Whole Azorean arthropod diversity: understanding the trophic relations and functional diversity at a plot scale

Tese de Doutoramento

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“The Road goes ever on and on
Down from the door where it began.
Now far ahead the Road has gone,
And I must follow, if I can,
Pursuing it with eager feet,
Until it joins some larger way,
Where many paths and errands meet.
And whither then? I cannot say. "

J.R.R. Tolkien, *The Lord of the Rings*

Abstract

Island ecosystems are home to a disproportionate amount of unique floristic and faunistic diversity, but conversely, islands also host some of the most imperiled habitats and species on Earth. These island communities are in many cases extremely vulnerable to anthropogenic habitat disturbance and destruction, and to the introduction of exotic species. Most of the island terrestrial biodiversity is composed by arthropods, but the processes that structure their communities are still poorly understood. In order to preserve what is left of these unique insular biotas, our current knowledge regarding species, communities and habitats, and recovery processes under disturbance must be expanded, and new possibilities for conservation must be also evaluated.

Taking advantage of the unique characteristics of the canopy fogging (pyrethrum knockdown) sampling protocols, this thesis investigates for the first time in the Azores archipelago the impact of defaunation on the reassembly of canopy arthropod communities. A total of 24 native trees were sampled with insecticidal knockdown in 2014 and 2015, in a native forest patch on Terceira Island. Between 2015 and 2016 this same protocol was applied to five isolated Azorean cedar trees on a semi-natural pasture. Regarding the defaunation and recovery processes, changes in taxonomic (TD) and functional diversity (FD) for the initial communities for the control trees and for those of the recolonised trees were also investigated and null models created, to ascertain how these communities differed from randomly assembled ones.

The main objectives of this thesis were: 1) take advantage of the canopy fogging technique to do an exhaustive quantitative and qualitative study of the arthropod communities present in the canopies of three native Azorean tree species (*Juniperus brevifolia*, *Ilex perado* subs *azorica*, *Laurus azorica*); 2) to study the recovery processes of these communities after the defaunation of the canopies; 3) to study the arthropod communities present in the canopies of the isolated pasture trees, evaluating their role as repositories of indigenous fauna and as an element in the interconnection between extant native forest patches.

In the forest experiment, a total of 21275 arthropod specimens belonging to 75 species were collected. The community was in general dominated by some highly abundant endemic and to a certain extent native species. Most exotic species were locally rare, and most likely vagrants. Host tree species seemed to be of secondary importance in structuring the highly generalist arthropod community. Regarding functional diversity, there was no apparent saturation of functional trait-space.

Recolonisation of the defaunated trees was fast and complete, with the recovered arthropod community being similar to both the initial community or that of the control trees, particularly for endemic species. In general, functional and taxonomic diversity remained fairly unaltered both in the initial and recolonised communities and in the control trees. The recovered community also had a relatively lower proportion of exotic species, also observed as a decreased in both TD and FD for this group. Recolonisation and recovery seemed to be largely influenced by the structure of the canopies, the high level of interconnectedness of the canopies and the existing pool of highly abundant indigenous species. Also observed was that in general these communities had lower values of TD and FD than what would be expected by random assembly, most likely consequence of a filtering effect by the structure of the canopies, possibly allied with the fact that the indigenous Azorean fauna is somewhat depauperate.

In the pasture experiment, a total of 8056 specimens belonging to 58 species were collected. These communities still retained a high degree of similarity with the forest communities, reinforcing both the importance of the characteristics of the canopies in structuring the communities and the role of these trees as repositories of indigenous species. As with the forest communities there was no apparent saturation of functional trait space. These communities were nevertheless less resilient to the defaunation events, with the recovered community presenting an increase in the abundance of native specimens but a decrease in endemics, while simultaneously attracting a higher number of exotic vagrants. This was also mimicked by a decrease in TD and FD for the endemic species in the recolonised community, while exotic species had a considerable increase for these parameters. In these isolated trees, native species seemed to assemble in a random way, while exotic species, which were apparently suppressed in the initial communities, assembled indistinguishably from a null community in the recolonised trees.

Overall, this study seems to indicate that the indigenous canopy arthropod communities of Terceira retain a high degree of resilience towards disturbances and invasion by introduced arthropod species, in part due to the filtering effect exerted by the structure and characteristics of the canopies.

