small temperature increases can be substantial (Kingsolver et al., 2020).

The detritivores, arthropods that feed on decaying matter, did not show significant differences between the treatments. The rate of detrital decomposition depends on the quality of the detritus and the physical environment, including factors such as temperature and water availability (Wu et al., 2021). In the Azores, precipitation is highest from November to January, and it varies considerably within each month, depending on elevation and longitude. Humidity is generally high, with median relative humidity (RH) values around 80%, and the cooler months are typically January and February (Paredes et al., 2018), with temperatures above 0 °C in our experiment. Therefore, detritivores may be particularly dependent on the availability of decaying matter and less affected by temperature changes than other guilds.

For the beetles, increased temperatures impacted most of the functional traits studied, with stronger effects also observed during winter. This suggests that beetles may be more sensitive to temperature changes during colder months, potentially due to metabolic and physiological constraints. Ectotherms, such as beetles, rely on external sources of heat to regulate their body temperature, and their metabolic rates are strongly influenced by ambient temperatures (Lahondère, 2023; Sears et al., 2015). At lower temperatures, metabolic rates are typically slower, potentially limiting activity levels and overall fitness (Hannigan et al., 2022). Therefore, even small increases in temperature during winter could have a disproportionately large impact on beetle physiology and behavior, aligning with findings from other studies demonstrating the vulnerability of ectotherms to temperature changes, particularly during colder periods (Kingsolver et al., 2020).

During the winter season, the detritivore arthropod abundance may have been lower within the OTCs compared to the natural control plots due to several factors. Temperature variation within OTCs can disrupt the stable microhabitat that detritivores rely on (Bardgett et al., 2008). While OTCs are designed to elevate overall temperatures, the enclosed environment may lead to greater daily and seasonal fluctuations in temperature compared to the surrounding natural plots (Lutterschmidt et al., 1997). This could have adversely affected the physiology and behavior of these moisture-dependent organisms, making the environment less suitable for their survival and reproduction. In addition to temperature, OTCs may also alter moisture levels within leaf litter. By trapping heat, OTCs can potentially dry out the organic substrate, reducing the humidity levels that detritivores require (Bordier et al., 2017). Alternatively, the OTCs may have created a more condensed environment, leading to excessive moisture, which is also detrimental to detritivore communities. Furthermore, the physical presence of the OTC structures themselves could have interfered with the natural accumulation and distribution of organic matter, which serves as the primary food source for detritivore arthropods. This disruption of the microhabitat could have limited the availability of resources and led to a decreased abundance of these decomposer organisms within the OTCs compared to the control plots.

4.4.2.2. Ecological Traits

Interestingly, while the beetle body size peaked at middle elevations in both summer and winter, a larger average body size was observed within the OTCs during the summer. This contradicts the general trend of smaller body sizes in ectotherms under warmer temperatures, as suggested by (Kingsolver et al., 2008; Tseng et al., 2018). This discrepancy could be attributed to species-specific responses to temperature, altered resource availability within the OTCs, or interactions with other environmental factors not explored in this study. For instance, increased temperatures might have led to a greater quality and amount of food for certain beetle species (Chown et al., 2010).

The reduced activity of the nocturnal beetles, as well as the reduced activity of the diurnal and crepuscular arthropods and beetles within the OTC treatments during the winter, may indicate a means of avoiding thermal stress, as suggested by Thiele (Thiele, 1977). However, this result needs to be considered with caution, as in our case, the temperature within the OTCs during the winter was warmer than in the control plots, but not extreme. Therefore, it should be considered whether other factors, such as food availability, could have been responsible for the observed effect, and not only thermal stress, which should be low at this time of year. Pawar et al. (2024) also highlighted that thermal adaptation in arthropods is constrained by the temperature of peak performance for key life-history traits, which could also explain our results.

More low-dispersal arthropods were found in the OTCs than in the control plots. The opposite was found for the high-dispersal arthropods, which were more abundant in the control plots than in the OTCs. Thus, the high dispersers may have left the OTCs when the abiotic conditions became unsuitable, with only low dispersers remaining. This pattern is consistent with the finding that as climate change occurs, high dispersers are the first to seek out better abiotic conditions (García-Robledo et al., 2016; Lurgi et al., 2012).

During the summer, larger beetles were more prevalent in the OTCs, potentially indicating that increased temperatures within OTCs favor the presence of some larger beetle species. This finding opposes the prevailing trend in ectotherms, which tend to have smaller body sizes at warmer temperatures (Kingsolver et al., 2008), suggesting species-specific responses to temperature or altered resource dynamics within OTCs.

4.4.2.3. Feeding Behavior

The study found that the feeding behavior of arthropods, including piercing, sucking, chewing, cutting, and external digestion, was not impacted by increased temperatures within the OTCs. Although mouthparts are unique to each arthropod kingsofamily, this finding is also consistent with several studies suggesting that while temperature can affect metabolic rates and activity levels, the abundance of different arthropod feeding strategies often remains constant across temperature variations (Bale et al., 2002; Chown et al., 2004; Deutsch et al., 2008).

4.4.2.4. Beetle Color and Iridescence

The data showed an increased number of iridescent beetles inside the OTCs at lower elevations during winter, suggesting that elevated temperatures enhance the prevalence of iridescence. The increased presence of iridescent beetles inside the OTCs implies that iridescence may provide a thermoregulatory benefit under higher temperatures, aiding in heat reflection and reducing thermal stress (Davis et al., 2008; Vukusic, 2003). This ability to reflect sunlight and maintain lower body temperatures would be particularly advantageous during warmer periods, supporting the survival and activity of iridescent beetles (Stuart-Fox et al., 2017).

The higher abundance of black beetles in the OTCs during winter suggests potential thermal benefits associated with darker coloration. Darker colors can absorb more heat, providing significant thermal advantages in colder environments (Lindstedt et al., 2009; Young, 1960). This adaptation probably enhanced the survival and activity of the black beetles during the winter months, when ambient temperatures are lower. The observation of fewer black beetles in the control plots compared to the OTCs supports the hypothesis that the increased temperatures within the OTCs would create more favorable conditions for these beetles in winter. Such findings align with the theory that melanism confers thermal benefits by facilitating heat absorption, which is crucial for ectotherms to maintain metabolic processes in cooler climates (Trullas et al., 2007). The reddish-brown coloration might offer a balance between camouflage and thermal regulation, providing sufficient heat absorption without the risk of overheating in moderate environments (Badejo et al., 2020; Majerus, 1998; Stavenga et al., 2006). These findings contribute to our understanding of how beetles adapt to varying microclimatic conditions and offer a basis for further research on the ecological functions of beetle coloration and iridescence.

4.5. Conclusions

Overall, this study highlights the complex interplay between elevation, temperature, and season in shaping arthropod and beetle communities. The observed patterns emphasize the need to consider multiple environmental factors when assessing the impact of climate change on biodiversity. The functional traits approach unveiled more patterns among the studied arthropod communities in response to climatic changes than the taxonomical approach previously applied by Wallon, Tsafack, et al. (2023). Other studies comparing the taxonomical and the functional approach showed the importance of considering functional traits in analyzing arthropod communities and agreed that the functional approach enhances knowledge of the processes underlying patterns of diversity in complex ecological communities involving multiple trophic levels (Lamarre et al., 2016; Rabello et al., 2021; Wong et al., 2019). However, analyses including functional traits appear to be more complex to interpret due to various factors and interactions (Vergara et al., 2022).

Future research should further explore the underlying mechanisms driving these patterns and their implications for ecosystem functioning and resilience. The results of this study contribute to this growing body of knowledge and highlight the importance of examining arthropod responses at the community level and considering functional traits, rather than focusing solely on individual species.

In conclusion, the observed effects of increasing temperature and elevational gradients on the functional traits of arthropods and beetles highlight the complex and functional-group-specific nature of thermal responses within these communities.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/insects15090677/s1 : Species collected over the winter and the summer at all sites studied; Table S2: Beetle species collected over the winter and the summer at all sites studied.

4.6. Appendices

Table A1. Results of the ANOVA performed to investigate the effects of the elevation and the treatment on functional traits of all arthropods, including the interaction terms (Elev:Treatment) on each CWM variable. Adjusted *p* values are also presented. Significant results are marked in bold. Traits presented are Herbivore; Predator; Fungivore; Detritivore, Coprophagous; External digestion and sucking (IngestEDS); Chewing and cutting (CC); Piercing and sucking (PS); Standardized body size (Body size) in (mm); High dispersal ability (Hdisp) and low dispersal ability (Ldisp); Diurnal arthropods (ActDay); Nocturnal arthropods (ActNig); and arthropods active during twilight (ActTwi).

Season	Trait	Factor	Df	Sum Sq.	Mean Sq.	F Value	Pr(>F)	*p* Adjust
Summer	Herbivore	Elevation	2	0.847	0.424	212.617	**<0.001**	**<0.001**
		Treatment	1	0.001	0.001	0.360	0.551	0.605
		Elev:Treatment	2	0.029	0.015	7.359	**0.001**	**0.004**
		Residuals	54	0.108	0.002			
Winter	Herbivore	Elevation	2	0.147	0.073	22.520	**<0.001**	**<0.001**
		Treatment	1	0.075	0.075	23.106	**<0.001**	**<0.001**
		Elev:Treatment	2	0.006	0.003	0.981	0.382	0.477
		Residuals	54	0.176	0.003			
Summer	Predator	Elevation	2	0.029	0.014	8.667	**0.001**	**0.002**
		Treatment	1	0.000	0.000	0.235	0.629	0.659
		Elev:Treatment	2	0.011	0.005	3.227	**0.047**	0.082
		Residuals	54	0.089	0.002			
Winter	Predator	Elevation	2	0.079	0.040	12.293	**<0.001**	**<0.001**
		Treatment	1	0.031	0.031	9.772	**0.003**	**0.008**
		Elev:Treatment	2	0.003	0.001	0.400	0.672	0.756
		Residuals	54	0.174	0.003			
Summer	Fungivore	Elevation	2	0.204	0.102	97.826	**<0.001**	**<0.001**
		Treatment	1	0.008	0.008	8.028	**0.006**	**0.014**
		Elev:Treatment	2	0.004	0.002	1.87	0.164	0.217
		Residuals	54	0.056	0.001			
Winter	Fungivore	Elevation	2	0.135	0.068	28.955	**<0.001**	**<0.001**
		Treatment	1	0.018	0.018	7.510	**0.008**	**0.020**
		Elev:Treatment	2	0.002	0.001	0.339	0.714	0.765
		Residuals	54	0.126	0.002			
Summer	Detritivore	Elevation	2	0.140	0.070	53.575	**<0.001**	**<0.001**
		Treatment	1	0.014	0.014	10.820	**0.002**	**0.004**
		Elev:Treatment	2	0.006	0.003	2.318	0.108	0.147
		Residuals	54	0.070	0.001			
Winter	Detritivore	Elevation	2	0.003	0.001	0.516	0.600	0.711
		Treatment	1	0.000	0.000	0.138	0.712	0.765

Season	Trait	Factor	Df	Sum Sq.	Mean Sq.	F Value	Pr(>F)	*p* Adjust
		Elev:Treatment	2	0.003	0.002	0.595	0.555	0.675
		Residuals	54	0.146	0.003			
Summer	Coprophagous	Elevation	2	0.234	0.117	99.245	**<0.001**	**<0.001**
		Treatment	1	0.004	0.004	3.712	0.059	0.098
		Elev:Treatment	2	0.004	0.002	1.638	0.204	0.262
		Residuals	54	0.064	0.001			
Winter	Coprophagous	Elevation	2	0.083	0.041	20.037	**<0.001**	**<0.001**
		Treatment	1	0.022	0.022	10.808	**0.002**	**0.005**
		Elev:Treatment	2	0.000	0.000	0.087	**0.917**	0.923
		Residuals	54	0.111	0.002			
Summer	IngestEDS	Elevation	2	0.212	0.106	81.22	**<0.001**	**<0.001**
		Treatment	1	0.004	0.004	3.212	**0.079**	0.116
		Elev:Treatment	2	0.014	0.007	5.306	**0.008**	**0.016**
		Residuals	54	0.070	0.001			
Winter	IngestEDS	Elevation	2	0.152	0.076	37.49	**<0.001**	**<0.001**
		Treatment	1	0.008	0.008	3.999	0.051	0.099
		Elev:Treatment	2	0.004	0.002	1.098	0.341	0.477
		Residuals	54	0.110	0.002			
Summer	IngestCC	Elevation	2	0.147	0.074	46.258	**<0.001**	**<0.001**
		Treatment	1	0.001	0.001	0.572	0.453	0.536
		Elev:Treatment	2	0.023	0.012	7.307	**0.002**	**0.004**
		Residuals	54	0.086	0.002			
Winter	IngestCC	Elevation	2	0.115	0.057	29.110	**<0.001**	**<0.001**
		Treatment	1	0.012	0.012	5.907	**0.018**	**0.041**
		Elev:Treatment	2	0.005	0.003	1.360	0.265	0.426
		Residuals	54	0.107	0.002			
Summer	IngestPS	Elevation	2	0.013	0.006	23.312	**<0.001**	**<0.001**
		Treatment	1	0.001	0.001	3.653	0.061	0.098
		Elev:Treatment	2	0.002	0.001	3.530	**0.036**	0.065
		Residuals	54	0.015	0.000			
Winter	IngestPS	Elevation	2	0.004	0.002	10.916	**<0.001**	**<0.001**
		Treatment	1	0.001	0.001	4.348	**0.042**	0.086
		Elev:Treatment	2	0.000	0.000	0.186	0.831	0.869
		Residuals	54	0.009	0.000			
Summer	Body size	Elevation	2	2350.500	1175.300	61.207	**<0.001**	**<0.001**

Season	Trait	Factor	Df	Sum Sq.	Mean Sq.	F Value	Pr(>F)	*p* Adjust
		Treatment	1	61.200	61.200	3.187	0.080	0.116
		Elev:Treatment	2	102.000	51.000	2.657	0.079	0.116
		Residuals	54	1036.900	19.200			
Winter	Body size	Elevation	2	809.300	404.600	21.583	**<0.001**	**<0.001**
		Treatment	1	15.000	15.000	0.801	0.375	0.477
		Elev:Treatment	2	66.700	33.300	1.778	0.179	0.309
		Residuals	54	1012.400	18.700			
Summer	Hdisp	Elevation	2	0.544	0.272	213.338	**<0.001**	**<0.001**
		Treatment	1	0.031	0.031	24.141	**<0.001**	**<0.001**
		Elev:Treatment	2	0.013	0.006	4.923	**0.011**	**0.021**
		Residuals	54	0.069	0.001			
Winter	Hdisp	Elevation	2	0.354	0.177	46.911	**<0.001**	**<0.001**
		Treatment	1	0.049	0.049	13.067	**<0.001**	**0.002**
		Elev:Treatment	2	0.004	0.002	0.457	0.636	0.733
		Residuals	54	0.204	0.004			
Summer	Ldisp	Elevation	2	0.018	0.009	10.41	**<0.001**	**<0.001**
		Treatment	1	0.016	0.016	18.81	**<0.001**	**<0.001**
		Elev:Treatment	2	0.008	0.004	4.41	**<0.001**	**0.032**
		Residuals	54	0.047	0.001			
Winter	Ldisp	Elevation	2	0.011	0.005	2.207	0.120	0.225
		Treatment	1	0.022	0.022	9.226	**0.004**	**0.009**
		Elev:Treatment	2	0.000	0.000	0.08	0.923	0.923
		Residuals	54	0.131	0.002			
Summer	ActivDay	Elevation	2	0.492	0.246	159.662	**<0.001**	**<0.001**
		Treatment	1	0.001	0.001	0.794	0.377	0.471
		Elev:Treatment	2	0.008	0.004	2.578	0.085	0.120
		Residuals	54	0.083	0.002			
Winter	ActivDay	Elevation	2	0.458	0.229	74.253	**<0.001**	**<0.001**
		Treatment	1	0.018	0.018	5.734	**0.020**	**0.043**
		Elev:Treatment	2	0.011	0.006	1.826	0.171	0.308
		Residuals	54	0.167	0.003			
Summer	ActivNight	Elevation	2	0.014	0.007	11.8	**<0.001**	**<0.001**
		Treatment	1	0.000	0.000	0.027	0.869	0.869
		Elev:Treatment	2	0.001	0.000	0.501	0.609	0.652
		Residuals	54	0.032	0.001			

