Universidade dos Açores

Doutoramento em Gestão Interdisciplinar da Paisagem

Biodiversity conservation in island protected areas: the case of plant-insect pollinating networks

Orientador:

Professor Doutor Paulo Alexandre Vieira Borges

Co- orientador:

Professor Doutor François Rigal

Doutoranda:

Ana Luísa Coderniz Picanço

Angra do Heroísmo
2018

"Biological diversity must be treated more seriously as a global resource, to be indexed, used, and above all, preserved. (…) The biological diversity most threatened is also the least explored, and there is no prospect at the moment that the scientific task will be completed before a large fraction of the species vanish."

E. O. Wilson (1988) *Biodiversity* (p. 3, 3)

"The role of scientists is to collect data and transform them into understanding. (…) However, going from data to understanding is a multi-step process."
Schimel (2012) *Writing Science* (p. 11)

Agradecimentos

O trabalho desenvolvido para a realização desta tese, não teria sido possível sem a preciosa ajuda de muitas, muitas pessoas, às quais quero dizer obrigada.

Em primeiro lugar, ao Prof. Paulo Alexandre Vieira Borges, não só pelo empenho e dedicação como orientador, como também pela fé, confiança e optimismo que depositou em mim ao longo do doutoramento. E, ao meu co-orientador Dr. François Rigal: -"Incroyable, c'est déjà fini. C'été seulement possible grâce à toi aussi. Un grand et gros merci beaucoup".

Aos colaboradores e co-autores Dr. Artur Gil, Dr. Pedro Cardoso, Dr. Thomas J. Matthews, Prof. Jens M. Olesen muito obrigada por todos os vossos contributos, desde o simples comentário ou opinião até à análise mais complexa, permitiram-me realizar esta tese.

Aos investigadores Dr. Virgílio Vieira e Dr. Matthias Jentzsch, no auxílio da identificação de morfoespécies de lepidópteros e da espécie *Xanthandrus azorensis*, respectivamente.

À FRUTER, mais concretamente à Sra. Conceição Carvalho e ao Serviço Desenvolvimento Agrário da Ilha Terceira, o Sr. Eng. Jorge Martins pela disponibilização dos dados que permitiram efectuar a análise económica apresentada no Capítulo 4.

A todos os elementos do Grupo da Biodiversidade dos Açores, mas em especial à Enésima Mendonça, ao Luís Barcelos, ao Reinaldo Pimentel, à Carla Rego, ao Mário Boeiro, à Débora Henriques, ao Rui Nunes, ao Rui Carvalho, ao Orlando Guerreiro, à Teresa Ferreira, à Rita Godinho, à Isabel Amorim, à Prof. Rosalina Gabriel, ao Prof. Rui Elias e ao Fernando Pereira (aka Pardal), desde os simples momentos de partilha, ao auxílio na identificação de espécies, no domínio do sistema de informação geográfica até à colaboração nas saídas de campo, todos os contributos para a minha formação "avançada" foram de grande valor.

Em último, mas não menos importante à minha família, pai Valeriano e mãe Iva, por implantarem o "bichinho da curiosidade", ao meu marido Bruno e filho Miguel, aos meus irmãos e cunhadas pelo apoio ao longo deste caminho.

Esta dissertação foi desenvolvida no âmbito do projecto de doutoramento - M3.1.2/F/031/2011 financiado pelo Fundo Regional da Ciência e Tecnologia, Secretaria Regional do Mar, Ciência e Tecnologia do Governo Regional dos Açores.

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Abstract

Worldwide declines in biodiversity have prompted concerns about the functioning of ecosystems that may rely on it. This is particularly true for insect pollinators that provide a key ecosystem service (ES): the pollination of plants, which is essential in the maintenance of plant biological diversity and food production. However, pollinator communities are currently under threat throughout the planet mainly because of land use changes that is considered to be one the most important contemporary drivers of biodiversity loss. Land-use changes are nowhere more apparent than on remote oceanic islands that have been disproportionately affected by anthropogenic disturbances since the last centuries. Therefore, there is an urgent need to better identify the pathways responsible for the alteration of insect pollinator communities and its respective plant-pollinator insects network structure in order to better plan their conservation, restoration and to preserve the ES that they may supply for humans. Here, I investigated the impact of land-use changes: (i) on flower-visiting insect species community structure (chapter 2), (ii) on plant-insect interaction networks (chapter 3), (iii) on pollination ecosystem services provision taking also into account its economic value (chapter 4), and (iv) I propose priority areas for the insect pollinator conservation (chapter 5). Flower-visiting insects were sampled over two years using a standardized protocol along 50 transects across five different habitats corresponding to a land-use gradient in Terceira Island (Azores). The results revealed that the studied flower-visiting insect communities were dominated by indigenous species (mostly native non-endemic species) with a prevalence of species of intermediate abundance. Communities of flower-visiting insects were also highly simplified across the entire gradient with little differences between habitats, except between native forest and intensive pastures. In the absence of strong exotic competitors, indigenous pollinating insects have expanded their range and occupied new anthropogenic habitats, also possibly facilitating the expansion of a large number of exotic plant species. Remarkably, pristine vegetation areas, but also the orchards and agricultural areas have relatively high values of pollination services, even though both land uses have opposite disturbance levels. Concerning the plant-insect network structures, they were small and highly simplified, nested and non-significantly modular. The generalist nature and relative abundance of individual insect pollinators was found to be one of the main drivers of the network structure, which was expected for a young and small oceanic island. Moreover, when I pooled all habitats in one global network, there was no evidence for modularity which suggest that habitats differences did not generate any specific structures highlighting the fact that the modern Azorean island landscape is relatively uniform or homogeneous with respect to pollinator species. Concerning the economic valuation of pollinator insect communities, insect species contribution totals 36.2% of the total mean annual agricultural income of the pollinator-dependent crops, emphasizing the importance of insect pollinators in agricultural production. In addition, and to complement this latter result, I assessed the overall different land uses as possible conservation areas and realized that apart from the well preserved and protected native forest of Terceira, other land uses, such as naturalized vegetation areas, exotic forests, and semi-natural pastures, could serve as a continuum to protected areas network. This result has profound implications for the conservation of Terceira Island insect pollinators, implying the need of sustainable management practices across the landscape.

Location

Terceira Island, Azores

Taxa

Coleoptera, Diptera, Hymenoptera and Lepidoptera

Keywords

Ecosystem services (ES), economic valuation, conservation, land-use change, mutualistic networks, nestedness, priority areas, pollinator insects, species abundance distribution (SAD), oceanic island, Azores.

Resumo

As preocupações relativamente ao funcionamento dos ecossistemas surgiram com o declínio mundial da biodiversidade. Esta relação é particularmente evidente para os insectos polinizadores responsáveis por um importante serviço de ecossistema: a polinização das plantas, essencial para a manutenção da diversidade biológica das plantas e produção de alimentos. Porém, actualmente as comunidades de polinizadores encontram-se ameaçadas por todo o planeta, principalmente devido às alterações do uso do solo, considerado um dos factores contemporâneos mais importantes pela perda da biodiversidade. As alterações do uso do solo revelam ser mais proeminentes em ilhas oceânicas isoladas que foram desproporcionalmente afectadas pelas perturbações antropogénicas nos últimos séculos. Como tal, é urgente identificar devidamente as vias responsáveis pela mudança das comunidades de insectos polinizadores e subsequente estrutura das redes plantas - insectos polinizadores de modo a planear adequadamente a sua conservação, restauro e para a preservação dos serviços de ecossistemas que podem suprir os humanos. Nesta tese foi investigado o impacto das alterações dos usos do solo: (i) na estrutura da comunidade dos insectos polinizadores (capítulo 2), (ii) nas redes da interacção planta-insecto (capítulo 3), (iii) nos serviços de polinização tendo em conta o seu valor económico (capítulo 4), (iv) e foram propostas áreas prioritárias para a conservação dos insectos polinizadores (capítulo 5). Os insectos polinizadores foram amostrados durante dois anos através de um protocolo de amostragem padronizado em 50 transectos, em cinco tipos de habitat diferentes correspondendo a um gradiente do uso do solo na ilha Terceira (Açores). Os resultados revelam que as comunidades de insectos polinizadores estudadas são constituídas maioritariamente por espécies indígenas (sendo a maioria espécies nativas não endémicas) com prevalência por espécies de abundância intermédia. As comunidades de insectos polinizadores são também muito simplificadas ao longo de todo o gradiente com poucas diferenças entre os habitats, excepto entre a floresta nativa e as pastagens intensivas. Na ausência de fortes competidores exóticos, os insectos polinizadores indígenos expandem e ocupam novos habitats antropogénicos, facilitando assim a expansão de um vasto número de espécies de plantas exóticas. Notavelmente, não só as áreas de vegetação pristina, mas também as áreas agrícolas e de pomares possuem valores elevados de serviços de polinização, apesar de ambos os usos do solo possuírem níveis de perturbação opostos. Quanto às estruturas de rede planta-insecto, estas são basicamente redes pequenas e muito simplificadas, aninhadas e de modularidade não significativa. A natureza generalista e abundância relativa individual dos insectos polinizadores foi considerada como uma das principais causas para a estrutura da rede, o que seria de esperar de uma ilha oceânica recente e pequena. Inclusivé, ao agregar as redes dos habitats numa só matriz, foi verificado que não existe modularidade, sugerindo que as diferenças entre habitats não são suficientes para formar subgrupos interligados, evidenciando assim que a moderna paisagem da ilha Açoreana é uniforme ou homogénea em relação às espécies polinizadoras. Relativamente à valoração económica das comunidades de insectos polinizadores, os insectos contribuem com um total de 36,2% da média anual total do rendimento agrícola das colheitas dependentes dos polinizadores, o que enfatiza a importância dos insectos polinizadores para a produção agrícola. Por fim, a complementar estes resultados, a avaliação dos diferentes usos do solo para a conservação,

permitiu verificar que para além das áreas protegidas e bem preservadas de floresta nativa da Terceira, outros usos do solo, como as áreas de vegetação naturalizada, florestas exóticas e pastagens semi-naturais poderão servir como um continuum para a rede de áreas protegidas. Este resultado tem implicações consideráveis para a conservação dos insectos polinizadores da ilha Terceira, implicando a necessidade de uma gestão mais sustentável das práticas humanas nos ecossitemas agrícolas.

Local

Terceira, Açores

Taxa

Coleoptera, Diptera, Hymenoptera e Lepidoptera

Palavras-chave

Serviços de ecossistema, valoração económica, conservação, alteração do uso do solo, redes mutualistas, aninhamento, áreas prioritárias, insectos polinizadores, distribuição da abundância de espécies, ilha oceânica, Açores.

Chapter 1

General Introduction

1.1 Conservation biology

Biodiversity can be defined as the variability among living organisms from all sources, including diversity within species (e.g. genetic diversity), between species, and of ecosystems. Biodiversity forms also the foundation of the vast array of ecosystem services (hereafter ES, see Box 1 for definition) that critically contribute to human well-being (Magurran, 2007; Cardinale *et al*., 2012). However, it is increasingly being recognized that human activities are having a profound impact on the biodiversity worldwide, unparalleled by any other single species, leading scientists to suggest I have entered a new geological era: the anthropocene (Vitousek *et al.*, 1997). Furthermore, the world's ecosystems have changed even more rapidly and intensely over the last centuries, causing an unprecedented decline of the global biodiversity, which, in turn, has deeply impaired ecosystem functioning and ES provisioning throughout the world (Godfray *et al*., 2010). Biodiversity loss is mainly driven by the alteration of the natural ecosystems through habitat destruction, degradation and fragmentation, human-induced climate change and the introduction of exotic species (Gaston & Spicer, 2004). Since the impacts of those drivers are likely to become even more pronounced in the future (Thuiller, 2007), there is an urgent need to better identify the pathways responsible for the alteration of biodiversity under human pressure in order to better plan its conservation, restoration and to preserve the ES that it may supply for humans. One major impact responsible for biodiversity alteration and subsequent vulnerability of ES, being, therefore, necessary more research applied to it, is on the land-use change (see Box 2 for definition), where increased anthropogenic disturbance often leads to declines in species diversity (Tilman, 1999; Kremen *et al*., 2002; Tscharntke *et al*., 2005, 2012; Chacoff and Aizen, 2006) and is recognized as a major driver of species extinction (Fahrig, 1997; Brooks *et al*., 2002). However, the response of biodiversity to disturbance differs, depending on the level of the latter. So, the implementation of appropriate management actions to mitigate the impact of human disturbance on biodiversity requires, therefore, a better understanding of how species diversity, distribution and abundance patterns are altered in response to land-use change.

Box 1: Defining Ecosystem Services (ES)

Ehlrich & Mooney (1983) were the first authors to define ecosystem service, by mentioning that the "ecosystems are an important source for the human well-being and biocenosis degradation affect its functioning and therefore the providing services to humans". Some years later Daily (1997) defined ecosystem services as "the conditions and processes through which natural ecosystems, and the species that make them, sustain and fulfil human life". With another approach Constanza *et al*. (1997) evaluated the value of ecosystem services and its natural capital at 33 millions of US dollars. Finally, a definition was published in the Millennium Ecosystem Assessment Report, where ecosystem services are considered the benefits that humankind gets from ecosystems without acting in them to obtain these services (MEA, 2005). The services are classified in four categories: (1) services of "maintenance" or "support" (nutrient recycling, photosynthesis), (2) services of "supply" (goods directed exploited by Human as fresh water, timber or food), (3) services of "regulation" (climate regulation, water filtration by soils, pollination), and (4) services "cultural" (recreational, educational and aesthetic vision of the ecosystem).

Conserving biodiversity can be motivated by multiple goals, from cultural and aesthetic to ethical. Maintaining biodiversity like insect pollinating species is also essential to preserve key ecosystem processes or ES that this diversity provides to humans. For instance, most natural systems in tropical and temperate regions unfold an exceptionally large ecosystem volume, providing crucial ES ranging from timber, watershed protection and carbon sequestration to medicinal plants, but also recreation and tourism (Gaston & Spicer, 2004). So, incorporating ES into conservation planning might also promote biodiversity conservation to the stakeholders and public (Cimon-Morin *et al.*, 2013). However, so far, most conservation approaches have only considered biodiversity and, in practice, linking biodiversity conservation, that is to say that ES remains a challenging task in most ecosystems (Cimon-Morin *et al.*, 2013). Furthermore, ES varies greatly in space and time, with the majority of ES providing benefits locally. ES conservation would therefore be better ensured at this scale (i.e. local), where there are human beneficiaries. Hence, ES conservation calls for protected areas to be established close to human populations. Ecosystems in their original natural state provide for potential services, as supporting and regulating services. Priority areas for ES have mostly been assessed based on their potential, e.g. amount of stored carbon or drinkable water (Cimon-Morin *et al.*, 2013), much previous attention has focused on the use of set-aside areas for conservation; however, different combinations of land-use, from no use to extensive, can generate different contributions of ES. In fact, there is an increasing recognition that protected areas are not sufficient to slow down the biodiversity decline, attention now being turned towards the potential utility of managed land for conservation (Tscharntke *et al.*, 2005). For example, agriculture has long been perceived as incompatible in conservation plans, but nowadays scientists are advocating more mutual benefits in what concerns agricultural production and biodiversity conservation (Tilman *et al.*, 2001; Tscharntke *et al.*, 2002; Daily *et al.*, 2003, Chacoff & Aizen, 2006). The benefits among agricultural land-use and native biodiversity rest on a deep understanding of the influence of different land-uses on population and community dynamics.

Box 2: Defining Land-use change

Land-use change, described by Houghton (1994), occurs in various forms, but primarily in changes in the area and in the intensity of use. It is linked to economic development, population growth, technology and environmental change; basically, it is the result of global economy and international trade, with an increase of demand and supply of goods. The global effects of land-use includes: conversion of potential productive land to land with diminishing capacity for crops, forests and housing, its progressive loss of species and the emission of gases to the atmosphere. However, sustainable land-use may produce a great variety of ecological goods and services (Altieri, 1999).

One of the main goals of conservation is to maintain and promote the long-term persistence of species diversity and related ecological processes. Although conservation has traditionally focused on the protection of biodiversity through the design and the implementation of natural reserves, recent evidence indicates that natural reserves alone are not enough to effectively protect biodiversity (Wilson *et al*., 2010). Therefore, conservation practices must go beyond traditional protected areas (Fattorini *et al*., 2012; Vergílio *et al*., 2016) and include human-transformed agricultural landscapes (Daily, 2001; Polasky *et al*., 2005; Pressey *et al*., 2007).

1.2 Pollination: concept, importance and example of an ecosystem service

Pollination is the act of transferring pollen grains from the male anther (male organ) of a flower to the female stigma i.e. the surface of the pistil receptor (female organ). Pollination is essential to the sexual reproduction of the majority of flowering plants (Spermatophytes = Gymnosperms and Angiosperms). There are various types of pollination: auto-pollination, animal pollination (zoophilous) with the majority of these animal pollinators being insects (entomophilous), pollination by wind (anemophilous) and pollination by water (hydrophilous). Pollination can be completed within the same individual; this is the case of autogamy, resulting in the transfer of pollen within a hermaphrodite flower through passive auto-pollination, whether with the help of a carrier (autogamy strict), or by pollen transfer between flowers of a same individual (geitonogamy). This has to be opposed to allogamy, which implies that the pollen deposited in the stigma comes from a genetically different individual. Once in the stigma, the grain pollen (if viable) can germinate and send a pollinic tube that transverses the flower style. The pollinic tube channels the gametes males (spermatic core) to the ovules, allowing fecundation to occur (Fig. 1.1). It is also noteworthy to notice that many plant species have a mixed mating system. In a long-term species perspective, however, plants with mixed mating systems require animal pollination to maintain out-crossing among individuals of the same species.

Pollination of flowering plants represents a vital ES for the sustainable health of the planet and food security. In view of the fact that 74 – 98% of all flowering plants (i.e. about 308.000 plant species) are animal pollinated (Ollerton *et al*., 2011), the plant- animal relationship has been a focus for scientists for many decades, inquiring into some of the fundamental aspects of biology, from evolution and ecology to behaviour and reproduction (Willmer, 2011). Several types of plant-animal relationship exist, but entomophily (plant-insect relationship) is probably the most pervasive and diversified, resulting in great diversity of mutualistic relationships between plants and insects species; the flowering plants provide food resources (nectar and/or pollen), refuges or even the material for the insects' nests, while, in turn, insects assure the plants pollination and/or dispersal. Moreover, Klein *et al*. (2007) have reported that, globally, 87 primary subsistent crops, representing 35% of the worldwide food production, entirely or partially depend on insect pollinators. The total economic value of insect pollination worldwide amounted to €153 billion, which represented 9.5% of the value of the world agricultural production used for human food in 2005 (Gallai *et al.*, 2009).

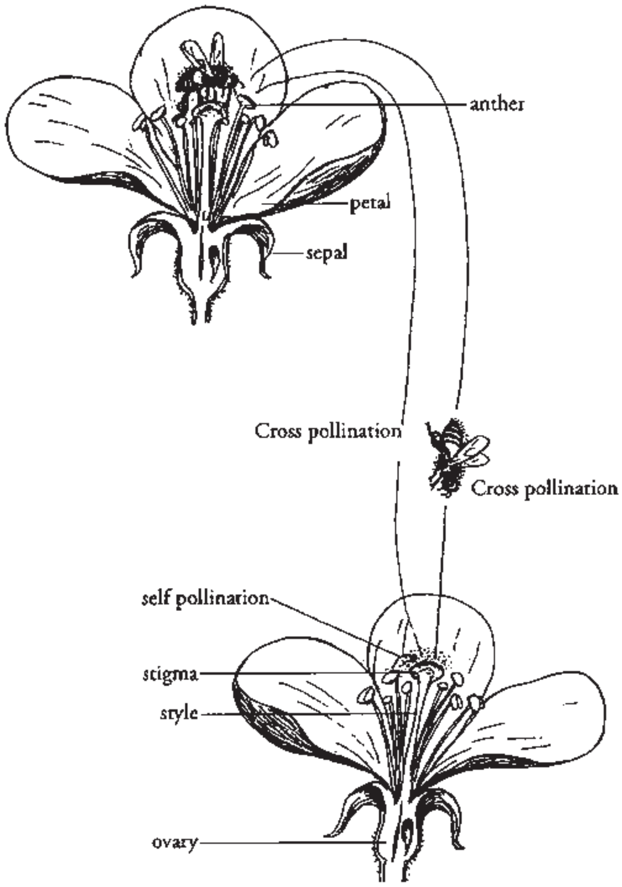


Figure 1.1 Diagram illustrating flower's structure and types of pollination (from Partap, 1999).

1.3 Insect pollinators: a general description

Among insects, pollinators species are particularly frequent within the large orders Hymenoptera (bees and wasps), Lepidoptera (moths and butterflies), Diptera (flies and mosquitoes) and Coleoptera (beetles):

Figure 1.2. Examples of insects from Hymnoptera, Lepidoptera, Diptera and Coleoptera orders. Upper left photo *Lasioglossum villosulum* by Julie A. Weissman (from Weissman *et al*., 2017), upper right photo Pieris brassicae azorensis by Paulo A. V. Borges (from Azorean Biodiversity Portal), down left photo *Stomorhina lunata* by Paulo A. V. Borges (from Azorean Biodiversity Portal) and down right photo *Anaspis proteus* by Paulo A. V. Borges (from Azorean Biodiversity Portal).

Hymenoptera*:* Hymenoptera constitute, after the Coleoptera, the most diversified order and are estimated to be more than 120.000 species described to daute (Leonhardt *et al*., 2013). The Anthophila group (bees) is probably the most studied group of insect pollinators and it is considered the largest one (Steffan-Dewenter, Potts & Packer, 2005). Bees feed mainly on both nectar and pollen.

Lepidoptera: Lepidoptera have mouth apparatus, composed of a proboscis that can enrol by itself, being able to forage in flowers with very long corollas. The majority of Lepidoptera feed on nectar, but they cannot generally suck viscous nectars (Kim, Gilet & Bush, 2011). In general, Lepidopterans are also effective pollinators, especially large and partially endothermic sphingid species (Willmer, 2011).

Diptera: Dipterans are the only flying insects with only one pair of wings. They are well adapted to the pollination due to their rapid and secure flight, their lightness and ability to land with precision on the flowers. Dipterans are important flower visitors in some tropical and semiarid zones, but their importance increases especially in regions where other visitor groups are uncommon, such as some oceanic islands and high-altitude habitats.

Coleoptera: Coleopterans are the most primitive inset pollinators (Forbes, 1922). They often feed on every part of the flower. In this sense, many flower-visiting beetles are destructive feeders and may damage or consume whole flowers, including petals and ovule tissues (Willmer, 2011). During the visit, the pollen is deposited in their body while passing along the anthers, then redeposit on stigmas of the same flower or in a new flower, in the following visit. To suck the flower nectars and extract the nectar very rapidly, some Coleoptera have morphological adaptations, like the frontal projection of mouth pieces or the prothorax elongation (Kevan & Baker, 1983). Beetles are often overlooked although they represent an important part of the insect pollinators, especially in the southern hemisphere and in arid or tropical climates. Beetles are less mobile than bees or flies, and are rarely sufficiently specific in their visits to the generalist flower types.

1.4. Species diversity and abundance distribution

The aforementioned information allows to recognize which type of insect species are part of the community composition this study addresses. Also to perform a community analysis, species diversity and abundance must be measured to understand the variation of spatio-temporal patterns. For this purpose, a considerable number of approaches of diversity indices and abundance models were taken into consideration and some have been used (Magurran, 2004). The indices are quantitative assessments of how many different species exist in a community, taking into account the abundance distribution of these species, e.g. Shannon index (Magurran, 2004).

Hence, species diversity, according to Whittaker (1960), can be spatially divided into three inter-related components: alpha (α), beta (β) and gamma (γ) diversity, with the total diversity of a geographic area (gamma diversity) being the product of diversity within (alpha diversity) and among (beta diversity) communities of that area. This diversity partitioning can also be done by an additive instead of multiplicative approach, where total diversity is the sum of its alpha and beta components (Landem, 1996). The most studied components are apha and beta (Cardoso *et al*., 2015).

In ecological communities, the species abundance distribution (SAD) influences the ability to distinguish biology (niche) and chance (neutral) driven factors of stability. In most communities, the SAD is skewed, i.e. a few species are abundant, and the majority are relatively rare (McGill *et al*., 2007). The skewed SAD can confound the differences between niche- and neutral-based drivers of plant – pollinator interaction patterns, so the relative importance of abundant species for a given ecological process, and the redundancy of rare species for that process, may be driven by species traits that are separate from abundance (e.g. pollen or nectar rewards of plants), or by abundance itself, but when species abundances are skewed, it is impossible to empirically tease apart those patterns (Blüthgen *et al*., 2008; Blüthgen, 2010).

The abundance models allow scientists to understand the relative abundance pattern of the species in a community, i.e. if the species are common or rare in comparison to other species. A large number of SAD models have been proposed (see Matthews & Whittaker, 2014). The most frequently ones are the logseries (Fisher *et al.*, 1943) and the lognormal (Preston, 1948) models. The logseries results from the Poisson sampling of a gamma distribution after a certain relevant limit is taken, and characterises a situation in which singletons represent the most common abundance class. The lognormal represents a situation in which the logarithms of the different species' abundances follow a Gaussian distribution, and thus it characterises a situation in which most species are of intermediate abundance (Preston, 1948). As the continuous lognormal distribution allows fractional abundances, the Poisson lognormal model is often used instead (Matthews & Whittaker, 2014). More recently, the Gambin SAD model was introduced to provide a useful tool for assessing variations in SAD form between samples (Ugland *et al.*, 2007). Gambin is a stochastic model, which combines the gamma distribution with a binomial sampling method. The model has a single free parameter, alpha (α), which characterises the distribution shape; communities dominated by rare species (logseries-like SADs) have low α values, whilst lognormal-like SAD shapes are characterised by higher α values (Ugland *et al.*, 2007; Matthews *et al.*, 2014).

1.5. Ecological networks: plant-insect interactions

Species interaction networks have been referred to as "the architecture of biodiversity" because of their importance for community composition and dynamics (Jordano *et al.*, 2006; Bascompte & Jordano, 2007). Several forms of interactions exist, such as symbiosis or mutualism, through which two species can get benefit (positive interactions) or the parasitism or predation, where one species gets benefit in detriment of the other (negative interactions). Plant-insect pollination is one form of mutualism, since, in most of cases, it benefits from the reproduction of plants while the insect pollinators benefit from the provision of resources (Ollerton & Waser, 2006). Effectively, plant-insect pollination will be the focus of this work.

An interaction network can be defined as a set of entities that establish links among them. Network analyses are increasingly being used in ecological studies. Understanding network structure and its underlying causes are, indeed, essential parts of any study of biodiversity and as of critical importance to better quantify how ecosystems respond to global change (Amaral *et al.*, 2000; Strogatz, 2001; Dorogovtsev & Mendes, 2002; Albert & Barabási, 2002; Newman, 2003, 2004).

Networks has been first analysed and described by the theory of graphs, a very important discipline in mathematics (Erdös & Rényi, 1959). Briefly, a network will be defined as a group of nodes and a probability p, where two chosen nodes by chance are established through a link. Innumerable mathematical theorems related to graph theory have been proposed. However, their application to real data, and particularly ecological data, has been questioned because the majority of networks are more heterogeneous than predicted by the theory, i.e. they show a wide variability in the number of links established by the nodes. Two kinds of networks can be distinguished: one-mode and two-mode networks. In one-mode networks, nodes are similar to each other and are, thus, assigned to the same category of objects. In two-mode networks, there are two well-defined categories of nodes, and the links are established between them, but not between the nodes of the same category. These two-mode networks are represented by the bipartite graphs (Fig. 1.3).

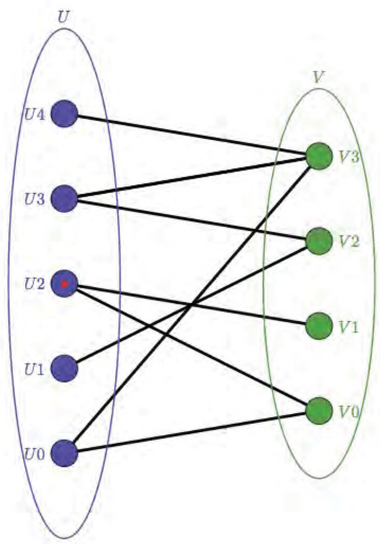


Figure 1.3. Example of a bipartite graph.

The plant-insect pollinators' mutualistic networks are, by definition, two-mode networks. The bipartite representation of the mutualistic networks demonstrates the implicit reciprocity implied in these types of interactions and contributes to understand the complexity of highly diversified mutualistic interactions (Jordano, 1987; Bascompte *et al*., 2003, 2006; Jordano *et al*., 2003, 2006). A pollination bipartite graph is defined as a matrix (R) of links composed of rows representing the plant species (i), and columns representing the insect pollinator species (j). If a pollinator interacts with a plant, then r_{ij} of the matrix is equal to the number of links between the plant species and the pollinator species, when related with a network of abundances, and with 1 (i.e. presence of a link) when related to a binary network. Moreover, a network can be further decomposed in different compartments, called *modules*, which correspond to groups of species within a network, being highly connected to each other. Specialist pollinator species usually tend to interact only with plant species within their own module.

The network theory described above allows the visualisation of the links in diversified communities and permits to statistically quantify and compare the network models between communities. In ecology, network studies are well represented for both mutualistic interactions (e.g. plant-pollinator, plant-seed disperser interactions) and trophic ecology (e.g. predator-prey) (Dunne *et al*., 2002; Blüthgen *et al*., 2007). Based on these studies, a large number of network parameters were developed to describe network interactions, at both network scale and/or species scale (see Dormann *et al*., 2009 for review).

In a network, a node is characterised by its degree, i.e. the number of links established towards other nodes. In complex networks, such as plant-pollinator interactions, it is important to characterise the intensity of interactions. A quantitative parameter of degree is the *strength* of a node, i.e. sum of nodes dependences connected to that node (Bascompte *et al*., 2006).

Understanding the underlying structure of such networks may give insights into the functionality and behaviour of the systems they represent (Bascompte & Jordano, 2007). Two important structural patterns can be identified in bipartite networks: nestedness and modularity. Nestedness describes such a hierarchical ordering of nodes, such that more specialised nodes have interactions with a subset of the partners with which the more generalised nodes interact (Bascompte & Jordano, 2007). Modularity captures the community structure of a network as distinct clusters of interactions, such that there are more connections within communities than between communities. While these network architectures are easy to describe in writing, their quantitative measurement for a given network constitutes a difficult task. Several different methods have been proposed in each case but it is currently unclear which of them should be used in practice (Bascompte & Jordano, 2007).

Nestedness network parameter also allows the assessment of the level of specialization in a given pollinator network. The core of the network is usually composed of highly connected generalist species (i.e. a pollinator that interacts with many different species of plant), while specialist species interact with a small subset of the plant species that the generalists also interact with. This represents an asymmetrical network structure classified as *nested* (Bascompte *et al*., 2003; Thébault & Fontaine, 2008, 2010), which gives a network some resilience, also avoiding species' extinction (Memmott *et al*., 2004). Nested matrices are characterized by two main properties: i) first, they are the core of generalist species, plant or animal species, which interact with each other. As a consequence, some species can interact with a wide number of other species, allowing functional redundancy to occur and the possibility of alternative interactions, due to the matrix persistence when some interactions disappear; ii) in addition, asymmetries exist in different levels of specialization, i.e. specialist plants also tend to interact with the majority of generalist pollinator species (Vázquez & Aizen, 2004).

Prior to complex network analysis, as described above, it is also essential to properly investigate how diversity, composition and abundance of both insects and plants communities are distributed and how they might correlate through direct and/or indirect effects e.g. the diversity of plant species in a community is positively correlated to the abundance and diversity of the associated pollinating fauna (Potts *et al*., 2003). Insect and plants communities are composed of different types of species, from the most specialists to the most generalists. After Darwin's evolution theory (1862), the interactions among plants and pollinators were during a long time considered as dominated by specialization. Floral traits (or phenotype) were considered as the adaptations to a type of pollinator, allowing to know the potential pollinator of that plant (Fenster *et al*., 2004). The most known example is the one of the Sphingidae moths with the long proboscis specialised in an orchid species (Darwin, 1862). These morphological adaptations have led to the pollination syndrome concept (Johnson & Steiner, 2000; Fenster *et al*., 2004). However, it is now commonly accepted that the specialist behaviour is not the most common one. Generalism appears to be the most common type of interaction in natural communities (Waser *et al*., 1996; Ollerton, 1996; Memmott, 1999). The majority of plants species are pollinated by various pollinating species and, on the same way, one pollinating species has the tendency to visit several species of plants in same genus or family. Moreover, the spatial and temporal variability of these interactions show, without any doubt, generalism to be the most common, once a spatial and/or temporal scale of a study increases (Herrera, 1988; Fenster & Dudash, 2001).

The degree of specialization of plants or animals is well studied and discussed, and in a range of network studies we can observe that it goes from a strict specialization to a strong generalization (Jordano, 1987; Waser *et al*., 1996; Olesen & Jordano, 2002; Bascompte *et al*., 2003; Ollerton & Waser, 2006). In summary, two levels of specialization measures can be distinguished as: (1) species characterisation apart from the network and (2) specialization degree in a network of interactions (Blüthgen *et al*., 2006). Hence, the species specialization level is very simple depending on its biological interpretation, where the analyses at network level allow comparisons to be made between different types of networks, i.e., the analyses made with the purpose to compare plant-pollinator networks across a geographical gradient (Ollerton & Cranmer, 2002; Olesen & Jordano, 2002). The comparable network analyses are equally used to study the patterns at community scale, like co-evolutionary adaptation (Waser *et al*., 1996), and ecosystem stability (Bascompte & Jordano, 2007; Dunne, Williams & Martinez, 2002; Vázquez & Simberloff, 2002). Frequently, at species scale, the specialization or the generalization of interactions are characterised as the number of connectors of that species (*degree*). In this qualitative approach, the interactions between a pollinator and a plant are only considered as binary (present or absent), this way ignoring the distinction between strong, weak or random interactions.

The measure usually used to characterise specialization at community scale is *connectance* (Jordano, 1987; Olesen & Jordano, 2002; Devoto *et al*., 2005) It is defined as the proportion of the number of observed interactions to the total number of possible interactions. In a network matrix with of *i* rows (plants species) and *j* columns (pollinator species), the *connectance* is defined as $C = I/(i * j)$, where I is the number of total interactions observed in the matrix. Consequently, as in the case of number of connectors described above (*degree*), the *connectance* only uses binary information and ignores the interaction strength. In addition, to compare networks, some studies have already used the average number of links per species (L) (Waser *et al*., 1996; Ollerton & Cranmer, 2002; Olesen & Jordano, 2002; Vázquez & Aizen, 2004; Devoto *et al*., 2005). However, the use of L to compare between networks can be problematic, due to the different sizes of networks.

Nevertheless, at an individual or community scale, the analyses based on binary data show evident gaps (Blüthgen *et al*., 2006; Vizentin-Bugoni *et al*., 2016) because they are strongly dependent on the sampling effort. Blüthgen *et al.* (2006) have proposed two specialization metrics: (1) an index of entropy Shannon (H_2') to the network scale, and (2) a standardised metric of the Kullback–Leibler distance (d') to the species scale. The advantage of these two metrics relies on the fact that they are based on quantitative data, i.e. the specialization measure of a given species has into account the information related to other species' level of specialization.

In addition, there are particular constraints concerning the establishment of some interactions, due to particular biological traits of two species. Such constraints are the so-called *forbidden links* (Jordano *et al*., 2003; Olesen *et al*., 2011), not possible to observe, i.e. the pollinators and/or plants functional traits can be responsible for their nature to be more or less specialist, limiting the number of interacting species. For example, Jordano *et al*. (2003) associated the non-observed interactions to the phenology mismatch and size restrictions.

In Azores, about 1199 species belonging to the major important pollinator insect groups can be found in the islands, 14% of which are considered endemic species, i.e. found only in the region (Borges *et al*., 2010; Weissmann *et al*., 2017). From the groups described above, beetles (Coleoptera) have the highest number of species and endemic species, followed by flies (Diptera) (Table 1.1). On the other hand, bees, wasps and ants (Hymenoptera) are the less diverse (Table 1.1) with few social species, apart from ants and *Apis mellifera*. On the opposite, butterflies and moths (Lepidoptera) is the group with the highest percentage of endemic species, with about 27% of endemism (Table 1.1). Nevertheless, the current list of Diptera and Hymenoptera needs a detailed revision, since these are two of the least studied insect orders in the Azores (see Borges *et al*., 2010; Weissmann *et al*., 2017).

Table 1.1. Total number of Azorean insects per order and colonisation status, according to Borges *et al*. (2010) and updates for Hymenoptera, by Weissmann *et al*. (2017).

Species	Native non-endemic	Native endemic	Introduced	Total
Coleoptera	121	72	326	519
Diptera	246	51	95	392
Hymenoptera	115	10	19	145
Lepidoptera	58	38	47	143

There are very few studies related to insect pollination in the Azores (Valido & Olesen, 2010). In fact, the unique case studies available investigating plant-pollinator networks in the Azores are the study of Olesen *et al*. (2002), who investigated the communities of insect pollinators in the island of Flores, and the recent study of Weissmann & Schaefer (2017), investigating complexes of generalist insect pollinators in Azorean endemic plants *Azorina vidalii*, *Euphrasia azorica*, *Myosotis azorica* and *Solidago azorica,* in Corvo island. Other available studies investigated pollination in the plant reproduction perspective, namely: Olesen *et al*. (2012), who investigated the Azorean endemic plant *Azorina vidalii* in Corvo, Flores, Santa Maria and Terceira; Pereira (2006, 2008) who studied *Vaccinium cylindraceum* and *Juniperus brevifolia* (Cupressaceae) in all islands, except Graciosa. In pollination network study carried out by Olesen *et al*. (2002) in Flores, the plant species were more frequently visited by one native species of Halictus (Apidae) and the introduced *Apis mellifera*. In the study of Olesen *et al*. (2012) the flower visitors recorded, associated with *Azorina vidalii* were: hawkmoth *Macroglossum stellatarum*

(Sphingidae) on Santa Maria, the introduced honeybee *Apis mellifera*, the monarch butterfly *Danaus plexippus* (Nymphalidae) and some unidentified Muscidae, Calliphoridae and Sepsidae (Diptera) on Terceira and Santa Maria; *Apis mellifera* and *Sepsis* spp. (Sepsidae, Diptera) were the only flower visitors in Corvo and Flores Islands. In the recent study of Weissmann & Schaefer (2017) the endemic plant studied in Corvo Island is pollinated by a large number of species (5 to 21 insect species, mostly belonging to Hymenoptera and Diptera).

In Pereira (2008), the endemic Azores Blueberry (*Vaccinium cylindraceum*, Ericaceae) was visited by Microlepidoptera *Scoparia semiamplalis* (Crambidae), by ants in Santa Maria, and some Macrolepidoptera *Hipparchia* spp. (Nymphalidae). The domestic honeybee *Apis mellifera* visited these flowers (in the same island), but only in low–altitude populations. Hence, no other solitary bees and the bumblebee *Bombus ruderatus* visit edthem. Also, the flower-visiting Microlepidoptera use the endemic *Juniperus brevifolia* as their host plant (Pereira, 2006).

1.6. Thesis outline: aims and research questions

Island plant-pollination networks have distinct ecological characteristics when compared to the mainland systems (Valido & Olesen, 2010). In fact, due the isolation, many groups of insect pollinators are unable to overcome the ocean barrier, favouring the colonization of strong and highly dispersive insects. Therefore, island plant-pollination networks are characterised by either the adaptation of specialist pollinators (e.g. birds, lizards) or generalist pollinators (e.g. flies) (e.g. Olesen *et al*., 2002; Olesen & Jordano, 2002; Dupont *et al*., 2003; Kaiser-Bunbury *et al*., 2009). Hence, there is a general knowledge that the simplified nature of ecological networks on island's systems make them prone to species extinction and vulnerable to habitat disturbance and invasive species in comparison to mainland (Hansen *et al*., 2002; Valido *et al*., 2002; Winfree *et al*., 2009). However, the high proportion of generalist pollinators for a given plant may also indicate some resilience in the plant perspective (Weissmann & Schaefer, 2017).

Pollination network studies are scarce in islands, particularly in the Azores. This thesis aims to contribute to fulfil this gap and respond to key ecological questions related to plant-pollinator interactions. Accordingly, Terceira Island was selected as the case study to investigate the impact of land-use changes: (a) on flower-visiting insect species community structure (chapter 2), (b) on plant-insect interaction networks (chapter 3), (c) on pollination services taking into account its economic value (chapter 4), (d) and proposed priority areas for the insect pollinator conservation (chapter 5; see Fig. 1.4).

This thesis is based on an observational study with emphasis on large-scale patterns operating at an island scale. Thus, Terceira Island, comparing to the other Azorean islands: i) is one of the best studied in the Azores, concerning arthropod diversity and community structure; and ii) has the best subset of well-preserved native forest in the Azores (Gaspar *et al*., 2011). The thesis is organized to answer several key ecological and conservation questions:

1- *How are flower visiting insect communities organised across different habitat types corresponding to a gradient of human disturbance?*

Despite reasonable knowledge on the impact of land-use changes on the Azorean arthropod community structure (Borges *et al.*, 2008; Cardoso *et al.*, 2009, 2010a; Florencio *et al.*, 2013, 2015), there is no study investigating the impact of human disturbance on the Azorean insect pollinator community structure.

The goal was to analyse and compare the composition of flower-visiting insect communities, the diversity, abundance and richness between different land-use types, following a gradient of disturbance (Fig. 2.1).

2- *What are the characteristics of the plant-insect interaction networks in the different habitat types?*

In chapter 3, the aims were to characterise the plant-insect pollinator networks structure relatively to size, species richness and abundance, connectance, nestedness, modularity and generalization, comparing each network along with a gradient of land-use disturbance and identifying the networks main linkage drivers.

3- *Which and where are the possible contributions of the insect species to the pollination services in Terceira Island?*

Ecosystem services are currently of key importance to human well-being, a way to value nature and to turn conservation more appealing to individuals and institutions (Daily *et al*., 2009). The current challenge is to measure the underlying role of biodiversity in providing services. In the Azores, the studies of Cruz *et al*. (2011), Mendonça (2013) and Vergílio *et al*. (2016) are the unique available quantifying ecosystem services but they do not consider pollination.

In chapter 4, the focus was in the investigation of the potential contribution of Azorean insects to pollination services. The research was performed to determine the spatial variations of the pollination services, and to inquire whether the variations of the pollination services were influenced by the different land-uses. In addition, I have investigated the number of crops, for which production has a certain level of dependence on insect pollinators (or vulnerability ratio), and have estimated the island's insect pollinators economic value.

4- *What is the best subset of areas to protect the insect pollinator communities in Terceira?*

Recent studies in Azores have identified key areas for conservation using arthropods (e.g. Gaspar *et al*., 2011; Fattorini *et al*., 2012), but no study is specifically available for insect pollinators.

To fulfil this gap, Chapter 5 was dedicated to develop and apply a different spatial planning approach that explicitly accounts for the contribution of a diverse range of land uses for the communities of insect pollinators' conservation in Terceira Island.

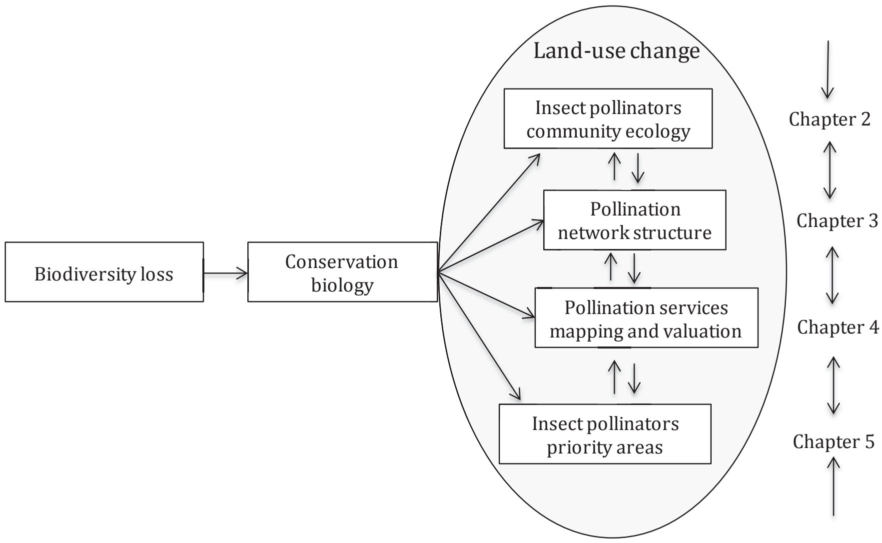


Figure 1.4. A schematic insight of doctoral thesis approach and contents.

Chapter 2

Impact of land use change on flower-visiting insect communities on an oceanic island

Ana Picanço, François Rigal, Thomas J. Matthews, Pedro Cardoso & Paulo A. V. Borges

In: *Insect Conservation & Diversity*, 10, 211-223. doi: 10.1111/icad.12216

2.1 Abstract

1. Land-use change has profoundly impacted pollinator communities throughout the world. However, the processes through which it acts on pollinator diversity and composition are still poorly understood, especially in highly vulnerable island ecosystems.

2. In this study, we investigated the distribution, abundance, richness and composition of flower-visiting insects to assess their response to land-use change in Terceira Island (Azores).

3. Flower-visiting were sampled over two years using a standardized protocol along 50 transects across five different habitats corresponding to a land-use gradient. Insect species were classified as indigenous or exotics. We assessed changes across habitats using multiple diversity indices, species abundance distribution models (SAD) and species composition metrics (β-diversity), along with plant species composition.

4. We observed that indigenous flower-visiting insects were dominant, both in abundance and species richness, across the entire land-use gradient. Species diversity vary only slightly across the gradient. SADs were lognormal in all habitats, with very few truly common and rare flower-visiting insects and a prevalence of species of intermediate abundance. Species replacement was significantly higher mainly between the two most contrasting habitats (i.e. natural forests and intensive pastures) but was significantly correlated with species replacement of host plant species across the gradient.

5. Our results revealed that the Azorean flower-visiting insect communities were highly simplified across the entire gradient with little difference between habitats. In the absence of strong exotic competitors, indigenous flower-visiting insects expand their range and occupy new anthropogenic habitats, also facilitating the expansion of a large number of exotic plant species.

Keywords

Community assembly, beta diversity, exotic species, flower-visiting insects, land-use change, oceanic islands, native species, pollinator networks, species abundance distribution.

2.2 Introduction

Land-use change is leading to the loss and degradation of natural habitats, resulting in the severe disruption of biodiversity processes and patterns throughout the world (Sala *et al*., 2000). In particular, land-use change has profoundly impacted species ranges and abundances and is now recognized as a major driver of the current extinction crisis (Fahrig, 1997; Brooks *et al*., 2002). As a consequence, key ecosystem processes such as pollination interaction networks have been severely affected, with dramatic consequences for ecosystem functioning and the provision of goods and services for humans (Cane, 2001; Kearns, 2001; Warren *et al*., 2001; Williams *et al*., 2001; Kremen *et al*., 2002; Biesmeijer *et al*., 2006; Klein *et al*., 2007; Steffan-Dewenter & Westphal, 2008; Winfree *et al*., 2009; Potts *et al*., 2010; Groom & Schwarz, 2011; Rader *et al*., 2014). The implementation of appropriate management actions to mitigate the impact of human disturbance on pollination interaction networks requires, therefore, a better understanding of how species diversity, distribution and abundance patterns of pollinators are altered in response to land-use change.