It also highlights the importance of isolated trees in pasture, and should also have some future implications on the habitat management and conservation strategies of the increasingly fragmented forests in the Azores.

Keywords: pyrethrum knockdown, arthropod communities, Macaronesia, community recovery, canopy arthropods.

Resumo

Os ecossistemas insulares albergam uma diversidade faunística e florística únicas e muito elevada proporcionalmente quando comparada com zonas continentais. No entanto, é também nas ilhas onde se encontram alguns dos habitats e espécies mais vulneráveis do planeta. Estas comunidades insulares são em muitos casos extremamente vulneráveis a perturbações antropogénicas e à destruição dos habitats, bem como à introdução de espécies exóticas. A maioria da biodiversidade insular terrestre é composta por artrópodes, mas existem ainda diversas lacunas no conhecimento sobre os processos que estruturam essas comunidades. Assim, de modo a poder preservar o que ainda resta destes biotas insulares únicos, o nosso conhecimento acerca destas espécies, das comunidades e dos habitats, bem como dos processos de recuperação após perturbações têm que ser expandidos e novas alternativas para a conservação devem também ser avaliadas.

Tomando partido das características únicas da amostragem por fumigação com insecticida das copas, esta tese propõe-se a investigar pela primeira vez nos Açores o impacto da defaunação e a recuperação das comunidades de artrópodes das copas. Entre 2014 e 2015 foram amostradas através de fumigação térmica com insecticidas um total de 24 árvores nativas das espécies *Juniperus brevifolia*, *Ilex perado* subs *azorica* e *Laurus azorica*, num fragmento de floresta nativa da Terceira. Em 2014 foram amostradas 16, das quais 15 voltaram a ser amostradas em 2015, em conjunto com outras oito árvores, fumigadas pela primeira vez, como controlo. Entre 2015 e 2016 o mesmo protocolo de amostragem foi aplicado a cinco exemplares de Cedro do mato (*Juniperus brevifolia*), isolado numa pastagem semi-natural. Três arvores foram fumigadas pela primeira vez em 2015, tendo voltado a ser amostradas em 2016, em conjunto com mais duas árvores controlo. No que diz respeito à defaunação e processos de recuperação das comunidades, alterações a nível da diversidade taxonómica (DT) e funcional (DF) foram investigadas para as comunidades iniciais, para as comunidades das árvores controlo e para as comunidades das árvores recolonizadas (as árvores fumigadas pela segunda vez, no ano seguinte). Foram também criados modelos nulos, de forma a tentar perceber como estas comunidades diferem de comunidades estabelecidas ao acaso.

Os principais objectivos desta tese são então: 1) tomar partido das características da técnica de fumigação das copas para fazer um estudo quantitativo e qualitativo exaustivo das comunidades de artrópodes presentes nas copas de três espécies de árvores nativas dos Açores (*Juniperus brevifolia*, *Ilex perado* subs *azorica*, *Laurus azorica*); 2) estudar os processos de recuperação destas comunidades após a defaunação das copas; 3) estudar as comunidades de artrópodes presentes nas copas de árvores nativas isoladas em pastagens, e simultaneamente avaliar o papel/potencial destas

árvores como repositórios de espécies indígenas de artrópodes e como elemento de interligação entre os fragmentos existentes de floresta nativa.

Na experiência da floresta, foram capturados um total de 21275 exemplares de artrópodes, pertencentes a 75 espécies. A comunidade é, em geral, dominada por algumas espécies endémicas extremamente abundantes, e em certa medida, também por algumas espécies nativas. A maioria das espécies exóticas é localmente rara e o mais provável será serem indivíduos errantes. A espécie de árvores hospedeira aparenta ter uma importância secundária na estruturação da comunidade constituída maioritariamente por espécies generalistas. No que diz respeito à diversidade funcional, não há uma aparente saturação do "espaço funcional".