Season	**Trait**	**Factor**	**Df**	**Sum Sq.**	**Mean Sq.**	**F Value**	**Pr(>F)**	***p* Adjust**
Winter	ActivNight	Elevation	2	0.357	0.178	161.993	**<0.001**	**<0.001**
		Treatment	1	0.002	0.002	1.59	0.213	0.355
		Elev:Treatment	2	0.002	0.001	1.066	0.352	0.477
		Residuals	54	0.060	0.001			
Summer	ActivTwi	Elevation	2	0.396	0.198	121.950	**<0.001**	**<0.001**
		Treatment	1	0.000	0.000	0.213	0.646	0.661
		Elev:Treatment	2	0.003	0.001	0.767	0.470	0.542
		Residuals	54	0.088	0.002			
Winter	ActivTwi	Elevation	2	0.082	0.041	17.828	**<0.001**	**<0.001**
		Treatment	1	0.028	0.028	12.182	**0.001**	**0.003**
		Elev:Treatment	2	0.006	0.003	1.218	0.304	0.472
		Residuals	54	0.124	0.002			

Table A2. Results of the post hoc pairwise comparisons performed on the different traits of all arthropods when the ANOVA models were significant. Significant results are marked in bold. Traits presented are Herbivore; Predator; Fungivore; Detritivore, Coprophagous; External digestion and sucking (IngestEDS); Chewing and cutting (CC); Piercing and sucking (PS); Standardized body size (Body size) in (mm); High dispersal ability (Hdisp) and low dispersal ability (Ldisp); Diurnal arthropods (ActDay); Nocturnal arthropods (ActNig); and arthropods active during twilight (ActTwi). Factors presented are the elevation, the treatment, and their interaction (Elev:Treatment). Low-elevation field (LOW); Middle-elevation field (MID); High-elevation field (HIGH); Control plots at low elevation (LOW C.); OTCs at low elevation (LOW OTC); Control plots at middle elevation (MID C.); OTCs at middle elevation (MID OTC); Control plots at high elevation (HIGH C.); OTCs at high elevation (HIGH OTC). See corresponding box plot in the main text in Figure 3.

Season	Trait	Factor	Pairwise Comparisons	Estimate	SE	df	t.Ratio	*p* Value	Trend
Summer	Herbivore	Elevation	LOW–MID	−0.045	0.014	54	−3.196	**0.007**	LOW < MID
			LOW–HIGH	0.227	0.014	54	16.045	**<0.001**	LOW > HIGH
			MID–HIGH	0.272	0.014	54	19.241	**<0.001**	MID > HIGH
Summer	Herbivore	Elev:Treatment	LOW C.–MID C.	−0.075	0.020	54	−3.763	**0.005**	LOW C. < MID C.
			LOW C.–HIGH C.	0.251	0.020	54	12.550	**<0.001**	LOW C. > HIGH C.
			LOW C.–LOW OTC	−0.011	0.020	54	−0.545	0.994	LOW C. = LOW OTC
			LOW C.–MID OTC	−0.026	0.020	54	−1.302	0.782	LOW C. = MID OTC
			LOW C.–HIGH OTC	0.192	0.020	54	9.596	**<0.001**	LOW C. > HIGH OTC
			MID C.–HIGH C.	0.326	0.020	54	16.313	**<0.001**	MID C. > HIGH C.
			MID C.–LOW OTC	0.064	0.020	54	3.218	**0.025**	MID C. > LOW OTC
			MID C.–MID OTC	0.049	0.020	54	2.460	0.155	MID C. = MID OTC
			MID C.–HIGH OTC	0.267	0.020	54	13.358	**<0.001**	MID C. > HIGH OTC
			HIGH C.–LOW OTC	−0.261	0.020	54	−13.095	**<0.001**	HIGH C. < LOW OTC
			HIGH C.–MID OTC	−0.277	0.020	54	−13.852	**<0.001**	HIGH C. < MID OTC
			HIGH C.–HIGH OTC	−0.059	0.020	54	−2.954	0.050	HIGH C. = HIGH OTC
			LOW OTC–MID OTC	−0.015	0.020	54	−0.757	0.973	LOW OTC = MID OTC
			LOW OTC–HIGH OTC	0.202	0.020	54	10.141	**<0.001**	LOW OTC > HIGH OTC
			MID OTC–HIGH OTC	0.218	0.020	54	10.898	**<0.001**	MID OTC > HIGH OTC
Winter	Herbivore	Elevation	LOW–MID	0.096	0.018	54	5.301	**<0.001**	LOW > MID

Season	Trait	Factor	Pairwise Comparisons	Estimate	SE	df	t.Ratio	*p* Value	Trend
			LOW–HIGH	0.112	0.018	54	6.215	**<0.001**	LOW > HIGH
			MID–HIGH	0.017	0.018	54	0.914	0.634	MID = HIGH
Winter	Herbivore	Treatment	Control–OTC	−0.071	0.015	54	−4.807	**<0.001**	C < OTC
Summer	Predator	Elevation	LOW–MID	−0.052	0.013	54	−4.026	**<0.001**	LOW < MID
			LOW–HIGH	−0.014	0.013	54	−1.094	0.522	LOW = HIGH
			MID–HIGH	0.038	0.013	54	2.932	**0.013**	MID > HIGH
Summer	Predator	Elev:Treatment	LOW C.–MID C.	−0.070	0.018	54	−3.841	**0.004**	LOW C. < MID C.
			LOW C.–HIGH C.	−0.047	0.018	54	−2.566	0.124	LOW C. = HIGH C.
			LOW C.–LOW OTC	−0.039	0.018	54	−2.138	0.284	LOW C. = LOW OTC
			LOW C.–MID OTC	−0.072	0.018	54	−3.991	**0.003**	LOW C. < MID OTC
			LOW C.–HIGH OTC	−0.020	0.018	54	−1.118	0.872	LOW C. = HIGH OTC
			MID C.–HIGH C.	0.023	0.018	54	1.274	0.797	MID C. = HIGH C.
			MID C.–LOW OTC	0.031	0.018	54	1.703	0.536	MID C. = LOW OTC
			MID C.–MID OTC	−0.003	0.018	54	−0.150	1.000	MID C. = MID OTC
			MID C.–HIGH OTC	0.049	0.018	54	2.722	0.087	MID C. = HIGH OTC
			HIGH C.–LOW OTC	0.008	0.018	54	0.428	0.998	HIGH C. = LOW OTC
			HIGH C.–MID OTC	−0.026	0.018	54	−1.425	0.712	HIGH C. = MID OTC
			HIGH C.–HIGH OTC	0.026	0.018	54	1.448	0.698	HIGH C. = HIGH OTC
			LOW OTC–MID OTC	−0.034	0.018	54	−1.853	0.442	LOW OTC = MID OTC
			LOW OTC–HIGH OTC	0.019	0.018	54	1.020	0.909	LOW OTC = HIGH OTC
			MID OTC–HIGH OTC	0.052	0.018	54	2.872	0.061	MID OTC = HIGH OTC
Winter	Predator	Elevation	LOW–MID	−0.085	0.018	54	−4.720	**<0.001**	LOW < MID
			LOW–HIGH	−0.019	0.018	54	−1.046	0.552	LOW = HIGH

Season	Trait	Factor	Pairwise Comparisons	Estimate	SE	df	t.Ratio	*p* Value	Trend
			MID–HIGH	0.066	0.018	54	3.675	**0.002**	MID > HIGH
Winter	Predator	Treatment	Control–OTC	−0.046	0.015	54	−3.126	**0.003**	C < OTC
Summer	Fungivore	Elevation	LOW–MID	0.043	0.010	54	4.205	**<0.001**	LOW > MID
			LOW–HIGH	0.140	0.010	54	13.656	**<0.001**	LOW > HIGH
			MID–HIGH	0.097	0.010	54	9.450	**<0.001**	MID > HIGH
Summer	Fungivore	Treatment	Control–OTC	−0.024	0.008	54	−2.833	**0.007**	C < OTC
Winter	Fungivore	Elevation	LOW–MID	0.013	0.0153	54	0.852	0.673	LOW = MID
			LOW–HIGH	0.1066	0.0153	54	6.975	**<0.001**	LOW > HIGH
			MID–HIGH	0.0936	0.0153	54	6.123	**<0.001**	MID > HIGH
Winter	Fungivore	Treatment	Control–OTC	−0.034	0.0125	54	−2.741	**0.008**	C < OTC
Summer	Detritivore	Elevation	LOW–MID	0.0504	0.0114	54	4.411	**0.000**	LOW > MID
			LOW–HIGH	0.1178	0.0114	54	10.315	**<0.001**	LOW > HIGH
			MID–HIGH	0.0674	0.0114	54	5.904	**<0.001**	MID > HIGH
Summer	Detritivore	Treatment	Control–OTC	−0.031	0.009	54	−3.289	**0.002**	C < OTC
Summer	Coprophagous	Elevation	LOW–MID	0.015	0.011	54	1.381	0.358	LOW = MID
			LOW–HIGH	0.139	0.011	54	12.833	**<0.001**	LOW > HIGH
			MID–HIGH	0.124	0.011	54	11.452	**<0.001**	MID > HIGH
Winter	Coprophagous	Elevation	LOW–MID	−0.009	0.014	54	−0.608	0.816	LOW = MID
			LOW–HIGH	0.074	0.014	54	5.153	**<0.001**	LOW > HIGH
			MID–HIGH	0.083	0.014	54	5.761	**<0.001**	MID > HIGH
Winter	Coprophagous	Treatment	Control–OTC	−0.039	0.012	54	−3.288	**0.002**	C < OTC
Summer	IngestCC	Elevation	LOW–MID	−0.036	0.013	54	−2.857	0.016	LOW = MID
			LOW–HIGH	0.082	0.013	54	6.526	**<0.001**	LOW > HIGH

Season	**Trait**	**Factor**	**Pairwise Comparisons**	**Estimate**	**SE**	**df**	**t.Ratio**	***p* Value**	**Trend**
			MID–HIGH	0.118	0.013	54	9.382	**<0.001**	MID > HIGH
Summer	IngestCC	Elev:Treatment	LOW C.–MID C.	−0.069	0.018	54	−3.867	**0.004**	LOW C. < MID C.
			LOW C.–HIGH C.	0.096	0.018	54	5.400	**<0.001**	LOW C. > HIGH C.
			LOW C.–LOW OTC	−0.005	0.018	54	−0.271	1.000	LOW C. = LOW OTC
			LOW C.–MID OTC	−0.008	0.018	54	−0.444	0.998	LOW C. = MID OTC
			LOW C.–HIGH OTC	0.064	0.018	54	3.558	**0.010**	LOW C. > HIGH OTC
			MID C.–HIGH C.	0.165	0.018	54	9.267	**<0.001**	MID C. > HIGH C.
			MID C.–LOW OTC	0.064	0.018	54	3.596	**0.009**	MID C. > LOW OTC
			MID C.–MID OTC	0.061	0.018	54	3.423	**0.014**	MID C. > MID OTC
			MID C.–HIGH OTC	0.133	0.018	54	7.424	**<0.001**	MID C. > HIGH OTC
			HIGH C.–LOW OTC	−0.101	0.018	54	−5.671	**<0.001**	HIGH C. < LOW OTC
			HIGH C.–MID OTC	−0.104	0.018	54	−5.844	**<0.001**	HIGH C. < MID OTC
			HIGH C.–HIGH OTC	−0.033	0.018	54	−1.843	0.448	HIGH C. = HIGH OTC
			LOW OTC–MID OTC	−0.003	0.018	54	−0.173	1.000	LOW OTC = MID OTC
			LOW OTC–HIGH OTC	0.068	0.018	54	3.828	**0.004**	LOW OTC > HIGH OTC
			MID OTC–HIGH OTC	0.071	0.018	54	4.001	**0.003**	MID OTC > HIGH OTC
Winter	IngestCC	Elevation	LOW–MID	0.094	0.014	54	6.683	**<0.001**	LOW > MID
			LOW–HIGH	0.092	0.014	54	6.530	**<0.001**	LOW > HIGH
			MID–HIGH	−0.002	0.014	54	−0.153	0.987	MID = HIGH
Winter	IngestCC	Treatment	Control–OTC	0.028	0.012	54	2.431	**0.018**	C > OTC
Summer	IngestEDS	Elevation	LOW–MID	0.016	0.011	54	1.413	0.341	LOW = MID
			LOW–HIGH	−0.117	0.011	54	−10.263	**<0.001**	LOW < HIGH
			MID–HIGH	−0.133	0.011	54	−11.676	**<0.001**	MID < HIGH

Season	**Trait**	**Factor**	**Pairwise Comparisons**	**Estimate**	**SE**	**df**	**t.Ratio**	***p* Value**	**Trend**
Summer	IngestEDS	Treatment	Control–OTC	−0.017	0.009	54	−1.792	0.079	C = OTC
Summer	IngestEDS	Elev:Treatment	LOW C.–MID C.	0.038	0.016	54	2.328	0.201	LOW C. = MID C.
			LOW C.–HIGH C.	−0.133	0.016	54	−8.222	**<0.001**	LOW C. < HIGH C.
			LOW C.–LOW OTC	−0.013	0.016	54	−0.793	0.968	LOW C. = LOW OTC
			LOW C.–MID OTC	−0.018	0.016	54	−1.122	0.870	LOW C. = MID OTC
			LOW C.–HIGH OTC	−0.114	0.016	54	−7.084	**<0.001**	LOW C. < HIGH OTC
			MID C.–HIGH C.	−0.170	0.016	54	−10.550	**<0.001**	MID C. < HIGH C.
			MID C.–LOW OTC	−0.050	0.016	54	−3.121	**0.033**	MID C. < LOW OTC
			MID C.–MID OTC	−0.056	0.016	54	−3.450	**0.013**	MID C. < MID OTC
			MID C.–HIGH OTC	−0.152	0.016	54	−9.412	**<0.001**	MID C. < HIGH OTC
			HIGH C.–LOW OTC	0.120	0.016	54	7.430	**<0.001**	HIGH C. > LOW OTC
			HIGH C.–MID OTC	0.115	0.016	54	7.101	**<0.001**	HIGH C. > MID OTC
			HIGH C.–HIGH OTC	0.018	0.016	54	1.138	0.863	HIGH C. = HIGH OTC
			LOW OTC–MID OTC	−0.005	0.016	54	−0.329	1.000	LOW OTC = MID OTC
			LOW OTC–HIGH OTC	−0.102	0.016	54	−6.292	**<0.001**	LOW OTC < HIGH OTC
			MID OTC–HIGH OTC	−0.096	0.016	54	−5.962	**<0.001**	MID OTC < HIGH OTC
Winter	IngestEDS	Elevation	LOW–MID	−0.102	0.014	54	−7.175	**<0.001**	LOW < MID
			LOW–HIGH	−0.111	0.014	54	−7.785	**<0.001**	LOW < HIGH
			MID–HIGH	−0.009	0.014	54	−0.610	0.815	MID = HIGH
Summer	IngestPS	Elevation	LOW–MID	0.024	0.005	54	4.510	**<0.001**	A > B
			LOW–HIGH	0.035	0.005	54	6.695	**<0.001**	A > C
			MID–HIGH	0.011	0.005	54	2.185	0.083	B = C
Summer	IngestPS	Elev:Treatment	LOW C.–MID C.	0.036	0.007	54	4.912	**<0.001**	LOW C. > MID C.