Over the last century, island ecosystems have been disproportionately affected by anthropogenic alterations and a large proportion of recorded extinctions have taken place on islands (e.g. Cardoso *et al*., 2010b; Rando *et al*., 2013; Alcover *et al*., 2015; Régnier *et al*., 2015; Terzopoulou *et al*., 2015). Land conversion of native forest to agricultural and exotic forest is now recognized as one of the major causes of island biodiversity decline, with many extant species predicted to be committed to future extinction as a result of land use change ('the extinction debt'; Triantis *et al*., 2010). These profound changes are known to have impacted several components of island ecosystems (see Connor *et al*., 2012), but very little is known about the impact of land-use change on island ecological networks, and in particular, on pollinating insects.

Insects are responsible for 78-94% of pollination across all flowering plants, and 75% of global food crops (Klein *et al*., 2007; Ollerton *et al*., 2011; Winfree *et al*., 2011). Guaranteeing a diversity of pollinators, particularly the species with a high degree of specialization (Steffan-Dewenter *et al*., 2006; Albrecht *et al*., 2012), is therefore crucial for maintaining gene flow and community stability in plant communities (Ricketts, 2004; Klein *et al*., 2007; Steffan-Dewenter & Westphal, 2008; Cranmer *et al*., 2012). Insular ecosystems usually support less complex networks with lower numbers of pollinator species, are mostly comprised of generalist species (Olesen *et al*., 2002; Whittaker & Fernández-Palacios, 2007) and have less redundancy between species in comparison with continental areas (Olesen *et al*., 2002). Thus, pollinator networks on oceanic islands are potentially highly vulnerable to any kind of disturbance (Traveset, 2002), and can be considered ideal model systems to evaluate the impact of land-use change on the diversity, distribution and abundance of pollinator species (Alarcón *et al*., 2014; Castro-Urgal & Traveset, 2014; Traveset *et al*., 2015; Kaiser-Bunbury & Blüthgen, 2015).

Over the last decade, a large range of negative impacts that can be attributed to land-use change have already been documented for pollinator communities. For instance, previous studies have identified a negative correlation between land-use intensity and the provision of functions sustained by pollinator species (Garibaldi *et al*., 2011, Winfree *et al*., 2011, Rader *et al*., 2014). With increasing land-use intensity, a clear increase of the dominance of common species has also been identified (Tylianakis *et al*., 2005), especially in small island populations that are more susceptible to the disruption of interaction networks (Kaiser-Bunbury *et al*., 2010). In response to intermediate disturbances, studies have also underlined the presence of an initial increase in local pollinator richness, but with some degree of regional homogenization, as the few specialists are replaced by abundant, often invasive, generalists (Kremen *et al*., 2005; Rader *et al*., 2014).

In the present study, we investigate the flower-visiting insect species communities of the Azores archipelago. Located in the North Atlantic Ocean, the archipelago is composed of nine main island, all volcanic and of recent origin (the oldest island being 8.12 Myr BP). The Azorean climate is temperate oceanic, characterized by high levels of relative humidity and small temperature fluctuations. Since the 15th century and the arrival of humans to the Azores, the native semi-tropical evergreen laurel forest (Laurisilva), originally covering most of the surface area across the islands, has been gradually replaced by agricultural land uses (i.e. intensively managed pastures for cattle and semi-natural pastures) and exotic forest (plantations of introduced wood species). Most of the native forest is nowadays confined to Juniperus-Ilex montane forests, characterized by reduced tree stature (usually up to 5 m, rarely reaching 10 m) on shallow soil and rugged terrain at high altitude, mostly between 800 and 1000 m.a.s.l (Martins, 1993; Borges *et al*., 2005; Cardoso *et al*., 2009, 2010a, Elias *et al*., 2016). Recent investigation of the impact of land-use changes in the Azores has shown that native forests and intensively managed pastures are the most important habitats influencing arthropods species composition and diversity, playing a fundamental role as source habitats for endemic and exotic species, respectively (Borges *et al*., 2008; Cardoso *et al*., 2009, 2010a). Intermediate-disturbed habitats, such as semi-natural pastures and exotic forests, also perform important functional roles, acting as corridors connecting native forest fragments for many indigenous arthropod species (Borges *et al*., 2008; Cardoso *et al*., 2009). However, despite the persistence of some Azorean native species in anthropogenic habitats (Fattorini *et al*., 2012), the large spread of exotic species throughout the landscape matrix tends to promote biotic homogenization of arthropod species at both local and island scales (Florencio *et al*., 2013).

In this contribution, we examine the impact of land-use change on flower-visiting insect species community structure in an Azorean island. Based on previous work on Azorean arthropod communities (Borges *et al*., 2008; Cardoso *et al*., 2009, 2010a; Florencio *et al*., 2013, 2015), we predict that: 1) native habitats such as natural forest should support a higher abundance and richness of indigenous flower-visiting insects in comparison to non-native land-uses; 2) species composition of flower-visiting insect communities should change from native habitats to non-native land-uses and 3) the dominance of a few common and many rare flower-visiting insect species should increase as disturbance increases.

2.3 Methods

Study area, sampling and species identification

Our study was conducted on Terceira Island. Terceira is an island from the central group of the Azores archipelago, located in the North Atlantic Ocean (38º 37´N - 38º 48´N, 27º 02´W - 27º 23´W) with an Area 402 km² and maximum elevation of 1023 m. Field work was conducted from June to September 2013 and from July to October 2014, due to favourable weather conditions and relatively high number of plant species in the flowering period. For the current study, I selected five distinct habitat types covering a large percentage of the total island area with, from the least to the most disturbed, **natural forests** (1NatFor) mainly characterized by *Juniperus-Ilex* montane forests and *Juniperus woodlands*; **naturalized vegetation areas** (2NatVeg) composed of both native and exotic plant species; **exotic forests** (3ExoFor) with *Criptomeria japonica* and *Eucalyptus* spp.; **semi-natural pastures** (4SemiPast) with both native and exotic plant species; and **intensively managed pastures** (5IntPast) with mostly *Lolium* spp. and *Trifolium* spp. (Cardoso *et al*., 2013). Compared with previous ecological studies undertaken in the Azores (Borges *et al.*, 2008; Cardoso *et al.*, 2009, 2010a; Florencio *et al.*, 2013, 2015) I added naturalized vegetation areas, dominated by *Erica azorica*, *Pittosporum undulatum* and *Rubus hochstetterorum*, as an important habitat for flower visiting insects, because of its recent growing extent due to pasture abandonment and combination of native and exotic flora. Detailed features regarding each habitat type are outlined in Table 2.1.

Table 2.1. Habitat descriptions with information on the altitude, main plant species (see Sjögren, 1973). NatFor (natural forests), NatVeg (naturalized vegetation areas), ExoFor (exotic forests), SemiPast (semi-natural pastures), IntPast (intensively managed pastures).

	NatFor	**NatVeg**	**ExoFor**	**SemiPast**	**IntPast**
Altitude (m)	460-950	76-649	126-624	433-641	73-334
Main plant species	*Juniperus brevifolia*; *Laurus azorica*; *Ilex perado* subsp. *azorica*; *Vaccinium cylindraceum*; *Myrsinea africana*; *Erica azorica*	*Erica azorica*; *Pittosporum undulatum*; *Rubus hochstetterorum*	*Cryptomeria japonica*; *Eucalyptus* sp.	*Lotus pedunculatus*; *Agrotis stolonifera*; *Anthoxanthum odoratum*; *Rumex azoricus*; *Holcus lanatus*	*Lolium perenne*; *Trifolium repens*; *Holcus lanatus*

In each habitat type we chose 10 sites in which 10m long line-transects (1m width) were set up (Pollard & Yates, 1993), making a total of 50 transects located across the entire island (Fig. 2.1, see Table 2.2 for details). To select the 10 sites per habitat type we tried to maximize the covered environmental diversity following Jiménez-Valverde & Lobo (2004) and Aranda *et al*. (2011). First, an environmental matrix for Terceira Island (see Borges *et al*., 2006) was compiled using climatic, topographic and geological variables with a resolution of 100x100m. Using the k-means non-hierarchical clustering algorithm we grouped all cells of each habitat type in 10 clusters, making a total 50 clusters (5 habitats x 10 groups). For each cluster, we ordered the cells according to their distance to the group's multidimensional centroid using Euclidean distance. The first cell in this ranking, deemed to be the most representative of the cluster, was chosen for sampling. If it was impossible to reach the selected cell in the field due to inaccessibility or lack of authorization from land owners, the second cell was chosen and so forth.

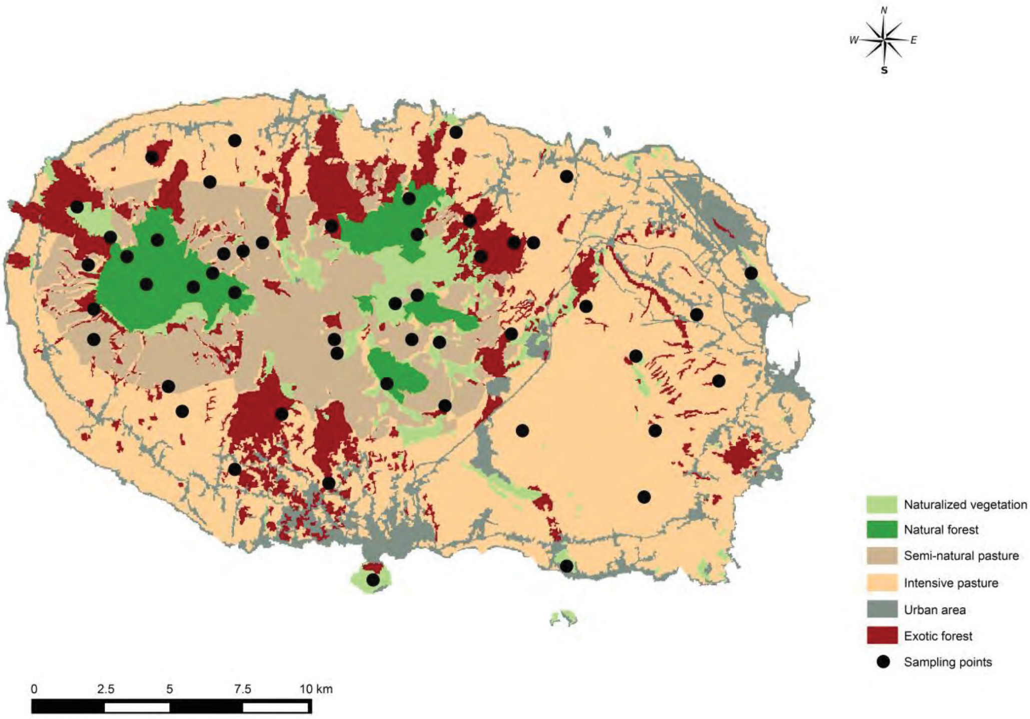


Figure 2.1. Land-use distribution map of Terceira Island with the selected sampling sites as black dots: NatFor (natural forests), SemiPast (semi-natural pastures), NatVeg (naturalized vegetation areas), ExoFor (exotic forests), IntPast (intensively managed pastures) (cartographic information from DROTRH (2008) and Gaspar (2007), see also Gaspar *et al.* (2011)).

Transect surveys were carried out once per year and repeated in the following year, in a randomised order, under sunlight (from 9 a.m. to 6 p.m) and only in sunny weather, with a duration of 180 minutes per transect. Transect location was selected to encompass spots of dense flowering. Each flower along every 10 m transect was surveyed for 4 minutes to guarantee effective contact of the insect, therefore only insects probing for nectar or eating/collecting pollen (foraging) were recorded. Flower-visiting insects were observed and collected with a pooter when it was not possible to identify them in the field. The specimens collected were sorted first into morphospecies and later identified to species-level under the supervision of Prof. Paulo Borges, following the taxonomic nomenclature in Borges *et al.* (2010). When species-level identification could not be resolved, individuals were identified to the lowest taxonomic unit possible and classified as morphospecies. Voucher specimens and a reference collection were deposited in EDTP – Entomoteca Dalberto Teixeira Pombo, University of Azores, Angra do Heroísmo, Portugal. All species were classified as indigenous or exotic species. Indigenous species may be endemic (i.e. found only in the Azores) or native non-endemic (i.e. species that colonized the Azores by natural long-distance dispersal mechanisms). Exotic species are those whose original distribution range did not include the Azores and are believed to have arrived as a consequence of human activities; these species often have a cosmopolitan distribution (see Borges *et al.*, 2010).

Table 2.2. Geographical coordinates for all sites in Terceira Island for each habitat type: NatFor (natural forests), NatVeg (naturalized vegetation areas), ExoFor (exotic forests), SemiPast (semi-natural pastures), IntPast (intensively managed pastures).

Habitat	Transect Code	Latitude	Longitude	Altitude
NatFor	NatFor1	4284392.5	480914.9	467.79
	NatFor2	4289592.5	472614.9	798.74
	NatFor3	4287992.5	472214.9	950.53
	NatFor4	4289792.5	482014.9	675.79
	NatFor5	4288992.5	471514.9	877.96
	NatFor6	4287892.5	473914.9	788.79
	NatFor7	4291092.5	481714.9	460.64
	NatFor8	4287592.5	482014.9	633.44
	NatFor9	4288392.5	474614.9	683.32
	NatFor10	4287692.5	475414.9	590.53
NatVeg	NatVeg1	4290792.5	469714.9	312.05
	NatVeg2	4285992.5	479014.9	500.11
	NatVeg3	4285892.5	482814.9	513.66
	NatVeg4	4286192.5	485414.9	323.31
	NatVeg5	4288392.5	494114.9	76.31
	NatVeg6	4293492.5	483414.9	82.17
	NatVeg7	4289692.5	470914.9	649.19
	NatVeg8	4287292.5	481214.9	632.95
	NatVeg9	4277292.5	480414.9	88.21
	NatVeg10	4277792.5	487414.9	88.04
ExoFor	ExoFor1	4284492.5	492914.9	126.89
	ExoFor2	4290292.5	483914.9	377.27
	ExoFor3	4289192.5	475714.9	471.40
	ExoFor4	4292592.5	472414.9	356.58
	ExoFor5	4280792.5	478814.9	139.04
	ExoFor6	4288992.5	484314.9	373.96
	ExoFor7	4290092.5	478914.9	537.45
	ExoFor8	4283292.5	477114.9	344.90
	ExoFor9	4287092.5	470314.9	624.26

	Transect Code	Latitude	Longitude	Altitude
	ExoFor10	4289492.5	485514.9	157.73
SemiPast	SemiPast1	4289092.5	475014.9	502.39
	SemiPast2	4285992.5	481814.9	574.22
	SemiPast3	4282692.5	490614.9	453.36
	SemiPast4	4285392.5	489914.9	438.35
	SemiPast5	4288692.5	470114.9	641.87
	SemiPast6	4284292.5	473014.9	433.89
	SemiPast7	4285992.5	470314.9	528.33
	SemiPast8	4285492.5	479114.9	494.89
	SemiPast9	4289492.5	476414.9	435.93
	SemiPast10	4283592.5	483014.9	491.48
IntPast	IntPast1	4281292.5	475414.9	157.85
	IntPast2	4287192.5	488114.9	310.22
	IntPast3	4291892.5	487414.9	82.61
	IntPast4	4280292.5	490214.9	222.26
	IntPast5	4291692.5	474514.9	327.37
	IntPast6	4286892.5	492114.9	73.09
	IntPast7	4283392.5	473514.9	254.43
	IntPast8	4293192.5	475414.9	160.41
	IntPast9	4289492.5	486214.9	209.37
	IntPast10	4282692.5	485814.9	334.88

Data analysis

Initially, we performed several statistical comparison tests (Chi-square, paired *t* test, analysis of variance (ANOVA) followed by Tukey HSD *post-hoc* tests) to identify potential differences between the 2 years of sampling (2013-2014), regarding habitat types, taxonomic orders, colonization status, abundance and richness. A statistically significant increase in species richness was observed between the two years (t = -4.4; p = 0.006; Table 2.3), which was primarily a result of the addition of rare species between years, although in absolute terms the increase was small. The difference in total abundance of individuals per species between years was found to be non-significant (t = 1.43; p = 0.22; Table 2.3). Therefore, in the following analyses we combined data from the same transects of both years to obtain a better sampling completeness.

Table 2.3. Abundance (N) and number of species/morphospecies (S) collected in 2013 and 2014 years per each habitat type: NatFor (natural forests), NatVeg (naturalized vegetation areas), ExoFor (exotic forests), SemiPast (semi-natural pastures), IntPast (intensively managed pastures).

	2013		2014	
Habitat	**N**	**S**	**N**	**S**
NatFor	459	20	255	23
NatVeg	177	31	152	32
ExoFor	218	22	170	28
SemiPast	251	24	127	28
IntPast	128	27	197	32

Using equivalent sampling effort in combination with the same standardized method in different habitat types may still result in differences in inventory completeness due to differences in the abundance of plant species in different transects. To analyse the variation in flower-visiting insect species accumulation between habitats and rule out possible biases in the sampling effort, we constructed species accumulation curves for the observed number of species, species richness estimates, singletons, and doubletons using the non-parametric estimators Chao 1 and Jackknife 1 (Chao1 and Jack1, both abundance-based). Species accumulation curves were constructed by randomly selecting the order of transect addition at each iteration. We repeated this process 1000 times, and used the mean of the 1000 random runs. To analyse the estimators' performance across all habitats, slopes were calculated along the entire curve. Sampling completeness was calculated in two ways: first, I calculated the ratio of observed richness to estimated richness ratio with Chao1, due to its higher precision (Hortal *et al*., 2006) and second, we recorded the final slope of species richness accumulation curves built with both observed and estimated richness as the inverse of the number of individuals needed to add the final single species to the accumulation curve (see Cardoso *et al*., 2009 for more details).

To investigate differences in flower-visiting insects' diversity between habitats, we calculated the mean number of individuals, species richness and two commonly used diversity indices namely Shannon-Wiener (H') and Pielou's evenness (J'). In addition, we calculated the Berger-Parker dominance index (D), which expresses the proportional abundance of the most abundant species, presented in the inverse format (1/D), so that an increase in the value of the index accompanies an increase in diversity and a decrease in dominance (Magurran, 2004). To test for statistically significant differences in diversity between habitats, I applied one-way ANOVAs followed by Tukey HSD *post-hoc* tests. ANOVAs were performed using generalized least square models (GLS; Pinheiro & Bates, 2000) to account for potential heteroscedasticity. Additionally, I also tested the ability of the GLS models to account for potential spatial structures by estimating the Moran's *I* spatial autocorrelation index for GLS residuals using the latitude and longitude of each transect site. When the overall GLS was statistically significant, the Tukey's post hoc test was used to identify statistically significant pairwise differences between habitats.

We studied the dissimilarity in flower-visiting species composition between sites of all habitat types using Jaccard's index as an overall beta diversity measure (β_{total}), and decomposing it into its replacement (β_{repl}) and richness difference (β_{rich}) components (Carvalho *et al*., 2012; Cardoso *et al*., 2014). β diversity indices were computed using presence/absence data. I also computed β diversity with log-transformed abundance data (results not shown), but the results were similar (Cardoso *et al*., 2015). Dissimilarity distances were visualized using non-metric multidimensional scaling ordinations (NMDS). To examine between-habitat differences in species composition, we used an analysis of similarities (ANOSIM) using the three beta diversity components as dissimilarity measures, followed by *post-hoc* tests with p-values adjusted using the Benjamini & Hochberg (1995) correction for multiple testing. I also computed β_{total}, β_{repl} and β_{rich} for plant species composition and correlated each β component of flower-visiting insects with its respective component for plants communities using Mantel tests with Spearman correlation.

In addition to examining patterns in flower-visiting species diversity and composition, we also explored variations in the species abundance distributions (SADs) of flower-visiting species (Matthews & Whittaker, 2015) across the five habitat types. To determine the shape of the SAD in each sample, we fitted logseries, lognormal and gambin SAD models to the observed abundance data, using both binned and un-binned data with the logseries and lognormal models, and only binned data with the gambin model (Matthews *et al*., 2014).

A large number of SAD models have been proposed (see Matthews & Whittaker, 2014), the most frequently applied models are the logseries (Fisher *et al.*, 1943) and the lognormal (Preston, 1948) models. The logseries results from the Poisson sampling of a gamma distribution after a certain relevant limit is taken, and characterises a situation in which singletons represent the most common abundance class. The lognormal represents a situation in which the logarithms of the different species' abundances follow a Gaussian distribution, and thus it characterises a situation in which most species are of intermediate abundance (Preston, 1948). As the continuous lognormal distribution allows fractional abundances, the Poisson lognormal model is often used instead (Matthews & Whittaker, 2014). More recently, the Gambin SAD model was introduced to provide a useful tool for assessing variations in SAD form between samples (Ugland *et al.*, 2007). Gambin is a stochastic model which combines the gamma distribution with a binomial sampling method. The model has a single free parameter, alpha (α), which characterises the distribution shape; communities dominated by rare species (logseries-like SADs) have low α values, whilst lognormal-like SAD shapes are characterised by higher α values (Ugland *et al.*, 2007; Matthews *et al.*, 2014).

To determine the shape of the SAD in each sample, we fitted a selection of SAD models to the observed abundance data, in both binned and un-binned form. The binning of abundance data into octaves prior to fitting SAD models is widespread in the SAD literature (e.g. see Gray *et al.*, 2006; Matthews & Whittaker, 2014) and allows for models to be fitted that only work with binned data (e.g. Matthews *et al.,* 2014); however, the binning of data has been criticised as it results in the loss of information (McGill *et al.*, 2007). First, for each sample, we binned the data into octaves, i.e. bin 1 corresponds to the number of species with 1 individual per species (i.e. singletons), bin 2 corresponds to the number of species with 2-3 individuals per species, bin 3 corresponds to the number of species with 4-7 individuals per species, etc.. As such, the bin interval is on a log 2 scale (method 3 of Gray *et al*., 2006; see also Matthews *et al*., 2014). We then fitted three SAD models to these binned data: the logseries, the Poisson lognormal (non-truncated; PLN), and the gambin model. The three models were compared using Akaike's information criterion corrected for small sample size (AIC_c; Burnham & Anderson, 2002). The best fitting model was taken as the model with the lowest AIC_c value; although all models with a ΔAICc value < 2 (the difference between each model's AICc and the lowest AICc) were considered as receiving equal statistical support (Burnham & Anderson, 2002). The use of an information theoretic approach to compare the fit of a suite of various SAD models to empirical data has been argued to represent one of the most effective approaches to SAD model comparison (Matthews & Whittaker, 2014). Since rigorous comparisons of α values across habitats should be based on keeping sample size constant (Matthews *et al.*, 2014) We calulated a standardized α by resampling the data to a fixed number of 1000 individuals. Finally, we again fitted the logseries and the PLN models to each of the five samples, but using the un-binned data. The Gambin model can only be fitted to binned data (see Matthews *et al*., 2014), and thus this model was not included in this analysis. The model fits were again compared using AIC_c, with the same aforementioned criteria used to determine the best fitting model with binned data.

Local (habitat) and regional (island) SADs were visualized using frequency histograms, where the number of individuals were binned into octaves following the same aforementioned method described above. We classified the 25% rarest species in terms of abundance as rare, as suggested by Gaston (1994). For this study it was equivalent to choosing all species with three or less individuals (see Borges *et al*., 2008). Likewise, common species were those in the top 25% of abundances, corresponding to species with 128 or more individuals. All other species were classified as being of intermediate abundance.

To classify types of rare species, we followed the description of Borges *et al.* (2008) with some adaptations, that allocates the rarest species in: a) "Regional rarity", i.e. with three or less individuals sampled in the island (region); and b) "Pseudo-rare species" for a given habitat are those species that are abundant in at least one or more habitats, but are sampled in small numbers in a specific habitat.

All analyses were performed with Microsoft Excel, IBM SPSS 20.0 (Nie *et al*., 2011) and the R statistical environment (R Core Team, 2016) using the R packages *BAT* (Cardoso *et al*., 2015, 2016), *vegan* (Oksanen *et al.*, 2013), *poilog* (Grøtan & Engen, 2009) and *gambin* (Matthews *et al.*, 2014).

2.4 Results

Species composition

Insects visited 2134 flowers (49% of the 4354 sampled flowers) belonging to 48 plant species from 21 families. The number of plant species surveyed per habitat type was distributed as follows: 17 plant species (1134 flowers) were identified in NatFor, 27 plant species (815 flowers) in NatVeg, 26 plant species (820 flowers) in ExoFor, 15 plant species (828 flowers) in SemiPast and 14 plant species (757 flowers) in IntPast (see Table A2; Appendix A).

The sampled flower-visiting insects belonged to 54 species and morphospecies from four orders namely Coleoptera, Diptera, Hymenoptera and Lepidoptera (Table A1; Appendix A). The most representative group was Diptera, with 51% of the individuals, followed by Hymenoptera with 25%, Coleoptera with 18% and finally the Lepidoptera with 6%. The most common species were *Sepsis neocynepsia* (Diptera) (17% of the individuals) and *Anaspis proteus* (Coleoptera) (16.5%), followed by *Bombus ruderatus* (6.3%), *Apis mellifera* (5%), *Lasioglossum villosulum* (all Hymenoptera) (4.5%) and *Stomorhina lunata* (Diptera) (4.6%) (Table A1; Appendix A). Flies (Diptera) were the most represented group in all habitats, invariably followed by bees (Hymenoptera) (χ^2= 4.81, df = 12, p=0.96). *Sepsis neocynepsia* (Diptera) had the highest number of individuals in three habitat types: NatVeg, SemiPast and IntPast, whereas *Anaspis proteus* (Coleoptera) was dominant in NatFor and *Bombus ruderatus* (Hymenoptera) in ExoFor.

At the island scale we observed that the majority of flower-visiting insects were native non-endemic species (82.1%) while only a small percentage was endemic (5.4%) or exotic (12.5%). These proportions were similar throughout all habitats (χ^2 = 0.89, df = 8, P = 1), showing that indigenous species dominated flower-visiting insect's communities across the entire gradient (Table 2.4). On the other hand, at the island scale the majority of host plants were exotic species (75%), and a small percentage was native non-endemic (14.6%) or endemic (10.4%). These proportions slightly differed between habitats (χ^2 = 17.5, df = 8, P = 0.025), although the introduced plant species were dominant in all habitats with the exception of NatFor (Table 2.4).

Table 2.4. Number of endemic, native non-endemic and introduced flower-visiting insects and plant species per each habitat type: NatFor (natural forests), SemiPast (semi-natural pastures), NatVeg (naturalized vegetation areas), ExoFor (exotic forests), IntPast (intensively managed pastures).

	Insect Species			Plant Species		
Habitats	Endemics	Natives	Introduced	Endemics	Natives	Introduced
NatFor	2	34	5	5	6	6
NatVeg	1	31	5	5	7	16
ExoFor	2	32	6	2	3	22
SemiPast	1	24	5	0	2	14
IntPast	2	27	5	0	2	13

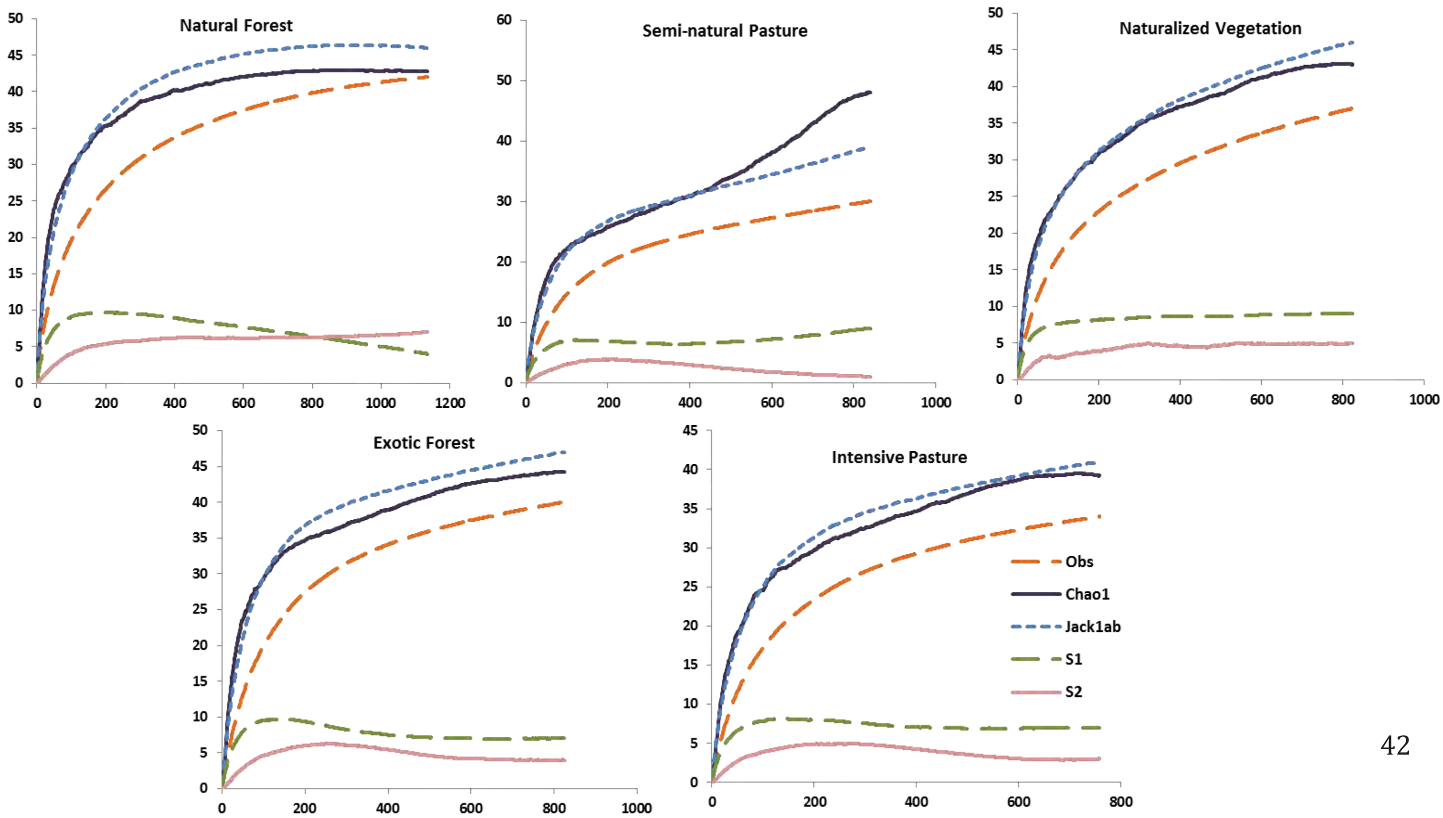
Sampling completeness

The average numbers of flower-visiting insect species per habitat estimated by the Chao1 and Jack1 estimators were found to be close to the observed richness values (Table 2.5). Considering the estimates obtained with Chao1, the sampling completeness values for each habitat varied between 98% for NatFor and 63% for SemiPast, with 90% for ExoFor, 87% for IntPast and 86% for NatVeg, all representing a good level of sampling completeness (Cardoso *et al*., 2009). The species accumulation curves (Fig. 2.2) approached an asymptote (with slope values between 0.002 and 0.08 by the end of the accumulation process) and the final slope values of estimators' curves were close to 0 for all habitats, which shows that the inventory was relatively complete in all habitats (Fig. 2.3).

Table 2.5. Number of individuals, species/morphospecies, singletons and doubletons studied in each habitat type: NatFor (natural forests), NatVeg (naturalized vegetation areas), ExoFor (exotic forests), SemiPast (semi-natural pastures), IntPast (intensive pastures). SREM is a mean of the species richness estimates (Chao 1 and Jackknife 1).

Habitats	Individuals (N)	Species (S)	Singletons	Doubletons	SREM (+-SE)
NatFor	713	41	4	7	40 (2.4)
NatVeg	329	37	9	5	35.3 (2.8)
ExoFor	388	40	7	4	38.1 (2.6)
SemiPast	378	30	9	1	31 (2.7)
IntPast	325	34	7	3	32.9 (2.4)

Figure 2.2. Species accumulation curves for several non-parametric estimators and for singletons and doubletons of the different habitat types. The observed species accumulation curve (Obs), abundance-based estimators Chao 1 and Jackknife 1 (Jack 1ab), species collected once (singletons, S1), species collected twice (doubletons, S2).



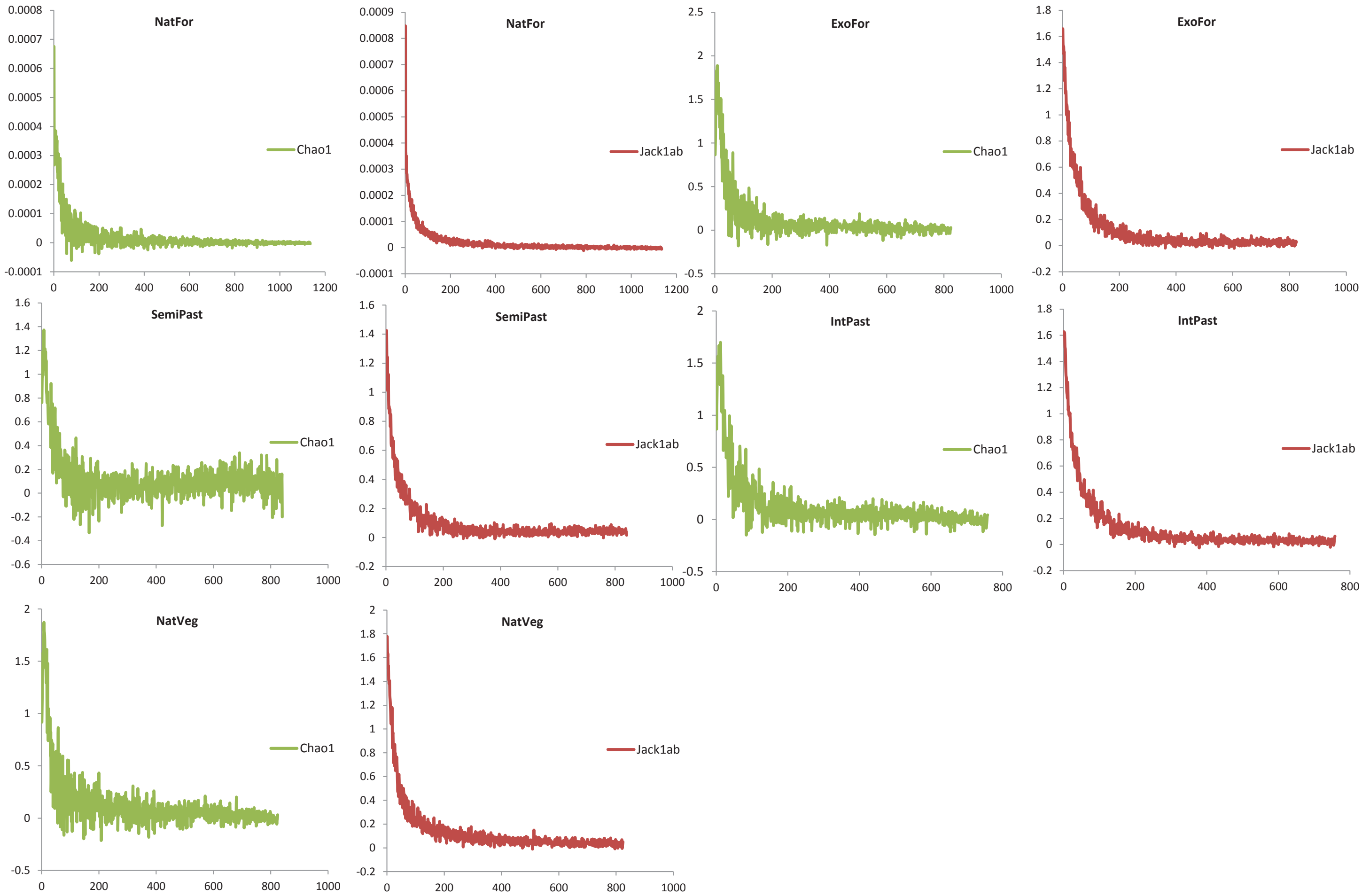


Figure 2.3. Slopes of species accumulation curves for non-parametric abundance-based estimators Chao 1 and Jackknife 1 (Jack 1ab) of the different habitat types: NatFor (natural forests), NatVeg (naturalized vegetation areas), ExoFor (exotic forests), SemiPast (semi-natural pastures), IntPast (intensive pastures).

Insect diversity in the different habitats

Mean number of individuals, species evenness (J') and dominance (1/D) for flower-visiting insects did not show any significant differences between habitats ($F_{1,4}$= 1.185, P = 0.330; $F_{1,4}$ = 1.682, P = 0.171 and $F_{1,4}$= 2.513 P = 0.055 respectively, Fig. 2.4a, d, e). However, species richness differed significantly between habitats ($F_{1,4}$= 4.231, P = 0.005) with NatFor being the richest habitat and NatVeg and SemiPast being the poorest (Fig. 2.4b). Shannon-Wiener H' index differed marginally between habitats ($F_{1,4}$= 2.711, P = 0.042) with ExoFor being significantly more diverse than SemiPast (Fig. 2.4c). No spatial autocorrelation was detected in the residuals of the GLS models (*I* = 0.007, P = 0.214; *I* = -0.006, P = 0.534; *I* = -0.020, P = 0.297; *I* = -0.011, P = 0.661 and *I* = -0.020, P = 0.872 for mean number of individuals, species richness, Shannon-Wiener, evenness and dominance respectively.

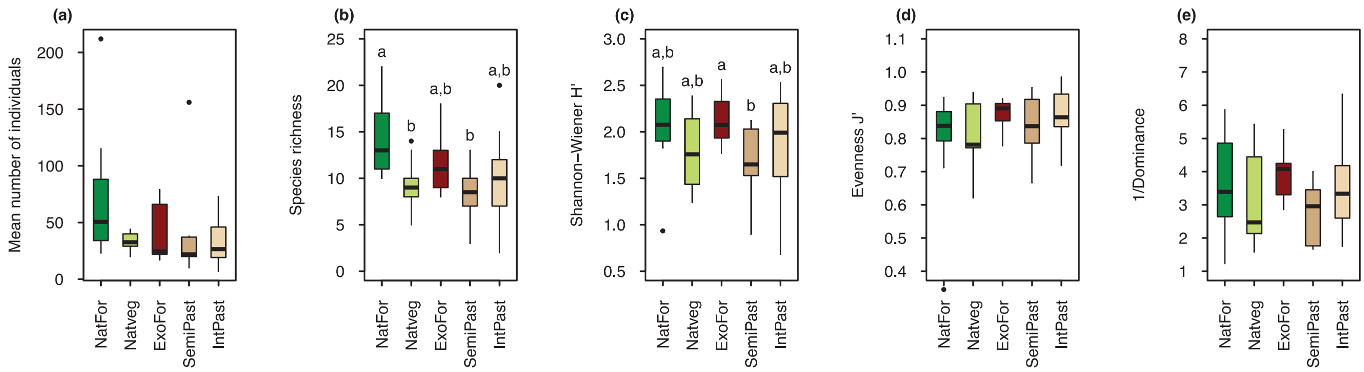


Figure 2.4. Species diversity metrics of flower-visiting insects across the different habitat types. (a)Mean abundance, (b) mean species richness, (c) Shannon-Wiener H´, (d) Pielou's Evenness J´ and (e) Inverse Berger-Parker 1/Dominance. For species richness (b), habitat types accompanied by a different letter are significantly different from each other (post hoc tests; P < 0.05). NatFor (natural forests), NatVeg (naturalized vegetation areas), ExoFor (exotic forests), SemiPast (semi-natural pastures), and IntPast (intensively managed pastures).

Habitat similarity

Overall, the analysis of flower-visiting insects β-diversity using Jaccard's index (β_{total}) showed significant differences in composition between habitat types (ANOSIM: r = 0.179, P = 0.001, Fig. 2.5a) with values ranging from 0.835 between NatFor and IntPast to 0.794 between NatFor and ExoFor (Table 2.6). NatFor was significantly more dissimilar to all anthropogenic habitats (Post-hoc ANOSIM $P < 0.05$, Table 2.7) while no significant differences were detected between anthropogenic habitats, except between ExoFor and SemiPast (Post-hoc ANOSIM $P = 0.02$). β_{repl} was the dominant component of β_{total}, with values ranging from 0.602 between ExoFor and both NatFor and NatVeg, to 0.494 between SemiPast and NatFor. β_{repl} had lower but still significant importance (ANOSIM: $r = 0.061$, $P = 0.023$, Fig. 2.5b) in explaining β diversity patterns. Significant differences in β_{repl} were found between NatFor and both ExoFor and IntPast (Post-hoc ANOSIM $P < 0.05$, Table 2.7), and between ExoFor and IntPast (Post-hoc ANOSIM $P = 0.02$). For β_{rich} values ranged from 0.316 between NatFor and SemiPast, to 0.192 between NatFor and ExoFor, but no significant difference between habitat types was found (ANOSIM: $r = 0.019$, $P = 0.233$).

Table 2.6. Comparison of total beta diversity (β_{total}), species replacement beta diversity (β_{repl}) and richness beta diversity (β_{rich}) values between habitat types. Values correspond to the average β diversity across all pairs of transect between pairs of habitats. NatFor (natural forests), NatVeg (naturalized vegetation areas), ExoFor (exotic forests), SemiPast (semi-natural pastures), and IntPast (intensively managed pastures).

β_{total}	NatFor	Natveg	ExoFor	SemiPast
Natveg	0.803			
ExoFor	0.794	0.800		
SemiPast	0.809	0.802	0.807	
IntPast	0.835	0.814	0.785	0.800
β_{repl}	NatFor	Natveg	ExoFor	SemiPast
Natveg	0.548			
ExoFor	0.602	0.602		
SemiPast	0.494	0.589	0.555	
IntPast	0.546	0.547	0.517	0.499
β_{rich}	NatFor	Natveg	ExoFor	SemiPast
Natveg	0.256			
ExoFor	0.192	0.199		
SemiPast	0.316	0.213	0.252	
IntPast	0.289	0.267	0.268	0.301

Table 2.7. P-values of the *post hoc* pairwise Analysis of similarities (ANOSIM) corrected for multiple tests. Post-hoc pairwise ANOSIM were performed for each pair of habitat type. P-values were adjusted by using the Benjamini & Hochberg (1995) correction for multiple testing. Significant results are marked in bold. NatFor (natural forests), NatVeg (naturalized vegetation areas), ExoFor (exotic forests), SemiPast (semi-natural pastures), IntPast (intensive pastures). Significant results are marked in bold.

β_{total}	NatFor	Natveg	ExoFor	SemiPast
Natveg	**0.020**			
ExoFor	**0.003**	0.346		
SemiPast	**0.003**	0.526	**0.020**	
IntPast	**0.003**	0.259	0.062	0.346
β_{repl}	NatFor	Natveg	ExoFor	SemiPast
Natveg	0.913			
ExoFor	**0.010**	0.278		
SemiPast	0.913	0.278	0.055	
IntPast	**0.010**	0.278	**0.020**	0.278

β_{rich}	NatFor	Natveg	ExoFor	SemiPast
Natveg	0.215			
ExoFor	0.907	0.907		
SemiPast	0.190	0.907	0.907	
IntPast	0.907	0.907	0.922	0.907

Significant correlations were found between the flower-visiting insects and plant species of the three β measurements (Fig. 2.6a, b, c) with the pattern of β_{total} being mostly driven by the β_{rich} component.

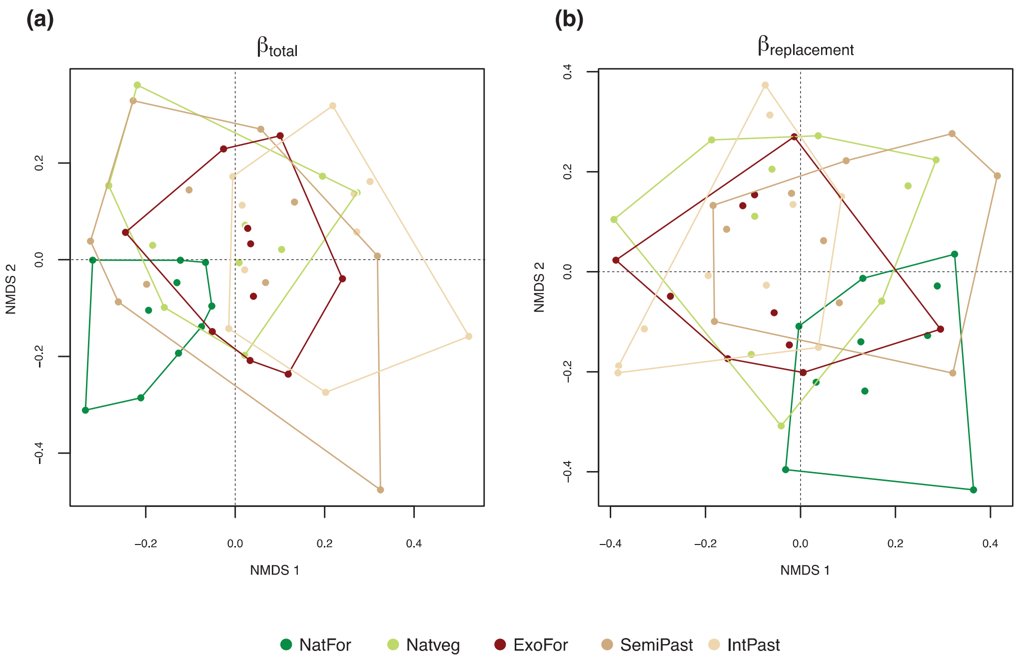


Figure 2.5. Two-dimensional ordination solution using non-metric multidimensional scaling (NMDS) with the β diversity measures β_{total} (a) and β_{repl} (b) for flower-visiting insects. Dots indicate transects while lines delimit the smallest polygon that encloses all transects for a given habitat. The stress value of NMDS was 0.17 and 0.18 for β_{total} and β_{repl} respectively. NatFor (natural forest), NatVeg (naturalized vegetation areas), ExoFor (exotic forest), SemiPast (semi-natural pasture), and IntPast (intensively managed pasture).