A recolonização das árvores fumigadas e a recuperação das comunidades foi rápida e total, sendo a comunidade presente nestas árvores similar à comunidade inicial e à comunidade das árvores controlo, especialmente no que diz respeito às espécies endémicas. No geral, a diversidade taxonómica e a diversidade funcional mantiveram-se relativamente inalteradas entre a comunidade inicial, a comunidade das árvores recolonizadas e a das árvores controlo. A comunidade reestabelecida apresentou também uma proporção relativamente menor de espécies exóticas, corroborado pelo decréscimo a nível de DT e DF para este subgrupo da comunidade. A recolonização das árvores e a recuperação da comunidade parecem ter sido em grande parte influenciadas pela estrutura das copas, pelo elevado nível de interligação destas e pelo pool de espécies imediatamente presente, composto maioritariamente por espécies endémicas e nativas de elevada abundância. Foi também observado que, em geral, estas comunidades possuem valores de DT e DF mais baixos do que o que seria de esperar se fossem estabelecidas ao acaso, muito possivelmente uma consequência de um efeito de filtro causado pela estrutura das copas, eventualmente aliado ao facto de a actual fauna indígena dos Açores ser algo depauperada.

Na experiência da pastagem, foram recolhidos um total de 8056 exemplares de artrópodes, pertencentes a 58 espécies. Estas comunidades das copas dos cedros de pastagem retêm ainda um elevado grau de similaridade com as dos cedros da floresta, reforçando quer a importância das características das copas na estruturação das comunidades de artrópodes, quer o papel destas árvores como repositório de espécies indígenas. Tal como no caso das comunidades da floresta, não foi aparente uma saturação do "espaço funcional". No entanto, estas comunidades das arvores de pastagem demonstraram ser menos resilientes ao episódio de defaunação, já que a comunidade reestabelecida apresentou um aumento na abundância de exemplares de espécies nativas, acompanhado por um decréscimo no que diz respeito a exemplares de espécies endémicas. Simultaneamente, houve também um aumento no número de espécies exóticas nestas novas

comunidades. Estas alterações nas comunidades reestabelecidas foram acompanhadas por um decréscimo a nível de DT e DF para as espécies endémicas, e por um aumento considerável destes parâmetros no que diz respeito às espécies exóticas. Nestas árvores isoladas, as espécies aparentam estabelecer-se de forma mais ou menos aleatória, ao passo que as espécies exóticas, aparentemente suprimidas nas comunidades iniciais, após a defaunação recolonizaram as árvores e estabeleceram-se nas copas de forma indistinguível do que seria de esperar de uma comunidade nula.

No geral, este estudo indica que as comunidades de artrópodes das copas indígenas da Terceira retêm um elevado grau de resiliência no que diz respeito a perturbações localizadas e a invasão por parte de espécies exóticas, em parte consequência do efeito de filtro exercido pela estrutura e características bióticas e abióticas das copas.

Este estudo realça também a importância de arvores nativas, isoladas em pastagem, como repositórios de fauna e como elementos de interligação, devendo ter implicações para as futuras estratégias de gestão ambiental e conservação das cada vez mais fragmentadas florestas nativas dos Açores, bem como no desenvolvimento sustentável da região.

Palavras-chave: comunidades de artrópodes, artrópodes arbóreos, recuperação de comunidade, Macaronésia, fumigação com piretrinas.

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To my parents

I would like to dedicate this work to my parents. For all their unconditional love and support, even when that meant having to see me leave again to a far away place, in this case, one of nine green islands in the middle of the Atlantic Ocean. The same could be said for the rest of my family, for whom I am so grateful for their love.

This work is also dedicated to the memory of two of the persons that I loved the most in this world and that passed away during the completion of this work, my grandfathers; Mário Abrantes Simões Ricardo and Américo Nunes. I regret the distance that prevented me from being able to spend more time with them, and not being able to see them again, for I still had much to learn from them.

But they live on, for one only dies when it passes from the memories of those that loved them.

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Any flaws with this work are mine alone and not theirs.

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Table of contents

Table of figures

Table of tables

Chapter 1
General Introduction

Since the early days of naturalist explorations of Hooker (1847) and Darwin (1859), islands have captured the interest of naturalists and ecologists as places of a unique fauna and flora. Islands are particularly important in the conservation of biodiversity because, as even if encompassing less than 5% of the planet's landmass (Caujapé-Castells *et al.* 2010), islands are home to a disproportionate amount of unique diversity (Paulay 1994, Rosenzweig 1995, Losos & Ricklef 2010, Warren *et al.* 2015). In fact, 20 of the current 36 biodiversity hotspots are islands or have an associated island component (Myers *et al.* 2000).