Season	Trait	Factor	Pairwise Comparisons	Estimate	SE	df	t.Ratio	*p* Value	Trend
			LOW C.–HIGH C.	0.036	0.007	54	4.947	**<0.001**	LOW C. > HIGH C.
			LOW C.–LOW OTC	0.018	0.007	54	2.394	0.177	LOW C. = LOW OTC
			LOW C.–MID OTC	0.028	0.007	54	3.860	**0.004**	LOW C. > MID OTC
			LOW C.–HIGH OTC	0.051	0.007	54	6.915	**<0.001**	LOW C. > HIGH OTC
			MID C.–HIGH C.	0.000	0.007	54	0.035	1.000	MID C. = HIGH C.
			MID C.–LOW OTC	−0.019	0.007	54	−2.518	0.137	MID C. = LOW OTC
			MID C.–MID OTC	−0.008	0.007	54	−1.052	0.898	MID C. = MID OTC
			MID C.–HIGH OTC	0.015	0.007	54	2.004	0.354	MID C. = HIGH OTC
			HIGH C.–LOW OTC	−0.019	0.007	54	−2.553	0.127	HIGH C. = LOW OTC
			HIGH C.–MID OTC	−0.008	0.007	54	−1.087	0.885	HIGH C. = MID OTC
			HIGH C.–HIGH OTC	0.015	0.007	54	1.969	0.373	HIGH C. = HIGH OTC
			LOW OTC–MID OTC	0.011	0.007	54	1.466	0.687	LOW OTC = MID OTC
			LOW OTC–HIGH OTC	0.033	0.007	54	4.522	**0.001**	LOW OTC > HIGH OTC
			MID OTC–HIGH OTC	0.023	0.007	54	3.056	**0.039**	MID OTC > HIGH OTC
Winter	IngestPS	Elevation	LOW–MID	0.012	0.004	54	2.931	**0.014**	A > B
			LOW–HIGH	0.019	0.004	54	4.617	**<0.001**	A > C
			MID–HIGH	0.007	0.004	54	1.686	0.220	B = C
Winter	IngestPS	Treatment	Control–OTC	−0.007	0.003	54	−2.085	**0.042**	C < OTC
Summer	Body size	Elevation	LOW–MID	−15.25	1.39	54	−11.004	**<0.001**	LOW < MID
			LOW–HIGH	−6.24	1.39	54	−4.504	**<0.001**	LOW < HIGH
			MID–HIGH	9.01	1.39	54	6.500	**<0.001**	MID > HIGH
Winter	Body size	Elevation	LOW–MID	−3.98	1.37	54	−2.908	**0.014**	LOW < MID
			LOW–HIGH	−8.98	1.37	54	−6.556	**<0.001**	LOW < HIGH

Season	Trait	Factor	Pairwise Comparisons	Estimate	SE	df	t.Ratio	*p* Value	Trend
			MID–HIGH	−4.99	1.37	54	−3.648	**0.002**	MID < HIGH
Summer	Hdisp	Elevation	LOW–MID	−0.108	0.011	54	−9.547	**<0.001**	LOW < MID
			LOW–HIGH	−0.233	0.011	54	−20.637	**<0.001**	LOW < HIGH
			MID–HIGH	−0.125	0.011	54	−11.090	**<0.001**	MID < HIGH
Summer	Hdisp	Treatment	Control–OTC	0.045	0.009	54	4.913	**<0.001**	C > OTC
Summer	Hdisp	Elev:Treatment	LOW C.–MID C.	−0.086	0.016	54	−5.389	**<0.001**	LOW C. < MID C.
			LOW C.–HIGH C.	−0.246	0.016	54	−15.429	**<0.001**	LOW C. < HIGH C.
			LOW C.–LOW OTC	0.051	0.016	54	3.187	**0.028**	LOW C. < LOW OTC
			LOW C.–MID OTC	−0.079	0.016	54	−4.926	**<0.001**	LOW C. < MID OTC
			LOW C.–HIGH OTC	−0.169	0.016	54	−10.569	**<0.001**	LOW C. < HIGH OTC
			MID C.–HIGH C.	−0.160	0.016	54	−10.040	**<0.001**	MID C. < HIGH C.
			MID C.–LOW OTC	0.137	0.016	54	8.576	**<0.001**	MID C. > LOW OTC
			MID C.–MID OTC	0.007	0.016	54	0.464	0.997	MID C. = MID OTC
			MID C.–HIGH OTC	−0.083	0.016	54	−5.180	**<0.001**	MID C. < HIGH OTC
			HIGH C.–LOW OTC	0.297	0.016	54	18.616	**<0.001**	HIGH C. > LOW OTC
			HIGH C.–MID OTC	0.168	0.016	54	10.504	**<0.001**	HIGH C. > MID OTC
			HIGH C.–HIGH OTC	0.078	0.016	54	4.860	**<0.001**	HIGH C. > HIGH OTC
			LOW OTC–MID OTC	−0.130	0.016	54	−8.112	**<0.001**	LOW OTC < MID OTC
			LOW OTC–HIGH OTC	−0.220	0.016	54	−13.756	**<0.001**	LOW OTC < HIGH OTC
			MID OTC–HIGH OTC	−0.090	0.016	54	−5.644	**<0.001**	MID OTC < HIGH OTC
Winter	Hdisp	Elevation	LOW–MID	−0.101	0.019	54	−5.175	**<0.001**	LOW < MID
			LOW–HIGH	−0.188	0.019	54	−9.678	**<0.001**	LOW < HIGH
			MID–HIGH	−0.088	0.019	54	−4.504	**<0.001**	MID < HIGH

Season	**Trait**	**Factor**	**Pairwise Comparisons**	**Estimate**	**SE**	**df**	**t.Ratio**	***p* Value**	**Trend**
Winter	Hdisp	Treatment	Control–OTC	0.057	0.016	54	3.615	**0.001**	C > OTC
Summer	Ldisp	Elevation	LOW–MID	0.034	0.009	54	3.609	**0.002**	LOW > MID
			LOW–HIGH	0.039	0.009	54	4.223	**<0.001**	LOW > HIGH
			MID–HIGH	0.006	0.009	54	0.614	0.813	MID = HIGH
Summer	Ldisp	Treatment	Control–OTC	−0.033	0.008	54	−4.337	**0.000**	C < OTC
Summer	Ldisp	Elev:Treatment	LOW C.–MID C.	0.040	0.013	54	3.010	**0.044**	LOW C. > MID C.
			LOW C.–HIGH C.	0.066	0.013	54	4.990	**<0.001**	LOW C. > HIGH C.
			LOW C.–LOW OTC	−0.011	0.013	54	−0.863	0.954	LOW C. = LOW OTC
			LOW C.–MID OTC	0.016	0.013	54	1.231	0.820	LOW C. = MID OTC
			LOW C.–HIGH OTC	0.002	0.013	54	0.119	1.000	LOW C. = HIGH OTC
			MID C.–HIGH C.	0.026	0.013	54	1.980	0.367	MID C. = HIGH C.
			MID C.–LOW OTC	−0.051	0.013	54	−3.873	**0.004**	MID C. < LOW OTC
			MID C.–MID OTC	−0.023	0.013	54	−1.778	0.488	MID C. = MID OTC
			MID C.–HIGH OTC	−0.038	0.013	54	−2.891	0.059	MID C. = HIGH OTC
			HIGH C.–LOW OTC	−0.077	0.013	54	−5.853	**<0.001**	HIGH C. < LOW OTC
			HIGH C.–MID OTC	−0.049	0.013	54	−3.758	**0.005**	HIGH C. < MID OTC
			HIGH C.–HIGH OTC	−0.064	0.013	54	−4.870	**<0.001**	HIGH C. < HIGH OTC
			LOW OTC–MID OTC	0.028	0.013	54	2.094	0.306	LOW OTC = MID OTC
			LOW OTC–HIGH OTC	0.013	0.013	54	0.982	0.922	LOW OTC = HIGH OTC
			MID OTC–HIGH OTC	−0.015	0.013	54	−1.112	0.874	MID OTC = HIGH OTC
Winter	Ldisp	Treatment	Control–OTC	−0.039	0.013	54	−3.038	**0.004**	C < OTC
Summer	ActivDay	Elevation	LOW–MID	0.124	0.012	54	9.954	**<0.001**	LOW > MID
			LOW–HIGH	0.221	0.012	54	17.829	**<0.001**	LOW > HIGH

Season	Trait	Factor	Pairwise Comparisons	Estimate	SE	df	t.Ratio	*p* Value	Trend
			MID–HIGH	0.098	0.012	54	7.875	**<0.001**	MID > HIGH
Winter	ActivDay	Elevation	LOW–MID	0.072	0.018	54	4.089	**<0.001**	LOW > MID
			LOW–HIGH	0.211	0.018	54	11.986	**<0.001**	LOW > HIGH
			MID–HIGH	0.139	0.018	54	7.897	**<0.001**	MID > HIGH
Winter	ActivDay	Treatment	Control–OTC	0.034	0.014	54	2.395	**0.020**	C > OTC
Summer	ActivNight	Elevation	LOW–MID	−0.034	0.008	54	−4.432	**<0.001**	LOW < MID
			LOW–HIGH	−0.031	0.008	54	−3.939	**0.001**	LOW < HIGH
			MID–HIGH	0.004	0.008	54	0.494	0.875	MID = HIGH
Winter	ActivNight	Elevation	LOW–MID	−0.134	0.011	54	−12.789	**<0.001**	LOW < MID
			LOW–HIGH	−0.182	0.011	54	−17.364	**<0.001**	LOW < HIGH
			MID–HIGH	−0.048	0.011	54	−4.575	**0.000**	MID < HIGH
Summer	ActivTwi	Elevation	LOW–MID	0.096	0.013	54	7.498	**<0.001**	LOW > MID
			LOW–HIGH	0.199	0.013	54	15.613	**<0.001**	LOW > HIGH
			MID–HIGH	0.103	0.013	54	8.115	**<0.001**	MID > HIGH
Winter	ActivTwi	Elevation	LOW–MID	−0.052	0.015	54	−3.417	**0.003**	LOW < MID
			LOW–HIGH	0.038	0.015	54	2.532	**0.037**	LOW > HIGH
			MID–HIGH	0.090	0.015	54	5.949	**<0.001**	MID > HIGH
Winter	ActivTwi	Treatment	Control–OTC	0.043	0.012	54	3.490	**0.001**	C > OTC

Table A3. Results of the ANOVA performed to investigate the effects of the elevation and the treatment on beetles functional traits including the interaction terms (Elev:Treatment) on each CWM variables. Adjusted *p* values are also presented. Significant results are marked in bold. Traits presented are Herbivore; Predator; Fungivore; Detritivore; Body size; High dispersal ability (Hdisp); Diurnal beetles (ActDay); Nocturnal beetles (ActNig); Beetles active during twilight (ActTwi); Black coloration (Black); Blackish coloration (Blackish); Reddish brown coloration (Reddish brown); and the presence of iridescence (Iridescence).

Season	Trophic Guild	Factor	Df	Sum Sq.	Mean Sq.	F Value	Pr(>F)	*p* Adjust
Summer	Herbivore	Elevation	2	1.102	0.551	99.625	**<0.001**	**<0.001**
		Treatment	1	0.003	0.003	0.585	0.448	0.562
		Elev:Treatment	2	0.033	0.016	2.968	0.060	0.104
		Residuals	54	0.299	0.006			
Winter	Herbivore	Elevation	2	0.099	0.049	12.186	**<0.001**	**<0.001**
		Treatment	1	0.003	0.003	0.826	0.367	0.481
		Elev:Treatment	2	0.011	0.006	1.395	0.257	0.385
		Residuals	54	0.219	0.004			
Summer	Predator	Elevation	2	0.071	0.036	10.111	**0.000**	**0.001**
		Treatment	1	0.000	0.000	0.012	0.915	0.969
		Elev:Treatment	2	0.005	0.002	0.666	0.518	0.622
		Residuals	54	0.190	0.004			
Winter	Predator	Elevation	2	0.052	0.026	4.172	**0.021**	**0.041**
		Treatment	1	0.085	0.085	13.641	**0.001**	**0.002**
		Elev:Treatment	2	0.008	0.004	0.627	0.538	0.652
		Residuals	54	0.336	0.006			
Summer	Fungivore	Elevation	2	0.030	0.015	23.373	**<0.001**	**<0.001**
		Treatment	1	0.004	0.004	6.674	**0.013**	**0.032**
		Elev:Treatment	2	0.001	0.001	1.09	0.344	0.468
		Residuals	54	0.034	0.001			
Winter	Fungivore	Elevation	2	0.034	0.017	8.521	**0.001**	**0.002**
		Treatment	1	0.000	0.000	0.116	0.734	0.749
		Elev:Treatment	2	0.001	0.000	0.166	0.848	0.848
		Residuals	54	0.108	0.002			
Summer	Detritivore	Elevation	2	0.001	0.001	3.459	**0.039**	0.074
		Treatment	1	0.000	0.000	0.28	0.599	0.703
		Elev:Treatment	2	0.001	0.000	1.72	0.189	0.283
		Residuals	54	0.010	0.000			
Winter	Detritivore	Elevation	2	0.011	0.006	2.104	0.132	0.217
		Treatment	1	0.077	0.077	29.021	**<0.001**	**<0.001**
		Elev:Treatment	2	0.006	0.003	1.092	0.343	0.460
		Residuals	54	0.143	0.003			