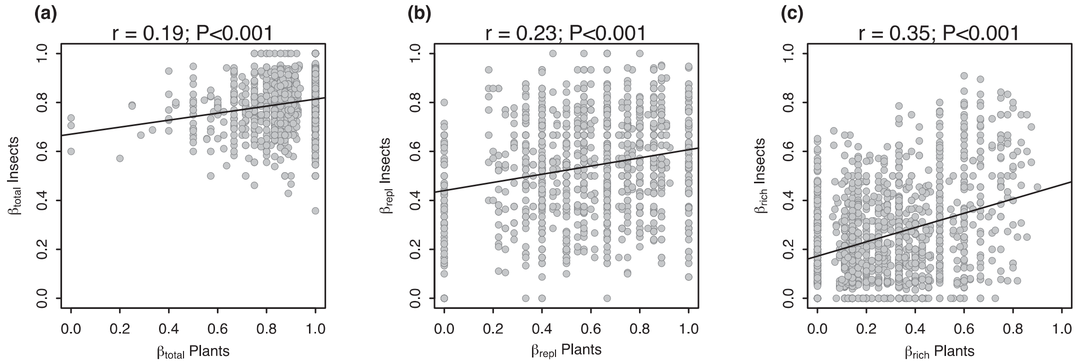


Figure 2.6. Correlations between species composition (β diversity) of flower-visiting insects and plants across the 50 transects. Correlations were performed with β_{total} (a) β_{repl} (b) and β_{rich} (c). Spearman correlation coefficient and its associated p-values of the Mantel test are given on the top of each panel. NatFor (natural forest), NatVeg (naturalized vegetation areas), ExoFor (exotic forest), SemiPast (semi-natural pasture) and IntPast (intensively managed pasture).

Species abundance distributions (SADs) and rarity patterns

Considering the binned data, the gambin model provided the best fit to all five habitat types ($\Delta AIC_c = 0$, Table 2.8), although for the NatFor the PLN had a $\Delta AIC_c < 2$. The PLN always provided a better fit to the binned data than the logseries. However, when the logseries and PLN were fitted to the unbinned data, the logseries provided a better fit to all five habitat types, indicating a greater number of rare species than predicted by the PLN (Table 2.8). The gambin model provided a good fit to the data in all habitat types according to the Pearson's chi-square (χ^2) goodness of fit test for NatFor: $\chi^2 = 6.376$, $P = 0.605$; NatVeg: $\chi^2 = 5.963$, $P = 0.31$; ExoFor: $\chi^2 = 1.568$, $P = 0.905$; SemiPast: $\chi^2 = 11.303$, $P = 0.079$ and IntPast: $\chi^2 = 2.656$, P=0.753. The α parameter of the gambin model did not show substantial variations between habitats with values of 2.364 for NatFor, 2.348 for SemiPast, 3.244 for NatVeg, 4.502 for ExoFor and 3.965 IntPast. Alpha values in this range indicate positively skewed lognormal-like (i.e. more rare species than predicted by a standard lognormal model) to standard lognormal SAD shapes (Fig. 2.7), with the lower values of α in NatFor and SemiPast denoting a relatively higher proportion of rarer species in these two habitat types.

Table 2.8. AIC$_c$ values for the SAD model selection. The three SAD models (logseries, PLN and gambin) were fitted to flower-visiting insect data from five land use types: NatFor (natural forests), NatVeg (naturalized vegetation areas), ExoFor (exotic forests), SemiPast (semi-natural pastures), and IntPast (intensively managed pastures). The model comparison was undertaken twice: once using binned abundance data, and once using non-binned data. The gambin model can only be fitted to binned data and was thus not used in the non-binned data comparison. The best fitting model in each instance is highlighted in bold.

	AICc (binned data)			AICc (non- binned data)	
HABITATS	LOG SERIES	PLN	GAMBIN	LOG SERIES	PLN
NatFor	188.53	**157.49**	**156.47**	**292.45**	295.75
SemiPast	125.98	119.75	**113.06**	**197.66**	210.34
NatVeg	152.73	139.90	**131.94**	**226.58**	240.74
ExoFor	174.38	148.40	**140.76**	**261.91**	266.41
IntPast	145.60	128.22	**120.90**	**217.30**	224.44

In regards to the species classified as common species (i.e. the 25% most abundant), there is only one habitat type with one species having more than 128 specimens: NatFor with *Anaspis proteus* (264 specimens). However, when considering regional abundance in the island, there are three true common species (*Sepsis neocynepsia* with 362 specimens, *Anaspis proteus* with 352 specimens and *Bombus ruderatus* with 134 specimens) (Fig. 2.7). The proportions of rare flower-visiting insect species represented in the first two bins of the SADs histograms in Figure 2.7 were decomposed into pseudo-rare and regionally rare species. The pseudo-rare species are relatively high in numbers when data from all habitats are aggregated, but are rare in some particular habitats and are the species primarily responsible for the differences in proportions of rare species between habitat types. The regionally rare species i.e. the number of species with less than four individuals (Fig. 2.7 Island; i.e. the first quartile of available bins) only comprise 5 species. These are the truly rare species. All habitats revealed a high number of intermediate abundance species (Fig. 2.7), as is to be expected in lognormal shaped SADs (Table 2.9).

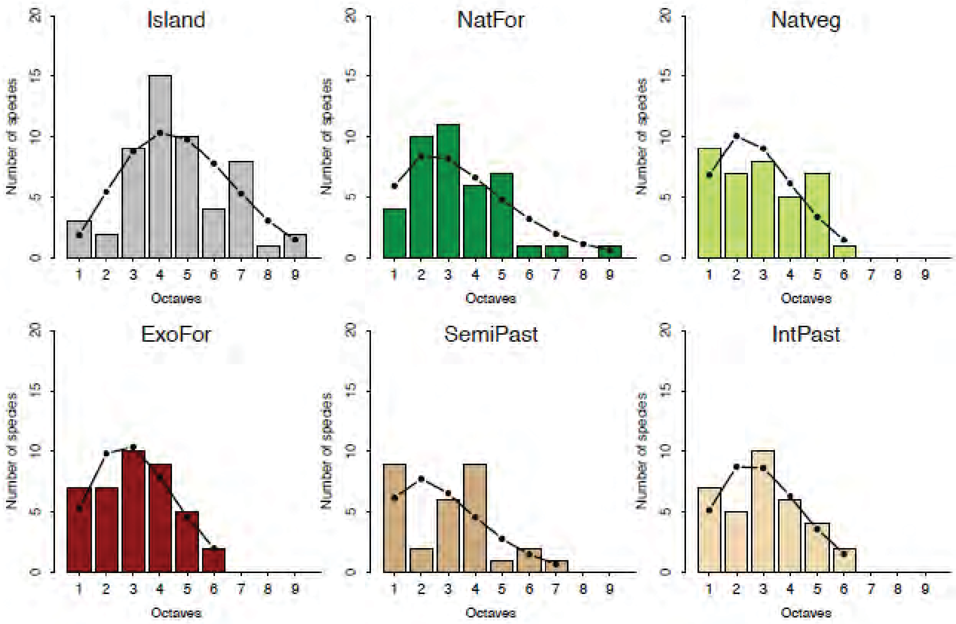


Figure 2.7 Species abundance distribution (SADs) histograms for flower-visiting insects, with predicted values of the gambin model (black dots), for all habitats, (a), natural forest (b), naturalized vegetation (c), exotic forest (d) semi-natural pasture (e), and intensively managed pasture (f). The following binning system was used: bin 1 corresponds to the number of species with 1 individual per species, bin 2 corresponds to the number of species with 2-3 individuals per species, bin 3 corresponds to the number of species with 4-7 individuals per species, etc. (see Gray *et al.*, 2006 and Matthews *et al.*, 2014).

Table 2.9. Number of regionally rare, habitat rare, pseudo-rare intermediate and common species of flower-visiting insects for NatFor (natural forests), SemiPast (semi-natural pastures), NatVeg (naturalized vegetation areas), ExoFor (exotic forests), and IntPast (intensively managed pastures) and island (region).

Habitats	Regionally Rare	Pseudo-rare	Intermediate	Common
Island	5	--	46	3
NatFor	1	13	26	1
NatVeg	2	14	21	0
ExoFor	2	12	26	0
SemiPast	0	11	19	0
IntPast	1	11	22	0

2.5 Discussion

In this study, we documented the influence of different levels of disturbance on the distribution, composition, richness and abundance of flower-visiting insect species on an Azorean island. First, we revealed that the island flower-visiting insect community is dominated by widespread generalist native species of intermediate abundance, despite the high representation of exotic plant species. Second, we showed that the species diversity, species abundance distribution (SAD) and species composition of flower-visiting insect species vary only slightly across the land-use gradients. Species replacement was significantly higher mainly between the two most contrasting habitats (i.e. natural forests and intensive pastures). Finally, species composition of flower-visiting insects was influenced by the distribution of host plant species regardless of the landscape matrix.

With the exception of the study of Olesen *et al.* (2002), to our knowledge there is no other study investigating flower-visiting insect communities in the Azores. In fact, although there are many studies investigating the impacts of land-use change on the community structure of pollinator insects on continental regions, such studies are scarce on oceanic islands. In one of the few examples, Sahari *et al*. (2010), in contrast to our results, showed that landscape change in Java Island (Indonesia) strongly affects insect pollinating species composition and richness with increasing rainforest isolation and land-use intensity, indicating significant changes in species composition between habitat types in the tropics, with emphasis on case-studies of wild and crop plants from Indonesia.

Insect diversity in the different habitats

The results demonstrated a surprising uniformity of several community metrics across the different habitats, suggesting that similar mechanisms may control flower-visiting species diversity across our land-use gradient. In most of the habitats, native non-endemic flies were the group with the largest number of species, a pattern already documented for island pollination networks (Castro-Urgal & Traveset, 2014). Concerning our original aims and hypotheses, as expected, natural forest was found to be a favourable habitat for indigenous flower-visiting insects, although we did not observe statistical differences between habitat types in terms of abundance (Fig. 2.3a, 2.2 and Table 2.3). This could be explained by adaptation or cross-scale resilience and response diversity of the native flower-visiting insect species to non-native habitats (see also Winfree & Kremen, 2009 and Cardoso *et al*., 2010a), a possible consequence of the island small area relative to the flower-visiting species foraging area (Miller *et al*., 2015) and loss of native habitats. Hence these differences in insect flower-visiting community could have been also influenced by the variation of altitude through the different habitat types; native forest being always at higher altitude than intensively managed pastures (Table 2.1). In conclusion, and even considering that exotic plants dominate all habitats with the exception of native forest, indigenous flower-visiting insects' diversity did not greatly vary, both in terms of abundance and species diversity, across the entire gradient.

Habitat similarity

As in previous studies focusing on the impact of land use change in Azorean arthropod communities (e.g. Borges *et al*., 2008; Cardoso *et al*., 2009, 2010a; Meijer *et al*., 2011), native forest and intensively managed pasture showed the most contrasting flower-visiting species composition. This difference was mostly a consequence of replacement differences (species substitution), with only a minor contribution of species richness variation (Fig.

2.5). This result differs from a previous work conducted with epigean arthropods in Terceira (see Cardoso *et al.*, 2009), where strong differences in species composition were reported between all types of habitats. This finding illustrates the need for further investigation concerning the role of landscape dynamics on Azorean insect pollinator species. The few differences in community composition reported across habitats could also be explained by the 'habitat heterogeneity hypothesis' (e.g. MacArthur & Wilson, 1967), where the flower-visiting species, due to low interspecific competition, predation and parasitic pressures (Olesen *et al.*, 2002; Ribeiro *et al.*, 2005) subdivide the landscape into suitable habitats (i.e. niche partitioning), based on plant communities (Tews *et al.*, 2004; Cramer & Willig, 2005). In fact, flower-visiting species composition was found to be mostly influenced by host plant species composition across all habitats (Fig. 2.6). The fact that differences in flower-visiting insects' composition correlated with differences in host plant species composition across habitat types (Fig. 2.6) implies that any changes in vegetation composition (i.e. replacement of native by exotic or invasive plants) might have a profound impact on pollinating insect community structure in the Azores. Interestingly, the high correlation between similarity values of plant and arthropod community structure was also observed by Borges (1999) for phytophagous insects and predatory arthropods from sown and semi-natural pastures in the Azores. In an additional study, Fründ *et al.* (2010) reported positive diversity correlation between 1764 individuals of 131 pollinator species with 77 plant species (n = 27 networks) across sites at a regional scale, even though only parts of the variation of bees and hoverfly diversity was explained by the diversity of flower species.

Species abundance distributions (SADs) and rarity patterns

The structure of flower-visiting insect species relative abundances did not differ substantially between habitats (Fig. 2.4a and Fig. 2.7), in spite of the clear land-use gradient present in Terceira, and the fact that previous studies have reported a clear effect of land-use change on SAD form for epigean arthropods on the same island (see Matthews *et al*., 2014). In fact, we found only slight variation in the form of the SAD between habitat types as highlighted by the small differences in gambin's α values calculated using binned data, and the fact that the logseries model provided the best fit to the non-binned data from all five habitat types. The SAD form in the different habitat types was accurately assessed by the gambin model for which the range of α values were characteristic of lognormal-like SADs (Ugland *et al*., 2007; Matthews *et al*., 2014), albeit with a relatively higher than expected proportion of rare species in native forest and semi-natural pasture (Table 2.9; Fig. 2.7). These results reveal therefore that most flower-visiting species, across all habitats, were of intermediate abundance. This could be explained by the fact that Azorean communities are largely unsaturated with ample resources, both features associated with low competition for food (Preston, 1948; Borges *et al*., 2008; Miller *et al*., 2015) (Table 2.8; Fig. 2.7). However, we also documented the presence of rare species although these were mostly considered to be pseudo-rare species (i.e. these species are rare in a given habitat but more frequent in others) that were likely present due to source-sink dynamics across habitat types. This work supports the view that Azorean arthropod communities are highly simplified, characterized by a dominance of generalist species (see also Olesen *et al.*, 2002; Ribeiro *et al.*, 2005; Whittaker & Fernández-Palacios, 2007; Traveset *et al.*, 2015), the presence of multiple local habitat pseudo-rarities, and few regionally rare species (see also Borges *et al.*, 2008). Borges *et al.* (2008) also reported another example of a functional group in the Azorean arthropod community with a high proportion of pseudo-rare species, in that case spiders which, similarly to pollinator insects, have many species able to use diverse resources, not limited to one specific habitat.

2.6 Conclusions

This finding supports the observations of Olesen *et al.* (2002) reported for a different Azorean island (Flores), where indigenous super-generalist species tend to include exotic plants in their set of pollinated plants without any clear evidence for facilitation between exotic plant and pollinator species. Therefore, our findings emphasize the need for further studies on pollination networks on islands to investigate the spread of exotic and invasive plants by indigenous pollinating insects that could in turn threaten the endemic flora. Finally, also further work is needed to clarify whether the Azorean indigenous pollinating insect species are behaving as "jacks of all trades, masters of none", i.e., what is the efficacy of these species in pollen transport and plant reproduction in the Azores? Given that we documented only a slight variation in pollinator community according to a land-use gradient, we suggest this is a starting point for assessing the insects' pollinators' behaviour along a disturbance gradient in the other islands of the Azores archipelago, and compare it at island-level with Terceira flower-visiting insect communities. In conclusion, our study offers one of the first exhaustive assessments of the impact of land-use change on an Azorean island flower-visiting insect community, revealing (1) the influence of plant species composition on flower-visiting insect species composition, and (2) providing evidence for potential occupation of native flower-visiting insects in new anthropogenic habitats.

Chapter 3

Structural patterns of small, simple and homogeneous pollinating communities

Ana Picanço, François Rigal, Jens M. Olesen & Paulo A. V. Borges

In: preparation

3.1 Abstract

Many studies suggest that abundance of species in plant-animal mutualistic networks might explain and have an important role in developing network patterns, is this the case of the Azorean insect pollinating networks? Our results reveal that: i) truncated power-law and exponential models insects and plants show a distribution of links that decays faster than expected, promoting the growth or establishment of new links, ii) land-use of moderate disturbance seems to promote the establishment and development of structural robust, nested, asymmetrical and specialized plant-insect networks, iii) nested and non-modular patterns across habitats and for global network, in combination with strong positive relationships between incidence links and abundance, highlights the importance of abundance as key driver for interactions and associated network structure pattern in Azorean insect pollinating communities.

Keywords

Abundance, pollination, network, insects, interactions, neutral explanation.

3.2 Introduction

Understanding the organization of mutualistic networks is a key issue in community and functional ecology. The diversity and structure of mutualistic networks can be constrained by a wide range of processes, including relative species abundances, populations spatial structure, species dispersal limitation and stochasticity, together with various niche-based processes (Blüthgen *et al*., 2006; Stang, *et al*., 2007; Krishna *et al*., 2008; Vázquez *et al*., 2009a,b; Canard *et al*., 2012; Olito & Fox, 2015) such as niche partitioning (e.g. interspecific competition) and/or niche breadth (Spiesman & Gratton, 2016). These processes can be grouped into two main hypotheses: (i) a neutral hypothesis claiming that interactions (i.e. links) among species are random and are proportional to their abundances in the observed community i.e. resulting from ecological drift or demographic stochasticity (Vázquez, 2005; Krishna *et al*., 2008); and (ii) a niche-based hypothesis claiming that biological constraints, i.e. forbidden links and niche-driven mechanisms (Santamaría & Rodríguez-Gironés, 2007) should prevail in explaining network structure. The relative influence of neutral and niche-based processes is at the core of current debates on the assembly of communities and the coexistence of species.

Mutualistic network analysis has been extensively applied to the study of plant–pollinator interactions (Memmott, 1999; Dicks *et al*., 2002; Olesen & Jordano, 2002; Bascompte *et al*., 2003; Jordano *et al*., 2003; Vázquez & Aizen, 2004; Santamaría & Rodríguez-Gironés, 2007; Petanidou *et al.,* 2008; Bosch *et al*., 2009). The plant-pollinator interactions imply two sets of interacting communities, and the diversity, composition and abundance of both communities may show unforeseen repercussions to each other through the network structure; e.g. the diversity of nectar plants in a community is positively correlated with the diversity and abundance of the associated pollinating fauna (Potts *et al*., 2003; Fründ *et al*., 2010).

The emergent topological properties of plant-pollinator networks result from complex interactions between plants and animals across time and space (Vázquez *et al*., 2009a). The two most frequently niche-based patterns observed in mutualistic networks are nestedness and modularity, both being related to the stability and persistence of the network structure , and therefore, interpreted as the results of complex eco-evolutionary processes (Bascompte *et al*., 2003; Lewinsohn *et al*., 2006; Olesen *et al*., 2007; Fortuna *et al*., 2010; Thébault & Fontaine, 2010; Dalsgaard *et al*., 2013). Nestedness measures the degree to which interactions of specialists are a subset of interactions of generalists. Interactions between plants and pollinators were for long considered to be dominated by specialized interactions, but recently their generalist-based nature has been highlighted (Waser *et al*., 1996; Ollerton, 1996; Memmott, 1999). This implies that a large majority of plants is pollinated by many pollinators and in the same way, a single pollinator species visit many plant species. Consequently, the number of interacting partners of a plant species might be partly explained by the abundance of the interacting species (Herrera, 1988; Armbruster *et al*., 2000; Olesen, 2000; Fenster & Dudash, 2001; Vázquez & Aizen, 2004; Montoya & Yvon-Durocher, 2007). In this way, a nested structure implies that new species entering the network tend to interact with already well-connected species (Olesen *et al*., 2008; Bosch *et al*., 2009; Dupont *et al*., 2009), and consequently generalists tend to be more abundant than specialists enhancing facilitation among species (Okuyama & Holland, 2008; Bastolla *et al*., 2009). Therefore, one could hypothesized than larger number of neutral interactions due to more abundant species in the network might partially explain patterns of nestedness (Dupont *et al*., 2003; Vázquez *et al*., 2009).

Modularity represents the propensity of the network to exhibit clusters of species that interact more strongly together than with the rest of the network (Olesen *et al*., 2007; Schleuning *et al*., 2014). The presence of modularity is mainly explained as the result of niche partitioning and complementary specialization (Blüthgen & Klein, 2011; Spiesman & Gratton, 2016), where interspecific competition increases as pollinator richness increases and an increase of plant resource richness and abundance (or density) promotes partition of niches enabling flexible foraging (Spiesman & Gratton, 2016).

Along with nestedness and modularity, other network features might also be driven by species abundance. This could be the case for the degree distribution and species interactions (i.e. Interaction strength). The degree distribution characterizes the distribution of number of links per node (Solé & Montoya, 2001). In plant-pollinators networks this relationship is usually truncated, i.e. the most linked nodes have fewer links than expected according to a power law relationship (Jordano *et al*., 2003; Bascompte & Jordano, 2007). Species interactions are often asymmetrical in strength, i.e. interacting species pairs are not equally dependent upon each other (Bascompte *et al*., 2006). Interaction strength (or species dependence) in plant-animal mutualisms is usually measured by the frequency of interactions between species pairs (Bascompte & Jordano, 2007). So, Macleod (2016) demonstrated that the relative importance of degree compared to strength depended on the underlying species abundance distribution (SAD), such that when SAD were even, the degree distribution (i.e. distribution of the links) was more influential to the network structure stability than strength (i.e. number or amount of links), but when SAD were skewed, degree distribution and strength were both very important to promote stability.

All these studies suggest therefore that abundance of species in plant-animal mutualistic networks might have an important explanatory power (Morales & Vázquez, 2008), in particular in young systems lacking of a long co-evolutionary history among its species (Traveset *et al*., 2015).

Oceanic islands often lack many families of pollinators most likely due to their isolation (Gillespie & Roderick, 2002; Olesen & Jordano, 2002; Traveset *et al*., 2015), and consequently their pollination networks are known to be small, topologically simple, and also disharmonic compared to mainland networks. Island area has usually no effect on network structure (Traveset *et al*., 2015), whereas a network property like nestedness is usually more pronounced in the isolated and low-elevation islands, than high-elevation and low-latitude islands with display of high species richness interactions (Traveset *et al.*, 2015). Strong nestedness can emerge as a consequence of adaptations that increase species-level and total community abundance (Suweis *et al*., 2013)

Here, we analyse a set of pollination network from an isolated oceanic archipelago, the Azores. Our specific aims are: (i) the characterization of plant-insect pollinator network topology, (ii) the comparison of networks across different habitat types, and (iii) the estimation of the role of species abundance as a driver of the pollination networks structures.

3.3 Methods

Study sites and sampling procedure

The fieldwork was undertaken from June to September 2013 and from July to October 2014 on Terceira Island (Azores) locate in the North Atlantic Ocean (38º 37´N 38º 48´N, 27º 02´W 27º 23´W). We used five relevant habitat types, corresponding to an increasing gradient of disturbance (1-5), namely natural forests (1NatFor), naturalized vegetation areas (2NatVeg), exotic forests (3ExoFor), semi-natural pastures (4SemiPast) and intensively managed pastures (5IntPast) (for details see Chapter 2 and Picanço *et al*., 2017). In each habitat type we chose 10 sites in which 10 m long line-transects (1m width) were set up (Pollard & Yates, 1993), making a total of 50 transects located across the entire island (for details see Chapter 2 and Picanço *et al*., 2017). Transect surveys, with subsequent season annual repetition, were carried out from 9 a.m. to 6 p.m and in sunny weather, with a duration of 180 minutes per transect. Transect location was selected to encompass patches of dense flowering. Each insect flower visit was surveyed for four min to ensure sufficient time for probing for nectar or consuming/collecting pollen (foraging). Only insects exhibiting these types of behaviour (probing or foraging) were considered as potential pollinators. Flower-visiting insects were collected with a pooter if it was not possible to identify them in the field. The specimens collected were sorted into morphospecies and later identified to species-level according to the taxonomic nomenclature in Borges *et al*. (2010). When species-level identification could not be achieved, individuals were identified to the lowest possible taxonomic unit and labelled as morphospecies. Voucher specimens are deposited in EDTP – Entomoteca Dalberto Teixeira Pombo, University of Azores, Angra do Heroísmo, Portugal.

Data analysis

For the two consecutive sampling years (2013-2014), we performed a statistical comparison test (paired *t* test) to identify potential differences between the years, which revealed a small but significant increase in species richness between the two years ($t = -4.4$; $p = 0.006$), and a non-significant difference in species abundances between years ($t = 1.43$; $p = 0.22$). So, I pooled data from both years to obtain a better sampling completeness.

For each of five habitat types, we constructed binary and quantitative (weighted) plant-flower visitor interaction matrices as well as one "global" matrix by merging all five networks (Table B1-B5 Appendix B; Fig. 3.1). These matrices are based on count data information due to its reliability when studying network structure relative to interaction frequency (Reitan & Nielsen, 2016). Matrix columns and rows represent plant and pollinator species, respectively, and cell values represent interactions ($x_{ij} \geq 1$ for presence/abundance and $x_{ij} = 0$ for absence of an interaction between pollinator species i, and plant species j).

We analysed the topological structure of the networks in relation to the rank of the habitats . Analytical output included numbers of plant (P) and animal (A) species, total number of species (A+P), total number of interactions (I) between plants and animals, system size (AP), connectance ($C = I/(AP)$), nestedness ($NODF$) and modularity level (M), these latter corresponding to binary unweighted metrics and weighted metrics: network-level specialization (H_2') (range: 0, extreme generalization to 1, extreme specialization; Blüthgen *et al*., 2006), interaction evenness, weighted nestedness (wNODF) and weighted modularity (Q).

Connectance is the number of interaction partners of a species, a measure of its degree of generalization. To characterize connectance distribution, we constructed cumulative degree distributions separately for plant and animal communities to fit exponential, power law and truncated power law decay models to the distribution of links of our five matrices (Jordano *et al*., 2006). The Akaike information criterion (AIC) was obtained for each fit. The model with the lowest AIC was selected as the best fit (Burnham and Anderson, 2002). H_2' values characterize the degree of specialization among species in the entire network (Blüthgen *et al*., 2006) and was assessed using 10000 randomizations networks (Maruyama *et al*., 2014). Interaction evenness based on Shannon diversity index, is a measure of variation in the number of interactions, i.e. visits, among distinct links (Blüthgen *et al*., 2008; Sahli & Conner, 2006), but calculated only for the realized links (Bersier *et al*., 2002; Tylianakis *et al*., 2007) to ease comparison among habitat networks.

Nestedness is a network structural pattern, in which interactions tend to form around a core of generalist species and asymmetrical tails between many specialists and a few generalists. To calculate unweighted (or qualitative) nestedness level (*NODF*) and whether NODF values deviate significantly from a random distribution, we used the software *ANINHADO* v. 3.0.3 3 (Almeida-Neto *et al*., 2008; Guimarães & Guimarães, 2006). We selected a null model assuming that the probability of an interaction is proportional to the product of the degrees of both the plant and the animal species. Hence, generalist species have a higher probability of being assigned to an interaction than specialist species (null model 2 in Bascompte *et al*., 2003 and null model Ce in *ANINHADO*). Compared to other models, this null model has the smallest type-I errors (Rodríguez-Gironés & Santamaría, 2006). For weighted (or quantitative) nestedness metric we calculated wNODF developed by Almeida-Neto & Ulrich (2011). wNODF was assessed relative to 1000 randomizations of the networks (see below and in Vizentin-Bugoni *et al*., 2016).

Modularity level of a network describes the extent to which it consists of sub-groups or modules, each consisting of tightly interacting species (Olesen *et al*., 2007; Dupont & Olesen, 2009; Schleuning *et al*., 2014). We used the algorithm *NETCARTO* for an unweighted (or qualitative) analysis (M) that maximizes M using simulated annealing (Guimerà & Amaral, 2005a, b) and for a weighted (or quantitative) analysis (Q), we applied the QuaBiMo algorithm developed by Dormann & Strauss (2013, 2014) following Vizentin-Bugoni *et al*. (2016) specifications. Both values of modularity were tested against M and Q random values generated by 100 randomizations of the networks (see below and in Olesen *et al*., 2007 and Vizentin-Bugoni *et al*., 2016).

The significance of the above described weighted metrics (nestedness, modularity and H_2') was assessed by comparing the realized values against the random values obtained from null model randomizations. To create these null models, except for H_2'which was used *shuffle.web* that only keeps connectance constant, I used *vaznull* function, which keeps constrained connectance and the proportion of unrealized interactions, which might represent forbidden links (Dormann *et al*., 2008). Realized values were considered significant if they were greater or less than 95% of confidence intervals of the values in randomized networks.

Linear regression analyses were also performed between incidence links (i.e. interactions at species-level) as response variable and insect pollinator species abundance as explanatory variable. Both variables were log-transformed to improve normality. It may reasonably be assumed that closely related species are on average more likely to display similar traits than less closely related species, raising issues of independence of data points in statistical analyses. Were therefore re-evaluate the relationship between the incidence links (i.e. interactions at species-level) and insect pollinator species abundance using phylogenetic regressions. Analyses were performed with phylogenetic generalized linear mixed models (PGLS) with a correlated error structure based on a phylogenetic distance matrix that assumes Pagel’s evolutionary model (Pagel, 1999). The associated parameter

Pagel's λ increases towards 1 as the phylogeny has an increasing impact on model structure (Pagel, 1999). Because no well-resolved phylogeny exists for all insects, I constructed our own phylogenetic tree based on recent phylogenies of each groups found in our study. We first reconstruct the topology in a newick format following Misof *et al*. (2014) for the relationship between Hymenoptera, Coleoptera, Diptera and Lepidoptera, Pena *et al*. (2006) and Brady *et al*. (2006) for Lepidoptera, Sharkey *et al.* (2012), Dowton *et al*. (2009), Davis *et al*. (2010), Danforth *et al*. (2003) and Danforth *et al*. (2013) for Hymenoptera, Rotheray & Gilbert (1999), Feng-Yi *et al*. (2008), Bernasconi *et al*. (2000), Ding *et al*. (2015) and Wiegmann *et al.* (2011) for Diptera and Hunt *et al*. (2007) for Coleoptera. Second, to obtain a time-calibrated phylogeny, I identified a total of 18 nodes that were in common between our phylogeny and the large-scale compilation of phylogenetic divergence dates provided by Hedges and Kumar (2009). Based on this set of nodes and putative dates, we applied a pseudo-calibration procedure by interpolating undated nodes at equal intervals between dated ones (the BLADJ algorithm; Webb *et al*., 2008).

All analyses, except nestedness and modularity binary metrics were performed using R v. 3.2.5 statistical environment (R Core Team, 2016) using the packages bipartite v.2.0.7 (Dormann *et al*., 2016), sna v. 2.4 (Butts & Butts, 2016) and vegan v. 2.3-3 (Oksanen *et al*., 2013) and caper (Orme *et al*., 2013).

3.4 Results

Network structure

Across the five habitats, a total of 54 species of insects were observed visiting 48 species of flowering plants and forming a total of 2134 interactions (Fig. 3.1). The largest and most specialized networks, but with the lowest connectance C values were the 2NatVeg and 3ExoFor (Table 3.1, Table B2-B3, Fig. 3.1). While in the pastures habitats (4SemiPast and 5IntPast), corresponding to the most disturbed and smallest networks size (i.e. less number of insect and plant species), the connectance C values were higher highlighting more frequent interactions between plants and insects in comparison to the other habitats (Table 3.1). Overall, networks have low to moderate C values indicating that these networks are relatively small and simple.

Table 3.1. Habitat types networks structure parameters or metrics.

Habitat matrix	A	P	A+P	AP	I	C (%)	H_2'	Interaction evenness	*M*	*Q*	NODF	wNODF
1NatFor	41	16	57	656	114	17.3	0.35*	0.69	0.36†	0.07†	19.2*	27.2*
2NatVeg	37	26	63	962	110	11.4	0.53*	0.89	0.47†	0.30†	29.6*	11.1*
3ExoFor	40	24	64	960	147	15.3	0.45*	0.92	0.38†	0.29†	16.0*	11.7*
4SemiPast	30	14	44	420	90	21.4	0.43*	0.83	0.34†	0.20†	18.6*	19.8*
5IntPast	34	14	48	476	101	21.2	0.40*	0.88	0.31†	0.26†	29.0*	19.8*
All 5 pooled									0.24†	0.11†		

Note: Abbreviations: NatFor, natural forests; NatVeg, naturalized vegetation areas; ExoFor, exotic forests; SemiPast, semi-natural pastures; IntPast, intensive pastures; A, number of flower-visitor species; P, number of flowering plant species; I, number of interactions between A and P; A+P = species richness; AP = network size; C (connectance) =100 I/(AP); H_2', specialization network index (Blüthgen *et al*., 2006); Interaction evenness (Blüthgen *et al*., 2008); *M*, binary modularity level; Q, weighted modularity level; NODF, binary nestedness level; wNODF, weighted nestedness level; *, $P < 0.05$, significant; †, non-significance level. All values are absolute, i.e. not corrected by network size.

For all habitat networks, the degree distributions or distribution of connectivity had the best fit models with exponential and truncated power-law function (Tables 3.2-3.3).

Table 3.2. The five habitat types' insect species data: NatFor (natural forests), NatVeg (naturalized vegetation areas), ExoFor (exotic forests), SemiPast (semi-natural pastures), IntPast (intensive pastures) fitting to three degree distribution models: exponential, power-law and truncated power-law, and respective fit comparison three AIC values. The best fit corresponding to the lowest AIC value is in bold.

Habitat	Insects degree distribution functions	Estimate	Standard error	Pr(>|t|)	R2	AIC
NatFor	Exponential	0.42	0.02	3.36E-06	0.99	-26.7
	Power-law	0.94	0.13	8.27E-04	0.97	-8.8
	Truncated power-law	-0.22	0.14	1.95E-01	0.99	**-27.9**
NatVeg	Exponential	0.37	0.02	4.73E-06	0.99	-25.0
	Power-law	0.91	0.08	2.87E-05	0.98	-17.3
	Truncated power-law	0.31	0.15	9.44E-02	0.99	**-28.1**
ExoFor	Exponential	3.21E-01	0.01	5.57E-10	0.99	**-46.0**
	Power-law	8.65E-01	0.09	6.11E-06	0.96	-17.5
	Truncated power-law	5.45E-03	0.09	9.57E-01	0.99	-44.0
SemiPast	Exponential	0.38	0.02	4.61E-06	0.99	**-25.0**
	Power-law	0.91	0.12	2.90E-04	0.96	-10.6
	Truncated power-law	-0.03	0.22	8.71E-01	0.99	-23.1
IntPast	Exponential	0.37	0.02	4.32E-06	0.99	**-26.4**
	Power-law	0.87	0.13	1.01E-03	0.96	-8.3
	Truncated power-law	-0.13	0.15	4.28E-01	0.99	-25.7

Table 3.3. The five habitat types' plant species data: NatFor (natural forests), NatVeg (naturalized vegetation areas), ExoFor (exotic forests), SemiPast (semi-natural pastures), IntPast (intensive pastures) fitting to three degree distribution models: exponential, power-law and truncated power-law, and respective fit comparison threw AIC values. The best fit corresponding to the lowest AIC value is in bold.

Habitat	Plants degree distribution functions	Estimate	Standard error	Pr(>|t|)	R2	AIC
NatFor	Exponential	0.14	0.01	2.25E-06	0.98	**-26.1**
	Power-law	0.53	0.08	1.65E-04	0.93	-10.1
	Truncated power-law	-0.04	0.12	7.71E-01	0.98	-24.2
NatVeg	Exponential	0.25	0.01	8.01E-09	0.99	-39.6
	Power-law	0.75	0.07	2.99E-06	0.96	-19.7
	Truncated power-law	0.15	0.09	1.29E-01	0.99	**-40.9**
ExoFor	Exponential	1.64E-01	0.01	2.42E-08	0.99	-34.9
	Power-law	5.71E-01	0.09	2.12E-04	0.91	-7.0
	Truncated power-law	-2.12E-01	0.05	2.95E-03	0.99	**-46.2**
SemiPast	Exponential	0.14	0.01	3.84E-09	0.99	**-40.8**
	Power-law	0.54	0.06	2.31E-05	0.94	-14.7
	Truncated power-law	0.03	0.06	6.89E-01	0.99	-39.0
IntPast	Exponential	0.13	0.01	4.13E-06	0.99	-26.0
	Power-law	0.50	0.06	1.26E-04	0.95	-12.2
	Truncated power-law	0.13	0.08	1.27E-01	0.99	**-27.4**

All habitat networks and the habitat pooled networks were found to be nested but non-modular for both binary and quantitative networks (Table 3.1). Hence for both NODF and wNODF, the networks present a relatively low nested pattern with values (Table 3.1) below the 95% confidence interval. Complementary specialization values for all networks are significant, but also presenting a relatively low specialization in comparison to randomised null model values. These small networks nested or asymmetrical patterns show high values of interaction evenness, i.e. high variation in the number of interactions or visits among links, in 3ExoFor and 2NatVeg (intermediate-disturbed habitats) followed by 5IntPast, 4SemiPast and 5NatFor.

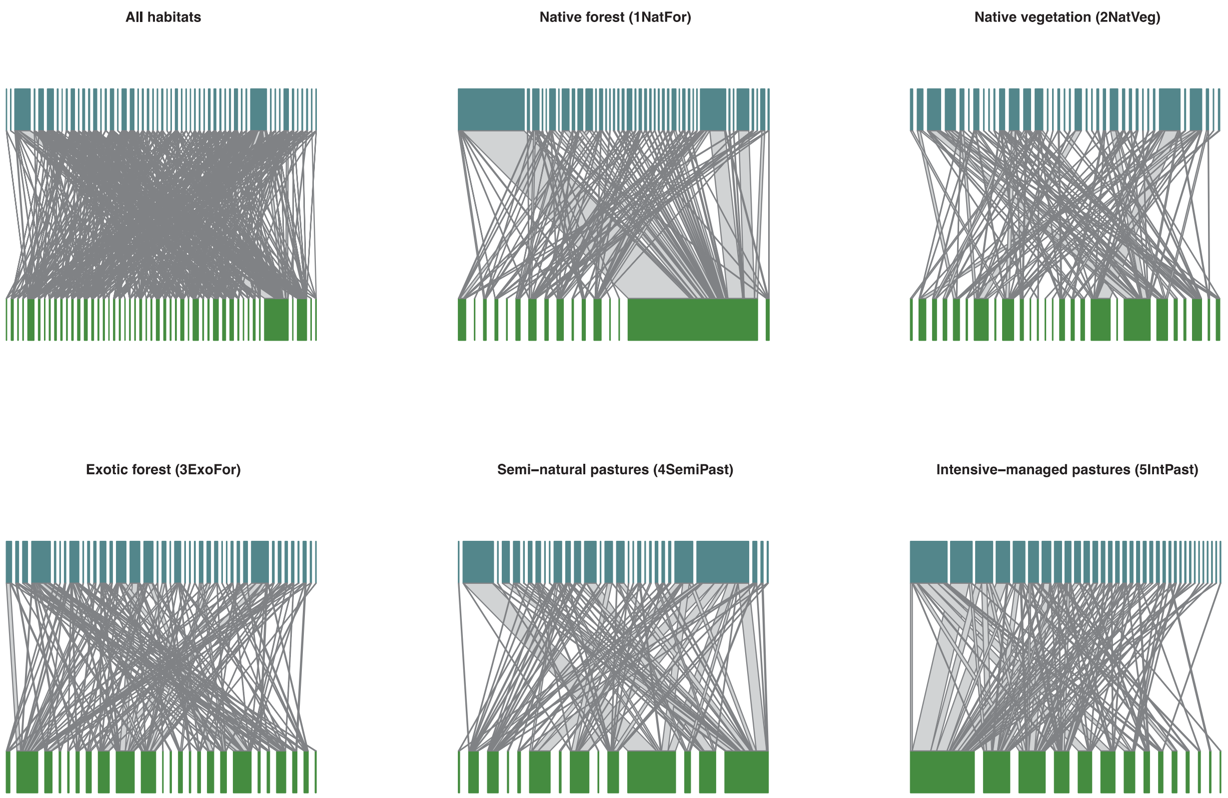


Figure 3.1. Bipartite graphs for quantitative pollination network of insects and plants, for the five habitats pooled together and for each habitat separately. Insect species are shown as rectangles at the top and plant species at the bottom. Lines connecting upper and lower boxes represent interactions between pollinator insects and plant species, and line thickness is scaled to the number of interactions.

Effect of species abundance on the pairwise interactions and network structure

The full re-constructed phylogenetic tree presented in Figure 3.2 and results of the PGLS in Table 3.4 shows that there is no phylogenetic effect or influence on the regressions.

For all habitats, pollinator abundance and incidence links of insect species were positively correlated (Table 3.4; Fig. 3.3). The strongest correlations of link incidence-abundance were in the 5IntPast (R^2 = 0.79; Table 3.4; Fig. 3.3), 3ExoFor (R^2 = 0.78; Table 3.4; Fig. 3.3) and 2NatVeg (R^2 = 0.75; Table 3.4; Fig. 3.3).

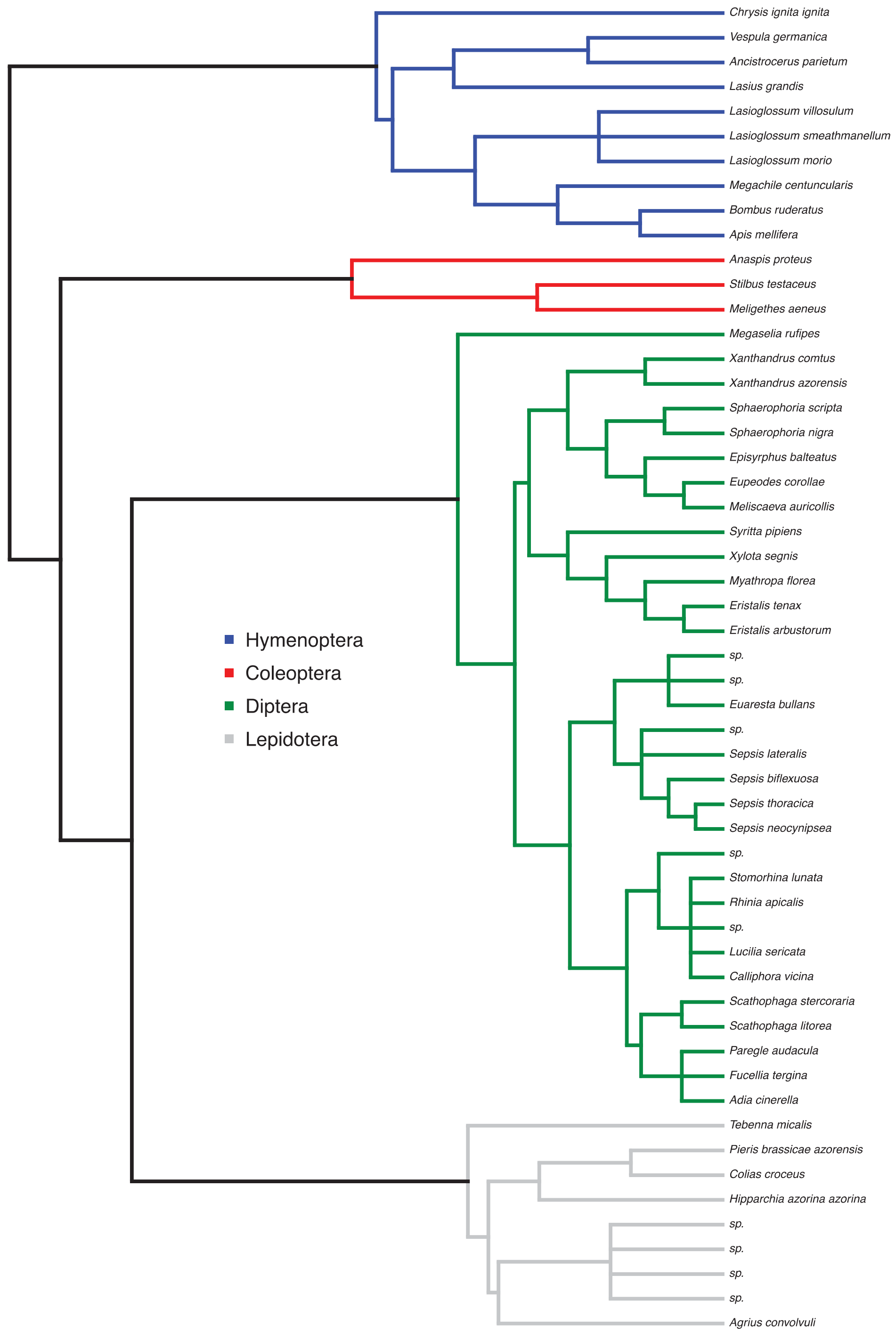


Figure 3.2. The phylogenetic tree for the 54 species of insects collected in the present study with the four orders represented in different colours.

Table 3.4. Results of the phylogenetic least square regressions performed between the link incidence (i.e. interactions at species-level) and insect pollinator species abundance. The correlated error structure was based on a phylogenetic distance matrix derived from the phylogenetic tree presented in Figure 4.2 assuming Pagel's evolutionary model. The associated parameter Pagel's λ increases towards 1 as the phylogeny has an increasing impact on model structure (Pagel, 1999). The effect size (standardized slope for the predictor), the *t* of two tail-student test, the associated P-values (*P*), Pagel's λ as well as the R^2 are given. Abbreviations: NatFor, natural forests; NatVeg, naturalized vegetation areas; ExoFor, exotic forests; SemiPast, semi-natural pastures; IntPast, intensive pastures.

		1NatFor	2NatVeg	3ExoFor	4SemiPast	5IntPast
Link incidence	*Effect size*	0.499	0.659	0.702	0.579	0.698
	t	7.426	10.355	11.684	6.906	10.839
	P	<0.001	<0.001	<0.001	<0.001	<0.001
	λ	0	0	0.484	0	0.539
	R^2	0.586	0.754	0.7823	0.6301	0.786

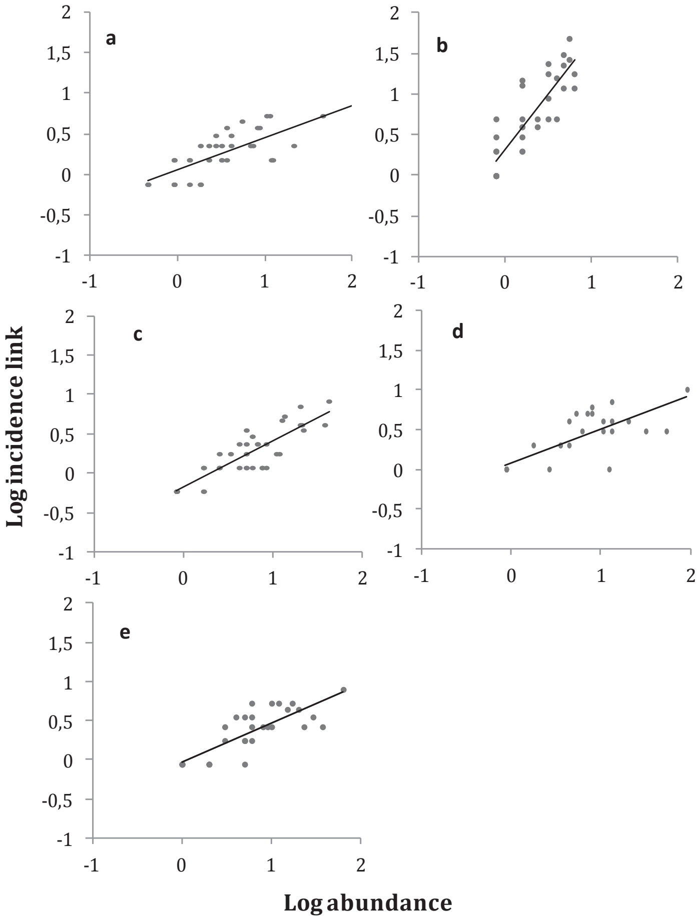


Figure 3.3. Linear regressions between log incidence link and log pollinator abundance. Regressions: a, correspond to natural forests; b, to naturalized vegetation areas; c, to exotic forests; d, to semi-natural pastures and e, to intensive pastures.