Conversely, islands include also some of the most endangered habitats and species on Earth, with its native communities being in many cases extremely vulnerable to anthropogenic habitat disturbance and destruction, and to the introduction of exotic species (Cronk 1997, Sadler 1999, Dunn 2005, Caujapé-Castells *et al.* 2010). Approximately 75% of documented animal extinctions constitute island species (Frankham 1998), and considering the current arthropod diversity, Dunn (2005) estimates that some 44.000 arthropod species might have become extinct in the last 600 years.

The natural terrestrial ecosystems of the Azores Archipelago have also suffered greatly over the last 600 years of human settlement (Martins 1993, Triantis *et al.* 2010a), and there is therefore an urgent need to preserve what is left of these unique insular biotas. In order to do so, our current knowledge regarding species, communities and habitats, and recovery processes under disturbance must be expanded, and new possibilities for conservation must be also evaluated. This will be particularly urgent in some islands in which there is an ongoing conflict between existing protected areas and the economic development of the region, given that a large portion of the population is directly or indirectly dependent on agriculture and cattle production (Cruz *et al.* 2007, Gil *et al.* 2018).

1.1. Current arthropod knowledge in the Azores

The Azores are an isolated archipelago, and historically little regard had been given by naturalists to its fauna and flora, save some early mentions in the works of Gaspar Frutuoso, in the 16th century (Frutuoso 2005a,b), or by other local chroniclers (*cf.* Vieira 2015). In 1836, on the return leg of its famous voyage on the Beagle, Charles Darwin went ashore in Terceira, but left little or no remark regarding the fauna and flora of the island (Keines 1988). This nevertheless spurred some

interest about the Azorean archipelago in the international scientific community and in the local naturalists, of which the prolific work of Francisco Arruda Furtado should be mentioned (see Arruda 1994).

Despite this, there was still a paucity of information regarding the local arthropod communities notwithstanding some important scientific expeditions like those of Chopard and Mequignon in 1930 (Vieira 2015) or that of Frey, Storå and Cedercreutz in 1938 (see Tjeder 1948), or some works by other authors, mainly of a taxonomic nature or species lists (e.g. Drouët 1859, 1861, Simon 1883, Tjeder 1963, Ohm 1969). Vieira (2015) gives a detailed account of the initial entomological studies in the Azorean archipelago.

This situation has greatly improved in the last twenty years, mainly due to the work of research groups from the University of the Azores, with many studies on both indigenous and exotic species having been carried out, such as exhaustive species inventories (Borges *et al.* 2005b; Borges *et al.* 2010), comprehensive biogeographical studies (Whittaker *et al.* 2008, 2014; Borges & Hortal 2009; Cardoso *et al.* 2010; Santos *et al.* 2010; Triantis *et al.* 2010a,b; Cameron *et al.* 2013; Aranda *et al.* 2014; Carvalho & Cardoso 2014; Carvalho *et al.* 2015), phylogenetic and evolutionary studies (Ferreira *et al.* 2011; Schaefer *et al.* 2011; Amorim *et al.* 2012; Rodrigues *et al.* 2013), or studies regarding the future effects of climatic changes in the archipelago (Ferreira *et al.* 2016).

In addition, there were several ecological studies at smaller spatial scales focusing on the communities of particular taxa, namely arthropods (e.g. Borges *et al.* 2006; Meijer *et al.* 2011; Florencio *et al.* 2013; Raposeiro *et al.* 2013, Florencio *et al.* 2016, Lamelas-López *et al.* 2017), but also of bryophytes (e.g. Gabriel & Bates 2005; Aranda *et al.* 2015) or vascular plants (e.g. Elias & Dias 2009; Rumeu *et al.* 2011; Marcelino *et al.* 2013).

However, there are so far very few studies dealing in detail with the specific biotic communities associated with each of the indigenous host tree species from the extant Azorean forests. Among them I would emphasise the works on arthropod canopy community biodiversity and structure (Markin *et al.* 1995; Ribeiro *et al.* 2005; Gaspar *et al.* 2008; Borges *et al.* 2008; Ribeiro & Borges 2010) and those dealing with the effects of herbivory on a specific indigenous host tree species (Vieira *et al.* 1993; Silva *et al.* 1995; Ribeiro *et al.* 2003).