Season	Trophic Guild	Factor	Df	Sum Sq.	Mean Sq.	F Value	Pr(>F)	*p* Adjust
Summer	Body size	Elevation	2	203.390	101.700	116.899	**<0.001**	**<0.001**
		Treatment	1	8.170	8.170	9.390	**0.003**	**0.010**
		Elev:Treatment	2	0.390	0.200	0.225	0.799	0.891
		Residuals	54	46.980	0.870			
Winter	Body size	Elevation	2	133.800	66.900	81.485	**<0.001**	**<0.001**
		Treatment	1	12.700	12.700	15.472	**0.000**	**0.001**
		Elev:Treatment	2	0.990	0.490	0.602	0.551	0.652
		Residuals	54	44.330	0.820			
Summer	Hdisp	Elevation	2	0.032	0.016	10.984	**<0.001**	**<0.001**
		Treatment	1	0.006	0.006	4.210	**0.045**	0.084
		Elev:Treatment	2	0.003	0.002	1.081	0.347	0.468
		Residuals	54	0.079	0.001			
Winter	Hdisp	Elevation	2	0.408	0.204	51.525	**<0.001**	**<0.001**
		Treatment	1	0.006	0.006	1.419	0.239	0.369
		Elev:Treatment	2	0.009	0.005	1.140	0.327	0.460
		Residuals	54	0.214	0.004			
Summer	ActivDay	Elevation	2	0.140	0.070	35.842	**<0.001**	**<0.001**
		Treatment	1	0.010	0.010	5.138	**0.027**	0.055
		Elev:Treatment	2	0.027	0.013	6.841	**0.002**	**0.007**
		Residuals	54	0.105	0.002			
Winter	ActivDay	Elevation	2	0.609	0.305	59.960	**<0.001**	**<0.001**
		Treatment	1	0.042	0.042	8.270	**0.006**	**0.013**
		Elev:Treatment	2	0.037	0.018	3.620	**0.033**	0.061
		Residuals	54	0.274	0.005			
Summer	ActivNight	Elevation	2	0.152	0.076	47.793	**<0.001**	**<0.001**
		Treatment	1	0.005	0.005	3.274	0.076	0.124
		Elev:Treatment	2	0.009	0.005	2.977	0.059	0.104
		Residuals	54	0.086	0.002			
Winter	ActivNight	Elevation	2	1.066	0.533	204.329	**<0.001**	**<0.001**
		Treatment	1	0.015	0.015	5.724	**0.020**	**0.041**
		Elev:Treatment	2	0.027	0.013	5.150	**0.009**	**0.020**
		Residuals	54	0.141	0.003			
Summer	ActivTwi	Elevation	2	0.018	0.009	5.694	**0.006**	**0.015**
		Treatment	1	0.000	0.000	0.163	0.688	0.790
		Elev:Treatment	2	0.002	0.001	0.685	0.509	0.622
		Residuals	54	0.083	0.002			

Season	Trophic Guild	Factor	Df	Sum Sq.	Mean Sq.	F Value	Pr(>F)	*p* Adjust
Winter	ActivTwi	Elevation	2	0.040	0.020	6.274	**0.004**	**0.009**
		Treatment	1	0.097	0.097	30.280	**<0.001**	**<0.001**
		Elev:Treatment	2	0.010	0.005	1.590	0.213	0.340
		Residuals	54	0.174	0.003			
Summer	Black	Elevation	2	2.085	1.042	129.16	**<0.001**	**<0.001**
		Treatment	1	0.138	0.138	17.06	**<0.001**	**<0.001**
		Elev:Treatment	2	0.037	0.018	2.26	0.114	0.176
		Residuals	54	0.436	0.008			
Winter	Black	Elevation	2	0.783	0.391	71.91	**<0.001**	**<0.001**
		Treatment	1	0.125	0.125	22.948	**<0.001**	**<0.001**
		Elev:Treatment	2	0.032	0.016	2.934	0.062	0.109
		Residuals	54	0.294	0.005			
Summer	Blackish	Elevation	2	0.333	0.166	51.586	**<0.001**	**<0.001**
		Treatment	1	0.019	0.019	5.866	**0.019**	**0.041**
		Elev:Treatment	2	0.028	0.014	4.268	**0.019**	**0.041**
		Residuals	54	0.174	0.003			
Winter	Blackish	Elevation	2	0.751	0.376	54.52	**<0.001**	**<0.001**
		Treatment	1	0.002	0.002	0.268	0.607	0.688
		Elev:Treatment	2	0.196	0.098	14.257	**<0.001**	**<0.001**
		Residuals	54	0.372	0.007			
Summer	Reddish brown	Elevation	2	0.586	0.293	61.002	**<0.001**	**<0.001**
		Treatment	1	0.055	0.055	11.486	**0.001**	**0.004**
		Elev:Treatment	2	0.013	0.006	1.317	0.276	0.398
		Residuals	54	0.259	0.005			
Winter	Reddish brown	Elevation	2	0.003	0.001	0.353	0.704	0.733
		Treatment	1	0.183	0.183	43.31	**<0.001**	**<0.001**
		Elev:Treatment	2	0.065	0.032	7.664	**0.001**	**0.003**
		Residuals	54	0.228	0.004			
Summer	Iridescence	Elevation	2	0.073	0.036	24.331	**<0.001**	**<0.001**
		Treatment	1	0.010	0.010	6.604	**0.013**	**0.032**
		Elev:Treatment	2	0.009	0.004	2.882	0.065	0.109
		Residuals	54	0.080	0.001			
Winter	Iridescence	Elevation	2	0.456	0.228	89.82	**<0.001**	**<0.001**
		Treatment	1	0.022	0.022	8.679	**0.005**	**0.012**
		Elev:Treatment	2	0.019	0.009	3.71	**0.031**	0.058
		Residuals	54	0.137	0.003			

Table A4. Results of the post hoc pairwise comparisons performed on the different beetles' traits when the ANOVA models were significant. Significant results are marked in bold. Traits presented are Herbivore; Predator; Fungivore; Detritivore; Body size; High dispersal ability (Hdisp); Diurnal beetles (ActDay); Nocturnal beetles (ActNig); Beetles active during twilight (ActTwi); Black coloration (Black); Blackish coloration (Blackish), Reddish-brown coloration (Reddish brown); and the presence of iridescence (Iridescence). Factors presented are the elevation, the treatment, and their interaction (Elev:Treatment). Low-elevation field (LOW); Middle-elevation field (MID); High-elevation field (HIGH); Control plots at low elevation (LOW C.); OTCs at low elevation (LOW OTC); Control plots at middle elevation (MID C.); OTCs at middle elevation (MID OTC); Control plots at high elevation (HIGH C.); OTCs at high elevation (HIGH OTC). See corresponding box plot in the main text in Figure 4.

Season	**Trait**	**Factor**	**Pairwise Comparisons**	**Estimate**	**SE**	**df**	**t.Ratio**	***p* Value**	**Trend**
Summer	Herbivore	Elevation	LOW–MID	−0.275	0.024	54	−11.692	**<0.0001**	LOW < MID
			LOW–HIGH	0.024	0.024	54	1.004	0.578	LOW = HIGH
			MID–HIGH	0.299	0.024	54	12.695	**<0.0001**	MID > HIGH
Winter	Herbivore	Elevation	LOW–MID	0.099	0.020	54	4.896	**<0.0001**	LOW > MID
			LOW–HIGH	0.038	0.020	54	1.903	0.148	LOW = HIGH
			MID–HIGH	−0.060	0.020	54	−2.994	**0.011**	MID < HIGH
Summer	Predator	Elevation	LOW–MID	−0.084	0.019	54	−4.466	**<0.0001**	LOW < MID
			LOW–HIGH	−0.050	0.019	54	−2.686	0.026	LOW = HIGH
			MID–HIGH	0.033	0.019	54	1.780	0.186	MID = HIGH
Winter	Predator	Elevation	LOW–MID	−0.066	0.025	54	−2.641	**0.029**	LOW < MID
			LOW–HIGH	−0.058	0.025	54	−2.334	0.060	LOW = HIGH
			MID–HIGH	0.008	0.025	54	0.307	0.949	MID = HIGH
Winter	Predator	Treatment	Control–OTC	−0.075	0.020	54	−3.693	**0.001**	C < OTC
Summer	Fungivore	Elevation	LOW–MID	0.053	0.008	54	6.585	**<0.0001**	LOW > MID
			LOW–HIGH	0.014	0.008	54	1.700	0.215	LOW = HIGH
			MID–HIGH	−0.039	0.008	54	−4.885	**<0.0001**	MID < HIGH
Summer	Fungivore	Treatment	Control–OTC	−0.017	0.007	54	−2.583	**0.013**	C < OTC
Winter	Fungivore	Elevation	LOW–MID	0.034	0.014	54	2.395	0.052	LOW = MID
			LOW–HIGH	0.058	0.014	54	4.109	**<0.0001**	LOW > HIGH

Season	**Trait**	**Factor**	**Pairwise Comparisons**	**Estimate**	**SE**	**df**	**t.Ratio**	***p* Value**	**Trend**
			MID–HIGH	0.024	0.014	54	1.714	0.209	MID = HIGH
Summer	Detritivore	Elevation	LOW–MID	0.006	0.004	54	1.493	0.302	LOW = MID
			LOW–HIGH	−0.005	0.004	54	−1.129	0.501	LOW = HIGH
			MID–HIGH	−0.011	0.004	54	−2.622	**0.030**	MID < HIGH
Winter	Detritivore	Treatment	Control–OTC	0.072	0.013	54	5.387	**<0.0001**	C > OTC
Summer	Body size	Elevation	LOW–MID	−4.218	0.295	54	−14.300	**<0.001**	LOW < MID
			LOW–HIGH	−0.726	0.295	54	−2.461	**0.044**	LOW < HIGH
			MID–HIGH	3.492	0.295	54	11.838	**<0.001**	MID > HIGH
Summer	Body size	Treatment	Control–OTC	−0.738	0.241	54	−3.064	**0.003**	C < OTC
Winter	Body size	Elevation	LOW–MID	−3.233	0.287	54	−11.285	**<0.001**	LOW < MID
			LOW–HIGH	−0.136	0.287	54	−0.473	0.884	LOW = HIGH
			MID–HIGH	3.098	0.287	54	10.811	**<0.001**	MID > HIGH
Winter	Body size	Treatment	Control–OTC	−0.920	0.234	54	−3.933	**<0.001**	C < OTC
Summer	Hdsip	Elevation	LOW–MID	−0.034	0.012	54	−2.782	**0.020**	LOW < MID
			LOW–HIGH	0.023	0.012	54	1.876	0.155	LOW = HIGH
			MID–HIGH	0.056	0.012	54	4.658	**<0.001**	MID > HIGH
Summer	Hdsip	Treatment	Control–OTC	0.020	0.010	54	2.052	**0.045**	C > OTC
Winter	Hdsip	Elevation	LOW–MID	−0.138	0.020	54	−6.954	**<0.001**	LOW < MID
			LOW–HIGH	−0.197	0.020	54	−9.882	**<0.001**	LOW < HIGH
			MID–HIGH	−0.058	0.020	54	−2.928	**0.014**	MID < HIGH
Summer	ActivDay	Elevation	LOW–MID	0.101	0.014	54	7.213	**<0.001**	LOW > MID
			LOW–HIGH	0.104	0.014	54	7.446	**<0.001**	LOW > HIGH
			MID–HIGH	0.003	0.014	54	0.232	0.971	MID = HIGH

Season	**Trait**	**Factor**	**Pairwise Comparisons**	**Estimate**	**SE**	**df**	**t.Ratio**	***p* Value**	**Trend**
Summer	ActivDay	Treatment	Control–OTC	−0.026	0.011	54	−2.267	**0.027**	C < OTC
Summer	ActivDay	Elev:Treatment	LOW C.–MID C.	0.050	0.020	54	2.511	0.139	LOW C. = MID C.
			LOW C.–HIGH C.	0.085	0.020	54	4.289	**0.001**	LOW C. > HIGH C.
			LOW C.–LOW OTC	−0.073	0.020	54	−3.686	**0.007**	LOW C. < LOW OTC
			LOW C.–MID OTC	0.079	0.020	54	4.005	**0.003**	LOW C. > MID OTC
			LOW C.–HIGH OTC	0.050	0.020	54	2.555	0.127	LOW C. = HIGH OTC
			MID C.–HIGH C.	0.035	0.020	54	1.778	0.488	MID C. = HIGH C.
			MID C.–LOW OTC	−0.122	0.020	54	−6.197	**<0.001**	MID C. < LOW OTC
			MID C.–MID OTC	0.030	0.020	54	1.493	0.670	MID C. = MID OTC
			MID C.–HIGH OTC	0.001	0.020	54	0.044	1.000	MID C. = HIGH OTC
			HIGH C.–LOW OTC	−0.158	0.020	54	−7.975	**<0.001**	HIGH C. < LOW OTC
			HIGH C.–MID OTC	−0.006	0.020	54	−0.284	1.000	HIGH C. = MID OTC
			HIGH C.–HIGH OTC	−0.034	0.020	54	−1.734	0.516	HIGH C. = HIGH OTC
			LOW OTC–MID OTC	0.152	0.020	54	7.690	**<0.001**	LOW OTC > MID OTC
			LOW OTC–HIGH OTC	0.123	0.020	54	6.241	**<0.001**	LOW OTC > HIGH OTC
			MID OTC–HIGH OTC	−0.029	0.020	54	−1.449	0.697	MID OTC = HIGH OTC
Winter	ActivDay	Elevation	LOW–MID	0.142	0.023	54	6.309	**<0.001**	LOW > MID
			LOW–HIGH	0.246	0.023	54	10.906	**<0.001**	LOW > HIGH
			MID–HIGH	0.104	0.023	54	4.597	**<0.001**	MID > HIGH
Winter	ActivDay	Treatment	Control–OTC	0.053	0.018	54	2.876	**0.006**	C > OTC
Winter	ActivDay	Elev:Treatment	LOW C.–MID C.	0.111	0.032	54	3.470	**0.013**	LOW C. > MID C.
			LOW C.–HIGH C.	0.185	0.032	54	5.810	**<0.001**	LOW C. > HIGH C.
			LOW C.–LOW OTC	−0.009	0.032	54	−0.268	1.000	LOW C. = LOW OTC

Season	Trait	Factor	Pairwise Comparisons	Estimate	SE	df	t.Ratio	*p* Value	Trend
			LOW C.–MID OTC	0.165	0.032	54	5.184	**<0.001**	LOW C. > MID OTC
			LOW C.–HIGH OTC	0.298	0.032	54	9.345	**<0.001**	LOW C. > HIGH OTC
			MID C.–HIGH C.	0.075	0.032	54	2.340	0.197	MID C. = HIGH C.
			MID C.–LOW OTC	−0.119	0.032	54	−3.738	**0.006**	MID C. < LOW OTC
			MID C.–MID OTC	0.055	0.032	54	1.714	0.529	MID C. = MID OTC
			MID C.–HIGH OTC	0.187	0.032	54	5.875	**<0.001**	MID C. > HIGH OTC
			HIGH C.–LOW OTC	−0.194	0.032	54	−6.078	**<0.001**	HIGH C. < LOW OTC
			HIGH C.–MID OTC	−0.020	0.032	54	−0.626	0.989	HIGH C. = MID OTC
			HIGH C.–HIGH OTC	0.113	0.032	54	3.536	**0.010**	HIGH C. > HIGH OTC
			LOW OTC–MID OTC	0.174	0.032	54	5.452	**<0.001**	LOW OTC > MID OTC
			LOW OTC–HIGH OTC	0.306	0.032	54	9.614	**<0.001**	LOW OTC > HIGH OTC
			MID OTC–HIGH OTC	0.133	0.032	54	4.161	**0.002**	MID OTC > HIGH OTC
Summer	ActivNight	Elevation	LOW–MID	−0.105	0.013	54	−8.334	**<0.001**	LOW < MID
			LOW–HIGH	−0.108	0.013	54	−8.594	**<0.001**	LOW < HIGH
			MID–HIGH	−0.003	0.013	54	−0.260	0.964	MID = HIGH
Winter	ActivNight	Elevation	LOW–MID	−0.209	0.016	54	−12.933	**<0.001**	LOW < MID
			LOW–HIGH	−0.322	0.016	54	−19.922	**<0.001**	LOW < HIGH
			MID–HIGH	−0.113	0.016	54	−6.988	**<0.001**	MID < HIGH
Winter	ActivNight	Treatment	Control–OTC	0.032	0.013	54	2.392	**0.020**	C > OTC
Winter	ActivNight	Elev:Treatment	LOW C.–MID C. -	0.168	0.023	54	−7.351	**<0.001**	LOW C. < MID C. -
			LOW C.–HIGH C.	−0.274	0.023	54	−11.987	**<0.001**	LOW C. < HIGH C.
			LOW C.–LOW OTC	0.091	0.023	54	3.978	**0.003**	LOW C. > LOW OTC
			LOW C.–MID OTC	−0.159	0.023	54	−6.962	**<0.001**	LOW C. < MID OTC