3.5 Discussion

Network structure analysis is fundamental to better understand how plant and pollinator insect interact between each other. In such analysis, it is also essential to take into consideration the environmental context, e.g. the influence of environmental conditions as well as and its spatial-temporal variation (Olesen *et al.*, 2011). In this context, our study aimed to assess how different habitat types might influence plant-insect pollinator networks assembly in Azores with as special focus on the role of species abundance in shaping network structure.

Overall, our results suggest that patterns of interaction among Azorean insect pollinators and plant species follow two main patterns: (i) mutualistic interactions are mostly driven by the abundance of species (Fig. 3.3; Fig. 3.4), i.e. abundant species tend to get more links in the community than rare ones (Vázquez & Aizen, 2004), or by species interacting more often becoming generalists, which is frequent in pollination systems (Herrera, 1996; Waser *et al.*, 1996; Olesen, 2000), and (ii) the distributions of links per species follow a truncated power-law and exponential degree distribution model (Table 3.2-3.3). This last result is in accordance with what has been already reported in other studies (e.g. Jordano *et al.*, 2003; Bascompte & Jordano, 2007; Olesen *et al.*, 2008) in which the truncated power-law distribution model was considered as the better fit highlighting a faster decay than expected for the distribution of links (Dunne *et al.*, 2002; Jordano *et al.*, 2003). The power-law distribution (see Barabási & Albert, 1999) is common in large networks and is the consequence of two main mechanisms: (i) the continuous growth of the network by the addition of new links, and (ii) new species preferentially attach to other species that are already well connected. These two processes might explain the linkage pattern found for the Azorean networks (Tables B1 - B5; Fig. 3.1; Tables 3.2 – 3.3; Picanço *et al.*, 2017). In fact, the connectance tends to decrease with species richness or network size (Pearson's correlation between C and AP and between C and A+P: r_p = -0.94, P=0.01 and : r_p = -0.91, P=0.02 respectively) (Table 3.1).

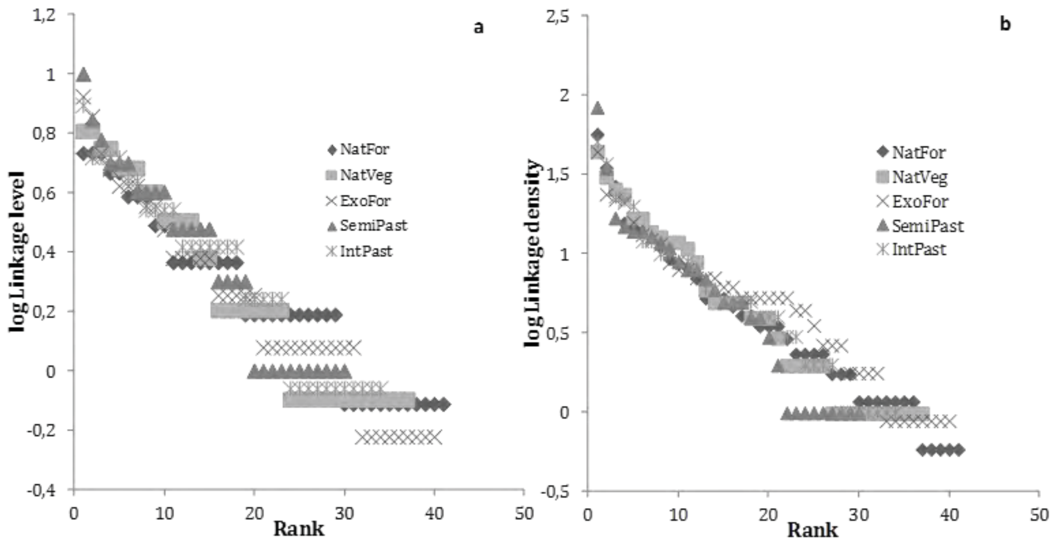


Figure 3.4. Rank abundance distribution of the plant-insect interactions: (a) linkage level and (b) linkage density, for the different habitat types: NatFor (natural forests), NatVeg (naturalized vegetation areas), ExoFor (exotic forests), SemiPast (semi-natural pastures), IntPast (intensive pastures).

Moreover, the habitats with the highest species number of species namely 2NatVeg and 3ExoFor which correspond to habitats with intermediate disturbance levels, showed low connectance and a corresponding low degree of generalization/high degree of specialization (H_2') (Table 3.1). This finding might reveal a tendency for the insect species to interact more often with the same type of plant species in these habitats which is in accordance with previous studies (Jordano *et al*., 2006, 2003; Vázquez & Aizen, 2006), where there is a tendency for specialization to increase with coevolution. These two habitats (2NatVeg and 3ExoFor) are the ones with the higher number of species (A+P) and interaction evenness (Table 3.1). Interestingly, they also show strong relationship among incidence links and abundance (Fig. 3.2; Table 3.4; Fig. 3.3). These results might support the fact that land-uses of moderate disturbance do not have a specific negative influence in the establishment of interactions and subsequent network structures, but rather, they might be seen as "hotspots" for plant-pollinator insect interactions. This finding supports somehow the hypotheses of Intermediate-disturbance postulating that species richness should be higher in communities with moderate levels of disturbance. However, the data did not allow us to properly test the presence of a significant hump-shaped relationship between habitat ranks and networks structure parameters since five observations was not enough to fit linear models with quadratic terms. Therefore, future works will be needed to further explore this issue.

Overall, although network structure is usually highly dependent of species richness (Olesen *et al*., 2007; Fonseca *et al*., 2005; Jordano, 1987), our findings reinforce the fact that species abundance should also be considered as a key variable for the understanding of pollinator-plant structure. Species abundance is one of several ecological factors affecting network structure (Olesen *et al*., 2008; Canard *et al*., 2012) but particularly in small and relatively young networks, abundance can be of overwhelming importance. In this case, it could be a consequence of the young age and the isolation of Azorean islands (Borges & Hortal, 2009; Triantis *et al*., 2012), which, in combination, has resulted in small and simplified networks dominating by generalist species, leading abundance to be one of the main driver of network structure in Azores. Moreover, the absence of modularity (M and Q) within the global network (i.e. the five habitats pooled together) (Table 3.1) suggests that even habitats differences did not generate any specific structures highlighting the fact that the modern Azorean island landscape is relatively uniform or homogeneous in respect to pollinator species. However, interestingly, recent studies in Galápagos and Canaries have shown that modularity prevailed in plant-pollinators networks, with the presence of both island and habitat modules, but also with modules defined by phylogenetic lineages, and differences in modularity are justified by each archipelago's specific evolutionary dynamics (Nogales *et al*., 2015).

The fact that all habitat networks show a nested structure (for both NODF and wNODF), might be in accordance with the fact that incoming pollinators associate preferentially with the most highly linked plants in a network (Olesen *et al*., 2008) which, again, supports the above statements that simple ecological variables such as species abundance is a major driver of the network structure. Hence our networks have a significant but low nested pattern which is expected for relatively small and simplified networks as already reported by Traveset *et al*. (2015) for oceanic islands. A recent work has found nestedness to be less important for individual species persistence than the simpler metric of number of interacting partners (James *et al*., 2012). However, nestedness may stabilize networks at the community level by increasing the number of insect pollinators shared by plants and the number of plants shared by animals, with their respective abundance promoting higher interactions (Vázquez & Aizen, 2004; Olesen, 2000) and, in turn, decreasing competition between plants and between animals (Bastolla *et al*., 2009). These processes structuring the networks are easily identified on very small and relatively homogeneous pollinating networks, such as in more generalized systems of temperate plant-insect networks (Olito & Fox, 2015).

The strong relationship between incidence link and pollinator abundance mirrors a well-known macroecological pattern: the positive interspecific abundance-occupancy relationship (IAOR), which shows that more abundant species tend to occupy more sites (Brown, 1984; Gaston, 1996). As far as I am aware, the IAOR analysis has not been yet applied to the study of ecological networks. Transferred to the plant-pollinators network, occupancy becomes the number of flowers visited by insect species, and abundance is simply the mean number individuals per plant species. Investigation of the position of species within the IAOR space can lead for instance, to a more accurate estimation of species particularly at risk of extinction and can also serves to highlight those species that dominate networks. By examining the residual variations around the IAOR, several authors have also been able to distinguish between specialists and generalist species, an approach that could be very useful for plant-pollinator networks. IAOR-based approach has been successfully applied to a wide variety of taxa and ecosystems (Gaston *et al*., 2000; Blackburn *et al*., 2006) and even recently to oceanic island systems (Rigal *et al*., 2013). Therefore, future IAOR studies on plant-pollinator networks might again demonstrate the importance of abundance in the networks structural patterns.

In conclusion, this study reveals that: i) truncated power-law and exponential models insects and plants show a distribution of links that decays faster than expected, promoting the growth or establishment of new links, ii) land-use of moderate disturbance seems to promote the establishment and development of structural robust, nested, asymmetrical and specialized plant-insect networks, iii) nested and non-modular patterns across habitats and for global network, in combination with strong positive relationships between incidence links and abundance, highlights the importance of abundance as key driver for interactions and associated network structure pattern in Azorean insect pollinating communities.

This study is one of the few attempts to explore the role of species abundance in shaping network structures. Because changes in network structural properties are associated with community stability (Thébault & Fontaine, 2010), understanding the influence of species abundance on network assembly should provide new insights into the mechanisms maintaining or threatening stability of plant-pollinators networks.

Chapter 4

Pollination services mapping and economic valuation from insect communities: a case study in the Azores (Terceira Island)

Ana Picanço, Artur Gil, François Rigal & Paulo A. V. Borges

In: *Nature Conservation*, 18, 1-25. doi:10.3897/natureconservation.18.11523

4.1 Abstract

Insect pollinators provide vital ecosystem services through its maintenance of plant biological diversity and its role in food production. Indeed, adequate pollination services can increase the production and quality of fruit and vegetable crops. This service is currently challenged by land use intensification and expanding human population growth. Hence, this study aims: (1) to assess the pollination services in different land uses with different levels of disturbance through GIS mapping technique using insect pollinators abundance and richness as indicators, and (2) estimate the economic value of pollination by insects in agricultural crops. Our study takes place in a small oceanic Island, Terceira (Azores, Portugal). Our results showed, remarkably, that not only the pristine vegetation areas, but also the orchards and agricultural areas have relatively high values of pollination services, even though both land uses have opposite disturbance levels. For the economic valuation, we analyzed 24 crops in the island and found that 18 depend on pollinators with one-third of these crops having 65% or 95% dependence on pollinators. The economic contribution of pollinators totals 36.2% of the total mean annual agricultural income of the dependent crops, highlighting the importance of insect pollinators in agricultural production and consequent economic gain productions.

Keywords

Ecosystem service, GIS, pollination, insects, agriculture, economic value.

4.2 Introduction

Research at the interface of ecology and economics to characterize, value, and manage ecosystem services (henceforth ES) has supported a paradigm shift in how society thinks about biodiversity, ecosystems and human relationships to them (MEA, 2005; TEEB, 2010; Garbach *et al.*, 2014). This awareness of the ES started with classical papers of Daily (1997) and Constanza *et al.* (1997); and in 2005, the Millennium Ecosystem Assessment (MEA) promoted and defined the concept of ES as "the benefits that humans recognize as obtained from ecosystems that support, directly or indirectly, their survival and quality of life". MEA suggests to group ES into four categories: (1) provisioning services, such as food, water, timber, and fiber; (2) regulating services that affect climate, floods, disease, wastes, and water quality; (3) cultural services that provide recreational, aesthetic, and spiritual benefits; and (4) supporting services such as soil formation, photosynthesis, and nutrient cycling (MEA, 2005).

The valuation and mapping of ES constitutes a continuous and very complex work for several national governments and organizations, and this process is only currently available for few countries (e.g. Portugal, Pereira *et al.*, 2009; UK, Maresca *et al.*, 2011; France, Watson *et al.*, 2011). ES assessment aims usually to estimate of the marginal values of these services to inform decisions and to evaluate how trade-offs in ES provision will affect human well-being. Therefore, researchers are interested in developing methods for quantifying the provision and value of ES so this information can be incorporated into mapping, planning and decision-making at different scales and in different public and private sectors (see e.g., Losey & Vaughan, 2006; Allsopp *et al.*, 2008; Gallai *et al.*, 2009; Nelson *et al.*, 2009; Tallis & Pollaski, 2009; Villa *et al.*, 2009; Maes *et al.*, 2012; Nemec & Raudsepp-Hearne, 2013; Nahuelhual *et al.*, 2013; 2015).

Pollination together with seed dispersal is considered as one of the key ES, classified by the Common International Classification of Ecosystem Services (CICES) coding system (Haines-Young & Potschin, 2013) as a "Regulation & Maintenance ES" with the code 2.3.1.1. Among other studies, Klein *et al*. (2007), Aizen *et al.* (2009), Gallai *et al*. (2009), Calderone (2012) and Giannini *et al.* (2015) show that pollination services contribute significantly to the agricultural production and subsequently assures 75% of food production worldwide (Klein *et al.*, 2007) (as well as to other flowering plants) by ensuring plant reproduction, fruit set development and dispersion (e.g. Ollerton *et al*., 2011; Altieri *et al*., 2015). Notably, the pollination of some vegetable crops (e.g. cabbage and other brassicas, carrots, turnips, lettuce, chicory and onions) increases the quality of the seed production (Gallai & Vassière, 2009). In addition, insect pollinators enhance fruit and seed quality (Garibaldi *et al.*, 2013; Bartomeus *et al.*, 2014; Garratt *et al.*, 2014; Marini *et al.*, 2015; Saeed *et al.*, 2016) and reinforces pest management (Cross *et al*., 2015) which constitutes an indirect and difficult benefit to measure, but extremely important for the agricultural market. Also, a recent study on pollination by wild insect pollinators has showed their capacity to increase the seed production in 41 agricultural systems globally, regardless of the abundance of honey bees (Garibaldi *et al.*, 2013). Additionally, it was also documented that wild insect pollinators can buffer the impact of climate change on crop production (Rader *et al.*, 2013), most likely due to their high biological diversity that can in turn stabilize ES against habitat disturbances (Cardinale *et al.*, 2012).

Besides these findings, there is also a general consensus that native pollinators abundance and richness are declining throughout the world (Ghazoul, 2005; Biesmeijer *et al.*, 2006; Winfree *et al.*, 2009). This global decline has sparked the formation of a global policy framework for pollinators, primarily through the International Pollinator Initiative within the Convention of Biological Diversity (CBD) and several other programs (e.g. Food and Agricultural Organization (FAO) Global Action on Pollination Services for Sustainable Agriculture; Bee Life European Beekeeping Coordination). All of these initiatives emphasize the need to assess and monitor the pollinators in different regions in order to better plan their conservation, restoration and to preserve the ES they supply for humans.

The Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) from United Nations Environment Programme (UNEP; Zisenis, 2015; Schmeller & Bridgewater, 2016) was recently created as a Knowledge-Policy interface (Díaz *et al.*, 2015; Schmeller & Bridgewater, 2016). In the fourth plenary of IPBES (IPBES-4) the agenda's item 5 (work programme of the Platform) included the development of works towards the approval of the thematic assessment on pollinators, pollination and food production ("Deliverable 3a" - see http://www.ipbes.net/workprogramme/pollination). This "Deliverable 3a" highlighted substantial knowledge gaps in different regions on the status and trend of pollinators and pollination, making the global assessment of insect pollinators (henceforth IP) not possible due to lack of data, although regional and national assessments indicated that more than 40 % of insect pollinators are threatened locally (Schmeller & Bridgewater, 2016).

These knowledge gaps unveil how the interactions between plants and insects are numerous and complex. So, the understanding of how plant-insect species' interactions affect ecological functions and are affected by land management (Kremen *et al.*, 2007) is central to maintain and enhance associated ES. As a vital and increasingly threatened ES, pollination (Klein *et al.*, 2007; Potts *et al.*, 2010) has become an often-cited example of how the ES are economically valuable (Hanley *et al.*, 2015). Two additional recent examples of studies about ES pollination in Europe (EU) that complement each other are from Leonhardt *et al.* (2013) and Schulp *et al.* (2014), both showing results that provide an overview of ES importance, variation and influence throughout European regions.

In this work, we assess the ES provision and values provided by insect pollinators in the Azores archipelagic region (Portugal) where few studies on ES assessment (e.g. Cruz *et al.*, 2011; Mendonça *et al.*, 2013; Vergílio *et al.*, 2016) or related to pollination and seed dispersal services have been undertaken (e.g. Pereira, 2008; Heleno *et al.*, 2009; Olesen *et al.*, 2002, 2012). We used a database on the spatial distribution of insect pollination in Terceira Island (Azores) recently collected (Chapter 2; Picanço *et al.*, 2017) to provide the first insight of the bees and other IP contribution to the pollination services and for assessing pollination-related ES in a small oceanic island. With this purpose, I applied two types of methodological approaches: (1) mapping pollination services with geographic information systems (GIS; e.g. Nemec & Raudsepp, 2013) using bees and other IP abundance and richness numerical values as indicators; and (2) economic valuation - through the production function approach - by using crops production estimates and crops dependence ratio (Klein *et al.*, 2007; Gallai & Vassière, 2009; Hanley *et al.*, 2015). The goals were to determine: (i) the spatial variations of the pollination services; (ii) whether the variations of the pollination services were influenced by the different land-uses and/or level of disturbance; (iii) the number of crops for which production has a certain level of dependence on IP (or vulnerability ratio); and (iv) estimation of the island's IP economic value.

4.3 Methods

Study area and sampling sites

Terceira Island, with an area of approximately 402 km2 (length=29 km and width =17 km) is a small island of the central group of the Azores archipelago (Portugal), located in the North Atlantic Ocean (38º 37´N 38º 48´N, 27º 02´W 27º 23´W). Like the other islands of the archipelago, Terceira is of volcanic origin and the third oldest island after Santa Maria and São Miguel, with an age of about 3,52 million years (Forjaz *et al*., 2004). The island is formed by four main volcanic complexes namely Cinco Picos, Guilherme Moniz, Pico Alto and Serra de Santa Bárbara, the latter corresponding the highest point of the island (1023 meters).

Terceira climate is temperate oceanic, characterized by both high levels of relative atmospheric humidity and low temperature fluctuations throughout the year. Particularly, winter and autumn are marked by heavy and regular precipitations often associated with strong winds. The average annual precipitation exceed 3400 mm in "Serra de Santa Bárbara" summit, and reaches almost 1000 mm per year in all the island. The average annual temperature varies between 9º C in "Serra de Santa Bárbara", to 17º C on the coast. Minimum temperature in the winter varies between 4º and 12º C while maximum temperature in the summer varies between 14º and 26º C (Azevedo et al 2004).

The insects (Table C1; Appendix C) were observed from five relevant habitat types, corresponding to an increasing gradient of disturbance, namely natural forests (NatFor) mainly characterized by *Juniperus-Ilex* montane forests and Juniperus woodlands, naturalized vegetation areas (NatVeg) composed by *Pittosporum* spp. and *Rubus* spp., exotic forests (ExoFor) with *Criptomeria japonica* and *Eucalyptus* sp., semi-natural pastures (SemiPast) with *Lotus* sp., *Holcus* sp., *Rumex* sp. and intensively managed pastures (IntPast) with Lolium sp. and Trifolium spp.. These habitat types were previously selected according to landscape disturbance index from Cardoso *et al*. (2013), with the aim to assess the impact of land-use change on flower-visiting insect species community structure in Terceira Island (for further details see Picanço *et al.*, 2017). In each habitat type, 10 sites were selected. In each site, 10 meters' linear transects with 1 meter width were set up (Pollard and Yates 1993), making a total of 50 transects located across the entire island (Fig. 4.1) (for further details on the sampling protocol see Picanço *et al*., 2017).

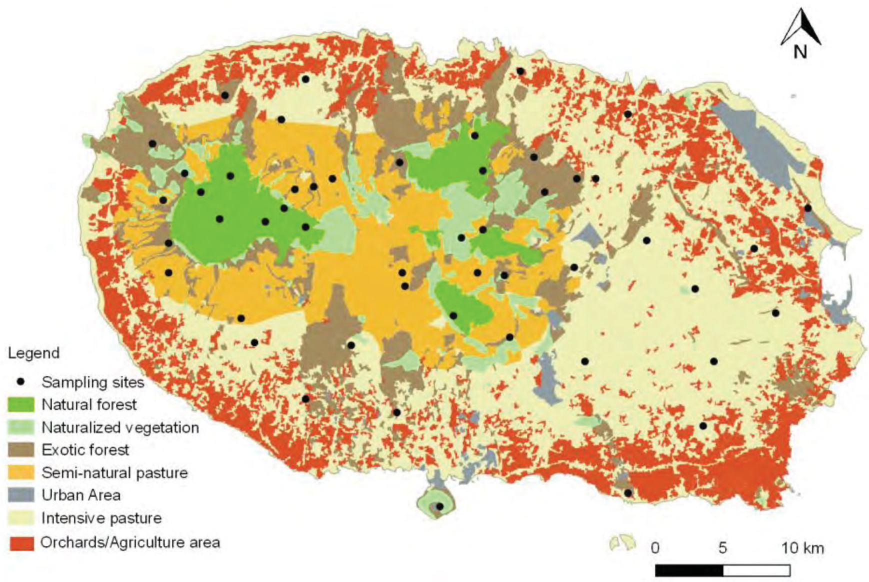


Figure 4.1. Land use distribution map of Terceira Island with the selected sampling sites as black dots: NatFor (natural forests), SemiPast (semi-natural pastures), NatVeg (naturalized vegetation areas), ExoFor (exotic forests), IntPast (intensively managed pastures), urban areas and agriculture areas. Land use cartographic sources: DROTRH (2008) and Gaspar (2007).

Ecosystem service mapping

Digital Elevation Models (DEM) are a numerical representation of topography, made up of squared equal-sized grid cells (pixels) with an elevation value associated to each pixel. DEM constitute the most widely used data structure to store and analyze topographic information in GIS (Rishikeshan *et al.*, 2014). The pollination service mapping was performed with the ArcGIS10© software, by applying the "Topo to Raster" interpolation technique, which was designed for the creation of hydrologically correct DEMs. This method uses an iterative finite difference interpolation technique. It is optimized to have the computational efficiency of local interpolation methods, such as inverse distance weighted (IDW) interpolation, without losing the surface continuity of global interpolation methods, such as Kriging and Spline. It is essentially a discretized thin plate spline technique for which the roughness penalty has been modified to allow the fitted DEM to follow abrupt changes in terrain. Furthermore, the quantity of input data can be up to an order of magnitude less than that normally required to adequately describe a surface with digitized contours, further minimizing the expense of obtaining reliable DEMs (Wahba, 1990, Hutchinson, 1988, 1993, 2011; ESRI, 2016). In this work, DEM were generated using respectively as elevation data the bees and insect pollinators' abundance and richness quantitative information collected from field surveys, of the 10 transects of each habitat type (or land-use). We have chosen to separate the bees and total insect pollinators data, because many studies about pollination services are more related to bees than to the insect pollinators in general, and also, to analyze if there would be differences between the DEM of the possible pollination services contribution from these two groups of data. This latter also applies relating to the abundance (i.e. number of individuals) and richness (i.e. number of species) information on both groups (Table C1; Appendix C). In this way, by applying all the fieldwork data, we intend to be more accurate as possible while developing DEM that deliver information on pollination services.

To complement this spatial analysis, we applied the formerly mentioned index of landscape disturbance metric based on the attributes of the landscape matrix (Cardoso *et al.*, 2013). This index, ranging from 0 to 100, corresponds to a local index of disturbance by taking into account the level of disturbance in the surrounding areas. Values of the disturbance index (D) was obtained by ranking the different land uses attributing a value of "local disturbance" (L) on a land use map of 100 x 100 m resolution built from aerial photography and fieldwork, and for each 100 x 100 m cell the D was calculated (see Cardoso *et al.*, 2013 and Appendix C1, Fig. C1).

For each analysis, we overlaid the respective pollination services' interpolation maps delivered by the fieldwork data on bees and other insect pollinators from Chapter 2 (see also Picanço *et al.*, 2017) with the land use and the disturbance index D. We have created thresholds to analyze disturbance index D influence on the amount and diversity of bees and other insect pollinators and mapped these categories in eight classes for bees' abundance (N) and richness (S); and in 12 classes for insect pollinators' abundance (N) and richness (S). The created thresholds values for the different classes are specified in Table 4.1. The numbers of classes established follow the minimum and maximum abundance and richness values (Table C1; Appendix C) obtained in Chapter 2 (see also Picanço *et al.*, 2017) for the different habitat types - natural forest, naturalized vegetation areas, exotic forest, semi-natural pasture and intensively managed pasture. The exceptions are urban, agriculture and orchard areas due to unavailable technical resources. Bees (Hymenoptera) a very important functional group, are constituted by the following most abundant species *Apis mellifera*, *Bombus ruderatus* and *Lasioglossum* spp., while the other wild insect pollinators groups are constituted by Coleoptera, Diptera and Lepidoptera, being the most abundant species *Anaspis proteus*, *Meligethes aeneus*, *Stomorhina lunata*, *Rhinia apicalis*, *Episyrphus balteatus*, *Eristalis tenax*, *Hipparchia azorina azorina* and *Pieris brassicae* (for further information related to the species list see Table C1 in Appendix C).

The disturbance level was organized in four classes, including a first one with very low disturbance level typical of high altitude native forests ($D<20$), two intermediate classes and finally a class with high levels of disturbance ($D>40$). The number of individuals of bees was divided in two classes in a logarithm scale (less than ten and more than ten individuals). The number of species of bees was divided in two classes with one species and two or more species. For insect pollinator abundance and richness three classes were prepared: for abundance we created one for the rarest species, one for intermediate and one for the most abundant; for species richness we divided the classes arbitrarily in less than 10 species, 10 to 15 and more than 15 (see Table 4.4). These created classes were evaluated through a quantitative analysis of the area covered by each class in Terceira Island.

Table 4.1. Distribution of disturbance index (D) for bees' and insect pollinators' abundance (N) and richness (S) per classes.

Bees class	D	N	S	IP class	D	N	S
1	D<20	≥10	≥2	1	D<20	≥73	>15
2	D<20	<10	<2	2	D<20	25≤S<73	10<S≤15
3	20<D<30	≥10	≥2	3	D<20	<25	<10
4	20<D<30	<10	<2	4	20<D<30	≥73	>15
5	30<D<40	≥10	≥2	5	20<D<30	25≤S<73	10<S≤15
6	30<D<40	<10	<2	6	20<D<30	<25	<10
7	>40	≥10	≥2	7	30<D<40	≥73	>15
8	>40	<10	<2	8	30<D<40	25≤S<73	10<S≤15
				9	30<D<40	<25	<10
				10	>40	≥73	>15
				11	>40	25≤S<73	10<S<15
				12	>40	<25	<10

Economic valuation

Terceira Island's main economic activity is agriculture, with the production of dairy products and raising livestock. Many small farmers practice subsistence agriculture or produce in small quantities to cooperatives. The island consumer is relatively similar to the southern Europe consumers, when comparing the GDP per capita of Azores region and Portugal to other countries of Europe (Tables 4.2 - 4.3), with Azorean economy comprising a conventional interval of prices elasticities -1.2 and -0.8, as in Gallai &Vassière (2009).

Table 4.2. Statistical data on Portugal and respective regions, emphasizing the Azores context (source: Instituto Nacional de Estatística, INE, 2014).

Regions **NUTS II (version 2013)**	**Total Population (2014)**	**Active Population (2014)**	**GDP (2013)**	**GDP per capita (PPP) a) (2013)**	
	Thousands	**Thousands**	**Millions €**	**Thousands**	**UE28=100**
Portugal	10,375	5,226	171,211	16.4	79
North	3,622	1,834	48,668	13.3	64
Centre	2,264	1,170	32,123	14	68
Lisbon Metropolitan Area	2,809	1,383	63,902	22.7	110
Alentejo	733	358	11,275	15.1	73

Algarve	441	227	7,310	16.5	79
Azores AR	**246**	**122**	**3,694**	**14.9**	**72**
Madeira AR	259	131	4,071	15.5	75

Note: a) ppc – purchasing power per capita.

Table 4.3. EU member states economic data of 2015. The GDP and the GDP (PPP) per capita for some European Union member states. The table can also be used as a rough gauge to the relative standards of living among member states, with Luxembourg the highest and Bulgaria the lowest. Source: Eurostat, 2015.

Member state	GDP (Nominal) in billions of euro	GDP (Nominal) per capita euro	GDP (PPS) per capita euro
Germany	3,032.8	37,100	36,000
United Kingdom	2,577.3	39,600	31,600
France	2,181.1	32,800	30,300
Italy	1,642.4	27,000	27,500
Spain	1,075.6	23,200	26,200
Netherlands	676.5	40,000	36,800
Sweden	447.0	45,600	35,600
Poland	429.8	11,200	19,800
Belgium	410.4	36,600	33,800
Austria	339.9	39,400	36,600
Denmark	271.8	47,800	36,200
Ireland	255.8	55,100	49,600
Finland	209.2	38,200	31,200
Portugal	179.5	17,300	22,300
Greece	176.0	16,200	20,300
Czech Republic	167.0	15,800	25,000
Romania	160.4	8,100	16,300
Hungary	109.7	11,100	19,700
Slovakia	78.7	14,500	22,200
Luxembourg	51.2	89,900	76,400
Bulgaria	45.3	6,300	13,300

FRUTER/Frutercoop is the "Association of Producers of Fruit, Vegetables and Flowers' in Terceira Island". Using their data from 2011 to 2015, we calculated the mean annual productions of 24 common fruits and vegetables in this island. Five-year means were used instead of the latest yearly production figures, in order to smooth out annual variations in crop output.

We estimated the value of pollination gain in agricultural crops and its respective vulnerability by using the crop production amount (Kasina *et al*., 2009), market and producer prices for each crop. This method was adapted to a regional rating scale, according to the methodology of FAO (Gallai & Vaissière, 2009) previously developed by Gallai *et al.* (2009). The data on crops were derived from multiple sources: Klein *et al*. (2007; only for crops grown in Terceira Island), FAO (Gallai & Vaissière, 2009), FRUTER/Frutercoop (2016), and Serviço de Desenvolvimento Agrário da Terceira (2016). We included all plants of economic importance in our dataset, such as those harvested for food, livestock, or for other uses.

The IP dependency for each crop was categorized according to Klein *et al*. (2007), and posteriorly adapted by Gallai & Vaissière (2009), into the following classes: essential, great, modest, little, increase seed production, increase breeding and no increase. We also corresponded the dependence ratio (DR) to these classes according to Gallai *et al*. (2009): essential, DR = 0.95 (meaning that the value of pollination-driven yield lies between 90 and 100%); great, DR = 0.65 (40–90% of yield is dependent on pollination); modest, DR = 0.25 (10–40% of yield is dependent on pollination) and little, DR = 0.05 (0–10% of yield is dependent on pollination). We multiplied this ratio by the economic value of the mean annual crop production to obtain the pollination services' economic value (Gallai & Vaissière 2009). The production value was obtained through the market prices and producer prices provided by the regional authority – "Serviços de Desenvolvimento Agrário da Terceira" (2016). For the current assessment we did not consider currency values, regional or seasonal variations in the crop labour costs and food prices.

4.3 Results

Ecosystem service mapping

By analysing together both the land use map of Terceira Island (Fig. 4.1) and the four pollination services' interpolation maps (Fig. 4.2) we can observe that: (i) bees abundance (N) comprised by some abundant species like *Bombus ruderatus* and *Lasioglossum morio* (Table C1; Appendix C) presented higher density values around the northwest, east, south-eastern coast and also at north, near the centre of Terceira Island, matching especially with the current areas occupied by orchards and agriculture; (ii) bees richness (S) high density values also correspond mostly to orchards and agricultural areas, namely in the north, along the west to the southern coast and in-between the centre and the eastern side of Terceira island; (iii) insect pollinators (IP) abundance (N) with the most abundant species being *Anaspis proteus*, *Stomorhina lunata*, *Eupeodes corollae*, *Sepsis neocynipsea* and *Pieris brassicae azorensis* (Table C1; Appendix C) presented higher density values around the north-western coast till near the center, and also in the eastern and central parts of the island, corresponding these higher density spots to the main Terceira island's biodiversity hotspots (pristine vegetation forests): "Serra de Santa Bárbara" and "Pico Alto" (that are both classified as protected areas). In the south-eastern coast of the island some orchards and agricultural areas also presented high IP abundance; finally, (iv) insect pollinators (IP) richness (S) comprised by many hoverfly species (Diptera, Syrphidae) when compared to the other insect pollinators groups Coleoptera and Lepidoptera (Table C1; Appendix C) followed a very similar spatial pattern to that of IP abundance. Nevertheless, orchards and agricultural areas in the north-western coast also presented high density values of IP richness.

In order to strengthen the previous analysis, we assessed the influence of the disturbance index (D), as calculated by Cardoso *et al*. (2013), in the pollination services and also assessed the area covered by bees and IP classes within the island (Tables 4.4 - 4.7).

As a result of overlaying each previous pollination service output with the matching disturbance index D spatial data (see full description of classes in Table 4.1), we observed that "Class 1" spatial distribution (areas with disturbance index D lower than 20 and high values for both abundance (N) and richness (S) of bees and IP) corresponded in every output to the small areas of pristine vegetation (biodiversity hotspots) at high altitudes and consequent most difficult human access, namely “Serra de Santa Bárbara” and “Pico Alto” protected areas (Fig. 4.2), which corresponds to the smallest % of island area (between 0.06 – 0.56%) occupied (Tables 4.4 – 4.7).

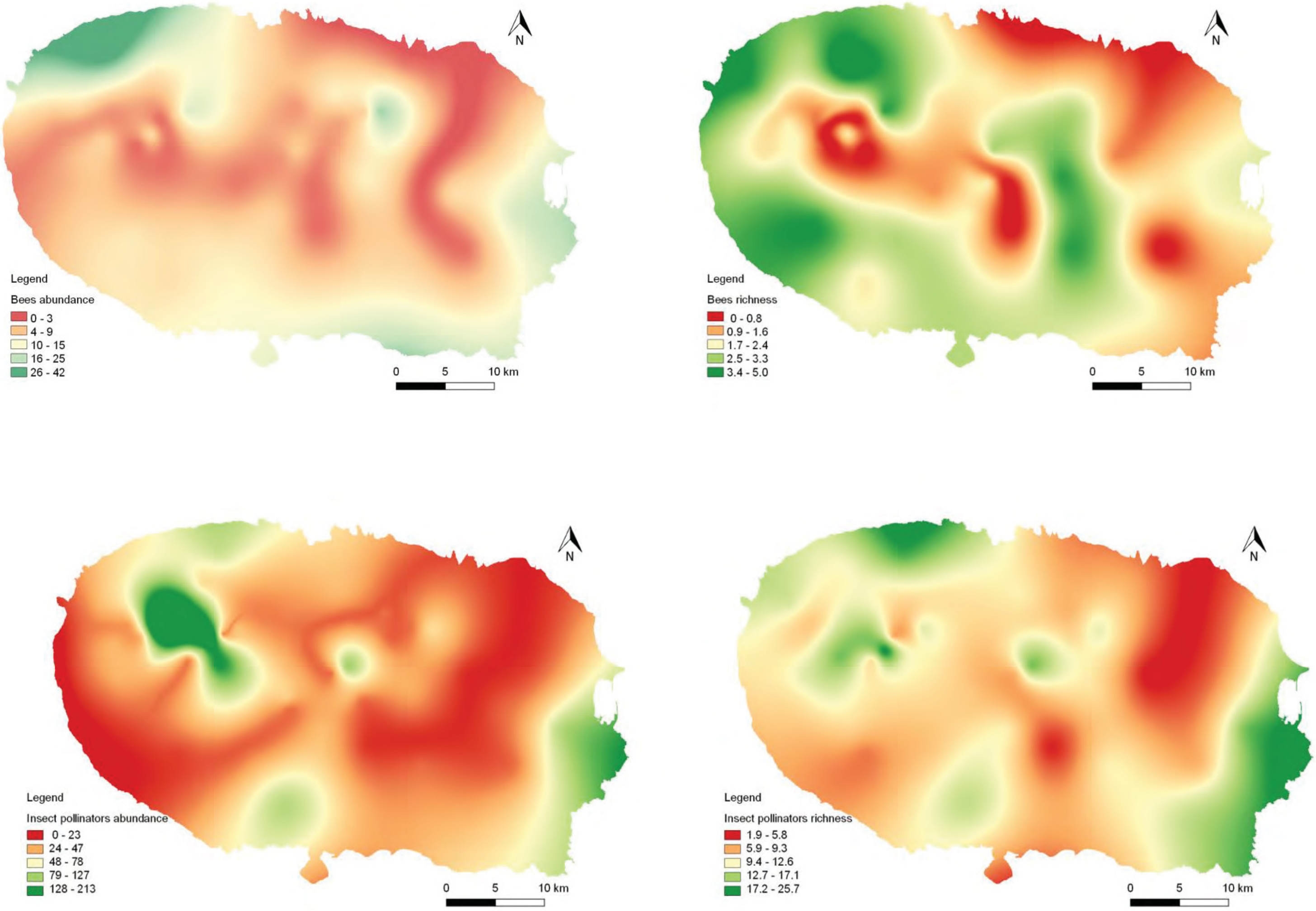


Figure 4.2. Pollination services' interpolation maps: (upper left) bees abundance (N); (upper right) bees richness (S); (lower left) insect pollinators abundance (N); (lower right) insect pollinators richness (S)

According to the same Fig. 4.3 and to Table 4.1, classes 4 and 6 for bees' abundance (N) and richness (S) (Table 4.4 and 4.5), as well as classes 5 and 8 for IP's abundance (N) and richness (S) (Table 4.6 and 4.7), respectively, are the predominant spatial patterns around class 1's areas.

Moreover, both bees-related maps (abundance - N and richness - S) in Fig. 4.3, Tables 4.4 and 4.5 show that the whole island is predominantly covered by highly disturbed areas (disturbance index D higher than 40) that seriously affect these pollination services, resulting in low abundance (N) and richness (S) for bees (classes 7 and 8). In fact, for the bees' abundance (N), class 8 covers the north to north-eastern coast, passing through the centre until the western coast. Class 7 is predominant from east to the southwestern coast. Regarding the bees richness

(S), the class 8 occupies the centre and the area from north to the south-eastern coast, as class 7 covers the areas from northwest to south and the territory between the centre and the eastern coast of the island. Both classes 7 and 8 mostly occur in orchards/agricultural areas, and in IntPast land use, respectively (see Fig. 4.1 and Fig. 4.3).

In the case of IP-related maps (Fig. 4.3, Table 4.6 and 4.7), the spatial pattern of disturbance versus pollination services is quite similar to that of bees' pollination services. Highly disturbed Class 11's areas (see Table 4.1) are predominant in the whole island for both IP's abundance (N) and richness (S), occupying around 39% and 20% respectively (Table 4.6 and 4.7). In the case of IP abundance (N), this class covers relevant areas in the north-western, eastern, south-eastern and southern territories of Terceira Island. For IP richness (S), class 11 covers large areas in the west, south and east of Terceira Island (Fig. 4.3). Most disturbed areas with lower IP-related services (abundance and richness) performance mostly occur in orchards, agricultural areas and other land uses strongly affected by human activity (Fig. 4.1).

Table 4.4. Spatial assessment of bees' abundance classes in Terceira Island.

Class	Total area (ha)	% of Terceira Island area
1	225	0.56
2	1325	3.29
3	103	0.26
4	2367	5.89
5	1006	2.50
6	3342	8.31
7	14342	35.66
8	17376	43.20
TOTAL	40086	99,67

Table 4.5. Spatial assessment of bees' richness classes in Terceira Island.

Class	Total area (ha)	% of Terceira Island area
1	24	0.06
2	276	0.69
3	142	0.35
4	2071	5.15
5	1192	2.96
6	3674	9.13
7	13880	34.51
8	15787	39.25
TOTAL	37046	92.11

Table 4.6. Spatial assessment of insect pollinators' abundance classes in Terceira Island.

Class	Total area (ha)	% of Terceira Island area
1	154	0.38
2	753	1.87
3	255	0.63
4	100	0.25
5	1504	3.74
6	390	0.97
7	136	0.34

8	2510	6.24
9	977	2.43
10	1997	4.97
11	15776	39.22
12	12782	31.78
TOTAL	37334	92.82

Table 4.7. Spatial assessment of insect pollinators' richness classes in Terceira Island.

Class	**Total area (ha)**	**% of Terceira Island area**
1	117	0.29
2	202	0.50
3	24	0.06
4	181	0.45
5	1055	2.62
6	320	0.80
7	101	0.25
8	1864	4.63
9	1065	2.65
10	2612	6.49
11	7922	19.70
12	8705	21.64
TOTAL	24168	60.09

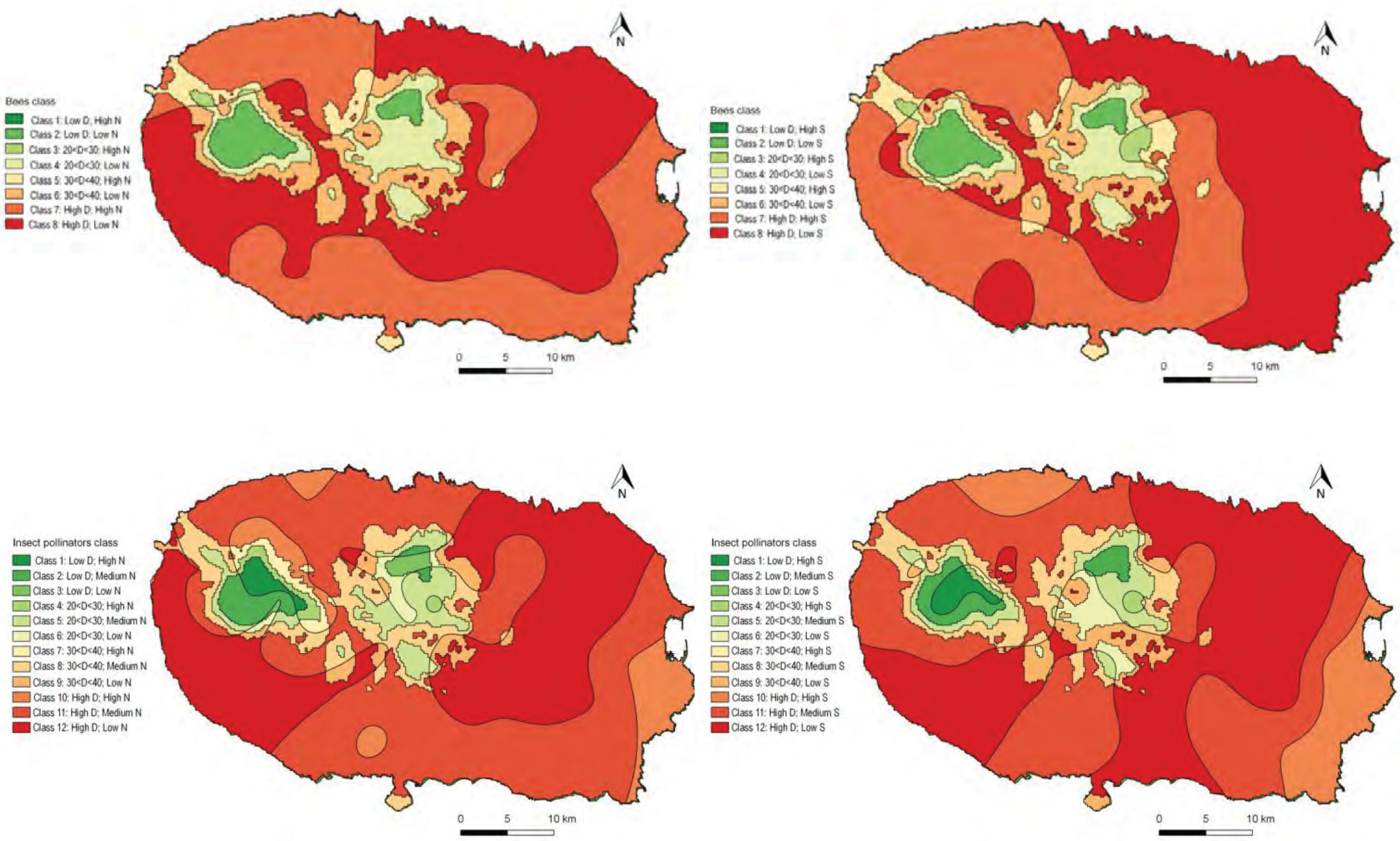


Figure 4.3. Classification maps of pollination services according to the influence of disturbance index (D): (upper left) bees abundance (N); (upper right) bees richness (S); (lower left) insect pollinators abundance (N); (lower right) insect pollinators richness (S).

Economic valuation

According to the data provided by Frutercoop for the period between 2011 and 2015, the total value of production for the 24 referred crops in Table 4.8 represented an amount of €874,925.51, from which only 29% of the production is from crops with known pollinator dependence ratio (see Tables 4.9 and 4.10).

Table 4.8. Array of crops used directly for human food following FAOSTAT and listed by common names of crops.