As such, it is possible to see that despite the considerable amount of studies regarding the biotic communities of the Azores, there are still several gaps regarding the knowledge of the diversity and the structure of the arthropod communities associated with Azorean tree canopies, particularly concerning the way these communities might recover after a disturbance event,

hindering conservation efforts regarding the indigenous biodiversity, and also the sustainable resource management and development (Summervile *et al.* 2003; Cardoso *et al.* 2011a) of the region.

Striving to increase the current knowledge about these communities, I proposed myself to use for the first time in the Azores canopy fogging to sample the arthropod communities present in three native tree species of significant importance in the natural forests of the Azores.

Canopy fogging (or pyrethrum knockdown) is a fairly unselective technique that allows to capture a "snapshot" of the community present on the tree at the moment of sampling. Its samples are a close reflection of the canopy arthropod community, irrespectively of the surface the arthropods are on, or their activity, dispensing with attractants and avoiding biases connected with activity-based traps (Stork & Hammond 1997). This technique also has the advantage of generating highly comparable samples, despite differences in latitude and altitude, in the time of collection, or differences in forest types and host tree species (Stork & Hammond 1997).

The use of this technique also opens the opportunity for another novelty in the Azorean archipelago, namely taking advantage of the defaunation of the trees, caused by the sampling protocol, to study how the arthropods recolonize the canopies of the native trees and how the community itself recovers from a major local disturbance and extinction.

Given the nature of the doctoral program where I enrolled (Integrated Landscape Management), I thought it would also be appropriate to study the arthropod communities and these same recolonization and recovery processes on the canopies of some of the relic trees present in several anthropogenic habitats of Terceira, particularly in the semi-natural pastures, ascertaining their importance in the conservation of the indigenous entomological fauna.

This thesis is organized in seven chapters and I summarize below the main objectives in each one:

Chapter 1

Here I give a brief rationale for my work, my motives and objectives

Chapter 2

In this chapter I give a brief description of the Azorean archipelago and particularly of Terceira island, its ontogeny, its climate, and of its fauna and flora, with emphasis on the three native tree species selected for this study, more precisely *Juniperus brevifolia* (Seub.) Antoine, *Ilex perado* Aiton subsp. *azorica* (Loes.) Tutin and *Laurus azorica* (Seub.) Franco.

I also do an appraisal of the suitability of the thermal fogging technique to fulfill my objectives, together with an overview of the history of the use of this technique.

Finally, I give a description of the two study sites where the sampling took place, in conjunction with the used sampling protocol and some details regarding the equipment and insecticide solution used, the sorting and identification of the specimens and the statistical analyses implemented.

Chapter 3

Here I investigate the already existing arthropod data regarding the species present in the canopies of *Juniperus brevifolia*, *Ilex perado* subsp. *azorica* and *Laurus azorica*, giving a brief overview of at the archipelago level, but focusing in Terceira island, to avoid confounding effects regarding island age, climatic variables, the different degree of anthropic disturbance or other factors that influence the composition of the arthropod community in each island (Borges 1997, Gaspar *et al* 2011, Nunes *et al.* 2015).

The arthropod data was collected between the years of 1999 and 2004 in the context of the BALA project (Ribeiro *et al.* 2005, Gaspar *et al.* 2008).

This chapter will allow a better understanding about the structure and species composition of the arthropod communities associated with each tree species at island level, as well as an evaluation of the relative weight of indigenous arthropod species in the canopies.

Therefore, data summarized in this chapter will be a baseline to be compared with the results obtained by pyrethrum knockdown/canopy fogging in a well preserved forest fragment of Terceira (Chapters 4, 5 and 6).