Season	**Trait**	**Factor**	**Pairwise Comparisons**	**Estimate**	**SE**	**df**	**t.Ratio**	***p* Value**	**Trend**
			LOW C.–HIGH OTC	−0.279	0.023	54	−12.209	**<0.001**	LOW C. < HIGH OTC
			MID C.–HIGH C.	−0.106	0.023	54	−4.636	**<0.001**	MID C. < HIGH C.
			MID C.–LOW OTC	0.259	0.023	54	11.328	**<0.001**	MID C. > LOW OTC
			MID C.–MID OTC	0.009	0.023	54	0.389	0.999	MID C. = MID OTC
			MID C.–HIGH OTC	−0.111	0.023	54	−4.859	**<0.001**	MID C. < HIGH OTC
			HIGH C.–LOW OTC	0.365	0.023	54	15.964	**<0.001**	HIGH C. > LOW OTC
			HIGH C.–MID OTC	0.115	0.023	54	5.025	**0.000**	HIGH C. > MID OTC
			HIGH C.–HIGH OTC	−0.005	0.023	54	−0.223	1.000	HIGH C. = HIGH OTC
			LOW OTC–MID OTC	−0.250	0.023	54	−10.940	**<0.001**	LOW OTC < MID OTC
			LOW OTC–HIGH OTC	−0.370	0.023	54	−16.187	**<0.001**	LOW OTC < HIGH OTC
			MID OTC–HIGH OTC	−0.120	0.023	54	−5.247	**<0.001**	MID OTC < HIGH OTC
Summer	ActivTwi	Elevation	LOW–MID	0.027	0.012	54	2.156	0.088	LOW = MID
			LOW–HIGH	0.041	0.012	54	3.326	**0.005**	LOW > HIGH
			MID–HIGH	0.015	0.012	54	1.171	0.476	MID = HIGH
Winter	ActivTwi	Elevation	LOW–MID	−0.050	0.018	54	−2.782	**0.020**	LOW < MID
			LOW–HIGH	−0.059	0.018	54	−3.290	**0.005**	LOW < HIGH
			MID–HIGH	−0.009	0.018	54	−0.507	0.868	MID = HIGH
Winter	ActivTwi	Treatment	Control–OTC	0.081	0.015	54	5.503	**<0.001**	C > OTC
Summer	Black	Elevation	LOW–MID	−0.452	0.028	54	−15.912	**<0.001**	LOW < MID
			LOW–HIGH	−0.170	0.028	54	−5.997	**<0.001**	LOW < HIGH
			MID–HIGH	0.282	0.028	54	9.915	**<0.001**	MID > HIGH
Summer	Black	Treatment	Control–OTC	−0.096	0.023	54	−4.130	**0.000**	C < OTC
Winter	Black	Elevation	LOW–MID	−0.140	0.023	54	−5.993	**<0.001**	LOW < MID

Season	Trait	Factor	Pairwise Comparisons	Estimate	SE	df	t.Ratio	*p* Value	Trend
			LOW–HIGH	0.140	0.023	54	5.999	**<0.001**	LOW > HIGH
			MID–HIGH	0.280	0.023	54	11.993	**<0.001**	MID > HIGH
Winter	Black	Treatment	Control–OTC	−0.091	0.019	54	−4.790	**<0.001**	C < OTC
Summer	Blackish	Elevation	LOW–MID	0.181	0.018	54	10.088	**<0.001**	LOW > MID
			LOW–HIGH	0.072	0.018	54	4.021	**0.001**	LOW > HIGH
			MID–HIGH	−0.109	0.018	54	−6.067	**<0.001**	MID < HIGH
Summer	Blackish	Treatment	Control–OTC	0.036	0.015	54	2.422	**0.019**	C = OTC
Summer	Blackish	Elev:Treatment	LOW C.–MID C.	0.234	0.025	54	9.198	**<0.001**	LOW C. > MID C.
			LOW C.–HIGH C.	0.097	0.025	54	3.805	**0.005**	LOW C. > HIGH C.
			LOW C.–LOW OTC	0.087	0.025	54	3.415	**0.015**	LOW C. > LOW OTC
			LOW C.–MID OTC	0.216	0.025	54	8.485	**<0.001**	LOW C. > MID OTC
			LOW C.–HIGH OTC	0.135	0.025	54	5.298	**<0.001**	LOW C. > HIGH OTC
			MID C.–HIGH C.	−0.137	0.025	54	−5.393	**<0.001**	MID C. < HIGH C.
			MID C.–LOW OTC	−0.147	0.025	54	−5.783	**<0.001**	MID C. < LOW OTC
			MID C.–MID OTC	−0.018	0.025	54	−0.713	0.980	MID C. = MID OTC
			MID C.–HIGH OTC	−0.099	0.025	54	−3.900	**0.004**	MID C. < HIGH OTC
			HIGH C.–LOW OTC	−0.010	0.025	54	−0.389	0.999	HIGH C. = LOW OTC
			HIGH C.–MID OTC	0.119	0.025	54	4.680	**<0.001**	HIGH C. > MID OTC
			HIGH C.–HIGH OTC	0.038	0.025	54	1.493	0.670	HIGH C. = HIGH OTC
			LOW OTC–MID OTC	0.129	0.025	54	5.069	**<0.001**	LOW OTC > MID OTC
			LOW OTC–HIGH OTC	0.048	0.025	54	1.882	0.424	LOW OTC = HIGH OTC
			MID OTC–HIGH OTC	−0.081	0.025	54	−3.187	**0.027**	MID OTC < HIGH OTC
Winter	Blackish	Elevation	LOW–MID	0.084	0.026	54	3.181	**0.007**	LOW > MID

Season	Trait	Factor	Pairwise Comparisons	Estimate	SE	df	t.Ratio	*p* Value	Trend
			LOW–HIGH	−0.184	0.026	54	−7.023	**<0.001**	LOW < HIGH
			MID–HIGH	−0.268	0.026	54	−10.204	**<0.001**	MID < HIGH
Winter	Blackish	Elev:Treatment	LOW C.–MID C.	0.091	0.037	54	2.457	0.155	LOW C. = MID C.
			LOW C.–HIGH C.	−0.059	0.037	54	−1.597	0.604	LOW C. = HIGH C.
			LOW C.–LOW OTC	0.077	0.037	54	2.086	0.310	LOW C. = LOW OTC
			LOW C.–MID OTC	0.153	0.037	54	4.128	**0.002**	LOW C. > MID OTC
			LOW C.–HIGH OTC	−0.232	0.037	54	−6.249	**<0.001**	LOW C. < HIGH OTC
			MID C.–HIGH C.	−0.151	0.037	54	−4.054	**0.002**	MID C. < HIGH C.
			MID C.–LOW OTC	−0.014	0.037	54	−0.372	0.999	MID C. = LOW OTC
			MID C.–MID OTC	0.062	0.037	54	1.670	0.557	MID C. = MID OTC
			MID C.–HIGH OTC	−0.323	0.037	54	−8.706	**<0.001**	MID C. < HIGH OTC
			HIGH C.–LOW OTC	0.137	0.037	54	3.683	**0.007**	HIGH C. > LOW OTC
			HIGH C.–MID OTC	0.213	0.037	54	5.724	**<0.001**	HIGH C. > MID OTC
			HIGH C.–HIGH OTC	−0.173	0.037	54	−4.652	**0.000**	HIGH C. < HIGH OTC
			LOW OTC–MID OTC	0.076	0.037	54	2.042	0.333	LOW OTC = MID OTC
			LOW OTC–HIGH OTC	−0.309	0.037	54	−8.335	**<0.001**	LOW OTC < HIGH OTC
			MID OTC–HIGH OTC	−0.385	0.037	54	−10.376	**<0.001**	MID OTC < HIGH OTC
Summer	Reddish brown	Field	LOW–MID	0.241	0.022	54	11.003	**<0.001**	LOW > MID
			LOW–HIGH	0.102	0.022	54	4.665	**0.000**	LOW > HIGH
			MID–HIGH	−0.139	0.022	54	−6.338	**<0.001**	MID < HIGH
Summer	Reddish brown	Treatment	Control–OTC	0.061	0.018	54	3.389	**0.001**	C > OTC
Winter	Reddish brown	Treatment	Control–OTC	0.110	0.017	54	6.581	**<0.001**	C > OTC
Winter	Reddish brown	Elev:Treatment	LOW C.–MID C.	0.014	0.029	54	0.469	0.997	LOW C. = Control

Season	Trait	Factor	Pairwise Comparisons	Estimate	SE	df	t.Ratio	*p* Value	Trend
			LOW C.–HIGH C.	−0.076	0.029	54	−2.618	0.111	LOW C. = HIGH C.
			LOW C.–LOW OTC	0.082	0.029	54	2.809	0.071	LOW C. = LOW OTC
			LOW C.–MID OTC	0.062	0.029	54	2.131	0.287	LOW C. = MID OTC
			LOW C.–HIGH OTC	0.125	0.029	54	4.309	**0.001**	LOW C. < HIGH OTC
			MID C.–HIGH C.	−0.090	0.029	54	−3.086	0.036	MID C. = HIGH C.
			MID C.–LOW OTC	0.068	0.029	54	2.341	0.196	MID C. = LOW OTC
			MID C.–MID OTC	0.048	0.029	54	1.663	0.562	MID C. = MID OTC
			MID C.–HIGH OTC	0.112	0.029	54	3.841	**0.004**	MID C. > HIGH OTC
			HIGH C.–LOW OTC	0.158	0.029	54	5.427	**<0.001**	HIGH C. > LOW OTC
			HIGH C.–MID OTC	0.138	0.029	54	4.749	**0.000**	HIGH C. > MID OTC
			HIGH C.–HIGH OTC	0.201	0.029	54	6.927	**<0.001**	HIGH C. > HIGH OTC
			LOW OTC–MID OTC	−0.020	0.029	54	−0.678	0.984	LOW OTC = MID OTC
			LOW OTC–HIGH OTC	0.044	0.029	54	1.500	0.666	LOW OTC = HIGH OTC
			MID OTC–HIGH OTC	0.063	0.029	54	2.178	0.265	MID OTC = HIGH OTC
Summer	Iridescence	Field	LOW–MID	0.010	0.012	54	0.817	0.694	LOW = MID
			LOW–HIGH	0.078	0.012	54	6.408	**<0.001**	LOW > HIGH
			MID–HIGH	0.068	0.012	54	5.591	**<0.001**	MID > HIGH
Summer	Iridescence	Treatment	Control–OTC	−0.026	0.010	54	−2.570	**0.013**	OTC > C
Winter	Iridescence	Field	LOW–MID	0.114	0.016	54	7.178	**<0.001**	LOW > MID
			LOW–HIGH	0.213	0.016	54	13.391	**<0.001**	LOW > HIGH
			MID–HIGH	0.099	0.016	54	6.214	**<0.001**	MID > HIGH
Winter	Iridescence	Treatment	Control–OTC	−0.038	0.013	54	−2.946	**0.005**	C < OTC
Winter	Iridescence	Elev:Treatment	LOW C.–MID C.	0.085	0.023	54	3.767	**0.005**	LOW C. > MID C.

Season	Trait	Factor	Pairwise Comparisons	Estimate	SE	df	t.Ratio	*p* Value	Trend
			LOW C.–HIGH C.	0.171	0.023	54	7.591	**<0.001**	LOW C. > HIGH C.
			LOW C.–LOW OTC	−0.086	0.023	54	−3.826	**0.004**	LOW C. < LOW OTC
			LOW C.–MID OTC	0.058	0.023	54	2.559	0.126	LOW C. = MID OTC
			LOW C.–HIGH OTC	0.170	0.023	54	7.522	**<0.001**	LOW C. > HIGH OTC
			MID C.–HIGH C.	0.086	0.023	54	3.824	**0.004**	MID C. > HIGH C.
			MID C.–LOW OTC	−0.171	0.023	54	−7.592	**<0.001**	MID C. < LOW OTC
			MID C.–MID OTC	−0.027	0.023	54	−1.208	0.831	MID C. = MID OTC
			MID C.–HIGH OTC	0.085	0.023	54	3.755	**0.005**	MID C. > HIGH OTC
			HIGH C.–LOW OTC	−0.257	0.023	54	−11.416	**<0.001**	HIGH C. < LOW OTC
			HIGH C.–MID OTC	−0.113	0.023	54	−5.032	**<0.001**	HIGH C. < MID OTC
			HIGH C.–HIGH OTC	−0.002	0.023	54	−0.069	1.000	HIGH C. = HIGH OTC
			LOW OTC–MID OTC	0.144	0.023	54	6.384	**<0.001**	LOW OTC > MID OTC
			LOW OTC–HIGH OTC	0.256	0.023	54	11.347	**<0.001**	LOW OTC > HIGH OTC
			MID OTC–HIGH OTC	0.112	0.023	54	4.963	**<0.001**	MID OTC > HIGH OTC

4.7. References

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Chapter 5. Assessing Temperature-Induced Changes in Arthropod Communities Over One Year Using Open Top Chambers: A Comparative Analysis

Abstract

Understanding how rising temperatures induced by climate change affect biodiversity and ecosystem function is of particular interest in fragile island environments. Terceira Island in the Azorean Archipelago (Portugal), located in the mid-Atlantic Ocean, was used for an *in situ* experiment to investigate the effects of simulated increased temperatures on arthropod diversity and grasses in intensive pastures. Over a one-year interval, we studied the impact of Open Top Chambers (OTCs) on arthropod community structure. Different diversity indices and multivariate models were employed to investigate the relationships between treatments, grass biomass, and arthropod communities. While the treatment did not significantly affect grass biomass, we observed a temporal increase in the three first Hill numbers (Species diversity, exponential Shannon and inverse Simpson diversity indices), indicating greater diversity and less species dominance over time. Species richness was also positively influenced by the grass biomass. The dbRDA analysis revealed a significant influence of OTCs on community composition, with certain species exhibiting a slight preference for the OTCs. These findings highlight the complexity of ecological responses to climate change, emphasizing the potential for long-term trends and the need for further investigation into the complex interactions between temperature, grass biomass, and arthropod communities.

Keywords: Arthropods, Temporal trends, Open Top Chambers, Global warming, Intensive grassland.

5.1. Introduction

Climate change represents one of the most urgent global challenges, with profound impacts on ecosystems, biodiversity, and agricultural productivity worldwide (Abhijeet et al., 2023; Hartmann et al., 2022; Portner et al., 2022). Rising temperatures, altered precipitation patterns, and increased frequency of extreme weather events are reshaping both natural and managed ecosystems (Papalexiou et al., 2019). These effects are particularly pronounced in oceanic archipelagos such as the Azores (Portugal) (Azevedo et al., 1998; PRAC, 2017; Santos et al., 2004), where unique climatic conditions foster distinct ecosystems like the Laurisilva forests (Gaspar et al., 2014; Pozsgai et al., 2024). Oceanic archipelagos are indeed particularly vulnerable to the effects of climate change due to their isolation and distinct environmental conditions (Harter et al., 2015; Taylor et al., 2016). The interplay of geographical isolation, limited land area, and a high level of endemism renders island ecosystems especially sensitive to environmental changes (Duvat et al., 2017; Petzold et al., 2019). Variations in temperature and precipitation can significantly impact island biodiversity, particularly for species inhabiting specialized or restricted habitats (Whittaker et al., 2007).