Crop common name	Crop species	Crop category following FAO	Dependence upon animal pollination	Dependence ratio (I consider only crops for which pollinators increase production of plant parts that are consumed)			Producer price per metric kg	Production	Total value of crop (TVC)	Economic value of insect pollinators (EVIP)	Consumer surplus loss (CSL) with elasticity =	
				Min	Max	Mean (DR)						
sources: FAOstat (http://faostat.org)			**sources: Klein *et al.* 2007**				**Sources = FRUTER/Serv. Desenvol. Agrário Terceira**		**Price * Production**	**TVC*D**	**-0.8**	**-1.2**
							€ / metric kg	metric kg	€	€	€	€
Apples	*Malus domestica*	Fruits	Great	0.4	0.9	0.65	1.50	40,424.70	60,738.11	39,479.77	70,952.49	57,515.02
Bananas	*Musa sapientum, M. cavendishii, M. nana, M. paradisiaca*	Fruits	Increase - breeding	-	-	-	1.00	405,642.60	405,642.60	-	-	-
Beans, green	*Vigna spp., V. unguiculata, V. subterranean* (syn. *Voandzeia subterranea*), *Phaseolus spp.*	Vegetables	Little	0	0.1	0.05	3.50	2,027.14	7,094.99	354.75	365.80	362.07
Cabbages and other brassicas	*Brassica chinensis, B. oleracea*	Vegetables	Increase - seed production	-	-	-	1.29	46,541.44	60,038.46	-	-	-
Carrots and turnips	*Daucus carota*	Vegetables	Increase - seed production	-	-	-	0.52	2,659.00	1,382.68	-	-	-
Chestnuts	*Castanea sativa*	Treenuts	Modest	0.1	0.4	0.25	1.00	6,104.60	6,104.60	1,526.15	1,807.69	1,706.62

Crop common name	Crop species	Crop category following FAO	Dependence upon animal pollination	Dependence ratio (I consider only crops for which pollinators increase production of plant parts that are consumed)			Producer price per metric kg	Production	Total value of crop (TVC)	Economic value of insect pollinators (EVIP)	Consumer surplus loss (CSL) with elasticity =	
				Min	Max	Mean (DR)						
Chillies and peppers, green	*Capscium annuum, C. frutescens*	Vegetables	Little	0	0.1	0.05	1.27	989.93	1,252.27	62.61	64.56	63.90
Citrus fruit, nes	*Citrus bergamia, C. medica* (var. *cedrata*), *C. myrtifolia, Fortunella japonica*	Fruits	Little	0	0.1	0.05	1.99	12,790.40	25,452.90	1,272.64	1,312.28	1,298.89
Cucumbers and gherkins	*Cucumis sativus*	Vegetables	Great	0.4	0.9	0.65	0.79	6,695.04	5,289.08	3,437.90	6,178.55	5,008.41
Figs	*Ficus carica*	Fruits	Modest	0.1	0.4	0.25	10.00	1,098.22	10,982.20	2,745.55	3,252.04	3,070.21
Lemons and limes	*Citrus aurantifolia, C. limetta, C. limon*	Fruits	Little	0	0.1	0.05	2.79	5,669.94	15,819.13	790.96	815.59	807.27
Lettuce and chicory	*Lactuca sativa, Cichorium intybus, C. endivia*	Vegetables	Increase - seed production	-	-	-	4.06	36,104.51	146,584.31	-	-	-
Onions (inc. shallots), green	*Allium cepa, A. ascalonicum, A. fistulosum*	Vegetables	Increase - seed production	-	-	-	0.88	4,732.20	4,140.68	-	-	-
Oranges	*Citrus aurantium, C. sinensis*	Fruits	Little	0	0.1	0.05	1.19	3,750.00	4,443.75	222.19	229.11	226.77
Other melons (inc.cantaloupes)	*Cucumis melo*	Vegetables	Essential	0.9	1	0.95	2.99	6,327.10	18,918.03	17,972.13	77,617.29	42,633.64

Crop common name	Crop species	Crop category following FAO	Dependence upon animal pollination	Dependence ratio (I consider only crops for which pollinators increase production of plant parts that are consumed)			Producer price per metric kg	Production	Total value of crop (TVC)	Economic value of insect pollinators (EVIP)	Crop Consumer surplus loss (CSL) with elasticity =	
				Min	Max	Mean (DR)						
Peaches and nestarines	*Prunus persica, Persica laevis*	Fruits	Great	0.4	0.9	0.65	1.99	90.22	179.54	116.70	209.73	170.01
Pears	*Pyrus communis*	Fruits	Great	0.4	0.9	0.65	1.50	463.10	694.65	451.52	811.47	657.79
Plums and sloes	*Prunus domestica, P. spinosa*	Fruits	Great	0.4	0.9	0.65	1.99	4,303.30	8,563.57	5,566.32	10,003.71	8,109.14
Pumpkins, squash and gourds	*Cucurbita maxima, C. mixta, C. moschata, C. pepo*	Vegetables	Essential	0.9	1	0.95	3.80	1,329.14	5,050.73	4,798.20	20,722.25	11,382.32
Strawberries	*Fragaria* spp.	Fruits	Modest	0.1	0.4	0.25	3.89	3,064.24	11,919.89	2,979.97	3,529.71	3,332.35
Sweet potatoes	*Ipomoea batatas*	Roots and Tubers	Increase - breeding	-	-	-	1.49	1,079.90	1,609.05	-	-	-
Tomatoes	*Lycopersicon esculentum*	Vegetables	Little	0	0.1	0.05	2.64	24,889.46	65,770.40	3,288.52	3,390.94	3,356.34
Watermelons	*Citrullus lanatus*	Vegetables	Essential	0.9	1	0.95	0.69	10,512.90	7,253.90	6,891.21	29,761.46	16,347.38
TOTAL OR MEAN				0.28	0.52	0.40	2.29	27,273.44	874,925.51	91,957.09	231,024.67	156,048.13

In terms of welfare, an assessment of the social to Terceira Island consumers resulting from pollinator decline estimated that the consumer surplus (economic measure of consumers benefit) loss was from €156K to €231K, which reflects the impact on the price of the crop on the market, based upon average price elasticities of −1.2 to −0.8, respectively (Table 4.10). When considering these values, we must also take into account that the production from Frutercoop represent approximately 54% of the entire island's production.

Table 4.9. Economic impact of insect pollination of the agricultural production used directly for human food and listed by the main categories.

Crop category following FAOSTAT	Average value per metric kg	Total value of crop (TVC)	Economic value of insect pollinators (EVIP)	Ratio of vulnerability (RV)	Consumer surplus loss (CSL) with elasticity equal to	
		Price * Production	TVC*DR	EVIP/TVC	-0.8	-1.2
	€ / metric kg	€	€		€	€
Fruits	1.14	544,436.34	53,625.63	9.8%	91,116.13	75,187.45
Roots and Tubers	1.49	1,609.05	0.00	0.0%	0.00	0.00
Treenuts	1.00	6,104.60	1,526.15	25.0%	1,807.69	1,706.62
Vegetables	2.26	322,775.52	36,805.31	11.4%	138,100.85	79,154.07
TOTAL		874,925.51	91,957.09	10.5%	231,024.67	156,048.13

Among the 18 crops relatively dependent to IP, the greatest economic value generated by the IP was originated by the class "little" or DR = 0.05, with 46.9% (€119,833), as well as the one originated by the class "great" or DR = 0.065, with 29.5% (€75,465) (Tables 4.8 and 4.9). In each class "little" and "great", the most representative crop productions were respectively "tomatoes" and "apples" (Table 4.8).

Table 4.10. Mean annual production values of crops with different pollinator dependency categories, for the period from 2011 to 2015.

Crop	Pollinator dependency class	Pollinators DR	Mean annual production (kg)
Beans, green; chillies and peppers, green; citrus fruit; lemons and limes; oranges; tomatoes	Little	0.05	50,116.87
Chestnuts, figs; strawberries	Modest	0.25	10,267.06
Apples; pears; peaches and nectarines; plums and sloes; cucumbers and gherkins	Great	0.65	51,976.36
Pumpkins; squash and gourds; watermelons and other melons	Essential	0.95	18,169.14
Bananas; cabbages and other brassicas; carrots and turnips; lettuce and chicory; onions (inc. shallots); sweet potatoes	Unknown	-	496,759.65
Total			627,289.08

On average, in recent years (2011-2015), IP contributed to pollination service in crop production with about €91,957 (total economic value of IP, EVIP), representing 10.5% crops ratio of vulnerability (VR) (Table 4.9), according to Frutercoop dataset. Extrapolating the IP contribution estimation from Frutercoop production data to the entire island, we can consider the IP value to be of approximately €170,291. This value represents about 36.2% of VR from the mean annual agricultural income (€469,867) resulting from the dependent crops.

4.5 Discussion and Conclusions

Under the same thematic as "Deliverable 3a" from IPBES (Schmeller and Bridgewater 2016) – i.e., assessment of the contribution of insect pollinators to the pollination and food production - our findings highlight the great importance of insect pollinators on a small oceanic island economy. Our results are relevant since they are based both in field and economic data with the aim of providing quantitative information as in Leonhardt *et al*. (2013) and Schulp *et al*. (2014), but by using a completely different approach to evaluate insect pollinators distribution in comparison to Lonsdorf *et al*. (2009) and Polce *et al*. (2013), which have used other biological indicators and modeling techniques. Concerning the field-based mapping of pollination-related ES, similar spatial patterns were revealed for both bees and overall insect pollinators (IP): (i) high values of abundance (N) and/or species richness (S) are directly associated to the pristine native forest areas with lower disturbance (D), on one side with low percentage of island area covered (Tables 4.4 – 4.7); and (ii) on the other side these same high values of pollination services are also observed in orchards and agricultural areas with high level of disturbance (D) covering large island areas (Tables 4.4 – 4.7). These results show that Azorean native pollinators (e.g. *Pieris brassicae azorensis*, *Anaspis proteus*, *Lasioglossum* spp., *Eupeodes corollae*, *Stomorhina lunata* - see Table C1; Appendix C) are providing key pollination services not only in native habitats for which they are originally adapted, but also in low altitude agro-ecosystems in which they expanded their range. This finding call for the need of a whole island integrated management strategy for pollinators in Terceira in order to decrease the 32.6% VR of crops production. However, intensive managed pastures, the most dominant land use in the island with highest disturbance index D (see classes 8 and 12 in Tables 4.4 – 4.7), showed low abundance (N) and/or richness (S) classes for both bees and IP (Fig. 4.3), evidencing therefore a low performance of pollination services, as observed in previous studies (e.g. Batary, 2010; Sjödin, 2007). Indeed, this land-use, subject to frequent and intense grazing events does not foster the occurrence of abundant pollinator populations.

Based on the results obtained for low altitude agricultural areas, the disturbance index D variable, in contrast to other studies (e.g. Boieiro *et al*., 2013; Cardoso *et al*., 2013, 2014; Florencio *et al*., 2013), do not fully and adequately explain the spatial abundance of native pollinators in this island. Unmeasured variables associated to current and past land uses that reflect specific agro-ecosystems management regimes in Terceira Island may have driven the current spatial heterogeneity of the pollinators' abundance and diversity. The numerous resources available for pollinators at low altitude (e.g. private gardens, abandoned orchards) together to a low input of pesticides in abandoned orchards are possibly fostering an ideal situation for the spread of native pollinators across the landscape (see also *Picanço et al*., 2017).

This study also highlights the fact that about one-third of Terceira Island crops have an essential or great dependence on pollinators, therefore complementing the above information on high values of insect pollinator abundance and richness in low altitude agro-ecosystems. The economic contribution of pollinators totalizes 36.2% (€170K) of the mean total annual agricultural income of the dependent crops (€469K). This EVIP percentage represents also the VR of agricultural production. Moreover, the consumer surplus loss was estimated between €156K and €231K based upon average price elasticities of −1.2 to −0.8 respectively. This interval of prices on the consumer surplus loss represents the difference between what island consumer are willing or able to pay for the ES relatively to its market price, in case of pollination services loss. These values referred to Frutercoop production that only represents 54% of the island's total crop productions (Tables 4.8 and 4.9). However, the presented estimates are underestimated values, since not all agricultural production is officially declared (family production, production in backyards, urban gardens, etc.).

Our study also indicates the high socioeconomic relevance of pollination-related ES in a small oceanic islands' context. Nevertheless, bio-economics based valuation studies have been inherently and generally unable to provide thorough and consistent results, due to frequent changes in currency values, labor costs and food prices. This type of approach has also failed to consider and propose realistic and cost-effective mitigation efforts that might reduce the impact of a pollination crisis. In general, the costs are still being strongly dependent on the local agro-ecological setting, namely the crops phenology, the local insect populations, and the existing ecological relationships between farmland and surrounding natural or semi-natural areas.

Some crops, despite their modest or little dependence, showed very high values of mean annual production and, therefore, even in these cases, the contribution of pollinators is significant (Gallai & Vassière, 2009; Tables 4.8 and 4.9). Moreover, there is no available information on pollinator dependence for some relevant crops, showing the urgent need to address this issue through basic research on reproductive biology and pollination ecology.

As a result, these pollinator-dependent crops are crucial for maintaining the agricultural food balance of the increasing population-growth of Terceira Island's consumers. Meanwhile, at the world scale, IP are becoming increasingly more vulnerable to (i) land-use intensification (Power *et al*., 2012); (ii) use of pesticides (Kevan, 1999; Suchail *et al*., 2001; Dos Santos *et al*., 2016; Geslin *et al*., 2016); (iii) use of insecticides (Sánchez-Bayo *et al*., 2016; Straub *et al*., 2016); (iv) use of fertilizers (McLaughlin and Mineau, 1995; Andersson *et al*., 2014); (v) cultivation of some genetically modified crops (Warwick *et al*., 2009); (vi) occurrence of biological invasions (Campbell *et al.*, 2015); (vii) climate change (Gill *et al*., 2016; Ferreira *et al*., 2016); and (viii) the interactions of these ecological stressors (Potts *et al*., 2010; Vanbergen, 2013). Nevertheless, it seems that intensive pastures aside, IP populations in Terceira Island are abundant and diverse in several agro-ecosystems (Fig. 4.3), and performing adequate pollination services to crops.

With the expected need for an increased production of vegetables and fruit in Terceira Island in the coming years, integrated mitigation measures (e.g. biological pest control, wild flowering plants production areas, promotion of organic farming), as well as (cost-) effective, innovative and attractive (for farmers) agri-environmental schemes are required in order to adequately promote pollination services and to compensate for some eventual crops' failing production (e.g. Wilson & Hart, 2001; Power *et al*., 2012; Andersson *et al*., 2014). It appears to be increasingly consensual that organic farming regimes benefit biodiversity, zoophilous wildflowers and IP abundance on a local scale (Gabriel & Tscharntke, 2007). As such, if strategically and effectively promoted and applied, this management practice may have the potential to benefit crop pollination and to increase IP abundance across the whole island. This needs to be taken into account for the sustainable long-term management and conservation of pollinator communities and insect-pollinated plants in Terceira Island (e.g. Power *et al*., 2012).

Agri-environmental schemes aiming to foster and to pay/compensate farmers for a more sustainable management of low-intensity pasture systems and to implement integrated farm management and organic agriculture practices should be especially encouraged in the north-western, eastern and south-eastern agro-ecosystem areas of Terceira Island.

Finally, this broad, straightforward and cost-effective methodological approach may be able to be applied in further small oceanic islands with the aim of improving the capacity of effectively assessing and monitoring pollination-related ecosystem services, in order to improve the existing decision support systems for land use planning/management policies, especially those related to agriculture and nature conservation.

Chapter 5

Area Prioritization for Insect Pollinator Communities on an Oceanic Island

Ana Picanço, François Rigal & Paulo A. V. Borges

In: *Arquipélago – Life and Marine Science*, 34, 85 -104. ISSN: 0873-4704

5.1 Abstract

Conservation studies usually assess the effectiveness of protected areas and draft proposals on the inclusion of new areas to gain legal protection status, paying little attention to the unprotected surrounding matrix of the respective protected areas network. By combining species distribution modelling and a site selection method, we aim to quantify the contribution of different land uses to insect pollinator conservation on a small oceanic island i.e. Terceira Island (Azores, Portugal). Our results showed that, in addition to well preserved and protected native forest in Terceira, other land uses, such as naturalized vegetation areas, exotic forests, and semi-natural pastures, could serve as a continuum for the protected areas network. This result suggests that protecting marginal non-natural areas may also be important, especially when areas with well-preserved natural habitats are scarce. This spatial planning approach can be easily applied to other islands in the archipelago and any similar island systems, to better plan conservation efforts (such as habitat restoration) and to design specific buffer zones around a protected areas network.

Keywords

Land-use planning, insect pollinator representation, spatial conservation planning, Zonation, species distribution modeling.

5.2 Introduction

Spatial conservation planning methods have been strongly influenced by the Island Biogeography Theory (IBT) of MacArthur & Wilson (1967), which has played a pivotal role in the establishment of the concept of natural reserves (Triantis & Bhagwat, 2011). IBT-based approaches usually make the assumption, which is often invalid, that reserves are isolated habitat islands embedded in a matrix of unfavorable terrain (Franklin & Lindenmayer, 2009). Despite affording some insights into reserve network design, the guidelines provided by IBT offer little explicit guidance for decision-makers who face specific choices about how many and which sites or which spatial configuration have to be incorporated into a reserve network.

There is currently a broad consensus that managing the landscape matrix also matters, because standard reserve systems will never cover more than a small fraction of the globe; and human-induced habitats dominate most terrestrial ecosystems (Vitousek *et al*., 1997; Pereira & Daily, 2006; Newbold *et al*., 2013). Therefore, proper conservation planning should take into consideration not only the human-perceived native habitat patches, but also the extensive areas that surround them (Franklin & Lindenmayer, 2009). For this reason, reserve selection shifted its focus to systematic conservation planning framework developed to efficiently identify conservation areas, with its emphasis on quantitative targets, that guarantee species representation and persistence (Margules & Pressey, 2000; Moilanen *et al*., 2009; Fattorini *et al*., 2012). Representation refers to the targets defined to reach the number of each species that should be contained within a system of conservation areas, and persistence refers to long-term survival of the species achieved by maintaining the ecological and evolutionary processes that sustain them (Carvalho *et al*., 2010; Margules & Pressey, 2000). In the last decade, with the aim of promoting the persistence of biodiversity and other natural values (Pressey *et al*., 2007), reserve selection has been advanced to spatial conservation prioritization (Kukkala & Moilanen, 2013). This has been achieved with the application of statistical modelling techniques and numerical methods and also with the assistance of decision-making theory to inform the rational allocation of resources that are available for conservation planning (Moilanen *et al.,* 2009). Biodiversity concerns have also to be incorporated into the policies and practices of sectors such as agriculture, tourism and transport, that operate outside protected areas, rendering essential the development of conservation planning products that are accessible and useful for local decision-makers into land-use planning (Pierce *et al.*, 2005). Unprotected land or alternative land uses make different contributions to the conservation of biodiversity, and have different implementation and management costs (Wilson *et al*., 2010).

Among the most threatened ecosystems on Earth, oceanic islands are probably the ones where the damages induced by the current global change are the more apparent (Whittaker & Fernández-Palacios, 2007). Since human colonization, most of the oceanic islands have undergone a dramatic human mediated habitat changes and massive species introduction driven by the development of local agriculture and urbanization, the increase in seaborne world trade routes (for which oceanic islands form a strategic node) and recently enhanced by the growing popularity of oceanic islands as world-class tourist destinations (Walker & Bellingham, 2011). Hence, there is an urgent need to improve the conservation of island ecosystems to better preserve their unique biota and the services that they may supply for human communities (Walker & Bellingham, 2011). Several policy conservation action strategies have already been produced for islands, namely The CBD Global Island Partnership (GLISPA http://www.cbd.int/island/glispa.shtml; visited 2 Nov 2016), the Samoa Pathway (see more at http://www.sids2014.org/samoapathway) and the BEST initiative (http://ec.europa.eu/environment/nature/biodiversity/best/index_en.htm) which mobilizes local stakeholders to identify priority areas for action and channels funding from different sources to research and conservation projects. However, little effort has been devoted specifically to island ecological networks, and in particular, to pollinating insects. Insects are responsible for 78 to 94% of pollination across all flowering plants and 75% of global food crops worldwide (Klein *et al*., 2007; Ollerton *et al*., 2011; Winfree *et al*., 2011). Therefore, maintaining the diversity of pollinators is of critical importance to preserve gene flow and community stability in plant communities (Steffan-Dewenter & Westphal, 2008; Cranmer *et al*., 2012). Oceanic islands usually feature less complex networks with lower numbers of pollinator species, a high number of generalist species and less redundancy in comparison with continental settings (Olesen *et al*., 2002, Whittaker & Fernandez-Palacios, 2007). Hence, pollinator networks on oceanic islands have been considered highly vulnerable to any kind of disturbance (Traveset, 2002), making them a priority target for future conservation planning on islands (Kaiser-Bunbury *et al*., 2017; Kaiser-Bunbury & Blüthgen, 2015).

The Azorean archipelago, which was mostly covered by several types of semi-tropical evergreen forest (e.g. Laurisilva; *Juniperus* mountain woodlands) prior to human settlement, has suffered a large land-use change since human settlement 600 years ago, resulting in the destruction of native habitats and introduction of many exotic species (Borges *et al*., 2000, 2013; Borges, 2005; Silva *et al*., 2008; Triantis *et al*., 2010; Gaspar *et al*., 2011). As a consequence, the region has already experienced a high number of species extinctions (Borges *et al*., 2000; Martín *et al*., 2008; Alcover *et al*., 2015; Terzopoulou *et al*., 2015) while recent estimations suggest that more than half of the extant forest arthropod species might eventually be driven to extinction in the near future (Triantis *et al*., 2010). However, previous studies have shown that some Azorean native and endemic arthropod species can persist and adapt in non-natural areas surrounding natural forest (Borges *et al*., 2000; Cardoso *et al*., 2008; Gaspar *et al*., 2011; Fattorini *et al*., 2012; Vergílio *et al*., 2016). Furthermore, in Chapter 2 and in Picanço *et al.* (2017) have demonstrated that Azorean endemic and native non-endemic insect pollinator species are widespread on the islands and are able to occur in non-native habitats. This supports the idea that there might be an opportunity to avoid biodiversity loss of pollinating insect species not only through the preservation of Azorean native forest but also by implementing better management of anthropogenic areas (Borges *et al*., 2008; Jackson *et al*., 2009).

In this study, we use an extensive dataset of the spatial distribution of pollinator insect on Terceira Island in the Azores (Chapter 2; Picanço *et al.*, 2017) in order to develop and apply a different spatial planning approach that explicitly accounts for the contribution of a diverse range of land uses to achieve conservation goals for the insect pollinator communities on the island.

5.3 Material and methods

To identify high representation areas of insect pollinator communities , we followed two steps: (i) use of species distribution models (SDMs) to estimate the potential distribution of insect pollinator species; and (ii) identification of areas of high priority for conservation in different land uses besides the island's protected areas network, i.e. Terceira Island Natural Park. By combining SDMs and priority areas (PA) selection method, our goal is to contribute to an optimal island PA design that promotes insect pollinator preservation and monitoring plans.

Study area

The Azores archipelago is located in the Central North Atlantic Ocean (37 - 40º N latitude, 25 – 31º W longitude), between Southern Europe (Portugal) and the east coast of North America. The Azores is a relatively recent archipelago comprising nine islands and several additional islets (França *et al*., 2005). At the time of human colonization, in the 15th century, the archipelago was almost totally covered by native forest consisting of Laurisilva forest i.e. a humid evergreen broadleaf laurel forest and other types of forest (e.g. mountain Juniperus woodlands) (see Elias *et al*., 2016). In 600 year human activities have led to the destruction of 95% of the original native forest (Gaspar *et al*., 2008) and presently, only seven out of the nine Azorean islands still have native forest fragments.

Our study was conducted on Terceira Island (Fig. 5.1). Terceira Island is the third largest island in the archipelago, after São Miguel and Pico with an area of 402 km^2 and with four main volcanic complexes (Cinco Picos, Guilherme Moniz, Pico Alto and Serra de Santa Bárbara). The Terceira climate is marked by heavy and regular precipitations, particularly in winter and autumn, often associated with strong winds. The average annual precipitation exceeds 3400 mm on "Serra de Santa Bárbara" summit (1023 meters), and reaches almost 1000 mm per year everywhere in the island. The average annual temperature varies between 9º C in "Serra de Santa Bárbara", to 17º C on the coast. Minimum temperature in winter varies between 4º and 12º C while the maximum summer temperature varies between 14º and 26º C (Azevedo et al. 2004). In Terceira, only five native forest fragments survived the severe deforestation, and now occupy less than 6% of the island surface (i.e. 23 km2) (Gaspar et al. 2008). Even so, a few of these forest fragments still harbor a substantial number of endemic species and were considered priority areas for biodiversity conservation in the Azores (Borges *et al*., 2005b; Gaspar *et al*., 2011; Fattorini *et al*., 2012). They are now included in a recently created protected area – the Terceira Island Natural Park (INP). Terceira INP (Fig. 5.1) is formed by 20 components including three nature reserves, two natural monuments, seven PAs for habitat/ species management, one protected landscape and seven PAs for resource management. The INP is regulated by Regional Legislative Decree no. 11/2011/A of 20th April, which applies a new juridical regime that classifies, manages and administrates the protected areas of Azores, according to the International Union for Conservation of Nature (IUCN) management categories system.

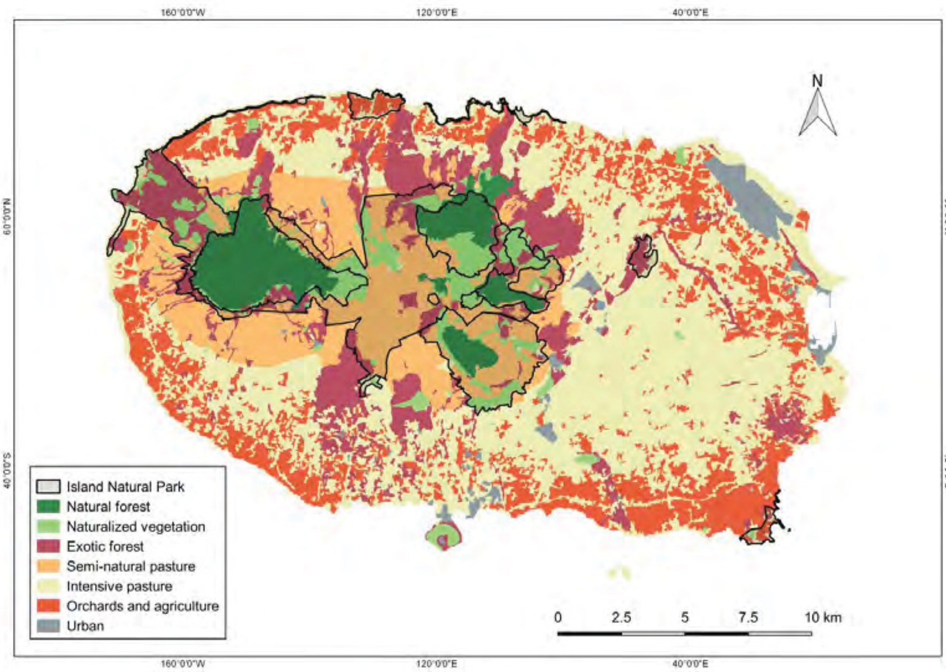


Figure 5.1. Terceira Island with respective land-use distribution, including the island protected areas network – Terceira Island Natural Park.

Species data

Distribution data from insect pollinator species were collected from June to September 2013 and from July to October 2014 in five distinct land uses covering a large percentage of the total island area, from the least to the most disturbed: natural forests mainly characterized by *Juniperus-Ilex* montane forests and Juniperus woodlands; naturalized vegetation areas formed by exotic and native species; exotic forests with *Criptomeria japonica* and *Eucalyptus* sp.; semi-natural pastures with *Lotus* sp., *Holcus* sp. and *Rumex* sp.; and intensively managed pastures with *Lolium* spp. and *Trifolium* spp.. In each land-use, 10 sites were sampled making a total of 50 transects located across the entire island. Within each land-use, sites were selected to maximize environmental diversity following the method developed by Jimenez- Valverde and Lobo (2004) and Aranda *et al*. (2011) (for more details see Picanço *et al*., 2017). In each site, a 10meter linear transect with 1 meter width was established (Pollard & Yates 1993) and transect surveys were carried out for 180 minutes once per year and repeated in the following year in a randomized order. Each flower along every 10 m transect was surveyed for 4 minutes to guarantee effective contact of the insect; therefore, only insects probing for nectar or eating/collecting pollen (foraging) were recorded. Each record includes information on location precision usually UTM point (Universal Transverse Mercator coordinate system) data. The specimens collected were identified to species-level but when species-level identification could not be resolved, individuals were identified to the lowest taxonomic unit possible and classified as morphospecies. All species were classified as indigenous or exotic species. Indigenous species may be endemic (i.e. found only in the Azores) or native non- endemic (i.e. species that colonized the Azores by natural long-distance dispersal mechanisms). Exotic species are those whose original distribution range did not include the Azores and are believed to have arrived as a consequence of human activities; these species often have a cosmopolitan distribution (see Borges *et al*., 2010). A total of 54 species/morphospecies belonging to Coleoptera, Hymenoptera, Lepidoptera, Syrphidae and other Diptera were collected (Chapter 2; Picanço *et al.*, 2017). Hoverflies (Syrphidae) were studied separately, due to the great importance of these dipteran insects for pollination (Jauker & Wolthers, 2008; Rader *et al*., 2015) and relatively high number of species observed. In the present study, I selected only species identified to species-level, totalling around 461 records of 45 species (Table D1 and D3; Appendix D). The 45 species comprise three beetle species (Coleoptera), 10 bees and wasps (Hymenoptera), five butterflies and moths (Lepidoptera), 12 hoverflies (Diptera, Syrphidae) and 15 other flies Diptera). These species include: (i) Azorean endemics occurring on Terceira Island (four species); (ii) native but non-endemic species (34 species); and (iii) exotic species seven species), according to Borges *et al*. (2010).

Species distribution modelling

For the following analysis, we used only incidence data (i.e. presence/absence data). We modelled the potential distribution of the 45 insect species (Table D1; Appendix D) using Maximum entropy modelling implemented in the software MaxEnt version 3.3.3 (http://www.cs.princeton.edu/~schapire/maxent). MaxEnt has been identified as one of the most accurate methods for species niche modelling since it combines ease of use with proven predictive ability (Moilanen *et al*., 2009). The method combines data of species incidence (presence-only data) with environmental grid data to estimate the probability of distribution of a species, subjected to the set of constraints provided by environmental characteristics of grid cells where the species has been recorded (Phillips *et al*., 2004, 2006; Elith *et al*., 2006). The environmental variables selected for the SDM procedure were the following:– annual averages for maximum annual temperature (tmax), minimum annual temperature (tmin), annual range of temperature (trange), minimum annual humidity (rhmin), maximum annual humidity (rhmax), annual range of humidity (rhrange), maximum annual precipitation (ppmax), minimum annual precipitation (ppmin), and annual range of precipitation (pprange). These variables were obtained from the CIELO model for the Azores (Azevedo, 1999), which models local scale climate variables. The geographical variables selected were altimetry and land-use, and they were based on maps provided by Cardoso *et al*. (2009; 2013) and the Azorean Government agencies (DROTRH, 2008), respectively. For all models, MaxEnt algorithm was used with default settings to randomly select 20% points of occurrence records for testing, with the remaining 80% for training (Philips *et al*., 2006). The models were tested with receiver operating characteristics (ROC), which plot the true-positive rate against the false-positive rate and with the average area under the curve (AUC) of the ROC plot as a measure of the overall fit for each model. In this context, the AUC could also serve as an index of habitat suitability ranging between 0 (highly unsuitable) and 1 (highly suitable) and it displays the probability that a randomly chosen presence site will be ranked above a randomly chosen absence site (Phillips *et al*., 2006). Models with AUC values above 0.7 were considered potentially useful (Pearce & Ferrier, 2000; Elith, 2002; Carvalho *et al*., 2010).

Contribution of each land-use and Island Natural Park to area prioritization

The software for spatial conservation prioritization, ZONATION v4.0 (Moilanen *et al*., 2014) which is based on a more recent and sophisticated heuristic algorithm (Moilanen, 2007; Moilanen *et al*., 2005) was used to identify priority areas for insect pollinator communities conservation. The Zonation algorithm produces a hierarchical prioritization of the landscape, by ranking cells on a scale from 0 to 1, starting from the selection of the whole planning region, and iteratively removing the area that causes the smallest marginal loss of conservation value, leaving the highest ranked with the highest conservation value (Moilanen *et al*., 2009). Because Zonation does not aim to achieve specific representation targets, this process is repeated for every area, thus producing a hierarchy of conservation priorities for the entire landscape. The critical part of the algorithm is the definition of marginal loss (called the cell-removal rule), which also allows species weighting and species-specific connectivity considerations to be applied. The probability of a species' presence in each cell is obtained from the MaxEnt models and total representation for each species is the sum of all the probabilities. Different cell-removal rules can be applied to emphasize different objectives. To perform the analysis, the Core-area Zonation function was applied as a removal rule for the retention of high-quality core areas (Moilanen, 2007) of the different land-use (natural forest, naturalized vegetation areas, exotic forest, semi-natural pasture, intensive pasture) and Island Natural Park (henceforth INP), for all species and for each one of the five taxonomic groups: Coleoptera, Hymenoptera, Lepidoptera, Syrphidae and other Diptera species. The option "edge removal" was selected to generate spatial aggregation into the solution. The warp factor (i.e., the number of cells removed at each iteration) and the boundary length penalty strength were defined as 1 and 0.01, respectively (Moilanen *et al*., 2014). All species were weighted equally. With this analysis, we calculated: (1) the ranking of priority areas, (2) percentages of land-use area covered by each different taxonomic group and total set of insects, both inside and outside INP, (3) the percentage of INP area covered by each different taxonomic group and total set of insects and (4) and average of species presence probability in each land-use for each different taxonomic group and total set of insects. For this latter result, I applied Kruskal-Wallis following by post-hoc Dunn tests to test for significant differences between land uses.

5.4. Results

Species distribution models

SDMs were performed for 45 species represented by 461 records (Table D1 and D3; Appendix D). The most important variables that contribute to over 30% of the selected insect pollinators were land-use, annual ppmin, annual rhrange and annual trange. AUC values for test data varied between 0.517 (the hoverfly *Eristalis arbustorum*) and 0.945 (the moth *Tebenna micalis*) (Table 5.1). Only three species – *Ancistrocerus parietum*, *Colias croceus* and *Eristalis arbustorum*, from Hymenoptera, Lepidoptera and Syrphidae taxonomic groups, respectively, had AUC values lower than 0.7 (Table 5.1). These species were not used in further analyses since SDMs presented both lower AUC values and a small number of records.

Table 5.1. Species included in the SDMs analyses for modeling, AUC values of training and test data.

	Test data AUC	Training data AUC
Coleoptera		
Anaspis proteus	0.822	0.906
Meligethes aeneus	0.764	0.818
Stilbus testaceus	0.705	0.936
Hymenoptera		
Ancistrocerus parietum	0.631	0.679
Apis mellifera	0.733	0.843
Bombus ruderatus	0.774	0.833
Chrysis ignita ignite	0.755	0.929
Lasioglossum morio	0.808	0.848
Lasioglossum smeathemanellum	0.784	0.976
Lasioglossum villosulum	0.752	0.826
Lasius grandis	0.839	0.856
Megachile centuncularis	0.754	0.929
Vespula germanica	0.824	0.834
Lepidoptera		
Agrius convolvuli	0.786	0.845
Colias croceus	0.529	0.599
Hipparchia azorina azorina	0.921	0.983
Pieris brassicae azorensis	0.789	0.779
Tebenna micalis	0.945	0.963
Syrphidae, Diptera		
Episyrphus balteatus	0.839	0.846
Eristalis arbustorum	0.517	0.579
Eristalis tenax	0.709	0.732
Eupeodes corolla	0.796	0.840
Meliscaeva auricollis	0.773	0.849
Myathropa florea	0.717	0.755
Sphaerophoria nigra	0.837	0.894
Sphaerophoria scripta	0.819	0.824
Syritta pipiens	0.753	0.793
Xanthandrus azorensis	0.850	0.887
Xanthandrus comtus	0.910	0.947
Xylota segnis	0.850	0.897
Other Diptera		
Adia cinerella	0.868	0.898
Calliphora vicina	0.746	0.860
Fucellia tergina	0.925	0.993

	Test data AUC	Training data AUC
Lucilia sericata	0.847	0.849
Megaselia rufipes	0.778	0.823
Paregle audacula	0.703	0.717
Rhinia apicalis	0.840	0.846
Scathophaga litorea	0.761	0.888
Scathophaga stercoraria	0.711	0.801
Sepsis biflexuosa	0.795	0.875
Sepsis lateralis	0.870	0.894
Sepsis neocynipsea	0.763	0.813
Sepsis thoracica	0.824	0.881
Stomorhina lunata	0.828	0.832

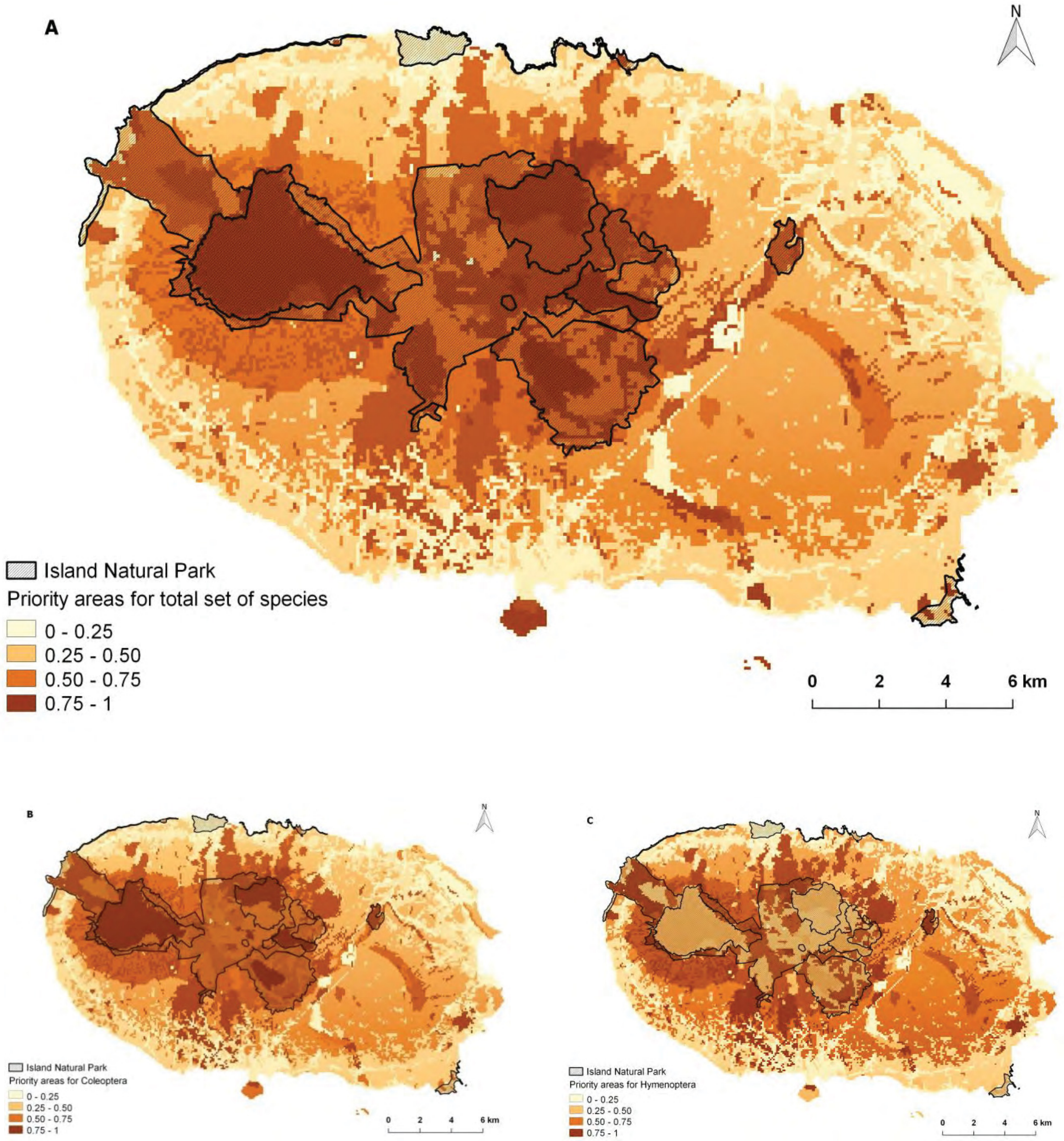
Contribution of each land-use and INP to areas prioritization

Natural forests, naturalized vegetation areas, exotic forests and semi-natural pastures currently cover more than 50% of the cells corresponding to Terceira Island, with highest rank (last quartile: 0,75-1), for the beetles (Coleoptera), hoverflies (Syrphidae) and total set of species (Fig. 5.2 (a), (b), (e); Table D2; Appendix D). These results are confirmed by the high probability mean incidence values and relatively high percentage of land-use area covered by these three groups of insects (Fig. 5.3; Fig. 5.5 All insects, Coleoptera, Syrphidae).

Hymenoptera (Fig. 5.2 (c)) and Lepidoptera (Fig. 5.2 (d)) species had above 34% of highly ranked areas (in the last quartile) covered by land-use areas (Table D2; Appendix D) and also, with corresponding high percentage area (Fig. 5.3), but with low values of probability mean incidence (Fig. 5.5 Hymenoptera, Lepidoptera).

Other Diptera species were the group with the lowest percentage of highly ranked areas (lower than 32% in the last quartile) covered by each different land-use (Fig. 5.2 (f); Table D2; Appendix D), and corresponding low percentage of overall land-use areas covered. Within the low percentage of high ranked areas, intensive pastures, and agriculture and orchards areas had 27 and 32, respectively (Fig. 5.3; Table D2; Appendix D). This latter result is opposed to the relatively high probability mean incidence values for natural forest, naturalized vegetation and orchards and agriculture areas (Fig. 5.5 Other Diptera).

The results of the Kruskal–Wallis test are significant ($H = 38290$, d.f.= 7, $P < 0.001$) and all pairwise differences between land-uses are also significant (post-hoc Dunn tests $P < 0.05$) for all species groupings. The mean ranks of probability of incidence per insect species groups (Coleoptera, Hymenoptera, Lepidoptera, Syrphidae and other Diptera) and per all insects group are significantly different among the land uses. Terceira INP's current area covers about 39% of the cells, with the highest rank (in the last quartile: 0.75–1) for the total set of pollinating insects, beetles (Coleoptera) and hoverflies (Diptera, Syrphidae) (Fig. 5.2 (a), (b), (e); Table D2; Appendix D). Lepidoptera was the taxonomic group with the largest number of highly ranked areas (about 69.2% in the last quartile; Fig. 5.2 (d); Table D2; Appendix D) and high percentage (84%) covered by current overall INP area (Fig. 5.4).



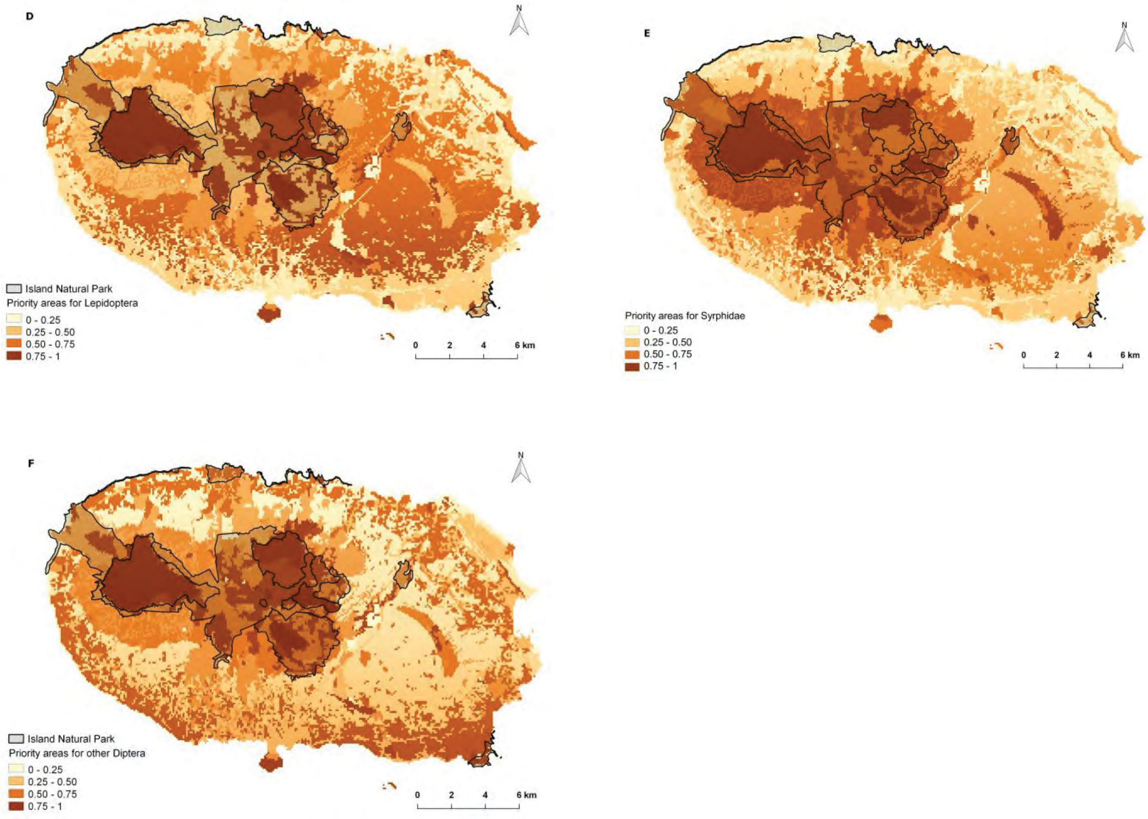


Figure 5.2. Ranking of priority areas for insect pollinators using zonation software: (A) all species, (B) Coleoptera, (C) Hymenoptera, (D) Lepidoptera, (E) Syrphidae, and (F) other Diptera.

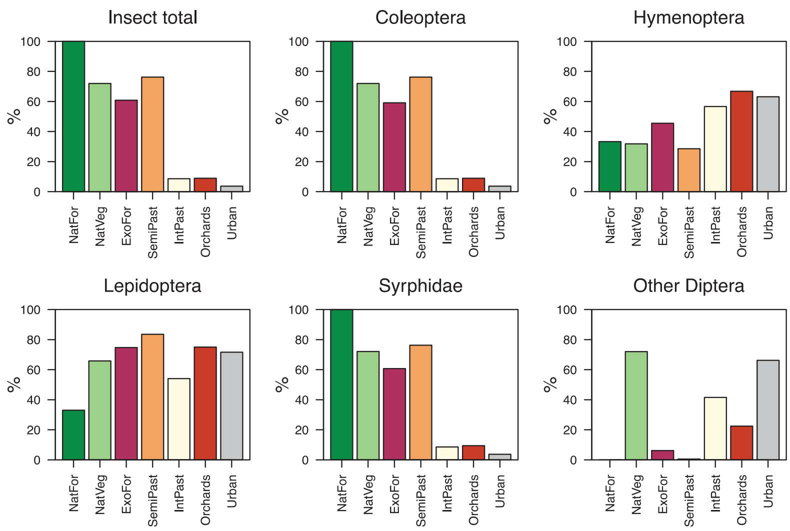


Figure 5.3. Percentage of land-use area - natural forest (Natfor), naturalized vegetation areas (Natveg), exotic forest (Exofor), semi-natural pasture (Semipast), intensively managed pasture (Intpast), agriculture/orchard areas (Orchards) and urban/industrial areas (Urban) - covered by each taxonomic group and all insect pollinators.

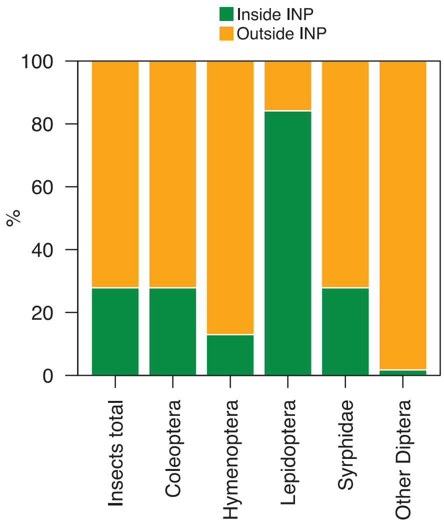


Figure 5.4. Percentage of Terceira Island Natural Park (INP) area inside and outside covered by each taxonomic group and all insect pollinators.