Chapter 4

In this chapter, I will use the samples collected by canopy fogging on the 16 trees fogged in the forest in 2014, together with those of eight extra trees that were also fogged for the first time in 2015, allowing me to:

a) describe in detail the diversity, abundance and spatial patterns of canopy arthropods in one of the best preserved extant forest patches in Terceira island, including previously less well studied groups such as Hymenoptera, Diptera, Collembola and Acari;

b) To compare the communities sampled by canopy fogging in a well preserved forest patch with previous canopy data for Terceira island, with a slight focus on the colonization status of the species present.

c) to ascertain if these tree species host distinct arthropod communities or if the previously reported high levels of generalists among the endemic and native arthropod species (Ribeiro *et al.* 2005) account for a somewhat homogeneous community through the different host-tree species;

Chapter 5

Chapter five aims to study the recovered arthropod canopy communities after fogging, comparing it with the initial community of those same trees and with that of control trees also fogged in 2015

I analyze and compare the overall structure of the recolonized community, ascertaining differences in species composition, abundance and colonization status, taxonomic and functional diversity and also create null models to investigate how the recovered community would differ from one that would be assembled purely by stochastic processes.

With this, I will try to validate the following predictions:

a) Given the generalist status of Azorean arthropod species (Ribeiro *et al.* 2005), a rapid recolonization process is expected to occur after defaunation leading to the rapid reestablishment of similar richness, composition and species abundance distribution in canopy arboreal communities;

b) The low diversity and abundance of introduced species in the canopies (see Chapter 4 and Florencio *et al.* 2016) suggests that these are vagrants and not a functional part of the community. Therefore, I expect higher levels of beta diversity for introduced species than for indigenous species with no increase in species richness as exotic introduced species should be filtered by the architecture of tree canopies and not by biotic resistance;

c) The fact that the arboreal arthropod fauna is resistant to exotic introduced species (Florencio *et al.* 2016,) may imply either a facilitation process in the spread of exotic species after defaunation (empty niche effect) if the exotics are filtered by competition, or no effect if exotics are filtered by the architecture and biotic and abiotic conditions in the tree canopies;

d) in addition, the lack of saturation in functional trait space of indigenous arthropod fauna in Azores (Whittaker *et al.* 2014) may also imply that the fauna of Azores will be vulnerable to further colonization and probably invasion of exotic species with new traits during the recolonization process.

Chapter 6

In here I study some Azorean cedar trees isolated in a semi-natural pasture, first comparing the arthropod communities present in them with those of other tree Azorean cedars fogged in the native forest within a short time period. I then proceed to analyze the recolonization of these trees by the arthropod community. In this process I aim to investigate the ecological importance of these trees in the ecosystems of Terceira and try to validate the following predictions:

a) Isolated trees in pastures, due to their architecture and biotic and abiotic conditions of their canopies, can potentially act as an indigenous species repository, maintaining a community similar to those of the extant native forests, despite the large scale disturbance suffered during the clearing of the pasture;

b) High elevation semi-natural pastures, with low grazing pressure and insecticide use (*cf*. Borges & Brown 2001) are still host to a high proportion of indigenous species (Borges *et al.* 2008, Cardoso *et al.* 2009), with exotic species favoring more disturbed lowland habitats. Therefore, as with the case of the forest communities, recolonization occurs quickly from the surrounding species pool, favoring the highly abundant native and endemic species from the nearby forests and heathland;

c) Even if isolated in a moderately disturbed matrix, the general biotic and abiotic conditions inside the complex canopies of these high altitude *J. brevifolia* trees will still favor the native and endemic species during the recolonization process after the defaunation event, filtering out the introduced species;

d) The lack of saturation in functional traits of indigenous species may imply lack of resilience in the case of disturbance of the natural environment (Whittaker *et al.* 2014), leaving the indigenous fauna of these isolated canopies vulnerable to further colonization and probable invasion of exotic species with new traits during the recolonization process.

Chapter 7

Chapter seven gives and overview of the present work and tries to convey to the reader the particular characteristics of the canopy arthropod communities of the native Azorean forests, as well as its resilience towards disturbance and invasion.

It will also strive to convey the role that isolated native trees in a moderately disturbed matrix might have as reservoirs of indigenous arthropod fauna and as stepping stones, increasing the interconnectivity between the extant patches of native forest.

Additionally, I will also supply in the form of Appendix I a list of all the identified arthropod species associated with the canopies of *J. brevifolia*, *I. perado* subs. *azorica* and *Laurus azorica* in Terceira island, which considering the present rates of biodiversity loss due to global changes could be a valuable asset for future studies regarding changes in the Azorean ecosystems.