Additionally, islands face heightened risks from rising sea levels, increasingly frequent and severe storms, and changing ocean currents, all of which can exacerbate the direct impacts of climate change on terrestrial ecosystems (Harter et al., 2015). These climatic shifts pose threats not only to the survival of native species but also to the ecological processes that underpin these delicate ecosystems. For instance, changes in rainfall patterns can affect relative air humidity and soil moisture, which are essential for the overall vitality of hyperhumid island ecosystems (Fernández-Palacios et al., 2021). Climate-induced shifts in temperature might affect different ecosystems, particularly in regions where agricultural sustainability and biodiversity conservation are intertwined as it is the case in the archipelago of the Azores.

Nowadays, the Azores' agricultural landscapes, including pastures, are of great importance as they are crucial for livestock production and therefore for the local economy (Almeida et al., 2021; Boval et al., 2012; Massot, 2015). Pastures serve as an essential resource for livestock, but they are also dynamic systems that respond to environmental changes (Henry et al., 2018; Soussana et al., 2010). Indeed, interactions between plant communities and their associated arthropod fauna are crucial for maintaining ecosystem functions (Joern et al., 2013). Of particular interest in these ecosystems, therefore, are arthropod organisms that contribute significantly to essential ecosystem functions such as pollination, nutrient cycling and pest regulation (Nagy et al., 2020; Solascasas et al., 2022; Teixeira et al., 2023; Verma et al., 2023). As a key component of the food web, arthropods are highly sensitive to environmental changes, making them valuable bioindicators for assessing ecosystem health (Gerlach et al., 2013; Harvey & Dong, 2023).

Arthropods are particularly vulnerable to shifts in temperature and habitat structure (Bale et al., 2002; Borges & Brown, 2004; Clark et al., 2004; González-Tokman et al., 2020; Meijer et al., 2011; Oyarzabal et al., 2024; Schmidt et al., 2005; Zarnetske et al., 2017). It is therefore key to understand the responses of arthropod communities to climate change in grasslands to build knowledge and advise stakeholders on future land management (risk assessment, grass selection, pasture elevation). Such studies are not yet common in the Azores, indicating an urgent need to fill this gap, as this research brings new knowledge to the field in the region.

Thus, this study employs Open Top Chambers (OTCs) in intensive pastures to simulate increased temperatures *in situ* and assesses their warming impact on arthropod communities across a one-year interval experimental period on the island of Terceira (Azores, Portugal). OTCs are practical and effective tools in ecological research for simulating temperature increases, providing a controlled environment that mimics realistic warming effects while minimizing interference with other environmental variables. Their accessibility and simplicity make them especially useful for long-term field experiments studying the ecological impacts of climate change (Hollister et al., 2023). By collecting data from the first and second years of the study, we aim to gain insight into immediate changes in arthropod community composition and shed light on rapid ecological responses to changing environmental conditions.

The aims of the study are:

i) to assess whether changes in arthropod community structure and species composition occur after one year of elevated temperature within OTCs.

ii) to identify whether temperature or grass biomass, or the combination of these, play a determining role in these potential changes.

5.2. Material and Methods

5.2.1. Study Area

The study took place on two intensively managed pastures located on Terceira Island, part of the Azores archipelago in Portugal (between 38°37′ N to 38°48′ N in latitude and 27°02′ W to 27°23′ W in longitude) during the boreal summers of 2020 and 2021. The island's area is 402 km^2 and its maximum elevation is 1,023 m. The two study sites are located at middle (301 m, above sea level) and high elevations (386 m, above sea level). The specific coordinates for each site are as follows: mid-elevation at 38.7016° N, −27.3258° W and high elevation at 38.6978° N, −27.1701° W (Figure 1). The two locations are spatially independent and classified as intensive pastures, with the mid-altitude field primarily covered by Italian ryegrass (*Lolium multiflorum* Lam., Poaceae) and high elevation field dominated by common velvet grass (*Holcus lanatus* L., Poaceae).

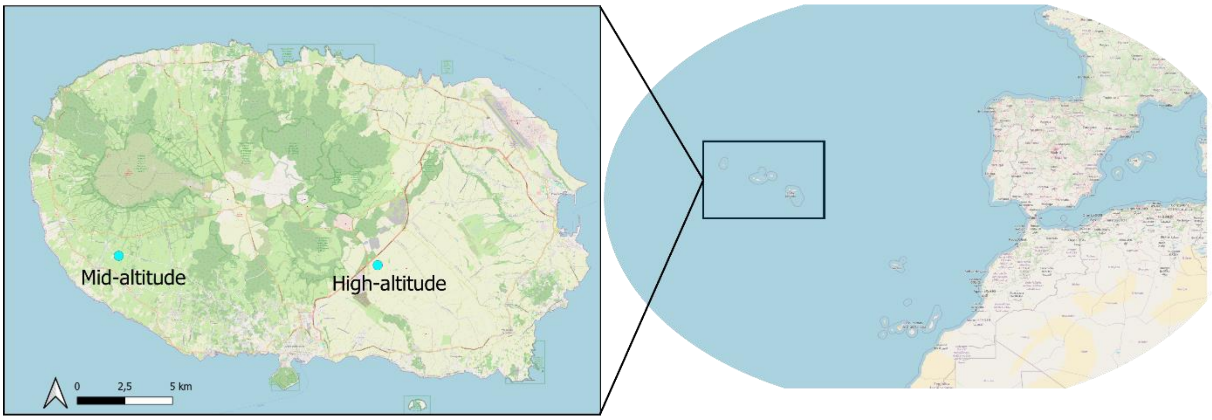

Figure 1. Location of the archipelago of the Azores, the island of Terceira as well as the two experimental fields.

5.2.2. Experimental Design

The field experiment was conducted using OTCs. OTCs are constructed with panels that act as wind barriers, minimizing heat loss through convection. Their open-top design allows rain to enter and air to circulate freely, creating small air vortices or eddies (Hollister et al., 2023).

In each field, twenty 1 × 1 m plots were arranged in a grid, spaced 1.5 m apart. Ten plots were randomly selected to serve as controls, while the remaining ten were enclosed by OTCs. The OTCs were designed to cover the 1 × 1 m plots and included an additional 25 cm border around each plot. This buffer zone allowed easy access for maintenance and monitoring while preventing damage to the plots. It also facilitated the placement of pitfall traps at each outer corner of the plots, all within the OTC boundaries. Additionally, the OTCs were elevated approximately 5 cm above the ground, allowing crawling arthropods to move freely throughout the sampling area. To track temperature differences, data loggers (Easy Log: EL-USB-2) were placed both inside the OTC plots and in the control plots. Over the two years, the average temperature in the OTCs was 1.2°C higher than in the control plots.

5.2.3. Arthropod Sampling and Identification

This research focused on arthropod communities found in intensively managed pastures. Since OTCs can act as barriers for flying insects and introduce bias, the study targeted ground-dwelling arthropods. Pitfall traps, which are designed to capture epigeal organisms crawling on the soil surface, were used for sampling. Four traps were placed at the outer corners of each plot, totaling 80 traps per field. In OTC-enclosed plots, the traps were set in the 25 cm margin surrounding each plot (see also the Experimental Design section). The traps consisted of 330 ml plastic cups, ca. 12 cm deep and 8 cm in diameter, filled with a solution of 20% ethylene glycol (car coolant) and a few drops of soap to break the surface tension. To protect the traps from rain, they were covered with plastic dishes raised on small metal supports, which left the trap openings accessible to arthropods. All collected specimens were preserved in 96% ethanol.

Catch data from one of the four traps in each plot were used for this analysis. Arthropod sampling was conducted in the summers of 2020 and 2021, with traps left open for 14 days. An exception occurred in the mid-altitude field during the summer of 2020, when traps were only functioning for 13 days. In this case, arthropod abundance was extrapolated to 14 days based on data from other traps, though species richness was not extrapolated. For data analysis, only adult specimens were considered.

All sampled arthropods were sorted and, where possible, identified to species level for the following groups: Arachnida (including Araneae, Opiliones, and Pseudoscorpiones), Diplopoda, Chilopoda, and Insecta (excluding Diptera and Hymenoptera, but including Formicidae), and Lepidoptera). To each specimen that could not be identified to the species level, a morphospecies code was assigned. Initial sorting and identification were performed by the first author (SW) and a team of students acting as parataxonomists (see Acknowledgements), followed by verification by a taxonomic expert (PAVB). Species names and colonization status were based on the most recent checklist of Azorean arthropods (Borges et al., 2022). Data analysis focused on the activity-density of adult individuals identified to the morphospecies level. While earlier studies on Azorean arthropods (e.g., Cardoso et al., 2009) included juvenile spiders, this study excluded them due to the dominance of Erigoninae linyphiid spiders, which made the identification challenging.

All specimens are preserved and stored in the Dalberto Teixeira Pombo (DTP) Collection at the University of the Azores on Terceira Island. Data from 2020 are publicly accessible in Wallon, Melo, et al., (2023), available at: http://ipt.gbif.pt/ipt/resource?r=pasturclim_otc. 2021 data are available on request.

5.2.4. Grass sampling

The experimental plots were established for the entire duration of the experiment. In 2020 and 2021, the grasses in each plot were manually harvested in each season, after the collection of pitfall traps. For each plot, the freshly harvested grasses were weighed green and then dried in a drying oven at 60°C to a constant weight (i.e. when all the water in the grasses had evaporated). The analysis was carried out using the dry weight of the grass, which will be referred to as "grasses" or “grass biomass” henceforth.

5.2.5. Data Analysis

The analysis of arthropod abundance and its relationship with environmental factors was conducted in R (version 4.2.3). The arthropod abundance data, encompassing two summer seasons (2020 and 2021) and two fields (mid and high-altitude), was used for the analysis.

We analyzed the diversity and community composition of arthropods using a series of statistical models and visualizations. The analysis aimed to explore the relationships between arthropod diversity, environmental factors, and treatment effects across two years.

First, to examine the relationship between grasses and treatment, a generalized mixed model was constructed using the glmer() function in R, using gaussian family and log link. This model evaluated the significance of the treatment (Control vs. OTCs) on the biomass, treating it as the response variable. The year accounted for a random effect. The results enabled us to incorporate grasses as an independent response variable, distinct from the treatment effects.

To quantify the diversity of arthropod assemblages, we employed the iNEXT package, which estimates the first three Hill numbers ($q = 0$, 1, and 2) for multiple diversity indices. Hill numbers (Legendre et al., 1999; Oksanen, 2022) are metrics used to quantify biodiversity by summarizing both the number of species and their relative abundances within a community into a single value. The importance assigned to dominant versus less dominant species varies with the value of the q parameter. Specifically, Hill number 0 corresponds to species richness, whilst Hill numbers 1 and 2 correspond to the exponential of the Shannon entropy index and the inverse of the Simpson index, respectively. Hill number 1 captures the effective number of species by weighing the contribution of each species according to its abundance, while Hill number 2 emphasizes the dominance of the most abundant species, highlighting the influence of species richness, the evenness and dominance on community structure. This approach allows for a comprehensive assessment of species richness, Shannon diversity, and Simpson diversity across treatment groups and years. Hill numbers were computed using bootstrapping techniques (n=500) to ensure robust estimates.

We employed linear models to assess the relationship between the Shannon and Simpson diversity indices and the independent variables year, treatment and grass biomass. Shannon and Simpson diversity indices were square root transformed for the linear models. For all models, we examined residuals using the Shapiro-Wilk term to check for normality. The models were fitted using the lm function in R. The goodness of fit was evaluated using the R-squared statistic. Significance was determined based on conventional thresholds, with a focus on identifying any meaningful relationships between the independent variables and the diversity measures.

In case when year showed a significant effect on the response variables, a mixed model, with including the year as a random effect, was used to estimate parameters. The models were fitted using the lmer function from the lme4 package in R (Bates et al., 2015), with the year included as a random effect to account for potential variability among years.

To assess the effects of year, treatment and biomass on species richness, a generalized linear model (GLM) was fitted using a Poisson distribution with a log link function for testing the year and the treatment and with Gaussian distribution with a log link function for testing the grass biomass. The model included year and either treatment or biomass as fixed effects, with the diversity indices as the response variable.

Finally, to assess the impact of treatment on community composition, we conducted a distance-based redundancy analysis (dbRDA) using the capscale() function from the vegan package in R. We applied the Hellinger method to transform the count data in our dataset using the decostand() function from the vegan R package (Oksanen et al., 2024). The dbRDA model was fitted with the treatment as the primary explanatory variable, using Bray-Curtis dissimilarity as the distance measure. The sampling year and the field were used as a conditional variable to control for the effect of temporal and spatial heterogeneity. The model's explanatory power was assessed using R^2 and adjusted R^2 values. Additionally, we performed a permutation-based ANOVA to test the significance of the treatment effect, applying 999 permutations to ensure robust results.

Finally, we used the similarity percentage (SIMPER) analysis to identify the arthropod taxa that contributed the most to the observed difference between the treatments (Clarke, 1993) and visualized the ordinations with ggplot2 package (Wickham, 2016).

5.3. Results

A total of 7,874 adult arthropod specimens were collected from two fields over two summers (2020 & 2021), belonging to 4 classes, 17 orders, 49 families, and 106 morphospecies. A total of 88 of these morphospecies were identified to the species level (which will be referred to as ‘species’ in this paper), while 16 were identified at the order, family, or genus level. The 88 species-level identifications represent about 97% of the specimens (n =7,674).

5.3.1. OTCs influence on grass biomass

The estimated mean biomass for the control treatment was approximately 115.96 grams (±10.80), while the mean for the OTCs treatment was around 114.44 grams (±15.27) (Figure 2). The generalized linear mixed model (Table 1) indicated no significant difference between the control and OTC treatments. Random effects for the year (Table 1) were included to account for inter-annual variability; however, the variance for this effect was estimated at 0, indicating negligible random variability across years and resulting in a singular fit.

Table 1. Fixed and Random effect from the generalized linear mixed model run to test the OTCs influence on grass biomass.

Fixed Effect	Estimate	Std. Error	t value	p-value
Intercept	1.52	0.02	72.66	< 0.01
Treatment	0.00	0.03	0.02	0.98

Random Effect	Variance	Std. Dev.
Year	0	0
Residual	0.37	0.61

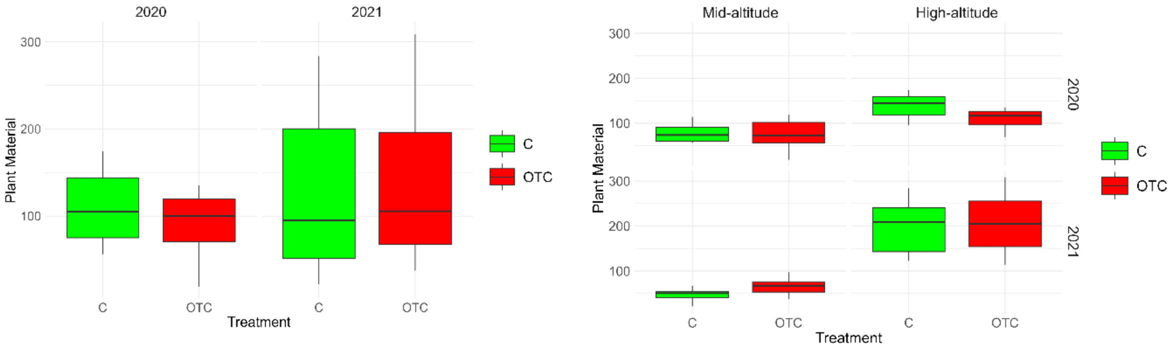

Figure 2. Boxplot of the grass biomass (in grams), a) separated by the sampling year and treatment and b) sampling year, treatment and field.