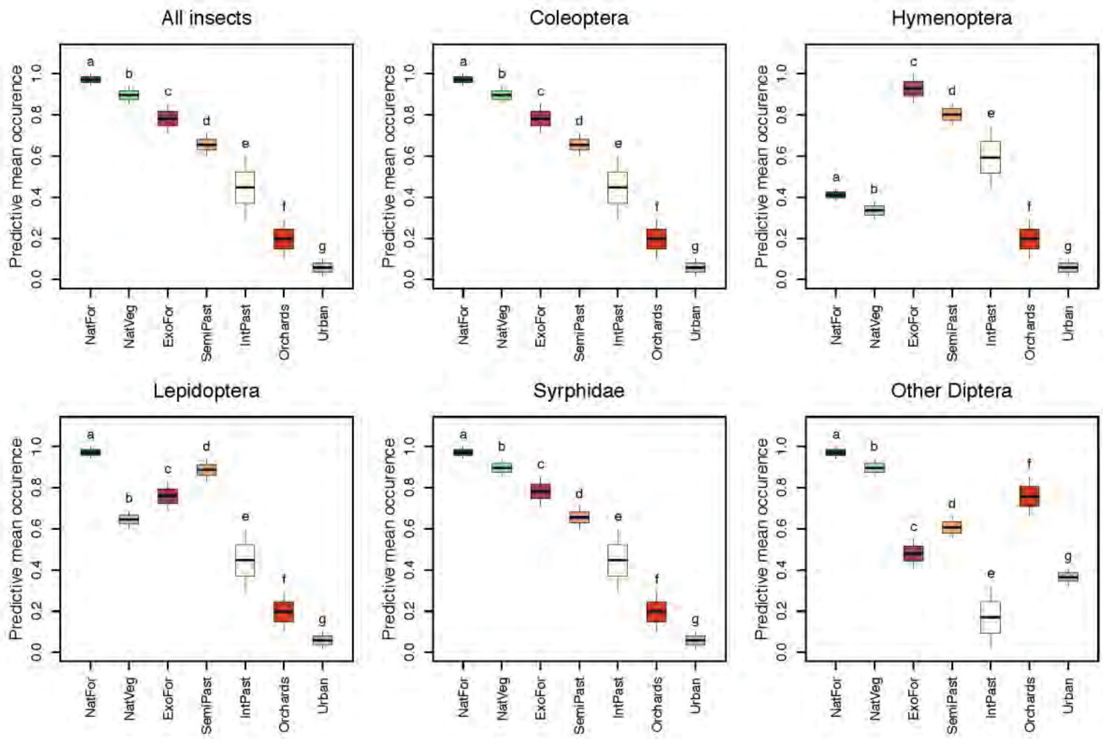


Figure 5.5. Probability or predictive mean of species' occurrence (values range: 0, absent - 1, very high probability) from Zonation software and standard deviation of each taxonomic group and all insect pollinators: (a) all species, (b) Coleoptera, (c)

Hymenoptera, (d) Lepidoptera, (e) Syrphidae, and (f) other Diptera, in different land uses: natural forest (Natfor), naturalized vegetation areas (Natveg), exotic forest (Exofor), semi-natural pasture (Semipast), intensively managed pasture (Intpast), agriculture/orchard areas (Orchards) and urban/industrial areas (Urban).

5.5 Discussion

This study first combined standardized data covering a large fraction of the area of an oceanic island and species distribution modeling to overcome the Wallacean shortfall (i.e. distribution of described species is mostly unknown) and fulfill one of the two most important conservation planning objectives, which is species representation in protected areas i.e. the proportion of known species in a region that occur in protected areas. In this context, SDM approaches have proved to be particularity useful since obtaining reliable and fine-scale distribution data for arthropods species is costly (Cardoso *et al*., 2011). Our SDM analyses implemented with the MaxEnt program provided robust predictions of occurrences for nearly all selected species with an AUC value above 0.7. Second, species persistence (Araújo & Williams, 2000; Cabeza & Moilanen, 2001; Cowling *et al*., 1999; Pressey *et al*., 2007) was estimated by using the information obtained from SDMs in the Zonation software as a decision support tool (Lehtomaki & Moilanen, 2013). Note that in our study, we did not integrate any socio-economic scenarios, due to the lack of information.

Our results show similar patterns for beetles, hoverflies and total insect species groups for the different land uses (natural forest, naturalized vegetation, exotic forest and semi-natural pasture) and INP area covered (Fig. 5.2 (a), (b), (e); Fig. 5.3; Fig. 5.4), and values of mean probability of occurrence (Fig. 5.5). The beetles and hoverflies seem to act as key groups in area prioritization patterns, which were obtained by the Core-area Zonation function and subsequently reflected in total set of insects group. Interestingly, for beetles the probability mean of occurrence decreases with land-use intensification (Fig. 5.5b), which is in accordance with previous results for other taxa on Azores (Cardoso *et al*., 2009). On the contrary, for Hymenoptera and Lepidoptera species, the high ranked areas with high percentage where identified in overall land uses, for some of which it is difficult to apply conservation efforts, like intensive pasture, agricultural and urban areas (Fig. 5.2 (c), (d)). The high widespread distribution of bees, butterflies and moths relative to other insect pollinators can be due to a larger range of food resources, habitat availability, beekeeping activity, and also large foraging area (Valido & Olesen, 2010) or to moderate human land–use intensification, where pollinator responses can be variable and sometimes positive (Winfree, 2013).

For a high representation of species or high ranking areas, all native fragments of natural forests are included in the priority areas (PA) optimal solutions for all groups, except other Diptera. Borges *et al*. (2005) and Gaspar *et al*. (2011) found similar results, where all fragments are included in the optimal solutions for 80% of abundance target representation of species.

For other Diptera species, the high ranked areas had relatively low percentage (above 32%), which reflects the low importance for conservation of the overall land-use areas for this group (Fig. 5.2 (f)), probably due to its high adaptability and dispersal ability. Nevertheless, other Diptera had its highest representativeness in naturalized vegetation areas (Fig. 5.3). Hence, the group had a low percentage of area covered in native forests and inside INP (Fig. 5.4). This can be the case reported by Gaspar *et al*. (2011) for some arthropod species with high dispersal ability, but with minimum solution sets of PA, possibly due to unsuccessful establishment of viable populations in these forests.

The central zone of the island, where PAs identified by Zonation are located, generally corresponded to natural forest areas, and overlapped most PAs classified in INP (see Fig. 5.1 and Fig. 5.2). The high ranked areas identified outside INP, located in the north and south of the island are naturalized vegetation areas, exotic forest and semi-natural pastures that are partially included in INP and extend to urban areas at the island coastal zones. These areas include Monte Brasil peninsula which corresponds to a naturalized vegetation area intertwined with exotic forest (see Fig. 5.1 and Fig. 5.2) that was also identified by Fattorini *et al*. (2012) as an important area. Although this high representation of pollinating insect species may be difficult to implement, these areas can potentially harbour numerous species, increasing the value of those areas for conservation and as a target for the restoration of the Azorean native forest (Kaiser-Bunbury *et al*., 2017). Even without legal protection, these areas can have a positive impact to the PA (Wilson *et al*., 2010). With this purpose, projects are under way, managed by Direcção Regional dos Recursos Florestais (DRRF) in some exotic forest areas, where *Criptomeria* sp. and *Eucalyptus* sp. plantations are being replaced by endemic/native plant species *Juniperus brevifolia*, *Ilex azorica*, *Prunnus azorica*, *Laurus azorica*, *Viburnum treleasei* (Engineer C. Meneses, pers. comm., June 6, 2016). This active measure is advantageous to promote conservation of native species, and possibly retain and/or decrease invasive species development, which endangers INP PA purpose. Therefore, we cannot consider only PA, but also the areas that might contribute to vast conservation goals, for example, application of environmental friendly techniques into agricultural and orchards areas for pollinator species conservation.

The implementation of PAs are usually constrained to the exiting reserve systems (Pressey, 2004), because the addition of other land-uses is too financially constrained to take them into consideration for conservation (Ferrier *et al*., 2000). However, additionally to the well preserved and protected native forest of Terceira, other habitats, such as naturalized vegetation areas, exotic forests, and semi-natural pastures, could serve as a continuum for the protected areas, with the possibility of creating some corridors between native forest areas. Therefore, our results suggests that protecting marginal non-natural areas may also be important, especially in systems when areas with well-preserved natural habitats are scarce.

In conclusion our study shows that (i) similar patterns of core-area zones are defined by Zonation for beetles (Coleoptera) and Syrphidae (Diptera), and that patterns for these two insect pollinator groups are again projected in the total set of insect species, which can imply that these can act as key groups for selection of areas for prioritization; and (ii) highly ranked areas for prioritization adjacent to already official priority areas are identified in naturalized vegetation areas, exotic forests and semi-natural pastures, making these potential areas ideal to create a buffer zone or corridors to maintain and preserve pollinating insect species. These outcomes indicate that the conservation of insect pollinating species will imply the combination of the management of existing PAs and the additional sustainable use of the surrounding matrix, taking into account pollinators' ecological interactions established in the different Azorean land uses. Based on our study and other similar research performed in Azores (e.g. Borges *et al*., 2000, 2005; Gaspar *et al*, 2011; Fattorini *et al*., 2012; Cardoso *et al*., 2013), we call for the implementation of a more integrative approach in future conservation planning on Terceira Island. Finally, we also believe that the approach introduced in the present study can be easily applied to other islands of the archipelago and any similar island systems, to improve conservation planning (such as habitat restoration) and to design specific buffer zones around protected area networks.

Chapter 6

General Discussion

Pollinators are a key component of global biodiversity, providing vital ecosystem services to crops and wild plants (Potts *et al*., 2010). Therefore, global pollinator declines may strongly affect pollination and reproduction of plants rely upon them (Brown & Paxton, 2009). Over the last century, island ecosystems have been disproportionately affected by human-made activities and a large proportion of the recorded extinctions have taken place on islands (e.g. Cardoso *et al*., 2010b; Rando *et al*., 2013; Alcover *et al*., 2015; Régnier *et al*., 2015; Terzopoulou *et al*., 2015). The impact of land-use changes is of particular concern (McLaughlin & Mineau, 1995; Benton *et al*., 2003), with native forest conversion to intensive managed agriculture recognized as one of the major causes of species loss on islands, with many extant species predicted to be committed to future extinction (Triantis *et al*., 2010). These profound changes are known to have impacted several components of island ecosystems (see Connor *et al*., 2012), but very little is known about the impact of land-use change on island ecological networks, and in particular, on pollinating insects. Therefore, there is an urgent need to better identify the pathways responsible for the alteration of oceanic pollinators networks under human pressure in order to better plan their conservation, restoration and to preserve the services that they may supply for humans.

It is my belief that this thesis contributes to better understand how island pollinators' networks respond to land-use changes, by describing and explaining the spatial structure of pollinating insect communities and plant-insect interaction network across different habitat types in Terceira Island, Azores.

To reach the goal, I used different approaches from classic communities analysis of pollinating insects species to more sophisticated network analysis and spatial assessment of ecosystems services. In addition, I also assessed different land-uses as possible priority areas for insect pollinators' conservation, in an oceanic island context.

Based on the results, answers were given to the following main questions that have been addressed in this thesis (research objectives, see general introduction in Chapter 1):

1) *How are flower-visiting insect communities organised across different habitat types corresponding to a gradient of human disturbance?*

This study revealed that flower-visiting insect communities are dominated by widespread generalist native species of intermediate abundance in the five main habitat types of Terceira Island (i.e. natural forests, naturalized vegetation areas, exotic forests, semi-natural pastures and intensively managed pastures), despite the high representation of exotic plant species in our 50 studied transects. Species diversity, species abundance distribution (SAD) and species composition of flower-visiting insect species vary only slightly across the different habitats. Species replacement (i.e. a measure of species turn-over quantified by the metric β_{repl}) was significantly higher mainly between the two most contrasting habitats (i.e. natural forests and intensive pastures). In addition, I also showed that species composition of flower-visiting insects was mostly influenced by the distribution of host plant species regardless of the habitats matrix, which implies that any changes in vegetation composition (i.e. replacement of native by exotic or invasive plants) might have a profound impact on pollinating insect community structure in the Azores. These results differ from previous works conducted with epigean arthropods in Terceira (see Cardoso *et al*., 2009; Matthews *et al*., 2014;), where authors reported strong differences in species composition between habitat types and a clear effect of land-use change on species abundance distribution (SAD) form.

The uniformity of several species diversity metrics across the different habitats (i.e. mean abundance, species evenness and dominance), suggest that similar mechanisms may control flower-visiting species diversity across the land-use gradients. This could be explained by adaptation or cross-scale resilience and response diversity of the native flower-visiting insect species to non-native habitats (see also Winfree & Kremen, 2009 and Cardoso *et al*., 2010a), a possible consequence of the island small area relative to the flower-visiting species foraging area (Miller *et al*., 2015) and loss of native habitats. In most of the habitats, native non-endemic flies were the group with the largest number of species, a pattern already documented for island pollination networks elsewhere (Castro-Urgal & Traveset, 2014). Hence, the differences in insect flower-visiting communities between native forest and intensively managed pastures could have been also influenced by the variation of altitude (and its related climatic variables) through the different habitat types; native forest being always at higher altitude than intensively managed pastures. Future works are needed to further disentangle the part due climatic variation and anthropogenic disturbance in explaining the spatial structure of flower-visiting insect communities in Terceira.

Beetles, flies, hoverflies, ants, bees, wasps, butterflies and moths were observed and sampled in all the five habitats, but I only recorded visits of insect species per flowering plants rather than their actual fitness. Consequently, it remains unclear, whether surrounding natural forest is a vital component of the life cycle of some or many of the species collected in pastures and whether forest served as a source for colonisation of agricultural areas (Chapter 2; Picanço *et al.*, 2017). Therefore, future ecological research are needed to further quantify the contribution of the different habitat types to the reproductive success of species (Kleijn *et al*., 2011). In addition, there is the need for more detailed information about pollination efficiency of native and exotic pollinators for reliably estimating the pollination function of insect pollinating communities in plant-insect interaction networks of different habitat types.

There are many studies investigating the impacts of land-use change on the community structure of pollinator insects in continental regions, but studies on oceanic islands are scarce. In one of the few examples, Sahari *et al*. (2010), in contrast to our results, showed that landscape change in Java Island (Indonesia) strongly affects insect pollinating species composition between habitat types in the tropics, as expectable based on the study of Traveset *et al*. (2015).

Research on flower-visiting insect communities in the Azores is restricted to very few studies, namely the works of Olesen *et al*. (2002), this study and another one that will be published soon (Weissmann & Schaefer, 2017). The problematic of pollinator decline (Valido & Olesen, 2010) and the recent discovery of new bee species records in Azores islands (Weissmann *et al*., 2017) highlights the need for more research related to the insect pollinators in Azores.

2) What are the characteristics of the plant-insect interaction networks in the different habitat types?

In this study system, overall plant-insect interaction networks were characterised as young, small, simplified and relatively generalized nested networks, with no existence of subgroups formation or modularity. This was true even for global network (the five habitats pooled together), reflecting the fact that Azorean island landscape might be considered as relatively uniform or homogeneous in regards to pollinator species and links. When comparing habitat networks between each other, I found the highest values for connectance, total number of species, specialization and interaction evenness (Table 3.1) along with a strong relationship among incidence links and abundance (Table 3.4; Fig. 3.3) for the habitats of intermediate-disturbance (naturalized vegetation and exotic forest). These results show that habitats of moderate disturbance do not have a specific negative influence in the establishment of interactions and related network structures. Interestingly, this result matches the classic observation of species diversity reaching its maximum at intermediate levels of disturbance. Future works are therefore needed to further study the underlying mechanistic processes generating this pattern. In addition, I showed that species abundance should also be considered as a key variable for the understanding of pollinator-plant interaction structure. In fact, in these relatively young Azorean plant-insect networks, abundance is a major driver of establishment of links (Table 3.4; Fig. 3.3), apart from species richness usually considered as one of the main explanation for network structure (Olesen *et al*., 2007; Fonseca *et al*., 2005; Jordano, 1987). Indeed, as Vázquez *et al*. (2009b) suggested, there is not a single factor that can explain mutualistic network diversity and structure. Increasing evidences indicate that species abundances, spatial structure, dispersal limitation and stochasticity act simultaneously with both neutral and niche-based processes in shaping network features (Vázquez *et al*., 2009a; Krishna *et al*., 2008; Canard *et al*., 2012). However, particularly in relatively young ecosystems such as Azorean islands (Borges & Hortal, 2009; Triantis *et al*., 2012) where complex evolutionary processes are almost negligible (Triantis *et al*., 2012), a basic ecological factor such as abundance could be considered as major driver of network structuring. Abundance is driving small, simple and homogeneous insect pollinating communities to form nested generalized habitat networks mostly influenced by host plant species composition (see also Chapter 2 and Picanço *et al*., 2017). To conclude, this study showed that generalist plant–pollinator interactions are prevalent in Azores.

3) Which and where are spatially located the possible contributions of the insect species to the pollination services in Terceira Island?

In this study, I estimate of the economic contribution of insect pollinators at 36.2% (€170K) of the mean total annual agricultural income of the dependent crops (€469K) in Terceira Island. The economic value of insect pollinators percentage represents also the vulnerability ratio of agricultural production. Moreover, using pollination ecosystem services mapping, I revealed similar spatial patterns for both bees and overall insect pollinators, for which I found: (i), on one hand, high values of abundance and/or species richness directly associated to the pristine native forest areas (i.e subject to a very low degree of, or no, human disturbance) but covering a small percentage of island area (Tables 4.4 – 4.7) and (ii) on the other hand, similar high values of pollination services in orchards and agricultural areas with high level of disturbance and covering large island areas (Tables 4.4 – 4.7).

Consequently, Azorean native pollinating insect species provide key pollination services not only in native habitats (Chapter 2 and Chapter 3; Picanço *et al.*, 2017) for which they are originally adapted, but also in low altitude agro-ecosystems in which they expanded their range. This finding call for the need of a whole island integrated management strategy for pollinators in Terceira in order to decrease the 32.6% vulnerability ratio of crops production (Chapter 4). However, intensive managed pastures, the most dominant agro-ecosystem in the island but also the most disturbed habitat (Cadroso *et al.*, 2009; 2013), host low species abundance and/or richness of both bees and insect pollinators (see classes 8 and 12 in Tables 4.4 – 4.7; Fig. 4.3), evidencing therefore a low performance of pollination services, as observed in previous studies (e.g. Batary, 2010; Sjödin, 2007). Therefore, this land-use, subject to frequent and intense grazing events and fertilization does not foster the occurrence of abundant pollinator populations emphasizing the need of adequate measures to: (i) prevent future land conversion to intensive managed pastures and (ii) promote habitat restoration of abandoned pastures (Kaiser-Bunbury *et al.*, 2017).

Finally, the design of proper corridors of native vegetation bordering the current stone-walls that divide the pasture fields in Terceira could possibly be a good management strategy to increase the diversity and abundance of insect pollinators and their ecosystem services in this island.

4) What is the best subset of areas to protect the insect pollinator communities in Terceira?

The last chapter of this thesis investigates the contribution of both protected areas and the surrounding matrix in the conservation of insect pollinators in Terceira island. Two main patterns were observed: (i) as expected, the central zone of the island, where priority areas identified by the ZONATION program are located, generally corresponded to the native forest areas, and overlap with most priority areas classified in Terceira Island Natural Park (see Fig. 5.1 and Fig. 5.2); (ii) the high ranked areas identified outside Terceira Island Natural Park, are located in the northern and southern parts of the island and comprise naturalized vegetation areas, exotic forest and semi-natural pastures that are partially included in Island Natural Park and extended to the urban areas at the island coastal zones. These areas include the Monte Brasil peninsula which corresponds to a naturalized vegetation area intertwined with exotic forest (see Fig. 5.1 and Fig. 5.2) that was previously identified by Fattorini *et al.*

(2012) as an important area for other endemic and native arthropods. Although pollinating insect communities may be difficult to manage in these non-protected areas, I suggest to increase the conservation values of those areas as a target for future restoration of the Azorean native forest (see other examples elsewhere in Kaiser-Bunbury *et al*., 2017).

Contrasting patterns were identified when selecting priority areas for Coleoptera, Syrphidae versus Hymenoptera and Lepidoptera. The first two groups (Coleoptera, Syrphidae) had high representation of their species and/or high ranking areas in natural forest, naturalized vegetation, exotic forest and semi-natural pastures with corresponding Island Natural Park area covered (Fig. 5.2 (a), (b), (e); Fig. 5.3; Fig. 5.4). On the other hand, the Hymenoptera and Lepidoptera species had high ranking areas identified in intensive pasture, agricultural and urban areas (Fig. 5.2 (c), (d)). This latter pattern can be explained by the widespread distribution of bees, butterflies and moths relatively to other insect pollinators due their abilities to feed on a larger range of resources and also their larger foraging area (Valido & Olesen, 2010). Hence for a high representation of species, all native fragments of natural forests need to be incorporated in the priority areas optimal solutions for all groups, except for some species of Diptera (e.g. *Scathophagidae* spp., *Sepsis* spp.). This is similar to the patterns reported by Gaspar *et al*. (2011) for some Azorean endemic forest arthropod species with high dispersal ability, but with minimum solution sets of priority areas, possibly due to no successful establishment of viable populations in these forests.

In summary, based in this study, additionally to well preserved and protected native forest of Terceira, other habitats, such as naturalized vegetation areas, exotic forests, and semi-natural pastures, could serve as a continuum to protected areas for the conservation of Azorean native pollinator insect communities, with the possibility of creating some corridors between native forest areas. Therefore, our result suggests that protecting marginal non-natural areas may also be important, especially in systems when areas with well-preserved natural habitats are scarce.

Conclusions and a roadmap for future research

The four studies that compose this thesis investigated the impact of land-use changes on insect pollinator communities in a small island using four different but complementary approaches: community ecology, functional, exosystemic and conservation based approaches. The main findings were particularly surprising, namely the fact that a large group of native insect pollinator species dominate the whole landscape and contribute to key pollination ecosystem services in highly modified habitats including important agro-ecosystems. This pattern has clear implications for the management of the matrix of non-natural habitats and might have important implications for the spread of exotic plant species across the landscape. This disservice has to be studied in more detail in future projects dealing explicitly with invasive species management. In addition, this thesis contributed to advance knowledge on the impact of land-use changes on both Azorean insect pollinator communities and community-wide interactions networks structure between plants and pollinators, reinforcing the fact that species diversity and abundance have a central role in shaping pollination network structure in small and young island systems.

Furthermore, our results stress the need to preserve pollination networks due to their important contribution and high economic importance to island crop production, presenting high values of potential pollination services not only in native forests fragments, but also in orchards and agricultural areas. Consequently, to achieve possible conservation goals for the island insect pollinators species, one must include in conservation planning other types of land uses apart from the already protected native forest fragments of Terceira Island.

Additionally, our results have profound implications for conversation policy, particularly for key stakeholders like beekeepers and Terceira Island Natural Park managers. Since our results have shown that pollination involve the whole landscape of Terceira and several interacted taxonomic groups (Chapter 4), conservation measures for pollinating insects should be undertaken at a community level and at larger spatial extents. I also suggest the design of proper corridors in order to create green infrastructures of native plants to favour the long-term preservation of native plant-pollinator networks. Finally, considering the strong link observed between the abundance of insect pollinators and network structure, I suggest that any potential drivers of change of pollinator abundance should be carefully monitored.

Several questions remain however unanswered and should be addressed in future works: (i) what will be the impact of the spread of exotic pollinator on plant-pollinator networks structure across habitat types and along environmental gradient (e.g. altitudinal)?; (ii) how plant-insect interactions in Terceira might facilitate the spread of invasive plants across habitat types, (iii) to what degree these newly modified biological communities and networks are self-sustaining and stable on the long-term and (iv) what will be the impact of climatic changes on pollinators' adaptation and agriculture productivity in Azores, namely wine and orchards?

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Appendix A

Table A1. Number of individuals per insect species/morphospecies in each habitat type: NatFor (natural forests), NatVeg (naturalized vegetation areas), ExoFor (exotic forests), SemiPast (semi-natural pastures) IntPast (intensive pastures)

Order	Family	Specie	Colonization Status	NatFor	NatVeg	ExoFor	SemiPast	IntPast	Total
Coleoptera	Nitidulidae	*Meligethes aeneus*	introduced	4		10	15	2	31
	Phalacridae	*Stilbus testaceus*	native	2		7			9
	Scraptiidae	*Anaspis proteus*	native	264	13	14	61		352
Diptera	Anthomyiidae	*Adia cinerella*	native		5		1		6
		Fucellia tergina	native			6		1	7
		Paregle audacula	native	5	5	9	3	12	34
	Calliphoridae	*Calliphora vicina*	introduced	2	9	3	1		15
		Lucilia sericata	introduced		1	2	1	2	6
		MF32	native	9	15	16	1	6	47
		Rhinia apicalis	native	1	5		5	1	12
		Stomorhina lunata	native	47	27	6	8	10	98
	Dolichopodidae	MF18	native	18	4		1	2	25
	Phoridae	*Megaselia rufipes*	introduced	2			15	3	20
	Scathophagidae	*Scathophaga litorea*	native	9	4	1	4		18
		Scathophaga stercoraria	native	6	1	5	36	20	68
	Sepsidae	MF41	native	3					3
		Sepsis biflexuosa	native	1	2	6			9
		Sepsis lateralis	native	2	3	10			15
		Sepsis neocynipsea	native	101	49	45	104	63	362
		Sepsis thoracica	native	4				6	10
	Syrphidae	*Episyrphus balteatus*	native	23	12	24	9	4	72
		Eristalis arbustorum	native	1	1	1	1	1	5
		Eristalis tenax	native	27	1	5	1	6	40
		Eupeodes corollae	native	19	12	15	15	8	69
		Meliscaeva auricollis	native	4	1			5	10
		Myathropa florea	native	7	4	2	1	1	15
		Sphaerophoria nigra	endemic	15	5	1			21
		Sphaerophoria scripta	native		2	4		3	9
		Syritta pipiens	native	6	5	6	4	6	27

		Xanthandrus azorensis	endemic	16		3		1	20
		Xanthandrus comtus	native	4		1			5
		Xylota segnis	native		3		2	1	6
	Tephritidae	*Euaresta bullans*	introduced	9	2	6		5	22
	--	MF26	native		1				1
		MF31	native	3	2				5
Hymenoptera	Apidae	*Apis mellifera*	introduced	8	31	13	14	37	103
		Bombus ruderatus	native	25	24	50	12	23	134
		Lasioglossum morio	native	2	23	25	9	15	74
		Lasioglossum smeathmanellum	native					5	5
		Lasioglossum villosulum	native	12	16	26	12	29	95
		Megachile centuncularis	native			9			9
	Chrysididae	*Chrysis ignita ignita*	native			1			1
	Formicidae	*Lasius grandis*	native	2	18	24	23	17	84
	Vespidae	*Ancistrocerus parietum*	native			7	1	5	13
		Vespula germanica	native	2		8		5	15
Lepidoptera	Choreutidae	*Tebenna micalis*	introduced		1	2			3
	Crambidae	MF12	native	2		1			3
		MF35	native	7					7
		MF36	native	5	2	1			8
		MF7	native	2	1		6		9
	Nymphalidae	*Hipparchia azorina azorina*	endemic	26					26
	Pieridae	*Colias croceus*	native	1	1	3	7	9	21
		Pieris brassicae azorensis	endemic		18	8	5	10	41
	Sphingidae	*Agrius convolvuli*	native					1	1
	--	MF12	native	5					5
		MF7	native	1		2			3
Total				**714**	**329**	**388**	378	**325**	**2134**

Table A2. Number of flowers per plant species in each habitat type: NatFor (natural forests), NatVeg (naturalized vegetation areas), ExoFor (exotic forests), SemiPast (semi-natural pastures), IntPast (intensive pastures).

Order	Family	Specie	Colonization status	NatFor	NatVeg	ExoFor	SemiPast	IntPast	Total
Apiales	Apiaceae	*Daucus carota azorica*	endemic		14	10			24
Asterales	Asteraceae	*Crepis capillaris*	introduced		29	123	36	123	333
		Erigeron karvinskianus	introduced	23	21	32			76
		Gazania rigens	introduced			7			7
		Helminthotheca echioides	introduced			52			52
		Hypochaeris radicata	introduced					34	34
		Leontodon taraxacoides	introduced					37	37
		Osteospermum ecklonis	introduced			38			38
		Tolpis azorica	endemic	556	51				607
		Tolpis succulenta	native	10	20				20
Boraginales	Boraginaceae	*Myosotis stolonifera*	introduced			3	71		74
Cornales	Hydrangeaceae	*Hydrangea macrophylla*	introduced		34	71			105
Ericales	Ericaceae	*Calluna vulgaris*	native	71	55				126
		Erica azorica	endemic	18	63				69
		Vaccinium cylindraceum	endemic	15					15
	Primulaceae	*Anagallis arvensis*	introduced		12		12		24
		Lysimachia azorica	endemic	72	46	14			132
Fabales	Fabaceae	*Lotus corniculatus*	introduced			7	55		62
		Lotus parviflorus	introduced		1	14			15
		Lotus pedunculatus	introduced		6	13	10	14	43
		Lotus subbiflorus	introduced	4	19			8	31
		Trifolium repens	introduced		20		227	333	580
		Ulex minor	introduced			15	1		16
Gentianales	Gentianaceae	*Centaurium scilloides*	native	2	23				25
Lamiales	Lamiaceae	*Mentha suaveolens*	introduced		24	8		43	86
		Origanum vulgare	introduced			12			12
		Prunella vulgaris	introduced	1	9	29	65	12	116
		Scutellaria minor	introduced	8	12		68		88
	Verbenaceae	*Lantana camara*	introduced		4				4
Malvales	Malvaceae	*Malva pseudolavatera*	introduced					30	30
Myrtales	Lythraceae	*Lythrum hyssopifolium*	introduced				27		27

Papaverales	Papaveraceae	*Chelidonium majus*	introduced			12			12
Polygonales	Polygonaceae	*Persicaria capitata*	introduced	37	24	140			201
		Rumex conglomeratus	introduced				23	20	43
Ranunculales	Ranunculaceae	*Ranunculus flammula*	introduced				46		46
		Ranunculus trilobus	native				61	34	95
Rosales	Rosaceae	*Duchesnea indica*	introduced	43	8	12			63
		Potentilla erecta	native	130	129	13	114		409
		Rubus hochstetterorum	endemic	34	103				103
		Rubus ulmifolius	introduced		60	62		38	160
Scrophulariales	Plantaginaceae	*Plantago lanceolata*	introduced				12	30	42
	Scrophulariaceae	*Digitalis purpurea*	introduced			25			25
		Scrophularia scorodonia	introduced			32			32
Solanales	Solanaceae	*Salpichroa organifolia*	introduced		6				6
		Solanum mauritianum	introduced			31			31
Theales	Hypericaceae	*Hypericum foliosum*	native	80	20	8		1	109
		Hypericum undulatum	native	30	2				32
Zingiberales	Zingiberaceae	*Hedychium gardneranum*	introduced			37			37
Total				1134	815	820	828	757	4354

Appendix B

Table B1. The maximally packed plant-insect network of the NatFor (natural forest) system with respective codes and scientific names, according to the number of interactions. Numbers along the borders of the matrix indicate the generalization levels of the species.

Morphospecie code	Insect Order NatFor	Plant code	P44	P15	P33	P24	P2	P5	P8	P10	P31	P48	P16	P27	P3	P9	P34	P42	**Insect generalization level**
		Insect species\Plant species	*Tolpis azorica*	*Hypericum foliosum*	*Potentilla erecta*	*Lysimachia azorica*	*Calluna vulgaris*	*Crepis apillaris*	*Duchesnea indica*	*Erigeron karvinskianus*	*Persicaria capitata*	*Vaccinium cylindraceum*	*Hypericum undulatum*	*Mentha suaveolens*	*Centaurium scilloides*	*Erica azorica*	*Prunella vulgaris*	*Scutellaria minor*	
MF2	Diptera	*Episyrphus balteatus*	14			1	2	1		1	3				1				7
MF5	Diptera	*Sepsis neocynipsea*	60	5	11	11			4			4	6						7
MF42	Hymenoptera	*Bombus ruderatus*	6	7			3	1			4	3					1		7
MF11	Coleoptera	*Anaspis proteus*	250	2	4	2		5	1										6
MF15	Hymenoptera	*Lasioglossum villosulum*	5		1	1		1		3			1						6
MF8	Diptera	*Eupeodes corollae*	13	1				1		2			2						5
MF18	Diptera	MF18	11	1	1	2			3										5
MF32	Diptera	MF32	1			0			1		3			3					5
MF17	Diptera	*Scathophaga litorea*	5	1	1	2													4
MF47	Diptera	*Scathophaga stercoraria*	3	1	1						1								4
MF25	Diptera	*Euaresta bullans*	6			2				1									3
MF24	Diptera	*Platycheirus albimanus*	9		3					3									3
MF28	Diptera	*Stomorhina lunata*	41				4							2					3
MF9	Diptera	*Syritta pipiens*		1	1								4						3
MF52	Diptera	*Xanthandrus azorensis*	12	2			2												3
MF27	Diptera	*Xanthandrus comtus*		2					1			1							3
MF12	Lepidoptera	MF12	4	1								2							3
MF36	Lepidoptera	MF36	3	1			1												3

MF46	Diptera	*Calliphora vicina*					1				1								2
MF19	Diptera	*Eristalis tenax*	21							6									2
MF31	Diptera	MF31				1	2												2
MF41	Diptera	MF41	2	1															2
MF43	Diptera	*Myathropa florea*	5	2															2
MF6	Diptera	*Paregle audacula*	4		1														2
MF3	Diptera	*Sepsis lateralis*			1				1										2
MF23	Hymenoptera	*Apis mellifera*	7	1															2
MF1	Hymenoptera	*Lasioglossum morio*	1					1											2
MF53	Lepidoptera	*Hipparchia azorina*	12				14												2
MF35	Lepidoptera	MF35	5			2													2
MF10	Coleoptera	*Meligethes aeneus*	4																1
MF38	Coleoptera	*Stilbus testaceus*	2																1
MF37	Diptera	*Eristalis arbustorum*	1																1
MF14	Diptera	*Megaselia rufipes*			2														1
MF29	Diptera	*Meliscaeva auricollis*	4																1
MF50	Diptera	*Rhinia apicalis*										1							1
MF39	Diptera	*Sepsis biflexuosa*			1														1
MF40	Diptera	*Sepsis thoracica*	4																1
MF34	Hymenoptera	*Lasius grandis*	2																1
MF13	Hymenoptera	*Vespula germanica*														2			1
MF49	Lepidoptera	*Colias croceus*																1	1
MF7	Lepidoptera	MF7	3																1
Plant generalization level			31	15	12	10	8	6	6	6	5	5	4	2	1	1	1	1	114

Table B2. The maximally packed plant-insect network of the NatVeg (naturalized vegetation areas) system with respective codes and scientific names, according to the number of interactions. Numbers along the borders of the matrix indicate the generalization levels of the species.

Morpho specie code	Insect Order NatVeg	Plant code	P37	P44	P14	P33	P38	P9	P24	P6	P2	P3	P46	P15	P27	P31	P8	P5	P45	P18	P40	P1	P42	P10	P16	P22	P23	P34	
		Insect species\Plant species	*Rubus hochstetterorum*	*Tolpis azorica*	*Hydrangea macrophylla*	*Potentilla erecta*	*Rubus ulmifolius*	*Erica azorica*	*Lysimachia azorica*	*Daucus carota*	*Calluna vulgaris*	*Centaurium scilloides*	*Trifolium repens*	*Hypericum foliosum*	*Mentha suaveolens*	*Persicaria capitata*	*Duchesnea indica*	*Crepis capillaris*	*Tolpis succulenta*	*Lantana camara*	*Salpichroa organifolia*	*Anagallis arvensis*	*Scutellaria minor*	*Erigeron karvinskianus*	*Hypericum undulatum*	*Lotus pedunculatus*	*Lotus subbiflorus*	*Prunella vulgaris*	**Insect generalization level**
MF34	Hymenoptera	*Lasius grandis*				1		1	1			1						2		1	7	4							8
MF8	Diptera	*Eupeodes corollae*	2	1			1	2	1				1	3														1	8
MF5	Diptera	*Sepsis neocynipsea*	3		3	3 1			5	4									2								1		7
MF28	Diptera	*Stomorhina lunata*	2		1			8			1 3				1	1										1			7
MF23	Hymenoptera	*Apis mellifera*	18				5						4		2	1				1									6
MF1	Hymenoptera	*Lasioglossum morio*	2	5	8	1								1				6											6
MF2	Diptera	*Episyrphus balteatus*		2	2	4	1				1	2																	6
MF15	Hymenoptera	*Lasioglossum villosulum*	1	4								5		2									4						5
MF50	Diptera	*Rhinia apicalis*	1	1	1			1						1															5
MF42	Hymenoptera	*Bombus ruderatus*	8				8						2			6													4
MF44	Lepidoptera	*Pieris brassicae azorensis*	12				4					1	1																4
MF46	Diptera	*Calliphora vicina*	1					6		1	1																		4
MF24	Diptera	*Platycheirus albimanus*		2					1								1								1				4
MF6	Diptera	*Paregle audacula*	1			1									3														3
MF18	Diptera	MF18		1					2								1												3

MF32	Diptera	MF32						14			1																	2
MF11	Coleoptera	*Anaspis proteus*	6							7																		2
MF9	Diptera	*Syritta pipiens*					4												1									2
MF43	Diptera	*Myathropa florea*	3		1																							2
MF17	Diptera	*Scathophaga litorea*				3				1																		2
MF3	Diptera	*Sepsis lateralis*				2				1																		2
MF25	Diptera	*Euaresta bullans*		1					1																			2
MF51	Diptera	*Sphaerophoria scripta*			1												1											2
MF16	Diptera	*Adia cinerella*			5																							1
MF30	Diptera	*Xylota segnis*			3																							1
MF31	Diptera	MF31																						2				1
MF39	Diptera	*Sepsis biflexuosa*				2																						1
MF36	Lepidoptera	MF36		2																								1
MF37	Diptera	*Eristalis arbustorum*					1																					1
MF19	Diptera	*Eristalis tenax*					1																					1
MF21	Diptera	*Lucilia sericata*						1																				1
MF29	Diptera	*Meliscaeva auricollis*			1																							1
MF26	Diptera	MF26		1																								1
MF47	Diptera	*Scathophaga stercoraria*	1																									1
MF49	Lepidoptera	*Colias croceus*	1																									1
MF7	Lepidoptera	MF7		1																								1
MF33	Lepidoptera	*Tebenna micalis*													1													1
Plant generalization level			15	11	10	8	8	7	6	5	4	4	4	4	4	3	3	2	2	2	1	1	1	1	1	1	1	1	110

Table B3. The maximally packed plant-insect network of the ExoFor (exofic forest) system with respective codes and scientific names, according to the number of interactions. Numbers along the borders of the matrix indicate the generalization levels of the species.

Morphospecie code	Insect Order ExoFor	Plant code	P5	P31	P14	P13	P38	P12	P30	P6	P43	P10	P41	P4	P27	P34	P29	P11	P22	P33	P8	P7	P24	P21	P47	P15	**Insect generalization level**
		Insect species\Plant species	*Crepis capillaris*	*Persicaria capitata*	*Hydrangea macrophylla*	*Helminthotheca echioides*	*Rubus ulmifolius*	*Hedychium gardneranum*	*Osteospermum ecklonis*	*Daucus carota*	*Solanum mauritianum*	*Erigeron karvinskianus*	*Scrophularia scorodonia*	*Chelidonium majus*	*Mentha suaveolens*	*Prunella vulgaris*	*Origanum vulgare*	*Gazania rigens*	*Lotus pedunculatus*	*Potentilla erecta*	*Duchesnea indica*	*Digitalis purpurea*	*Lysimachia azorica*	*Lotus parviflorus*	*Ulex minor*	*Hypericum foliosum*	
MF42	Hymenoptera	*Bombus ruderatus*	2	13	4		9	4	1		2	1	3		1	2	3					3			2		14
MF2	Diptera	*Episyrphus balteatus*	2	1	6	3	2				1	2	1	1		1					1			3			12
MF32	Diptera	MF32	7	1	1			1	1		1	1	2		1												9
MF8	Diptera	*Eupeodes corollae*	2	4	1	3	1	1	1										2								8
MF5	Diptera	*Sepsis neocynipsea*		1	10	1		16		12	2									3							7
MF1	Hymenoptera	*Lasioglossum morio*	3	13				1	3			1							3			1					7
MF34	Hymenoptera	*Lasius grandis*		1				3						3			11	4		1	1						7
MF15	Hymenoptera	*Lasioglossum villosulum*	6		1	15	1								2		1										6
MF9	Diptera	*Syritta pipiens*	1	1	1		1			1		1															6
MF20	Hymenoptera	*Ancistrocerus parietum*				1	1		1	2			2														5
MF3	Diptera	*Sepsis lateralis*												3		1		5			1						4
MF13	Hymenoptera	*Vespula germanica*	1	1		3							3														4
MF44	Lepidoptera	*Pieris brassicae azorensis*				5	1		1	1																	4
MF28	Diptera	*Stomorhina lunata*	3	1	1			1																			4
MF47	Diptera	*Scathophaga stercoraria*	1	1	1			2																			4
MF11	Coleoptera	*Anaspis proteus*	10													1		3									3
MF23	Hymenoptera	*Apis mellifera*		8			4									1											3
MF39	Diptera	*Sepsis biflexuosa*									3				2		1										3

MF51	Diptera	*Sphaerophoria scripta*	2									1			1												3
MF46	Diptera	*Calliphora vicina*		1										1						1							3
MF10	Coleoptera	*Meligethes aeneus*				8																	2				2
MF6	Diptera	*Paregle audacula*	1		8																						2
MF22	Hymenoptera	*Osmia fulviventris*							5										4								2
MF38	Coleoptera	*Stilbus testaceus*			1	6																					2
MF25	Diptera	*Euaresta bullans*	5									1															2
MF4	Diptera	*Fucellia tergina*	5															1									2
MF19	Diptera	*Eristalis tenax*				2	3																				2
MF52	Diptera	*Xanthandrus azorensis*							2	1																	2
MF49	Lepidoptera	*Colias croceus*	2							1																	2
MF21	Diptera	*Lucilia sericata*	1																							1	2
MF43	Diptera	*Myathropa florea*				1	1																				2
MF7	Lepidoptera	MF7			2																						1
MF33	Lepidoptera	*Tebenna micalis*	2																								1
MF37	Diptera	*Eristalis arbustorum*								1																	1
MF24	Diptera	*Platycheirus albimanus*									1																1
MF17	Diptera	*Scathophaga litorea*									1																1
MF27	Diptera	*Xanthandrus comtus*																	1								1
MF45	Hymenoptera	*Chrysis ignita ignita*												1													1
MF12	Lepidoptera	MF12																					1				1
MF36	Lepidoptera	MF36			1																						1
Plant generalization level			18	13	13	11	10	8	8	7	7	7	5	5	5	5	4	4	4	3	3	2	2	1	1	1	147

Table B4. The maximally packed plant-insect network of the SemiPast (semi-natural pasture) system with respective codes and scientific names, according to the number of interactions. Numbers along the borders of the matrix indicate the generalization levels of the species.

	Insect Order SemiPast	Plant code	P46	P20	P35	P5	P33	P42	P36	P28	P39	P25	P1	P32	P22	P34	**Insect generalization level**
		Morphospecie code	*Trifolium repens*	*Lotus corniculatus*	*Ranunculus flammula*	*Crepis capillaris*	*Potentilla erecta*	*Scutellaria minor*	*Ranunculus trilobus*	*Myosotis stolonifera*	*Rumex conglomeratus*	*Lythrum hyssopifolium*	*Anagallis arvensis*	*Plantago lanceolata*	*Lotus pedunculatus*	*Prunella vulgaris*	
MF5	Diptera	*Sepsis neocynipsea*	21	3	8	7	19	1	15	24	5		1				10
MF8	Diptera	*Eupeodes corollae*		1	2	2		1	4	4			1				7
MF1	Hymenoptera	*Lasioglossum morio*	3	2	1	1		1				1					6
MF47	Diptera	*Scathophaga stercoraria*	7				1		13	12				3			5
MF2	Diptera	*Episyrphus balteatus*	1		2	1	1		4								5
MF28	Diptera	*Stomorhina lunata*	1	2		2	1				2						5
MF7	Lepidoptera	MF7	1	1	1				2	1							5
MF34	Hymenoptera	*Lasius grandis*		1				19			1				2		4
MF14	Diptera	*Megaselia rufipes*	1	4		1	9										4
MF42	Hymenoptera	*Bombus ruderatus*	8			1		2								1	4
MF50	Diptera	*Rhinia apicalis*	2	1	1		1										4
MF11	Coleoptera	*Anaspis proteus*	2				1		58								3
MF10	Coleoptera	*Meligethes aeneus*	11		1						3						3
MF15	Hymenoptera	*Lasioglossum villosulum*	8	2		2											3
MF49	Lepidoptera	*Colias croceus*	1			1		5									3
MF44	Lepidoptera	*Pieris brassicae azorensis*	2					3									2
MF17	Diptera	*Scathophaga litorea*		1								3					2
MF9	Diptera	*Syritta pipiens*	2		2												2
MF30	Diptera	*Xylota segnis*			1							1					2
MF23	Hymenoptera	*Apis mellifera*	14														1
MF6	Diptera	*Paregle audacula*					3										1

MF16	Diptera	*Adia cinerella*				1											1
MF46	Diptera	*Calliphora vicina*	1														1
MF37	Diptera	*Eristalis arbustorum*		1													1
MF19	Diptera	*Eristalis tenax*	1														1
MF21	Diptera	*Lucilia sericata*		1													1
MF18	Diptera	MF18			1												1
MF32	Diptera	MF32					1										1
MF43	Diptera	*Myathropa florea*		1													1
MF20	Hymenoptera	*Ancistrocerus parietum*			1												1
		Plant generalization level	18	13	11	10	9	7	6	4	4	3	2	1	1	1	90

Table B5. The maximally packed plant-insect network of the IntPast (intensively managed pasture) system with respective codes and scientific names, according to the number of interactions. Numbers along the borders of the matrix indicate the generalization levels of the species.

Morphospecie code	Insect Order IntPast	Plant code	P46	P5	P27	P38	P17	P19	P26	P36	P39	P23	P34	P32	P15	P22	**Insect generalization level**
		Insect species\Plant species	*Trifolium repens*	*Crepis capillaris*	*Mentha suaveolens*	*Rubus ulmifolius*	*Hypochaeris radicata*	*Leontodon taraxacoides*	*Malva pseudolavatera*	*Ranunculus trilobus*	*Rumex conglomeratus*	*Lotus subbiflorus*	*Prunella vulgaris*	*Plantago lanceolata*	*Hypericum foliosum*	*Lotus pedunculatus*	
MF5	Diptera	*Sepsis neocynipsea*	3	1	7	2	17	17	10	3	3						9
MF23	Hymenoptera	*Apis mellifera*	32	4							1						3
MF15	Hymenoptera	*Lasioglossum villosulum*	10	9	5	5											4
MF42	Hymenoptera	*Bombus ruderatus*	18	2									3				3
MF47	Diptera	*Scathophaga stercoraria*	4	8	2	2			4								5
MF34	Hymenoptera	*Lasius grandis*		1	3	2					2	7		2			6
MF1	Hymenoptera	*Lasioglossum morio*	2	1	10	1	1										5
MF6	Diptera	*Paregle audacula*	3	3		1		2				1	2				6
MF28	Diptera	*Stomorhina lunata*	2	1	1	4	1	1									6
MF44	Lepidoptera	*Pieris brassicae azorensis*	8							1						1	3
MF49	Lepidoptera	*Colias croceus*	6	1						2							3
MF8	Diptera	*Eupeodes corollae*	1	6	1												3
MF19	Diptera	*Eristalis tenax*	1		4		1										3
MF32	Diptera	MF32	3		1	1		1									4
MF40	Diptera	*Sepsis thoracica*	2			4											2
MF9	Diptera	*Syritta pipiens*	1	1	1	1		1		1							6
MF25	Diptera	*Euaresta bullans*		3		2											2
MF29	Diptera	*Meliscaeva auricollis*	1				1			2				1			4
MF20	Hymenoptera	*Ancistrocerus parietum*	1		4												2
MF54	Hymenoptera	*Lasioglossum smeathmanellum*	5														1
MF13	Hymenoptera	*Vespula germanica*	4						1								2

MF2	Diptera	*Episyrphus balteatus*		1	1		1		1								4
MF14	Diptera	*Megaselia rufipes*							1						2		2
MF51	Diptera	*Sphaerophoria scripta*	1		1				1								3
MF10	Coleoptera	*Meligethes aeneus*						2									1
MF21	Diptera	*Lucilia sericata*			2												1
MF18	Diptera	MF18		2													1
MF37	Diptera	*Eristalis arbustorum*	1														1
MF4	Diptera	*Fucellia tergina*					1										1
MF43	Diptera	*Myathropa florea*			1												1
MF50	Diptera	*Rhinia apicalis*		1													1
MF52	Diptera	*Xanthandrus azorensis*			1												1
MF30	Diptera	*Xylota segnis*	1														1
MF48	Lepidoptera	*Agrius convolvuli*									1						1
Plant generalization level			22	16	16	11	7	6	6	5	4	2	2	2	1	1	101

Appendix C

Table C1. List of insect species/morphospecies names

Order	Family	Specie	Colonization Status	NatFor	NatVeg	ExoFor	SemiPast	IntPast	Total
Coleoptera	Nitidulidae	*Meligethes aeneus*	introduced	4		10	15	2	31
	Phalacridae	*Stilbus testaceus*	native	2		7			9
	Scraptiidae	*Anaspis proteus*	native	264	13	14	61		352
Diptera	Anthomyiidae	*Adia cinerella*	native		5		1		6
		Fucellia tergina	native			6		1	7
		Paregle audacula	native	5	5	9	3	12	34
	Calliphoridae	*Calliphora vicina*	introduced	2	9	3	1		15
		Lucilia sericata	introduced		1	2	1	2	6
		MF32	native	9	15	16	1	6	47
		Rhinia apicalis	native	1	5		5	1	12
		Stomorhina lunata	native	47	27	6	8	10	98
	Dolichopodidae	MF18	native	18	4		1	2	25
	Phoridae	*Megaselia rufipes*	introduced	2			15	3	20
	Scathophagidae	*Scathophaga litorea*	native	9	4	1	4		18
		Scathophaga stercoraria	native	6	1	5	36	20	68
	Sepsidae	MF41	native	3					3
		Sepsis biflexuosa	native	1	2	6			9
		Sepsis lateralis	native	2	3	10			15
		Sepsis neocynipsea	native	101	49	45	104	63	362
		Sepsis thoracica	native	4				6	10
	Syrphidae	*Episyrphus balteatus*	native	23	12	24	9	4	72
		Eristalis arbustorum	native	1	1	1	1	1	5
		Eristalis tenax	native	27	1	5	1	6	40
		Eupeodes corollae	native	19	12	15	15	8	69
		Meliscaeva auricollis	native	4	1			5	10
		Myathropa florea	native	7	4	2	1	1	15
		Sphaerophoria nigra	endemic	15	5	1			21
		Sphaerophoria scripta	native		2	4		3	9
		Syritta pipiens	native	6	5	6	4	6	27
		Xanthandrus azorensis	endemic	16		3		1	20
		Xanthandrus comtus	native	4		1			5
		Xylota segnis	native		3		2	1	6
	Tephritidae	*Euaresta bullans*	introduced	9	2	6		5	22
	--	MF26	native		1				1
		MF31	native	3	2				5
Hymenoptera	Apidae	*Apis mellifera*	introduced	8	31	13	14	37	103
		Bombus ruderatus	native	25	24	50	12	23	134
		Lasioglossum morio	native	2	23	25	9	15	74
		Lasioglossum smeathmanellum	native					5	5

		Lasioglossum villosulum	native	12	16	26	12	29	95
		Megachile centuncularis	native			9			9
	Chrysididae	*Chrysis ignita ignita*	native			1			1
	Formicidae	*Lasius grandis*	native	2	18	24	23	17	84
	Vespidae	*Ancistrocerus parietum*	native			7	1	5	13
		Vespula germanica	native	2		8		5	15
Lepidoptera	Choreutidae	*Tebenna micalis*	introduced		1	2			3
	Crambidae	MF12	native	2		1			3
		MF35	native	7					7
		MF36	native	5	2	1			8
		MF7	native	2	1		6		9
	Nymphalidae	*Hipparchia azorina azorina*	endemic	26					26
	Pieridae	*Colias croceus*	native	1	1	3	7	9	21
		Pieris brassicae azorensis	endemic		18	8	5	10	41
	Sphingidae	*Agrius convolvuli*	native					1	1
	--	MF12	native	5					5
		MF7	native	1		2			3
Total				**714**	**329**	**388**	378	**325**	**2134**

Appendix C1. Description of the landscape disturbance index methodological approach according to Cardoso *et al.* (2013).

The index of "landscape disturbance" (D) reflects a gradient by considering landscape configuration. Based on aerial photography (DROTRH, 2008) and previous fieldwork on native forests from C. Gaspar (unpublished data) and on the proportion of endemic, native and exotic species typical to each land use type present in the island (Cardoso *et al*., 2009), a land use map of 100×100 m resolution depicting the location of all land use types was built. With this information, inferred the disturbance level of each land use relative to an undisturbed native forest and used it to rank the different land uses. To each rank, a value of "local disturbance" (L) was attributed: Natural forests=0, Natural(ized) vegetation or rocky outcrops=1, Exotic forests=2, Semi-natural pastures=3; Intensively managed pastures=4; Orchards/agriculture areas=5; Urban/industrial areas=6. To the ocean attributed the value of "no data". For the landscape disturbance index of each 100×100 m cell in the island the following equation was used:

$$D_{i,j} = \left(\frac{2L_{i,j} + \sum_{n=1}^{r} \sum_{m=1}^{c} \frac{L_{n,m}}{d^2_{(i,j)(n,m)}}}{2\max + \sum_{n=1}^{r} \sum_{m=1}^{c} \frac{\max}{d^2_{(i,j)(n,m)}}} \right) \times 100$$

where: Di,j is the final index value of the cell in row i and column j; L is the local disturbance value of each cell (as defined above); r is number of rows in the map; c is number of columns in the map; d is the distance between the centroids of each two cells; max is the maximum theoretical value of disturbance each cell may take (in this case max=6, corresponding to urban/industrial areas).

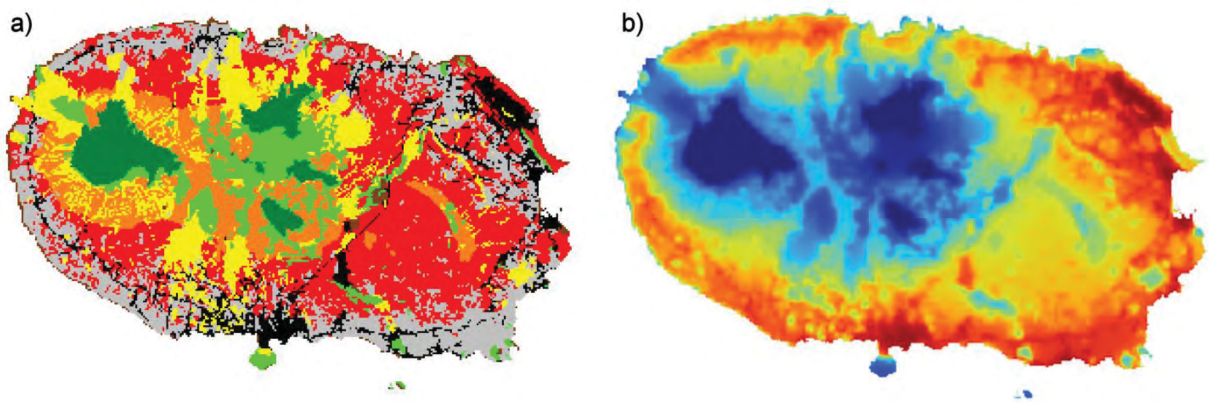


Figure C1. Maps of Terceira Island with (a) distribution of land use types and (b) value of landscape disturbance according to Cardoso *et al.* (2013). For land use types (a): dark green=natural forests, light green=natural(ized) vegetation, yellow=exotic forests, orange=semi-natural pastures, red=intensively managed pastures, grey=orchards/agriculture areas, black=urban/industrial areas and brown=rocky outcrops). For landscape disturbance gradient (b): values of landscape disturbance are represented in a gradient from blue for lowest values to red for highest values.

Appendix D

Table D1. Geographical coordinates of insect species records in Terceira Island with respective taxonomic information and colonization status.

Order	Family	Species	Status	Longitude	Latitude
Coleoptera	Nitidulidae	*Meligethes aeneus*	exotic	492915	4284493
				475715	4289193
				474515	4291693
				472615	4289593
				474615	4288393
				475015	4289093
				490615	4282693
	Phalacridae	*Stilbus testaceus*	native	492915	4284493
				470315	4287093
				471515	4288993
				474615	4288393
	Scraptiidae	*Anaspis proteus*	native	478815	4280793
				480915	4284393
				472615	4289593
				482015	4289793
				471515	4288993
				473915	4287893
				481715	4291093
				482015	4287593
				474615	4288393
				475415	4287693
				485415	4286193
				494115	4288395
				475015	4289093
				470115	4288693
Diptera	Anthomyiidae	*Adia cinerella*	native	469715	4290793
				470315	4285993
		Fucellia tergina	native	478815	4280793
				475415	4293193
		Paregle audacula	native	477115	4283293

				470315	4287093
				490215	4280293
				474515	4291693
				486215	4289493
				485815	4282693
				472615	4289593
				482015	4289793
				479015	4285993
				485415	4286193
				483015	4283593
	Calliphoridae	*Calliphora vicina*	exotic	483915	4290293
				478815	4280793
				478915	4290093
				471515	4288993
				481715	4291093
				494115	4288395
				483415	4293493
				470915	4289693
				487415	4277793
				470315	4285993
		Lucilia sericata	exotic	492915	4284493
				477115	4283293
				475415	4293193
				483415	4293493
				476415	4289493
		Rhinia apicalis	native	485815	4282693
				472215	4287993
				469715	4290793
				482815	4285893
				483415	4293493
				487415	4277793
				490615	4282693
				470115	4288693
				479115	4285493

				476415	4289493
		Stomorhina lunata	native	475715	4289193
				478815	4280793
				478915	4290093
				485515	4289493
				490215	4280293
				474515	4291693
				475415	4293193
				485815	4282693
				482015	4289793
				471515	4288993
				481715	4291093
				474615	4288393
				475415	4287693
				469715	4290793
				479015	4285993
				485415	4286193
				483415	4293493
				470915	4289693
				487415	4277793
				470115	4288693
				473015	4284293
				470315	4285993
				479115	4285493
	Phoridae	*Megaselia rufipes*	exotic	487415	4291893
				485815	4282693
				482015	4289793
				470115	4288693
				470315	4285993
				483015	4283593
	Scathophagidae	*Scathophaga litorea*	native	484315	4288993
				480915	4284393
				472615	4289593
				472215	4287993

				474615	4288393
				479015	4285993
				494115	4288395
				470315	4285993
				479115	4285493
		Scathophaga stercoraria	native	478915	4290093
				477115	4283293
				470315	4287093
				485515	4289493
				475415	4281293
				488115	4287193
				487415	4291893
				490215	4280293
				475415	4293193
				486215	4289493
				480915	4284393
				472215	4287993
				481715	4291093
				474615	4288393
				487415	4277793
				475015	4289093
				489915	4285393
				473015	4284293
				476415	4289493
				483015	4283593
	Sepsidae	*Sepsis biflexuosa*	native	478815	4280793
				484315	4288993
				485515	4289493
				472615	4289593
				479015	4285993
		Sepsis lateralis	native	478815	4280793
				472615	4289593
				472215	4287993
				479015	4285993

				494115	4288395
		Sepsis neocynipsea	native	492915	4284493
				475715	4289193
				472415	4292593
				478915	4290093
				470315	4287093
				485515	4289493
				487415	4291893
				490215	4280293
				474515	4291693
				492115	4286893
				475415	4293193
				485815	4282693
				480915	4284393
				472615	4289593
				472215	4287993
				482015	4289793
				471515	4288993
				473915	4287893
				481715	4291093
				482015	4287593
				474615	4288393
				475415	4287693
				469715	4290793
				479015	4285993
				482815	4285893
				485415	4286193
				494115	4288395
				470915	4289693
				475015	4289093
				481815	4285993
				490615	4282693
				489915	4285393
				470115	4288693

				473015	4284293
				470315	4285993
				479115	4285493
				476415	4289493
		Sepsis thoracica	native	490215	4280293
				492115	4286893
				472215	4287993
				475415	4287693
	Syrphidea	*Episyrphus balteatus*	native	492915	4284493
				475715	4289193
				478815	4280793
				484315	4288993
				478915	4290093
				477115	4283293
				470315	4287093
				485515	4289493
				487415	4291893
				490215	4280293
				475415	4293193
				472615	4289593
				472215	4287993
				482015	4289793
				471515	4288993
				473915	4287893
				481715	4291093
				482015	4287593
				474615	4288393
				475415	4287693
				469715	4290793
				479015	4285993
				482815	4285893
				494115	4288395
				470915	4289693
				481215	4287293

				475015	4289093
				470115	4288693
				473015	4284293
				479115	4285493
		Eristalis arbustorum	native	492915	4284493
				486215	4289493
				474615	4288393
				494115	4288395
				476415	4289493
		Eristalis tenax	native	492915	4284493
				483915	4290293
				490215	4280293
				475415	4293193
				482015	4287593
				474615	4288393
				475415	4287693
				494115	4288395
				473015	4284293
		Eupeodes corollae	native	492915	4284493
				483915	4290293
				475715	4289193
				472415	4292593
				475415	4281293
				473515	4283393
				475415	4293193
				486215	4289493
				485815	4282693
				480915	4284393
				472215	4287993
				482015	4289793
				471515	4288993
				481715	4291093
				482015	4287593
				474615	4288393

				475415	4287693
				482815	4285893
				494115	4288395
				483415	4293493
				470915	4289693
				481215	4287293
				487415	4277793
				475015	4289093
				481815	4285993
				490615	4282693
				470315	4285993
		Meliscaeva auricollis	native	492115	4286893
				475415	4293193
				472215	4287993
				475415	4287693
				469715	4290793
		Myathropa florea	native	492915	4284493
				475415	4293193
				480915	4284393
				482015	4287593
				474615	4288393
				469715	4290793
				487415	4277793
				470115	4288693
		Sphaerophoria nigra	endemic	485515	4289493
				482015	4287593
				474615	4288393
				481215	4287293
		Sphaerophoria scripta	native	478815	4280793
				484315	4288993
				477115	4283293
				487415	4291893
				490215	4280293
				475415	4293193

				469715	4290793
				481215	4287293
		Syritta pipiens	native	492915	4284493
				483915	4290293
				472415	4292593
				478915	4290093
				470315	4287093
				485515	4289493
				490215	4280293
				474515	4291693
				492115	4286893
				475415	4293193
				480915	4284393
				472615	4289593
				482815	4285893
				494115	4288395
				490615	4282693
				470315	4285993
				476415	4289493
		Xanthandrus azorensis	endemic	492915	4284493
				472415	4292593
				475415	4293193
				472615	4289593
				472215	4287993
				471515	4288993
				473915	4287893
				482015	4287593
				474615	4288393
		Xanthandrus comtus	native	472415	4292593
				472215	4287993
				473915	4287893
				482015	4287593
		Xylota segnis	native	473515	4283393
				469715	4290793

				490615	4282693
				479115	4285493
	Tephritidae	*Euaresta bullans*	exotic	478815	4280793
				477115	4283293
				485515	4289493
				490215	4280293
				472615	4289593
				472215	4287993
				471515	4288993
				482015	4287593
				474615	4288393
				481215	4287293
Hymenoptera	Apidae	*Apis mellifera*	exotic	483915	4290293
				484315	4288993
				478915	4290093
				485515	4289493
				475415	4281293
				488115	4287193
				487415	4291893
				474515	4291693
				492115	4286893
				473515	4283393
				475415	4293193
				486215	4289493
				485815	4282693
				482015	4287593
				474615	4288393
				469715	4290793
				485415	4286193
				494115	4288395
				480415	4277293
				487415	4277793
				489915	4285393
				473015	4284293

				476415	4289493
		Bombus ruderatus	native	492915	4284493
				483915	4290293
				475715	4289193
				472415	4292593
				478815	4280793
				484315	4288993
				478915	4290093
				477115	4283293
				470315	4287093
				485515	4289493
				475415	4281293
				474515	4291693
				492115	4286893
				473515	4283393
				475415	4293193
				486215	4289493
				485815	4282693
				480915	4284393
				472215	4287993
				471515	4288993
				481715	4291093
				482015	4287593
				474615	4288393
				469715	4290793
				485415	4286193
				494115	4288395
				481215	4287293
				487415	4277793
				481815	4285993
				489915	4285393
				473015	4284293
				470315	4285993
				476415	4289493

		Lasioglossum morio	native	472415	4292593
				478815	4280793
				484315	4288993
				477115	4283293
				490215	4280293
				474515	4291693
				475415	4293193
				482015	4289793
				481715	4291093
				469715	4290793
				479015	4285993
				485415	4286193
				470915	4289693
				480415	4277293
				481815	4285993
				470115	4288693
				473015	4284293
				470315	4285993
				479115	4285493
				476415	4289493
		Lasioglossum smeathmanellum	native	474515	4291693
				473515	4283393
				485815	4282693
		Lasioglossum villosulum	native	492915	4284493
				478815	4280793
				477115	4283293
				470315	4287093
				485515	4289493
				490215	4280293
				474515	4291693
				473515	4283393
				475415	4293193
				486215	4289493
				485815	4282693

				480915	4284393
				472615	4289593
				472215	4287993
				482015	4289793
				471515	4288993
				482015	4287593
				469715	4290793
				485415	4286193
				470915	4289693
				480415	4277293
				470115	4288693
				473015	4284293
				470315	4285993
				476415	4289493
		Megachile centuncularis	native	472415	4292593
	Chrysididae	*Chrysis ignita ignita*	native	478815	4280793
	Formicidae	*Lasius grandis*	native	478815	4280793
				478915	4290093
				485515	4289493
				475415	4281293
				490215	4280293
				474515	4291693
				475415	4293193
				485815	4282693
				474615	4288393
				475415	4287693
				479015	4285993
				482815	4285893
				483415	4293493
				480415	4277293
				481815	4285993
				490615	4282693
				476415	4289493
	Vespidae	*Ancistrocerus parietum*	native	492915	4284493

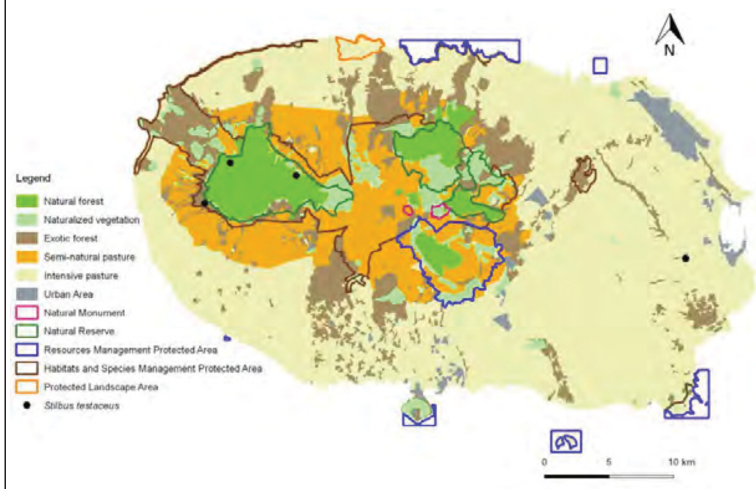
				472415	4292593
				470315	4287093
				475415	4293193
				486215	4289493
				490615	4282693
		Vespula germanica	native	492915	4284493
				483915	4290293
				472415	4292593
				470315	4287093
				487415	4291893
				486215	4289493
				474615	4288393
Lepidoptera	Choreutidae	*Tebenna micalis*	exotic	492915	4284493
				485415	4286193
	Nymphalidae	*Hipparchia azorina azorina*	endemic	472615	4289593
				472215	4287993
				473915	4287893
				482015	4287593
	Pieridae	*Colias croceus*	native	492915	4284493
				484315	4288993
				475415	4281293
				490215	4280293
				492115	4286893
				486215	4289493
				471515	4288993
				487415	4277793
				481815	4285993
				476415	4289493
		Pieris brassicae azorensis	endemic	492915	4284493
				472415	4292593
				484315	4288993
				475415	4281293
				492115	4286893
				486215	4289493

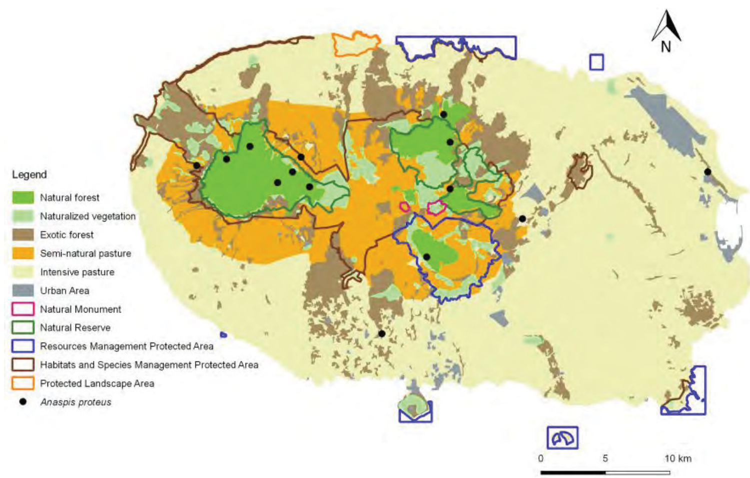
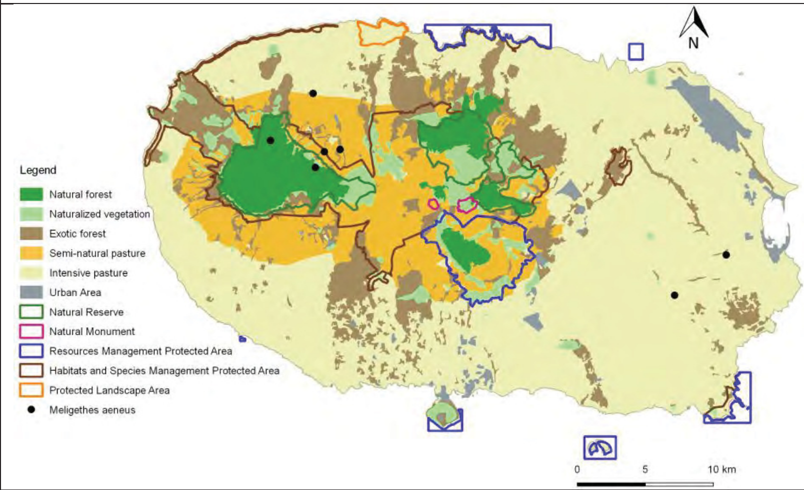
				485415	4286193
				494115	4288395
				480415	4277293
				487415	4277793
				481815	4285993
				489915	4285393
	Sphingidae	*Agrius convolvuli*	native	475415	4281293

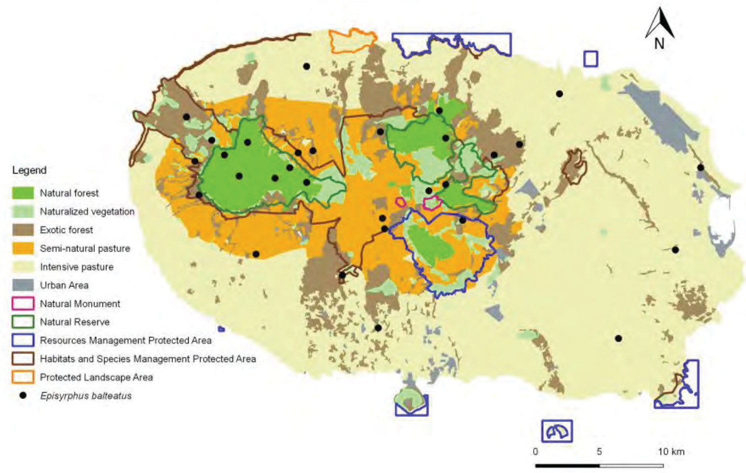
Table D2. Priority areas ranked in Zonation for each taxonomic group and total set of species, inside Terceira's land-use (natural forest, naturalized vegetation, exotic forest, semi-natural pasture, intensively managed pasture, agriculture and orchard, urban and industrial) and INP areas (ncells: number of cells; INP: Island Natural Park).

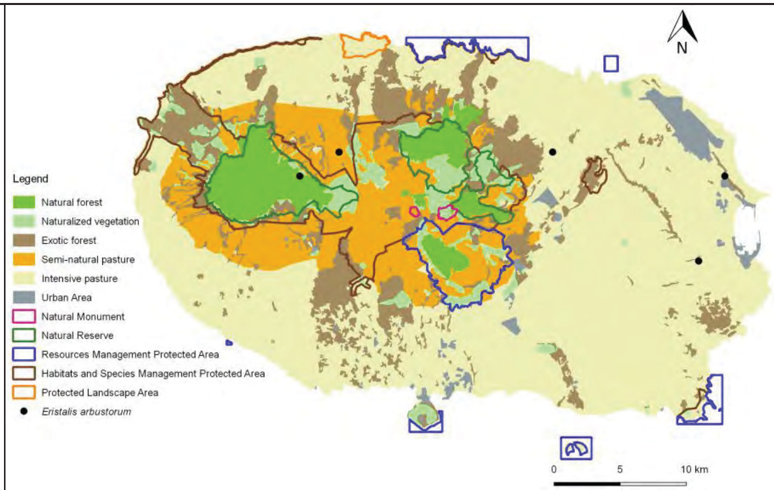
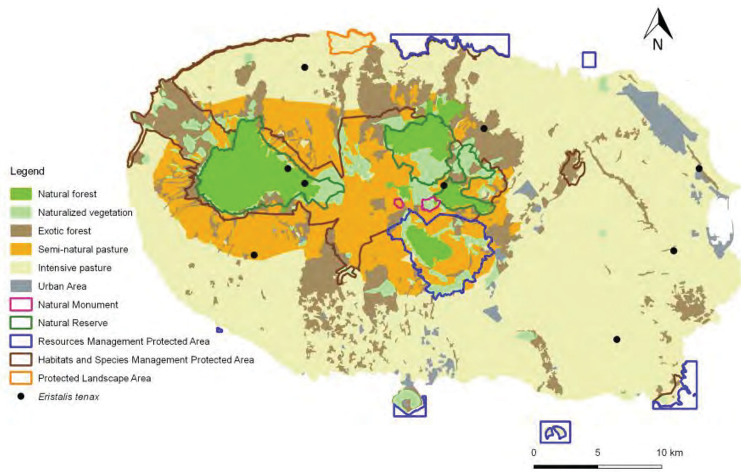
		Natural forest			Naturalized vegetation			Exotic forest			Semi-natural pasture			Intensive pasture			Agriculture/Orchards			Urban/Industrial			INP		
Group	Quartile	Total (ncells)	ncells	%	Total (ncells)	ncells	%	Total (ncells)	ncells	%	Total (ncells)	ncells	%	Total (ncells)	ncells	%	Total (ncells)	ncells	%	Total (ncells)	ncells	%	Total (ncells)	ncells	%
Coleoptera	0-0.25	5	1	20	70	18	25,7	586	254	43,3	117	21	17,9	419	345	82,3	521	422	81	52	42	80,8	13	8	61,5
	0.25-0.50	5	0	0	70	0	0	586	0	0	117	0	0	419	0	0	521	0	0	52	0	0	13	0	0
	0.50-0.75	5	0	0	70	0	0	586	0	0	117	0	0	419	0	0	521	0	0	52	0	0	13	0	0
	0.75-1	5	4	80	70	52	74,3	586	332	56,6	117	96	82,1	419	74	17,7	521	99	19	52	10	19,2	13	5	38,5
Hymenoptera	0-0.25	5	3	60	70	38	54,3	586	276	47	117	62	53	419	207	49,4	521	276	53	52	34	65,4	13	10	76,9
	0.25-0.50	5	0	0	70	0	0	586	0	0	117	0	0	419	0	0	521	0	0	52	0	0	13	0	0
	0.50-0.75	5	0	0	70	0	0	586	0	0	117	0	0	419	0	0	521	0	0	52	0	0	13	0	0
	0.75-1	5	2	40	70	32	45,7	586	310	52,9	117	55	47	419	212	50,6	521	245	47	52	18	34,6	13	3	23,1
Lepidoptera	0-0.25	5	3	60	70	20	28,6	586	251	42,8	117	42	36	419	193	88,1	521	246	47,2	52	26	50	13	4	30,8
	0.25-0.50	5	0	0	70	0	0	586	0	0	117	0	0	419	0	0	521	0	0	52	0	0	13	0	0
	0.50-0.75	5	0	0	70	0	0	586	0	0	117	0	0	419	0	0	521	0	0	52	0	0	13	0	0
	0.75-1	5	2	40	70	50	71,4	586	335	57,2	117	75	64	419	226	53,9	521	275	52,8	52	26	50	13	9	69,2
Syrphid	0-0.25	5	1	20	70	18	25,7	586	254	43,3	117	21	17,9	419	345	82,3	521	422	81	52	42	80,8	13	8	61,5
	0.25-0.50	5	0	0	70	0	0	586	0	0	117	0	0	419	0	0	521	0	0	52	0	0	13	0	0
	0.50-0.75	5	0	0	70	0	0	586	0	0	117	0	0	419	0	0	521	0	0	52	0	0	13	0	0
	0.75-1	5	4	80	70	52	74,3	586	332	56,6	117	96	82,1	419	74	17,7	521	99	19	52	10	19,2	13	5	38,5
Other diptera	0-0.25	5	4	80	70	4	5,7	586	50	8,5	117	9	7,7	419	51	23,3	521	73	14	52	12	23,1	13	3	23,1
	0.25-0.50	5	0	0	70	0	0	586	0	0	117	0	0	419	0	0	521	0	0	52	0	0	13	0	0
	0.50-0.75	5	0	0	70	0	0	586	0	0	117	0	0	419	0	0	521	0	0	52	0	0	13	0	0
	0.75-1	5	1	20	70	7	10	586	64	10,9	117	2	1,7	419	112	26,7	521	168	32,2	52	0	0	13	2	15,4
Total insects	0-0.25	5	1	20	70	18	25,7	586	254	43,3	117	21	17,9	419	345	82,3	521	422	81	52	42	80,8	13	8	61,5
	0.25-0.50	5	0	0	70	0	0	586	0	0	117	0	0	419	0	0	521	0	0	52	0	0	13	0	0
	0.50-0.75	5	0	0	70	0	0	586	0	0	117	0	0	419	0	0	521	0	0	52	0	0	13	0	0
	0.75-1	5	4	80	70	52	74,3	586	332	56,6	117	96	82,1	419	74	17,7	521	99	19	52	10	19,2	13	5	38,5

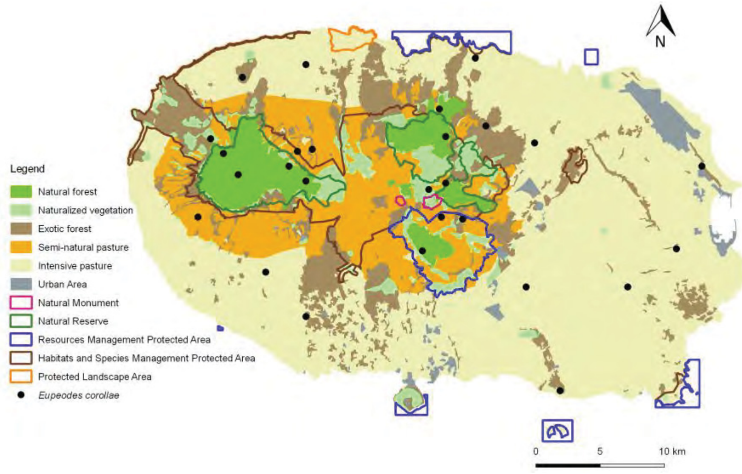
Table D3. Brief description, characterization, taxonomic identification (following Borges *et al*., 2010) and sampling sites of collected insects to species-level.

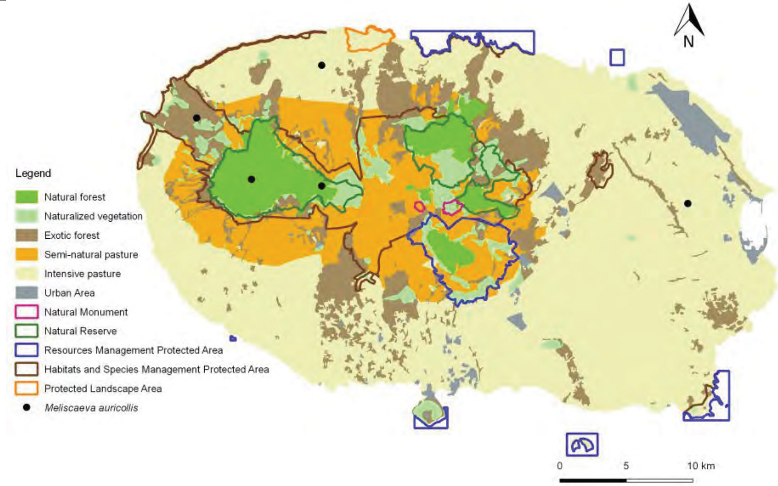
Species name	Taxonomic identification	Description and characterization	Colonization status	Sampling sites
Stilbus testaceus Panzer, 1797	Order Coleoptera Suborder Polyphaga Infraorder Cucujiformia Superfamily Cucujoidea Family Phalacridae	• Small specie with less than 3 mm long, with globular appearance and microsculpturing characteristic on the dorsal side. • Adults are often seen on flowers, but the larvae are found on a variety of plant material. This species is very common, and usually associated with reeds or dried grass.	Native	

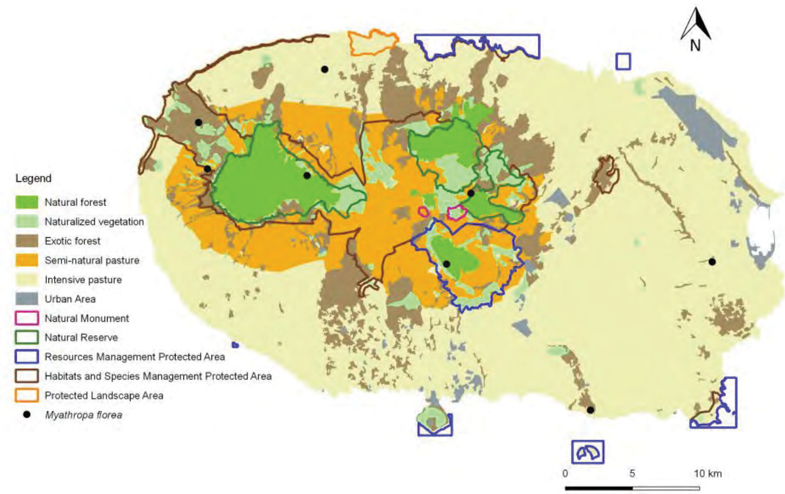
Anaspis proteus Wollaston, 1854	Order Coleoptera Suborder Polyphaga Infraorder Cucujiformia Superfamily Tenebrionoidea Family Scraptiidae	• Small species around 2 – 4 mm long. • Frequently seen in large numbers on flowers.	Macaronesia endemic	
Meligethes aeneus Fabricius, 1775	Order Coleoptera Suborder Polyphaga Infraorder Cucujiformia Superfamily Tenebrionoidea Family Nitidulidae	• Small black beetle with a metallic brassy or blue-green sheen.	Exotic	

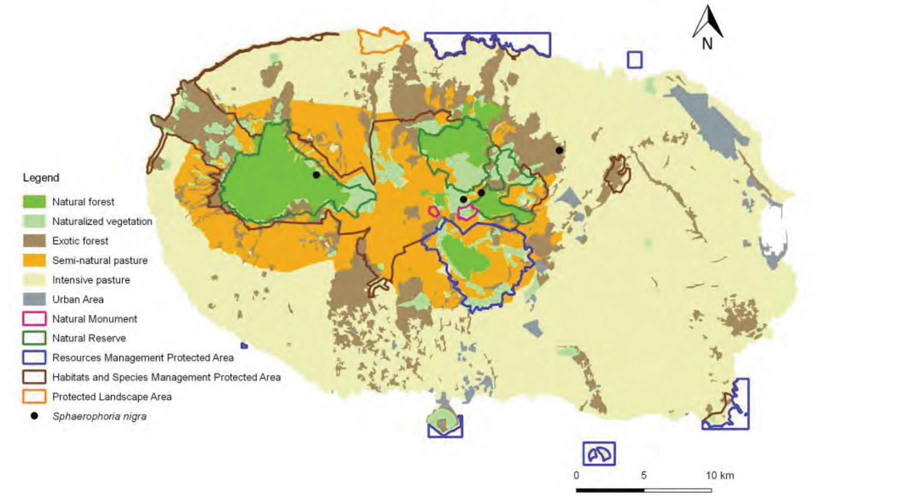
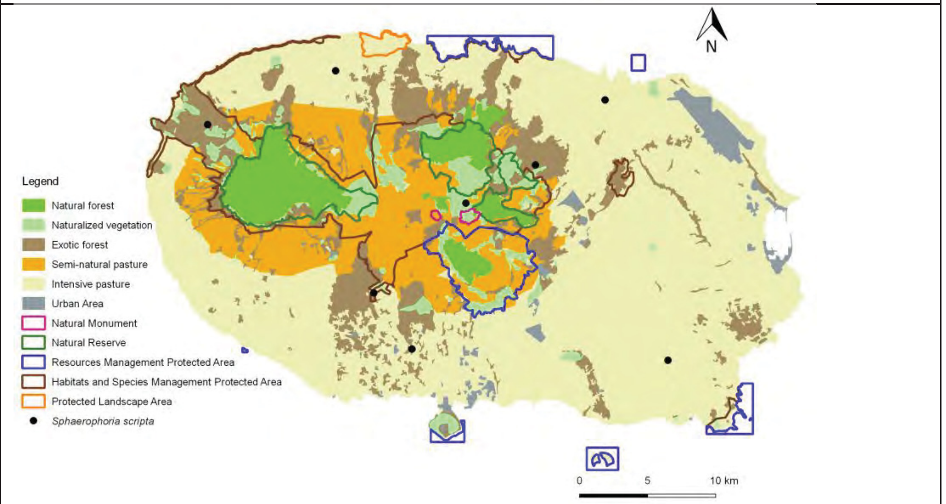
Episyrphus balteatus De Geer, 1776	Order Diptera Suborder Brachycera Infraorder Muscomorpha (Aschiza) Superfamily Syrphoidea Family Syrphidae	• Very well-known hoverfly, sometimes called the marmalade hoverfly, is a relatively small hoverfly (9–12 mm). • The upper side of the abdomen is patterned with orange and black bands. Two further identification characters are the presence of secondary black bands on the third and fourth dorsal plates and faint greyish longitudinal stripes on the thorax. • Conspicuous habit of hovering around flowers. Regularly visit flowers to feed on nectar and pollen, they can be an important pollinating species. • They are predatory on aphids and related insects that are similar plant pests; in fact they exploit a very wide range of habitats and food resources, like sap fluid of the plant and decaying wood or vegetation.	Native	

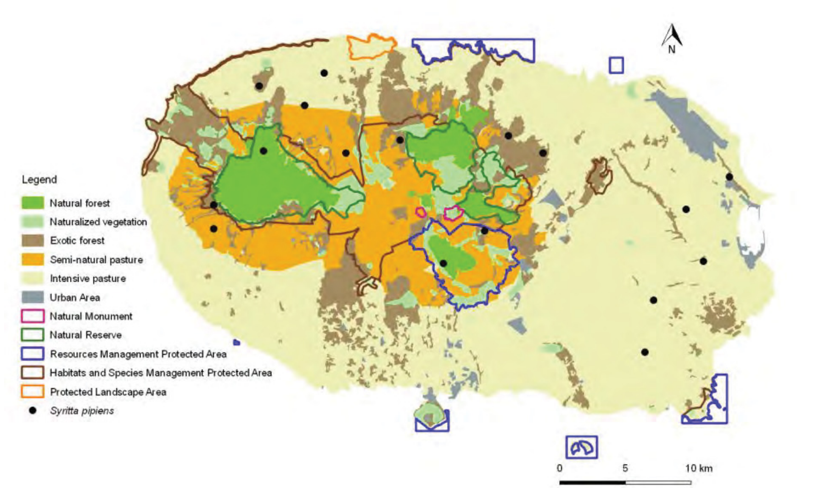
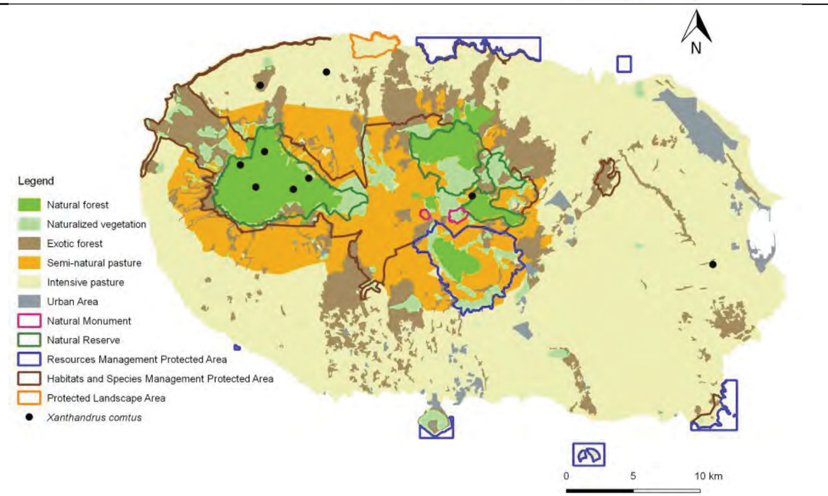
Eristalis arbustorum Linnaeus, 1758	Order Diptera Suborder Brachycera Infraorder Muscomorpha (Aschiza) Superfamily Syrphoidea Family Syrphidae	• Very known hoverfly with wasp-like coloration - yellow bright colour. • The larvae of which are aquatic, and breathe through a long, snorkel-like appendage, hence the common name rat-tailed maggots.	Native	
Eristalis tenax Linnaeus, 1758	Order Diptera Suborder Brachycera Infraorder Muscomorpha (Aschiza) Superfamily Syrphoidea Family Syrphidae	• One of the most common species in the genus Eritalis, is also known as the dronefly, because it bears a superficial resemblance to honeybee drones. • Dronefies and their relatives are fairly common generalist pollinators, the larvae of which are aquatic, and breathe through a long, snorkel-like appendage, hence the common name rat-tailed maggots.	Native	

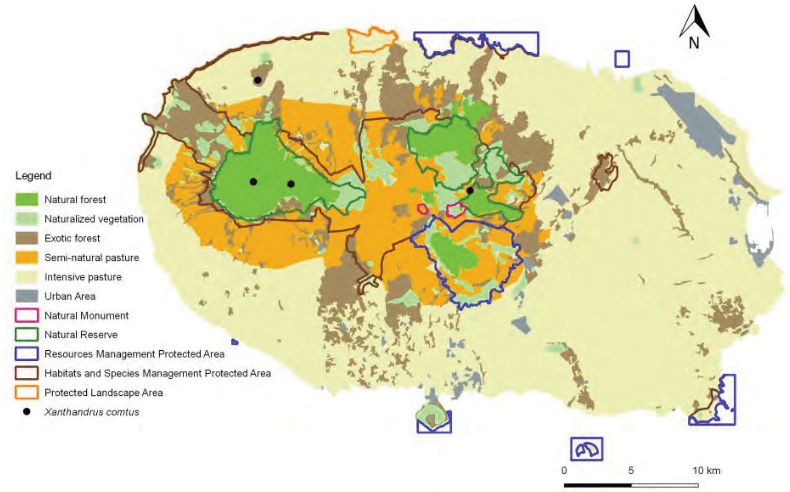
Eupeodes corolla Fabricius, 1794	Order Diptera Suborder Brachycera Infraorder Muscomorpha (Aschiza) Superfamily Syrphoidea Family Syrphidae	• Adults are 6–11 millimetres in body length. • Males and females have different marking on the abdomen; males have square commas on tergites 3 and 4, whereas females have narrow commas. • The upper side of the abdomen is patterned with orange and black bands. Two further identification characters are the presence of secondary black bands on the third and fourth dorsal plates and faint greyish longitudinal stripes on the thorax. • Larvae feed on aphids. This species has been used experimentally in glasshouses as a method of aphid control, and to control scale insects and aphids in fruit plantations.	Native	

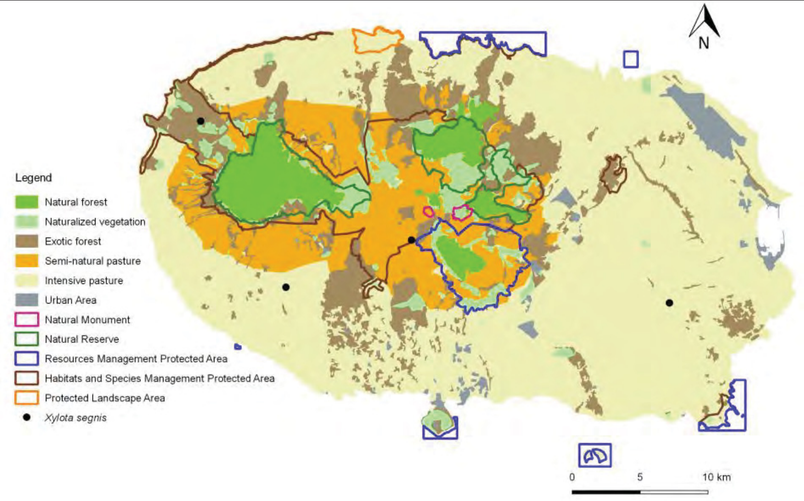
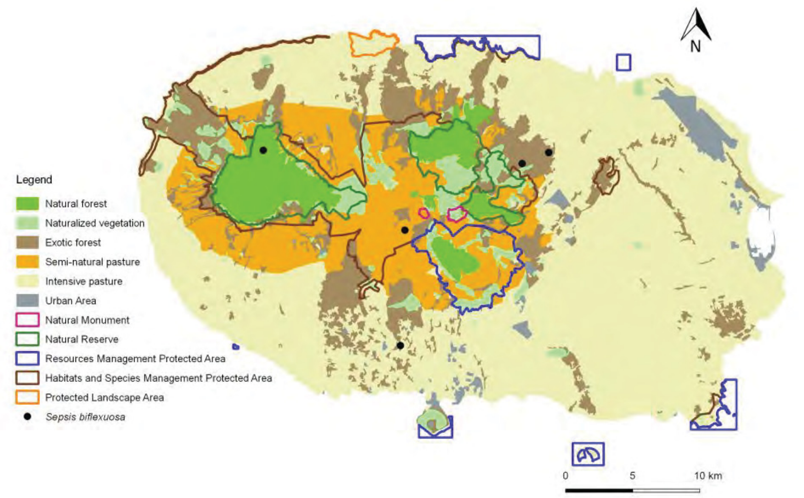
Meliscaeva auricollis Meigen, 1822	Order Diptera Suborder Brachycera Infraorder Muscomorpha (Aschiza) Superfamily Syrphoidea Family Syrphidae	• Though small and dark coloured, the slanting rear border of the yellow crescent marks on tergite 2, particularly in males, help to identify the species. • The spring generation tend to be darker bodied than those born later in the year. • Larvae are known to be associated with aphid colonies on shrubs such as Barberry and Broom and on the flowers and stems of umbellifers. • The adult hibernates.	Native	