5.3.2. *Effect of Year, Treatment, and Biomass*

Linear and mixed models were used to assess the relationships between year of sampling, treatment and grass biomass with the diversity indices (Hill numbers): Species richness, exponential Shannon diversity, and inverse Simpson diversity (Figure 3).

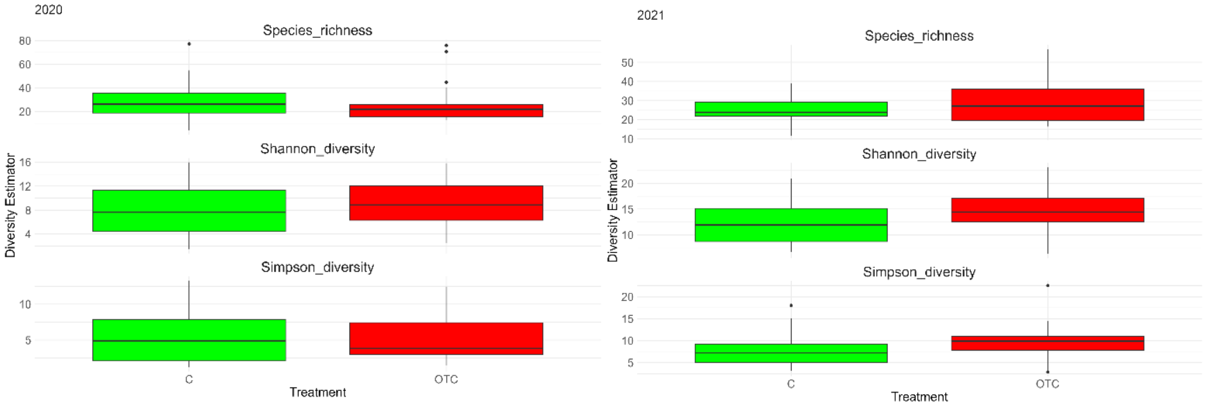

Figure 3. Box plot representing the different diversity indices, species richness (q0), exponential Shannon index (q1) and the inverse Simpson index (q2) in 2020 and 2021.

5.3.2.1. Diversity Indices and the Variable "Year"

Sampling year was a significant predictor for both Shannon and Simpson diversity when simple linear models were used (Table 2). The results indicate that from one year to the other, Shannon and Simpson diversity levels increase, suggesting a potential trend towards greater biodiversity over time. The R^2 for the Shannon and Simpson diversity index are respectively 0.25 and 0.19. Subsequently, for Shannon and Simpson diversity, the mixed-effects models confirmed the significant positive effects found in the linear models (Table 2).

Also, the generalized linear model revealed a significant effect of the year on species richness (z-value = 5.68, p-value < 0.001), indicating a notable increase in species richness from 2020 to 2021. The estimated coefficient for the year was 0.49 and the intercept was estimated at -995.63. Some variation in the deviance residuals is observed, with a minimum of -2.29 and a maximum of 3.89. The null deviance was 187.60 on 79 degrees of freedom, while the residual deviance was 154.35 on 78 degrees of freedom.

Table 2. Results from linear and mixed models assessing the effects of the year on species diversity levels, including Shannon Diversity and Simpson diversity.

Diversity Index	**Model Type**	**Coefficient Estimate (Year/Treatment)**	**Std. Error**	**t-value**	**p-value**	**R^2**	**Shapiro-Wilk (p-value)**
Shannon Diversity	Linear	0.79 (Year)	0.15	5.15	< 0.01	0.25	0.13
	Mixed	0.26 (Treatment)	0.15	1.72	0.09	NA	0.34
Simpson Diversity	Linear	0.67 (Year)	0.16	4.26	< 0.01	0.19	0.08
	Mixed	0.18 (Treatment)	0.35	7.08	0.07	NA	N/A

5.3.2.2. Diversity Indices and the Variable "Treatment"

The linear model indicated that the treatment did not show a statistically significant impact on any of the diversity indices examined (Table 3). The low R-squared values across treatment models suggest that treatment variations have minimal influence on the diversity levels in this study.

The treatment showed no significant relationship with the species richness either, with an estimate value of 0.14 (z = 1.68, p > 0.05). The null deviance of 187.60 indicates that the basic model, which does not include any predictors, accounts for some variability in the data and the lower residual deviance was estimated at 154.35. The intercept for the model was estimated at 1.88.

Table 3. Results from linear models assessing the effects of Treatment on species diversity levels, including Shannon diversity, and Simpson diversity.

Diversity Index	**Coefficient (Treatment)**	**Std. Error**	**t value**	**p-value**	**R^2**	**Adjusted R^2**	**Residual Std. Error**	**F-statistic**	**p-value (F-statistic)**
Shannon Diversity	0.26	0.17	1.49	0.14	0.03	0.02	0.77	2.22	0.14
Simpson Diversity	0.18	0.17	1.05	0.30	0.01	0.00	0.78	1.09	0.30

5.3.2.3. Diversity Indices and the Variable "Biomass"

The linear model indicated that the grass biomass has a significant effect on exponential Shannon and inverse Simpson diversity indices, while it does not significantly affect species richness. The mixed model analysis suggests that accounting for random effects, such as year, may enhance our understanding of these relationships. Indeed, while there is a suggestion of a biomass effect with the linear model, it is not strong enough to conclusively state that biomass significantly impacts Shannon and Simpson diversity when accounting for random effects (i.e. the sampling year) (Table 4.).

For species richness, the results from the generalized linear model showed that the intercept is significantly different from zero, with an estimate of 1.76 (z-value = 20.83, $p < 0.001$). The estimated effect of plant material was 0.0013 (t-value = 2.42, $p < 0.05$), suggesting a significant positive influence of plant material on species richness.

Table 4. Results from linear and mixed models, assessing the effects of the Biomass on species diversity levels, including Species Richness, Shannon Diversity, and Simpson Diversity.

Diversity Metric	Model Type	Coefficient Estimate (Year/Treatment)	Std. Error	t-value	p-value	R^2	Shapiro-Wilk (p-value)
Shannon Diversity	Linear	0.003 (Biomass)	0.00	2.39	**< 0.05**	0.07	0.67
	Mixed	0.002 (Biomass)	0.00	1.67	0.10	NA	0.08
Simpson Diversity	Linear	0.003 (Biomass)	0.00	2.06	**< 0.05**	0.05	0.09
	Mixed	0.002 (Biomass)	0.00	1.41	0.16	NA	0.11

5.3.3. dbRDA Analysis

The results of the distance-based redundancy analysis (dbRDA) indicate that the application of OTCs significantly influenced the community composition of the assemblages compared to the control group. The treatment accounted for a constrained inertia of 1.02 from the 18.25 of total inertia. This resulted in an R^2 value of 0.064, suggesting that approximately 6.4% of the variation in community composition can be attributed to the treatment.

After conditioning for sampling year and sampling field, as random factors, the constrained portion of the inertia attributable to the treatment variable was 1.021, representing approximately 5.60% of the total inertia. The proportion of variation explained by the conditioned variables (year and field) was 12.90%, while the unconstrained portion, indicating unexplained variation, was substantial at 81.50%.

The highly significant ($p < 0.001$) permutation-based ANOVA confirms that the OTC treatment had a substantial impact on community composition.

Indeed, the two treatments are distinctly represented in the dbRDA ordination plot (Figure. 4). Of the ten species most responsible for the separation of the treatments, the carabid *Pterostichus vernalis* (Panzer, 1796) (MF32) showed a clear preference for the OTCs, while the Linyphiid spider, *Erigone dentipalpis* (Wider, 1834) (MF246) as well as the ant, *Lasius grandis* Forel, 1909 (MFF1) showed a less clear tendency to be more linked to OTCs. The other species did not seem to show a strong preference for one or the other treatment.

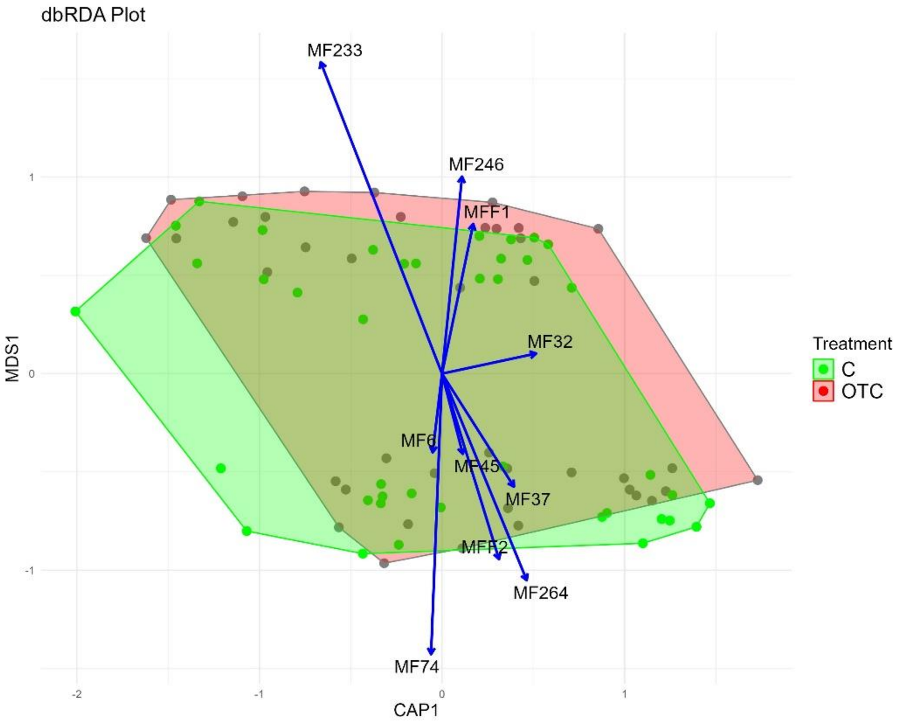

Figure 4. Ordination plot to represent the arthropods community while considering both years together. Species represented are the ones that most influenced the community: MF233: *Oedothorax fuscus* (Blackwall, 1834) - Araneae; MF246: *Erigone dentipalpis* (Wider, 1834) – Araneae; MF6: *Leiobunum blackwalli* Meade, 1861 – Opiliones; MF74: *Pseudoophonus rufipes* (De Geer, 1774) – Coleoptera; MF264: *Anotylus nitidifrons* (Wollaston, 1871) – Coleoptera; MF32: *Pterostichus vernalis* (Panzer, 1796) – Coleoptera; MF45: *Anisodactylus binotatus* (Fabricius, 1787) – Coleoptera; MF37: *Polydesmus coriaceus* Porat, 1870 – Polydesmida; MFF1: *Lasius grandis* Forel, 1909 – Hymenoptera; MFF2: *Hypoponera eduardi* (Forel, 1894) – Hymenoptera. Convex hulls indicate the two treatments: control plots are shown in green, while OTCs are indicated in red. The blue arrows represent the ten species that contributed the most to the observed difference between the treatments.

5.4.Discussion

The present study aimed to assess the effects of OTCs on grass biomass and arthropod diversity between two different years (2020 & 2021). The results indicate a nuanced relationship between treatment, time and the grass biomass with diversity indices.

5.4.1. Grass Biomass, Independent Variable from The Treatment

Our model observed no significant difference when testing the variable grass biomass with the treatment, using the year as a random effect. This suggests that the year of sampling did not contribute significantly to the variability in biomass and that the treatment did not influence grass biomass.

These results align with previous studies, which have shown that the responses of plant communities to simulated climate change can vary widely based on specific environmental metrics as the rain patterns (Hovenden et al., 2017). As our experiment did not include rain shelters, we can assume that other environmental factors, such as the amount of rainfall, may affect the structure of the grass more than the increased temperature within the OTCs. Also, in contrast to more mobile organisms such as arthropods, plant communities often exhibit slower responses to changes in their environment (Chapin et al., 2011; Walker et al., 2003) which may explain the lack of significant response in the relatively short time frame of our experiment.

5.4.2. *Temporal Change and Arthropod Diversity*

Regarding the temporal changes in arthropod diversity, significant positive results between sampling year and diversity indices indicated an arthropod diversity increase from the first to the second year of samplings.

The significant increase in arthropod species richness from 2020 to 2021 may suggest a positive response to changing environmental factors, although it could also reflect natural year-to-year variability. Most of the pasture-dwelling arthropods in Azores are habitat generalists, highly adapted to pasture intensification management. Agricultural systems monitored over 32 years in Switzerland showed an increase in species richness (Fürst et al., 2023). Obrist et al. (2010) also showed that over an 8-year period, the average number of species per year depended on temperature and increased only marginally significantly over time in agriculture. Therefore, a longer time frame for our experiment may reveal patterns that are not yet clear after only one year of study.

The higher exponential Shannon diversity values also indicate an increase in the overall diversity and a more even distribution of individuals among species from 2020 to 2021. Additionally, a higher value for the inverse Simpson diversity index suggests a less skewed dominance pattern and a more diverse community with a greater variety of species and a more balanced distribution of individuals among those species. These findings emphasize the potential for environmental changes over time to influence community dynamics (Van Klink et al., 2020).

Such trends are in line with observations from other ecosystems subjected to climate stressors, where arthropod communities have been documented to adapt to changing environmental conditions (Koltz et al., 2018; Schweiger et al., 2005). The increase in biodiversity indices suggests greater stability and balance within the arthropod community over the course of the one-year experiment. However, long-term monitoring is needed to ensure that these trends are sustained and to identify any underlying factors driving these increases.

5.4.3. *Increased Temperature and Arthropod Diversity*

The increased temperature inside the OTCs did not significantly alter diversity metrics. These results are consistent with Wallon, Tsafack, et al. (2023), who found no significant changes in arthropod diversity between treatments (OTCs versus control) when considering all species collected over different seasons in the same year. This lack of treatment effect challenges the assumption that increasing temperature in the magnitude that can be achieved via OTCs would lead to substantial changes in arthropod diversity. Such findings also support the idea that other ecological factors, such as fluctuating humidity, rainfall patterns or vegetation, may play a more important role in shaping community dynamics than the direct effects of increased temperature (Buchholz et al., 2013; Khaliq et al., 2014). A longer-term experiment might also detect slower changes in the ecosystem that our experiment did not detect because of its short duration.

5.4.4. *Relationships Between Grass Biomass and Arthropod Diversity*

While the linear model suggests a potential relationship between biomass and the Shannon and Simpson diversity indices, the evidence remains inconclusive, as the effect of biomass on diversity appears to diminish when accounting for interannual variability.

However, our results indicate a positive association between grass biomass and arthropod species richness, suggesting that increases in plant biomass may provide both direct resources and habitat structure, enhancing arthropod abundance and richness (Pommeresche, 2002; Scherber et al., 2010). This trend highlights the role of plant material in fostering diverse arthropod communities, aligning with findings from similar studies that emphasize the importance of vegetation structure and productivity in arthropod richness (Haddad et al., 2001; Siemanni, 1998).

5.4.5. dbRDA Analysis

Unlike the linear models, the distance-based redundancy analysis (dbRDA) demonstrated a significant influence of OTCs on community composition, with the treatment accounting for 6.4% of the total inertia in the assemblages. Although this value may seem low, it signifies that the conditions imposed by the OTCs led to observable changes in the assemblage structure. It also highlights the need to consider a variety analyses when assessing community responses to climate change and indicates a need for future research to identify additional environmental variables influencing arthropod communities.

The tendency of certain species to occur more frequently inside the OTCs may be influenced by a combination of ecological and trophic interactions, environmental conditions, and species-specific preferences. *Erigone dentipalpis* is a common introduced linyphiid spider in grasslands and while it tends to be less successful in areas with high disturbance and mixed grazing (Bell et al., 2001; Downie et al., 2000), it remains more abundant in grasslands and meadows with less disturbances (Bonte et al., 2000; Kromp et al., 1992; Pommeresche, 2002). The preference for OTCs may be due to the more stable microclimate they provide, which mimics the sheltered conditions and grass structures (not crushed by the wind) these spiders favor (Borges & Brown, 2004).

The ant *Lasius grandis*, is present in diverse habitats and is one of the most abundant native species of ants in the Azores (Wetterer et al., 2004). Sánchez-García et al. (2022), showed that the foraging activity of these ants was negatively impacted by increasing temperature. Finding them with a slight preference for OTCs in our study is therefore counter intuitive. However, several factors beyond temperature could contribute to this seemingly contradictory observation, such as nutritional benefits or predator avoidance. Further research is needed to understand the complex relationship between temperature, foraging behavior, competition with other species and habitat preference in *L. grandis*. (Cremer et al., 2006; C. Paris et al., 2012; C. I. Paris et al., 2009).

Pterostichus vernalis, a common and abundant carabid predator in agricultural area in Europe (Frank et al., 2007; Tudorache et al., 2020), showed a clear preference for the OTCs. It is considered as an introduced species in the Azores (Borges et al., 2022; Azores Bioportal, 2024). Limited information is available on this species, but we know that the habitat selection of carabids can be influenced by several factors, such as the temperature or humidity extremes (Thiele, 1977), as well as food availability (Guillemain et al., 1997; Purtauf et al., 2005) or the presence of competitors. Although even life history and season (Lövei, 2008), can be influential, in our study, the altered food availability in the OTCs can provide the most feasible hypothesis to test to explain *P. vernalis*'s preference to treatments over control (Holland, 2002). Thus, the tendency of certain species to prefer OTCs over control plots is likely driven by species-specific interactions with the altered microclimates, food availability, and habitat conditions created within these experimental chambers. These differences highlight the complex ecological dynamics and sensitivities of species to both direct and indirect effects of climate warming simulations.

Overall, the observed increase of these species in OTCs may result from a combination of trophic interactions, microhabitat modifications, all of which could favor species that are adaptable to changes in prey availability and environmental conditions. However, additional factors not assessed in this study, such as competition and indirect effects, may also influence these patterns.

Future studies, exploring factors such as inter- and intra-specific competition, food resource availability, trophic interactions, and seasonality could provide further insight into the patterns observed in our work (Holland, 2002).

While this study contributes to understanding the effects of climate change on grass biomass and arthropod diversity, certain limitations must be acknowledged. The focus on only two years may not capture long-term trends, and the results could be influenced by site-specific factors. Future research should consider longer temporal scales and a broader range of environmental variables, including soil composition, moisture levels, and other biotic interactions, to gain deeper insights into the mechanisms underlying these observed trends.

5.5. Conclusion

Overall, this study emphasizes the complexity of ecological responses to climate change. The lack of significant treatment effects on grass biomass, coupled with the observed increases in arthropod diversity indices over time, suggests that while immediate effects of temperature manipulation may be minimal, broader ecological dynamics are at play.

5.6. References

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Chapter 6. General Discussion

The present study contributes to our understanding of the complex interplay between climate change, arthropod diversity, and grass biomass within intensive pastures, particularly in the context of the Azorean intensively managed pasturelands. Through a series of experiments utilizing Open Top Chambers (OTCs) and examining elevational gradients, we have made significant advancements in identifying how increased temperature at a local scale may influence arthropod communities over time.

6.1. Impact of Increased Temperature on Arthropod Communities

To test the impact of increased temperature on arthropod communities, we prepared all our sampled data for 2020 and combined them into a dataset according to the standards of Darwin Core, intended to facilitate the sharing of information about species distribution and abundance and related metadata. The dataset was then used for part of the analysis presented in this thesis. It is available via the GBIF publication (Wallon, Elias, et al., 2023) as well as the paper presenting it (Wallon, Melo, et al., 2023), which constitutes Chapter 2. Data for 2021 will also be published shortly.

Using these datasets for analysis, our research highlights the nuanced effects of simulated warming by OTCs on arthropod diversity. Utilizing a taxonomical approach in both Chapters 3 and 5, we observed distinct patterns of response among different taxa.

Regarding diversity responses, in Chapter 3 (see also Wallon, Tsafack, et al., 2023), we identified a decrease in beetle richness under warmer conditions, while spider diversity exhibited an increase. This suggests that different taxonomic groups are responding differently to climate stressors, indicating the importance of understanding specific ecological traits that may enhance resilience.

Chapter 5 revealed significant positive correlations between year and key biodiversity indices as measured using the Hill Numbers framework (Exponential Shannon and Inverse Simpson indices), indicating an upward trend in arthropod diversity and decrease of species dominance over time. Higher diversity metrics suggest a more balanced community, emphasizing the dynamic nature of ecological interactions. The distance-based redundancy analysis (dbRDA) in Chapter 4 indicated a significant influence of OTCs on community composition, with the treatment accounting for 6.4% of the total inertia in the assemblages. This finding highlights the complexity of ecological responses and the need for diverse analytical approaches to fully understand community dynamics.

Our functional approach in Chapter 4 (see also Wallon et al., 2024) further emphasizes the importance of traits ecology. Our results indicate that functional diversity, measured through various traits such as body size, iridescence, and other morphological and behavioral characteristics, plays a critical role in the adaptive capacity of arthropod species to changing environmental conditions. The OTCs treatment, which increased temperatures, significantly affected arthropod and beetle traits, especially during winter. Higher temperatures led to increased abundances of herbivores, predators, coprophagous organisms, and fungivores, suggesting improved activity and survival. In contrast, detritivores showed no significant differences, likely due to their reliance on decaying matter and moisture. Beetles exhibited greater sensitivity to temperature changes in winter, with warmer conditions potentially reducing thermoregulation energy costs and enhancing foraging and development. Interestingly, larger beetle body sizes were observed in OTCs during summer, contradicting typical trends for ectotherms (Kingsolver et al., 2008; Tseng et al., 2018). Additionally, an increase in iridescent species in OTCs during winter at low altitude suggests that these traits may confer thermoregulatory advantages. Also, low-dispersal arthropods were more prevalent in OTCs, while high-dispersal species favored control plots, indicating a shift in community composition due to abiotic conditions.

Overall, the observed changes in both taxonomical and functional arthropods diversity underscore the varied responses of arthropod communities to increased temperatures. These two different approaches (taxonomic and functional) not only highlight different aspects of the arthropod community, but also demonstrate the importance of considering different types of analysis and variables when trying to disentangle the effects of climate change on arthropod communities.

6.2. Elevational Gradients and Arthropod communities

The influence of elevational gradients on arthropod communities was primarily explored through the functional approach presented in Chapter 4. This study revealed distinct patterns of abundance among different guilds along the elevation gradient. This highlights that elevation can create a variety of microhabitats, which can be used as an alternative way to study the effect of temperature on arthropod assemblages, as it naturally decreases linearly with elevation (Lessard et al., 2011; McCain et al., 2021, 2010).

Several key functional traits were examined to identify those that are critical for the adaptation of arthropod species to elevational gradients and associated abiotic conditions. One notable observation was the variation in body size, with larger-bodied species becoming more prevalent at higher elevations. Also, the results regarding the presence of iridescence on beetles along the elevational gradient were very interesting. Among the species studied, the clear pattern of this trait increasing with the decrease of elevation, were temperature and sun exposition were stronger, confirms that the presence of iridescence on beetles play a role for thermoregulation (Stuart-Fox et al., 2017). In contrast to the expected thermoregulation adaptations, the study revealed that beetles with orange and red nuances, such as blackish (mainly black with a reddish/orange shade) and reddish-brown (main tendency orange/brown color) species, exhibited higher abundances at low elevations, where these colorations may be more effective for thermoregulation and camouflage in warmer environments (Badejo et al., 2020; Young, 1960). Conversely, darker-colored beetles, particularly black beetles, were more abundant at mid-elevations, likely because their dark coloration helps them absorb heat in the cooler temperatures found at these elevations (Trullas et al., 2007). These results emphasize the need to continue studying beetles color adaptations in relation to different abiotic conditions associated with altitude.

Significant differences in feeding strategies among arthropod guilds in response to the elevational gradient have been also highlighted. Herbivorous arthropods exhibited lower abundances at high elevations. This decline in herbivore populations may influence the overall community structure of arthropods, as their interactions with other guilds are vital for maintaining ecological balance (Descombes et al., 2017; Garibaldi et al., 2011; Pitteloud et al., 2021). In contrast, predatory guilds displayed more consistent distributions along the gradient, with a peak in abundance at middle elevations. This suggests that these areas provide optimal conditions for predation and resource availability (Hodkinson, 2005).

We have highlighted the fact that different functional guilds of arthropods respond differently to changes along the elevational gradient. For future studies, as it is difficult to draw general conclusions and trends, it would be interesting to select some key species with key functional traits in intensive pastures and focus the analysis on them.

6.3. Temporal Changes in Diversity

Temporal changes in arthropod diversity were examined through both seasonal variations (Chapter 3) and across a one-year sampling period (Chapter 5). Our findings revealed significant seasonal fluctuations in arthropod diversity, with distinct community compositions emerging in different seasons as also found in other studies (Borges et al., 2017; Doležal et al., 2018; Pereira da Silva et al., 2011). Also, significant positive correlations between the two-year sampling and diversity indices suggests that arthropod communities may be adapting to changing environmental conditions over time. The stability of species richness despite shifts in community composition suggests that there may be a threshold beyond which environmental changes start to affect the number of species present, rather than just the abundance of individual species. Thomas et al. (2004) and Barnosky et al. (2011) found that changes in species abundances can occur before changes in species richness, and that these changes can be used as early indicators of climate change impacts on ecosystems. Also, Urban et al. (2016) found that changes in species abundances were more common than changes in species richness, and that these changes were often driven by changes in temperature and precipitation.

6.4. Interactions Between Grass Biomass and Arthropod Diversity

The relationship between grass biomass and arthropod diversity is complex and multifaceted, as highlighted in Chapter 5. Generally, higher grass biomass is often expected to correlate with increased species diversity or richness (Bell et al., 2001; Bonte et al., 2000; Haddad et al., 2001; Kromp et al., 1992). This expectation arises from the idea that greater biomass can provide more resources, such as food and habitat, potentially supporting a wider variety of species (Prather et al., 2020). Our results confirm this positive relationship, showing that higher grass biomass is indeed associated with greater arthropod species richness.

This positive correlation suggests that an increase in grass biomass may enhance the habitat's structural complexity, offering a wider range of microhabitats and resources that support various arthropod species. This aligns with findings from studies like Zarnetske et al. (2017), which highlight how habitat complexity can foster diversity by supporting niche differentiation and reducing competition. In our study, the increased biomass likely created more stable microclimates, helping to buffer arthropods from extreme temperatures and fluctuations in humidity, ultimately promoting a diverse community (Khaliq et al., 2014).

Moreover, the availability of more plant material may support complex trophic interactions, with an increase in prey availability potentially sustaining a more varied assemblage of predators and herbivores (Laws, 2017; C. Paris et al., 2012; Sánchez-García et al., 2022).

Further studies are needed on the composition of the grasses to assess whether any of these variables play a role in arthropod diversity. The present work is part of the project "PASTUCLIM - Impact of climate change on pasture's productivity and nutritional composition in the Azores". As part of this project, a first paper has been already published by Melo et al. (2022) regarding grass quality. This study investigated the effects of elevation and season on the productivity and nutritive value of pastures on Terceira Island in the Azores. The results revealed significant variations in forage net productivity across different altitudes and seasons. Soil chemical properties as soil pH, phosphorus, potassium, calcium, and magnesium contents also varied significantly among pastures. The average dry matter (DM) content across pastures was 16.15%, with crude protein (CP) averaging 17.60%. Noteworthy seasonal patterns were observed, with DM peaking in lowland pastures during summer and CP being highest in winter but declining as the growing season progressed. Increased fiber content, particularly neutral detergent fiber (NDF) and acid detergent fiber (ADF), negatively impact forage digestibility. Overall, Azorean pastures provide high-quality forage primarily in spring, but the quality declines with the stage of maturity of the plant. The CP content suffices for ruminant nutritional needs only at the beginning of the growing season, indicating a potential shortfall later. Thus, this paper highlights differences in grass quality at different seasons and elevations that could play a role in determining the arthropod community composition in intensively managed pastures. The effect of rising temperatures in OTCs on grass quality along different seasons has been analyzed for 2020 and 2021 (Elias et al., 2023). The results indicate the possibility that global warming will result in some decrease in forage quality due to a decrease in DM and an increase in fiber content: ADF and acid detergent lignin (ADL). Future analyses are planned to test how differences in grass quality parameters may affect the arthropod communities.

6.5. Implications for Future Research

While this study enhances our understanding of climate change's impacts on arthropod diversity, several limitations warrant further exploration. The relatively short temporal scale of the experiment may not capture long-term trends, and site-specific factors could influence the results. The project PASTURCLIM implied the collection of various data apart from sampling grass and arthropods. It also implied the collection of soil samples as well as soil moisture. These data need to be processed in order to be included in future analyses testing the complex interactions between local environmental variables and arthropod diversity and composition. Future research should consider longer time frames and a wider range of environmental variables, including soil composition, moisture levels and also biotic interactions across trophic levels, to gain deeper insights into the mechanisms underlying the observed trends.

6.6. Main Conclusion

This study underscores the complexity of ecological responses to climate change within agroecosystems. The nuanced relationships between temperature, elevation, grass biomass and arthropod diversity highlight the need for a multifaceted approach for understanding biodiversity dynamics in the face of climate change, especially increased temperature. A better understanding of arthropod communities and their biotic interactions in intensively managed pastures could help to model future arthropod assemblages under different temperature scenarios. This could prevent irreversible changes or changes that threaten the proper functioning of the grass ecosystem, with financial consequences for Azorean farmers.

In conclusion, it is important to remind that all facets of data analysis should be always considered, by integrating a taxonomical approach, functional traits, ecological interactions as well as relevant explanatory variables into future studies. In this way, we can better predict and mitigate the impacts of climate change on Azorean intensive pastures. Much work still needs to be done to gain a better understanding and overview of all the biological processes and their interrelationships in the grassland ecosystem. Achieving this general overview will then make it possible to produce reports for stakeholders and farmers to inform them and allow them to adapt their pasture management to new climatic conditions and limit potential financial impacts. Once again, we have proved that arthropods are "the little things that run the world" (E. O. Wilson, 1987).

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UNIVERSIDADE DOS AÇORES
Faculdade de Ciências Agrárias e do Ambiente

Rua Capitão João d'Ávila
9700-042 Angra do Heroísmo
Açores, Portugal