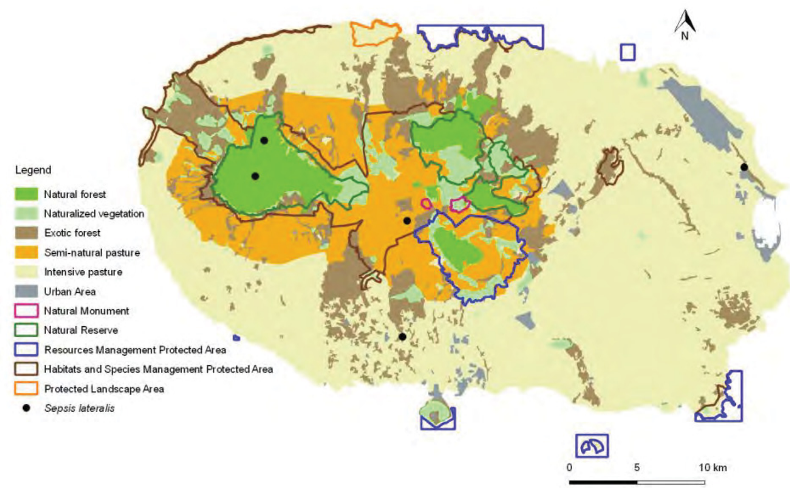
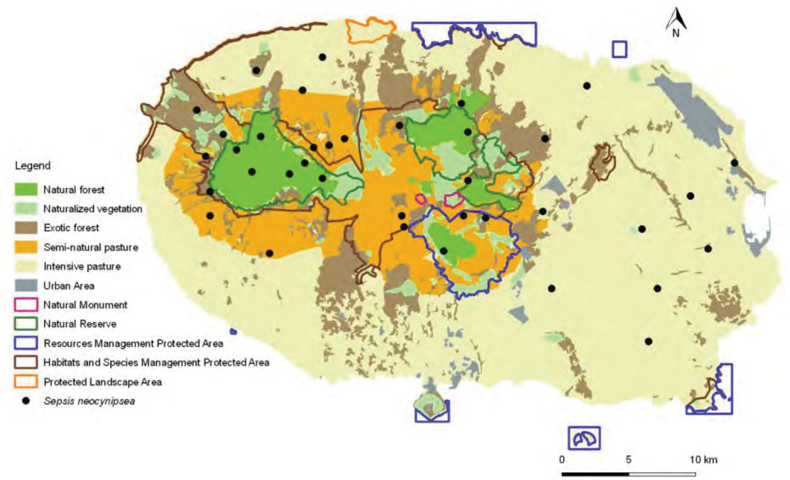
Myathropa florea Linnaeus, 1758	Order Diptera Suborder Brachycera Infraorder Muscomorpha (Aschiza) Superfamily Syrphoidea Family Syrphidae	• Is a very common European and North African species of hoverfly. • Adults may be seen on flowers from May to September. • It is of similar size as the drone fly, but are generally more yellow, with two light bands to the thorax, interrupted with a black central smudge. • Like most Eristalini, Myathropa are rather variable in size, shape and colour. • Larvae feed on bacteria in organic waterlogged detritus, often in the shallow rot holes of tree stumps.	Native	

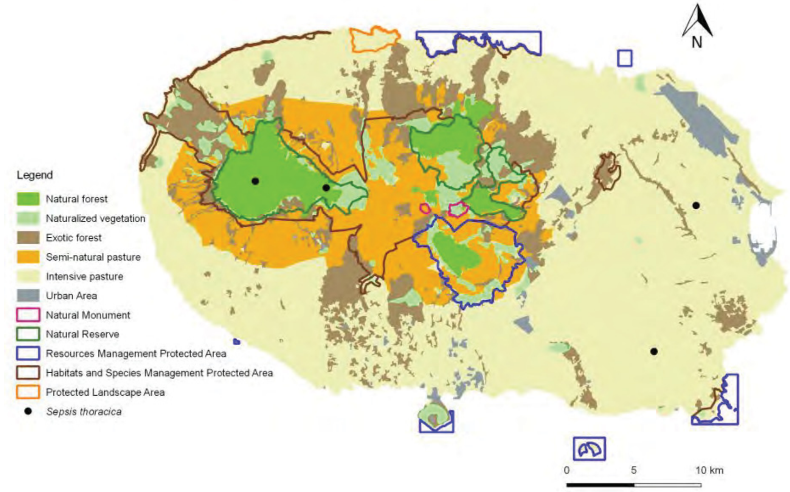
Sphaerophoria nigra Frey, 1945	Order Diptera Suborder Brachycera Infraorder Muscomorpha (Aschiza) Superfamily Syrphoidea Family Syrphidae	• The wings being shorter than the abdomen.	Endemic	
Sphaerophoria scripta Linnaeus, 1758	Order Diptera Suborder Brachycera Infraorder Muscomorpha (Aschiza) Superfamily Syrphoidea Family Syrphidae	• The wings being shorter than the abdomen.	Native	

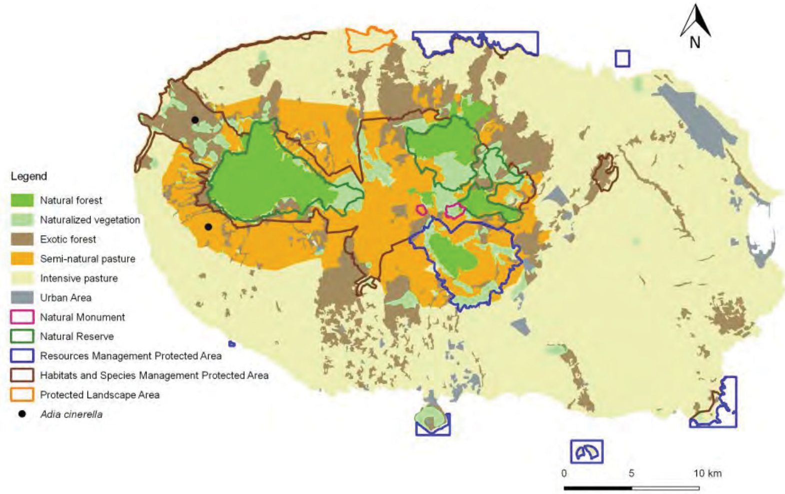
Syritta pipiens Linnaeus, 1758	Order Diptera Suborder Brachycera Infraorder Muscomorpha (Aschiza) Superfamily Syrphoidea Family Syrphidae	• Sometimes called the thick-legged hoverfly, from its distinctive broad hind femora. • They are fast nimble fliers. • Larvae feed in rotting organic matter.	Native	
Xanthandrus azorensis Frey, 1945	Order Diptera Suborder Brachycera Infraorder Muscomorpha (Aschiza) Superfamily Syrphoidea Family Syrphidae	• Conspicuous habit of hovering around flowers. • Regularly visit flowers to feed on nectar and pollen, they can be an important pollinating species.	Endemic	

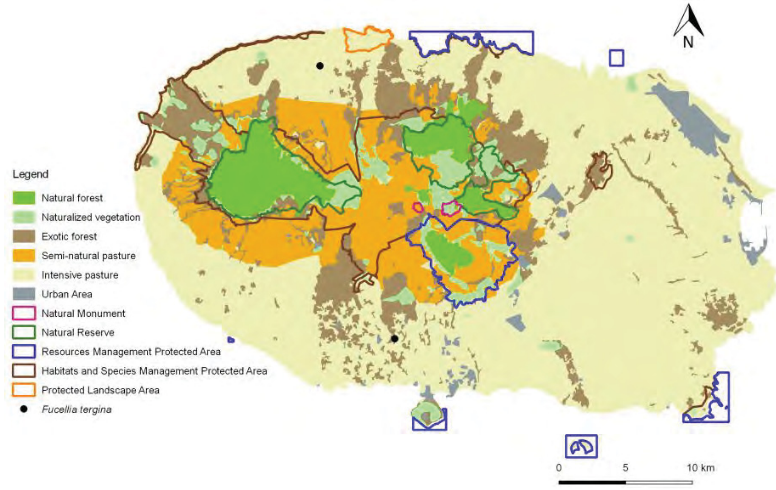
Xanthandrus comtus Harris, 1780	Order Diptera Suborder Brachycera Infraorder Muscomorpha (Aschiza) Superfamily Syrphoidea Family Syrphidae	• This genus is very close to Melanostoma Schiner, 1860, but it differs from this by possessing larger size of the body and the abdomen elliptic, wide and flat, arista bare, central portion of the epistoma moderately proeminent, face narrow and longer and wider susrtyli. • The most significant morphological characters to separate Xanthandrus specimens are: postpronotum bare, face and scutellum black, metaepisternum with some fine subappresses pile; metacoxa with a pile tuft at posteromedial apical angle; and antennal pits confluent.	Native	

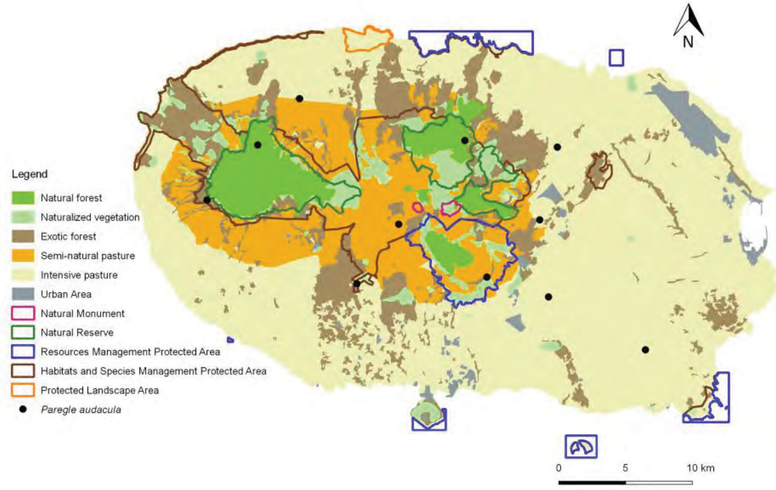
Xylota segnis Linnaeus, 1758	Order Diptera Suborder Brachycera Infraorder Muscomorpha (Aschiza) Superfamily Syrphoidea Family Syrphidae	• Like many other hoverflies, apart from their usually conspicuous colours and behavior, they can be easily recognized by one observable character: vein M1, it does not reach the wing margin but curves forward to meet the radial sector, resulting in a more or less continuous vein running parallel to the inconspicuous unthickened hind margin.	Native	
Sepsis biflexuosa Strobl, 1893	Order Diptera Suborder Brachycera Infraorder Muscomorpha (Schizophora Acalyptratae) Superfamily Sciomyzoidae Family Sepsidae	• The flies are small and rather ant-like, metallic and mostly black in colour and Sepsis species have a dark spot ate the wing-tip. • They are most often seen running around on vegetation, sometimes in large numbers, constantly "waving" their wings as part of their courtship display.	Native	

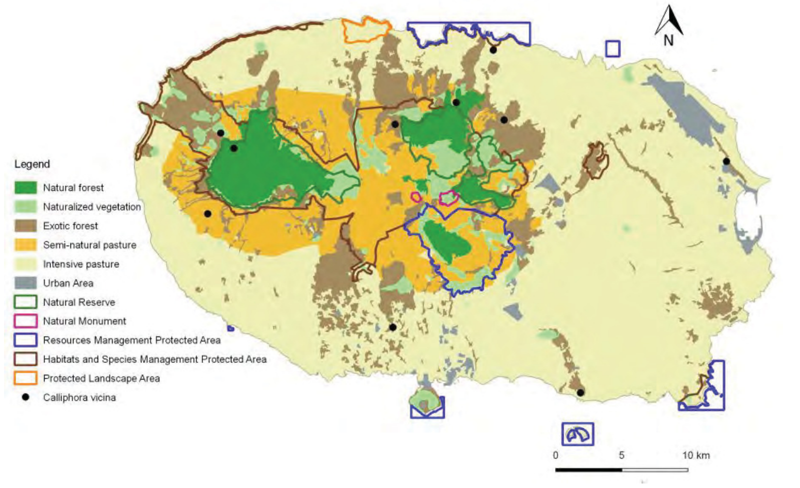
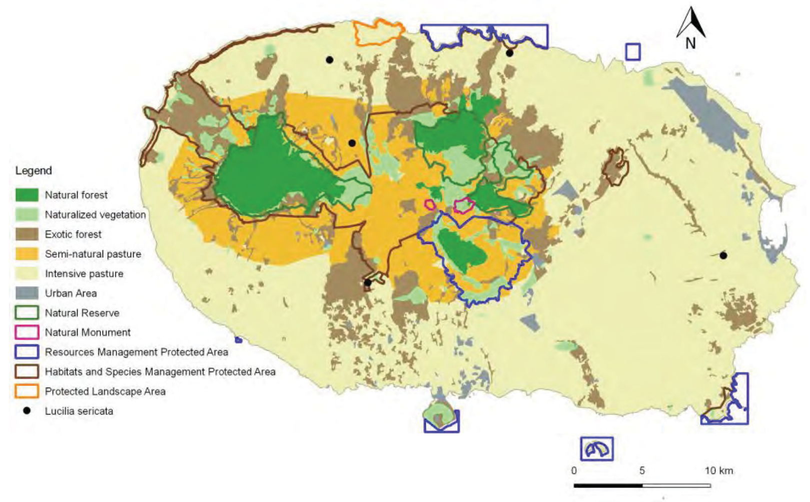
Sepsis lateralis Wiedemann, 1830	Order Diptera Suborder Brachycera Infraorder Muscomorpha (Schizophora Acalyptratae) Superfamily Sciomyzoidae Family Sepsidae	• The flies are small and rather ant-like, metallic and mostly black in colour and Sepsis species have a dark spot ate the wing-tip. • They are most often seen running around on vegetation, sometimes in large numbers, constantly "waving" their wings as part of their courtship display.	Native	
Sepsis neocynepsia Melander & Spuler, 1917	Order Diptera Suborder Brachycera Infraorder Muscomorpha (Schizophora Acalyptratae) Superfamily Sciomyzoidae Family Sepsidae	• The flies are small and rather ant-like, metallic and mostly black in colour and Sepsis species have a dark spot ate the wing-tip. • They are most often seen running around on vegetation, sometimes in large numbers, constantly "waving" their wings as part of their courtship display.	Native	

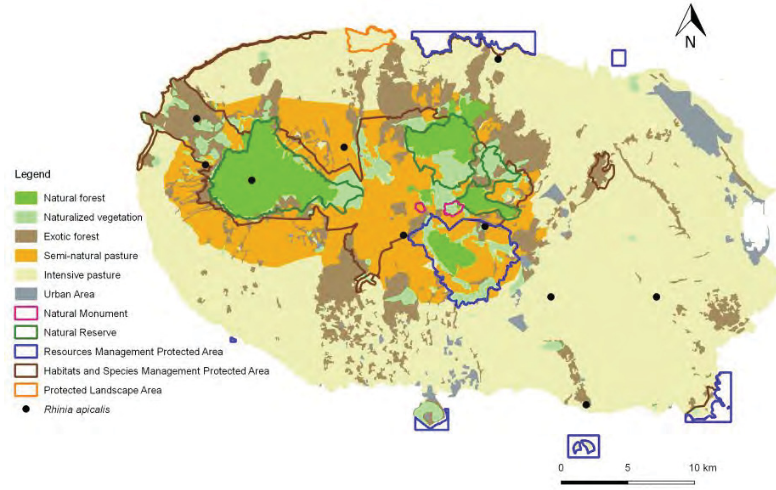
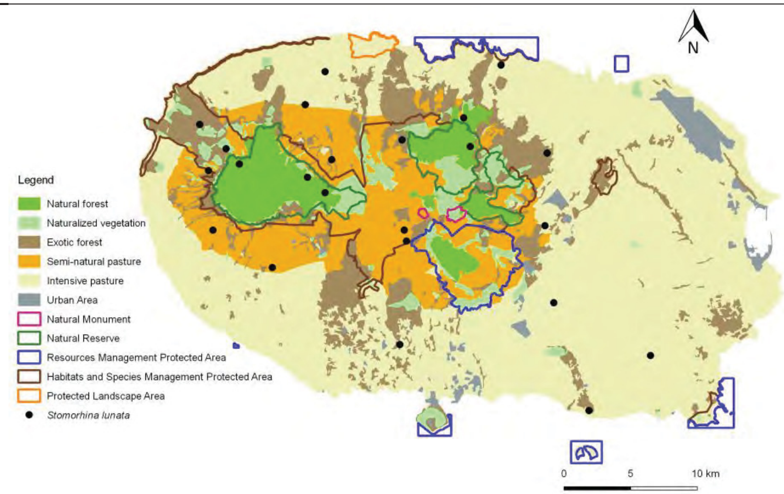
Sepsis thoracica Robineau-Desvoidy, 1830	Order Diptera Suborder Brachycera Infraorder Muscomorpha (Schizophora Acalyptratae) Superfamily Sciomyzoidae Family Sepsidae	• The flies are small and rather ant-like, metallic and mostly black in colour and Sepsis species have a dark spot ate the wing-tip. • They are most often seen running around on vegetation, sometimes in large numbers, constantly "waving" their wings as part of their courtship display.	Native	

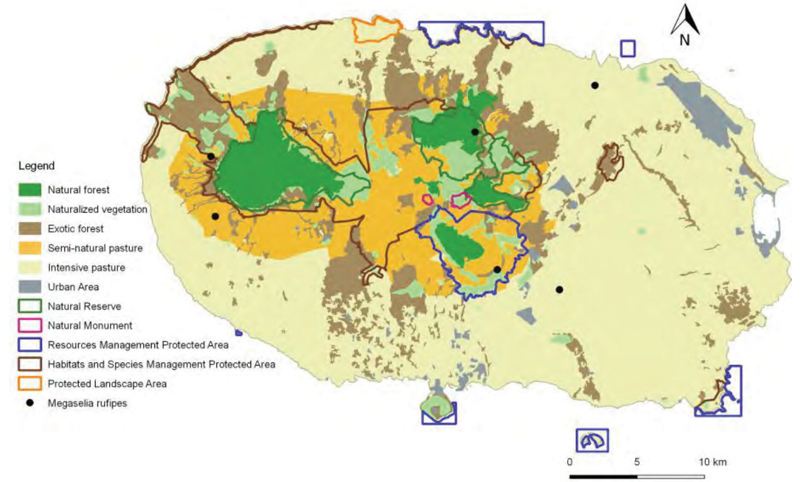
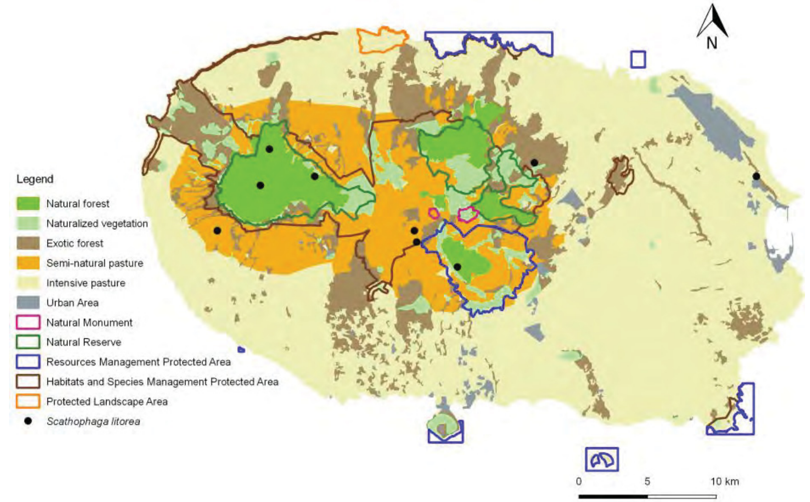
Adia cinerella Fállen, 1825	Order Diptera Suborder Brachycera Infraorder Muscomorpha (Schizophora Calyptratae) Superfamily Muscoidea Family Anthomyiidae	• Distinguished from the acalyptrates by the presence of a complete mesonotal suture on the thorax, and dorsal cleft on the athennal pedicel. Usually have well developed calypters or squamae behind the bases of the wings and are hairy or bristly. • Most species are grey, black or brownish, sometimes with distinctive markings, but apart from a few common species this is not an easy group to identify. • Adults are often seen on flowers. • The larvae of some species are saprophagous in habitats such as dung and fungi.	Native	

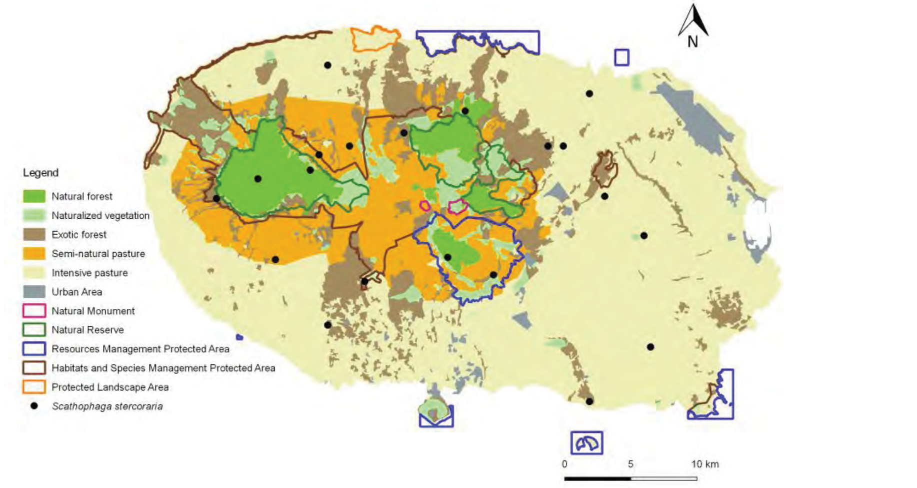
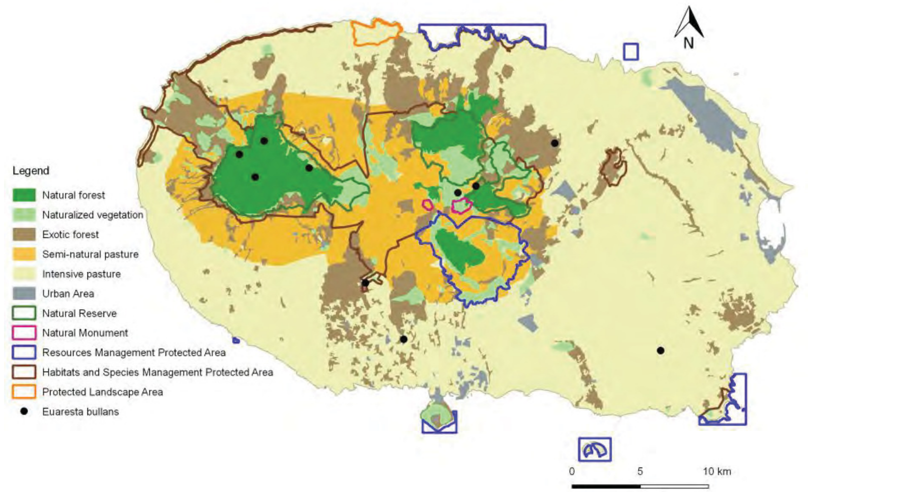
Fucellia tergina Zetterstedt, 1845	Order Diptera Suborder Brachycera Infraorder Muscomorpha (Schizophora Calyptratae) Superfamily Muscoidea Family Anthomyiidae	• Distinguished from the acalyptrates by the presence of a complete mesonotal suture on the thorax, and dorsal cleft on the athennal pedicel. Usually have well developed calypters or squamae behind the bases of the wings and are hairy or bristly. • Most species are grey, black or brownish, sometimes with distinctive markings but apart from q few common species this is not an easy group to identify.	Native	

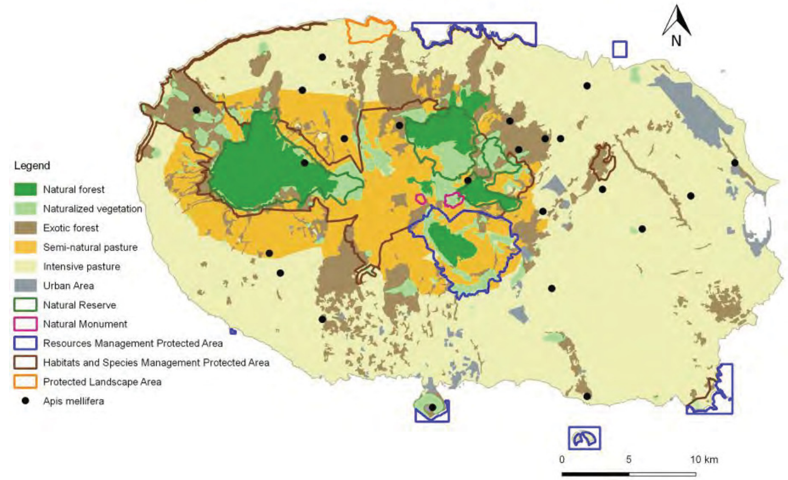
Paregle audacula Harris, 1780	Order Diptera Suborder Brachycera Infraorder Muscomorpha (Schizophora Calyptratae) Superfamily Muscoidea Family Anthomyiidae	• Distinguished from the acalyptrates by the presence of a complete mesonotal suture on the thorax, and dorsal cleft on the athennal pedicel. Usually have well developed calypters or squamae behind the bases of the wings and are hairy or bristly. • Most species are grey, black or brownish, sometimes with distinctive markings but apart from q few common species this is not an easy group to identify, mainly because there are no recent works covering this family.	Native	

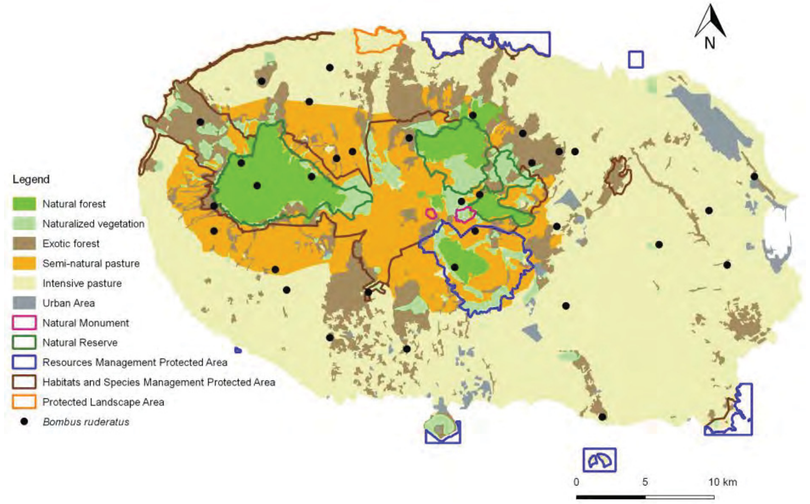
Calliphora vicina Robineau-Desvoidy, 1830	Order Diptera Suborder Brachycera Infraorder Muscomorpha (Schizophora Calyptratae) Superfamily Oestroidea Family Calliphoridae	• Commonly known as "blue bottle flies" due to metallic blue-gray coloration of its thorax and abdomen. • Is approximately 10–11 mm in length. • The sclerites at the base of the coxa are yellow or orange. By chaetotaxy, the study of bristle arrangement, characterized by having black bristles on the meron and two to three bristles on the notopleuron.	Exotic	
Lucilia sericata Meigen, 1807	Order Diptera Suborder Brachycera Infraorder Muscomorpha (Schizophora Calyptratae) Superfamily Oestroidea Family Calliphoridae	• Known as "common green bottle fly". • It is 10–14 mm long, slightly larger than a house fly, and has brilliant, metallic, blue-green or golden coloration with black markings. It has short, sparse black bristles (setae) and three cross-grooves on the thorax. • The wings are clear with light brown veins, and the legs and antennae are black.	Exotic	

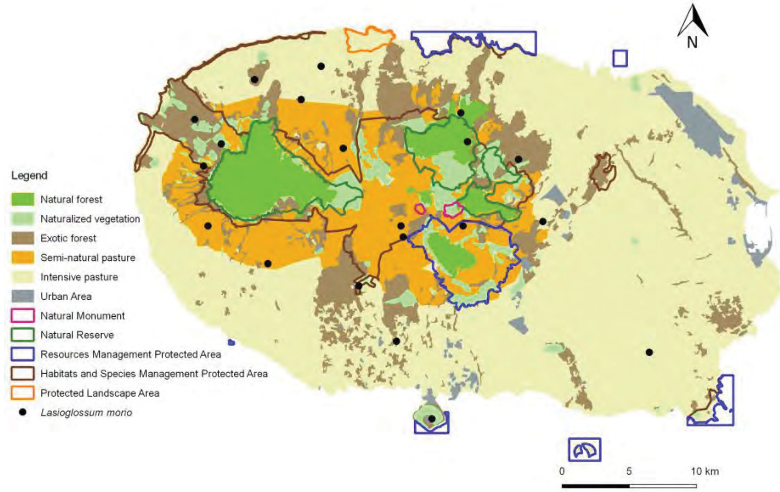
Rhinia apicalis Wiedemann, 1830	Order Diptera Suborder Brachycera Infraorder Muscomorpha (Schizophora Calyptratae) Superfamily Oestroidea Family Calliphoridae	• Dense covering of bristles. • Larvae are carrion-feeders and many are attracted to vertebrate bodies.	Native	
Stomorhina lunata Fabricius, 1805	Order Diptera Suborder Brachycera Infraorder Muscomorpha (Schizophora Calyptratae) Superfamily Oestroidea Family Calliphoridae Subfamily Rhiniinae	• Dense covering of bristles. • Larvae are carrion-feeders and many are attracted to vertebrate bodies.	Native	

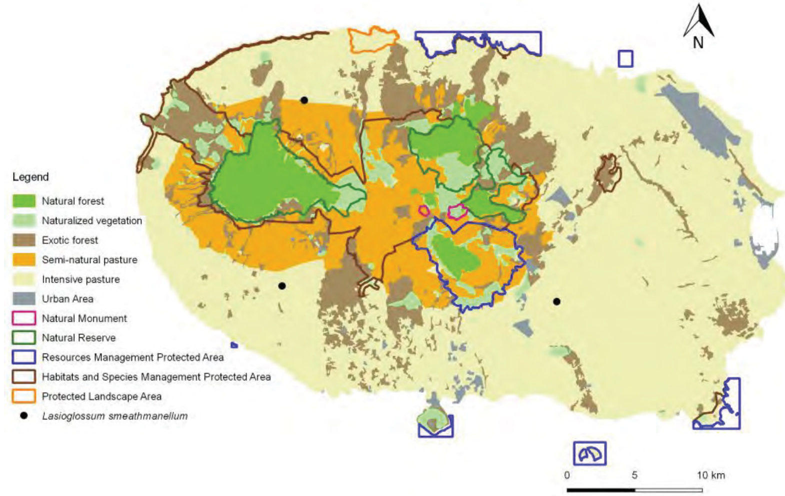
Megaselia rufipes Meigen, 1807	Family Phoridae	• Fly of very small size. Parasitoid and saprophag.	Exotic	
Scathophaga litorea Fallén, 1819	Order Diptera Suborder Brachycera Infraorder Muscomorpha (Schizophora Calyptratae) Superfamily Muscoidea Family Scathophagidae	• The adults are noticeably bristly or hairy and the long wings often have some faint marks or tinges of colour. • Commonly called the dung-flies. • The adults are predators with a preference for Dipteran prey.	Native	

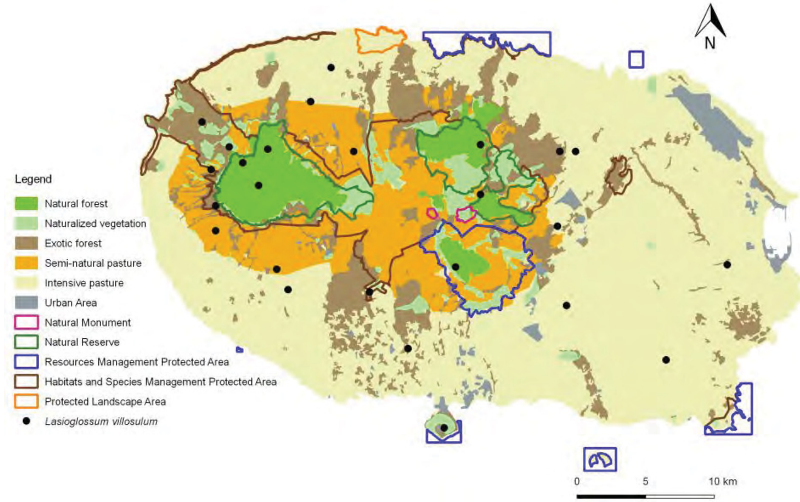
Scathophaga stercoraria Linnaeus, 1758	Order Diptera Suborder Brachycera Infraorder Muscomorpha (Schizophora Calyptratae) Superfamily Muscoidea Family Scathophagidae	• The adults are noticeably bristly or hairy and the long wings often have some faint marks or tinges of colour. • The best known species, the Yellow dung-fly. • Frequently seen in large numbers on cow-pats. • The adults are predators with a preference for Dipteran prey.	Native	
Euaresta bullans Wiedemann, 1830	Family Tephritidae	• Known as "mosca das frutas". • Can have positive or negative effect in agriculture.	Exotic	

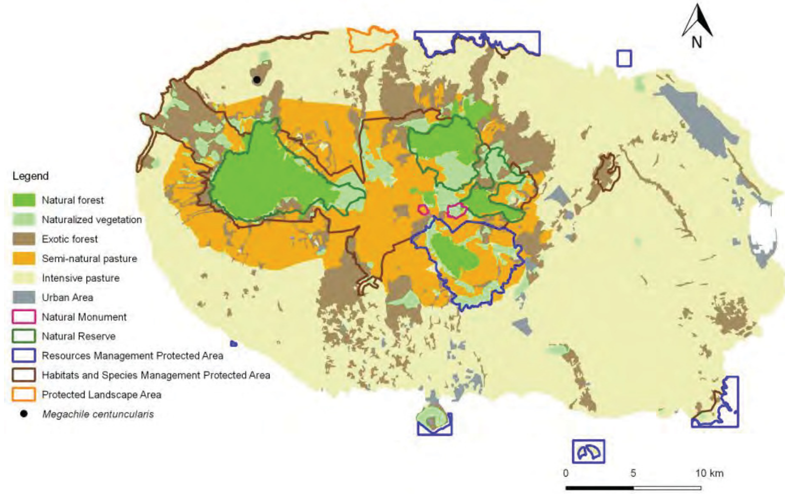
Apis mellifera Linnaeus, 1758	Order Hymenoptera Suborder Apocrita – Aculeata Superfamily Apoidea Family Apidae	• Known as domesticated western or European honey bee. • Is eusocial, creating colonies with a single fertile female (or "queen"), many sterile females or "workers", and small proportion of fertile males or "drones".	Exotic	

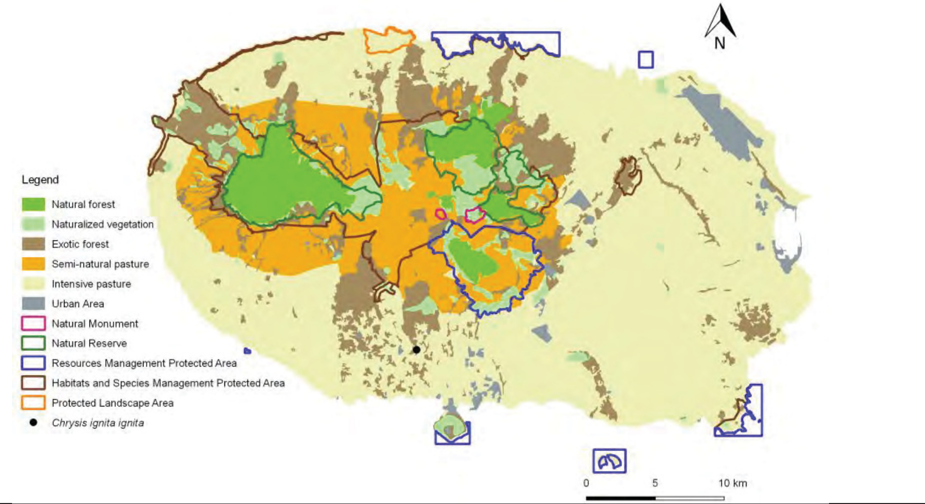
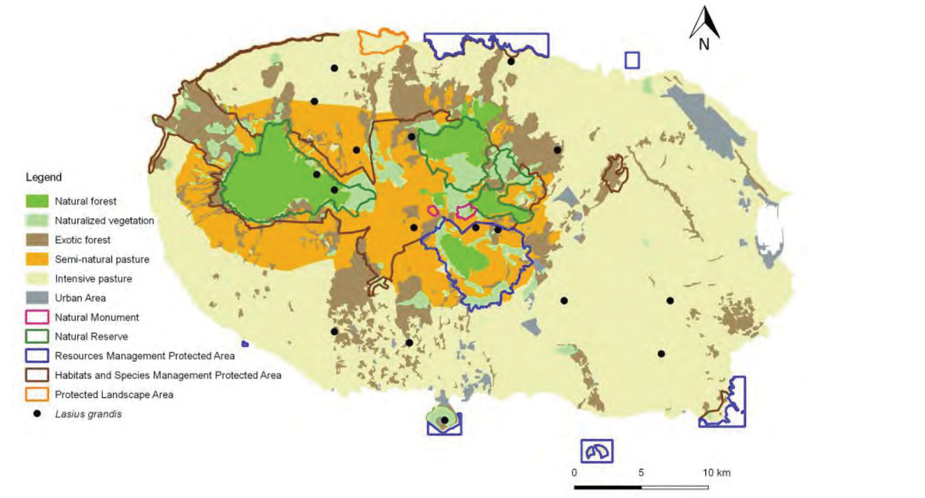
Bombus ruderatus Fabricius, 1775	Order Hymenoptera Suborder Apocrita – Aculeata Superfamily Apoidea Family Apidae	• The body lengths reach about 22 mm in queens, 16 mm in workers and 15 mm in males. • It has a long face and tongue, well adapted for feeding on long-tubed flowers. • The basic color of the body is black, with two yellow bands on the thorax and a single thin yellow band on the abdomen, while the tail is white. • Found in a range of open, flower-rich habitats, including coastal dunes, saltmarsh margins and shingle, grasslands, and occasionally gardens. In all cases, it requires very large expanses of suitable habitat to support viable populations. • The large garden bumblebee makes its nest underground, in the burrows of mice. • Nests are typically amongst vegetation on banks and slopes.	Native	

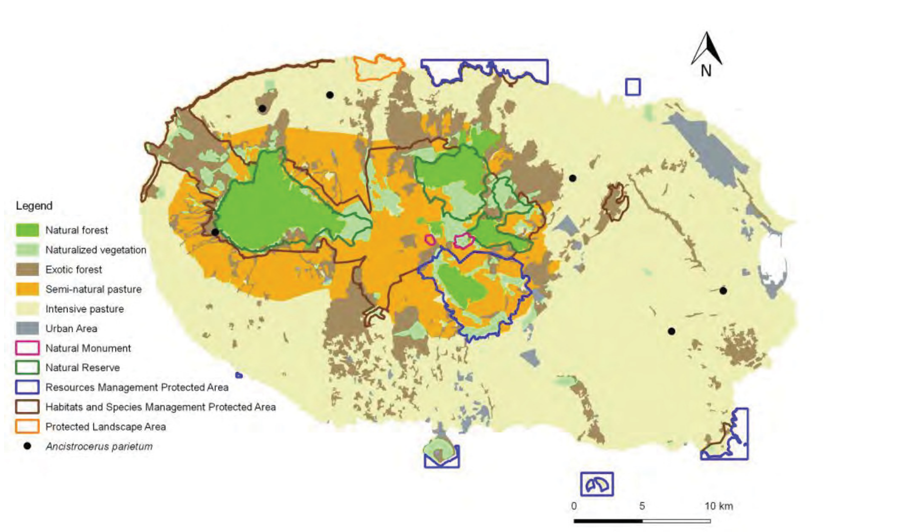
Lasioglossum morio Fabricius, 1793	Order Hymenoptera Suborder Apocrita – Aculeata Superfamily Apoidea Family Apidae	• The bee genus *Lasioglossum* - the sweat bees - is one of the largest of the bee genera, including over 1000 species of bees distributed on all continents, except Antarctica. • Common green furrow-bee or brassy mining bee. • Bees in this family are small to medium sized, ranging from 4 to 10 mm. • They generally are black or brownish coloured; however, there are species of sweat bees that are bright metallic green and some that have brassy yellow or red markings. • Sweat bees, also referred to as halictid bees (Halictidae) are so named for their habit of landing on people and licking the perspiration from the skin in order to obtain the salt. • Primitively eusocial. • The females normally nest in large aggregations in exposed soil.	Native	

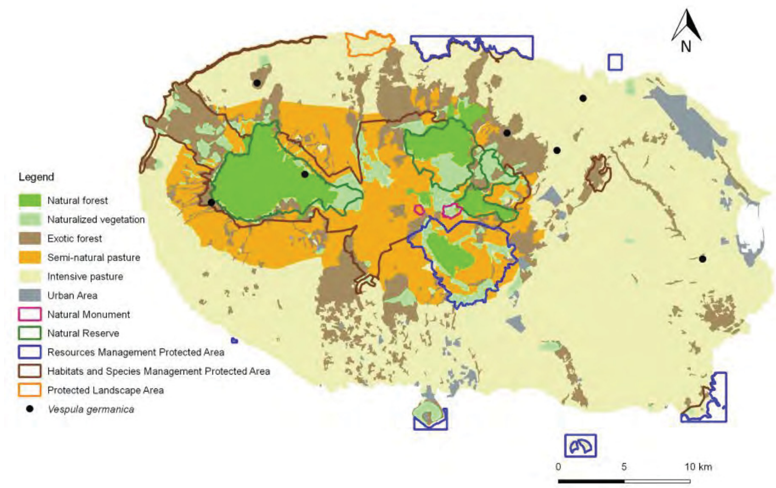
Lasioglossum smeathmanellum Kirby, 1802	Order Hymenoptera Suborder Apocrita – Aculeata Superfamily Apoidea Family Apidae	• The bee genus Lasioglossum - the sweat bees - is one of the largest of the bee genera, including over 1000 species of bees distributed on all continents, except Antarctica. • Bees in this family are small to medium sized, ranging from 4 to 10 mm. T • They generally are black or brownish coloured; however, there are species of sweat bees that are bright metallic green and some that have brassy yellow or red markings.	Native	

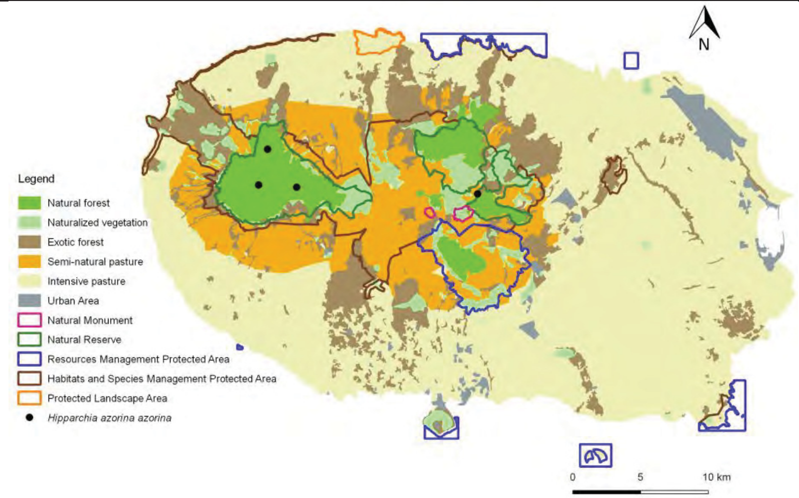
Lasioglossum villosulum Kirby, 1802	Order Hymenoptera Suborder Apocrita – Aculeata Superfamily Apoidea Family Apidae	• The bee genus *Lasioglossum* - the sweat bees - is one of the largest of the bee genera, including over 1000 species of bees distributed on all continents, except Antarctica. • Bees in this family are small to medium sized, ranging from 4 to 10 mm. T • They generally are black or brownish coloured; however, there are species of sweat bees that are bright metallic green and some that have brassy yellow or red markings. • Found in many habitats, including coastal soft rock cliffs.	Native	

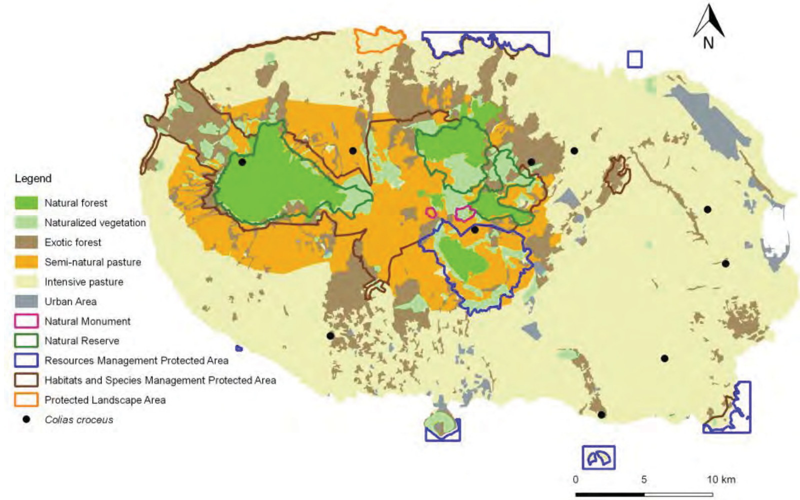
Megachile centuncularis Linnaeus, 1758	Order Hymenoptera Suborder Apocrita – Aculeata Superfamily Apoidea Family Apidae	• The genus Megachile is a cosmopolitan group of solitary bees, often called leafcutter bees or leafcutting bees. While other genera within the family Apidae may chew leaves or petals into fragments to build their nests, certain species within Megachile neatly cut pieces of leaves or petals, hence their common name. • Female bees are about 1 cm long, black in colour with conspicuous orange red fringes of hair, for carrying pollen, on the underside of their bodies. • These bees are important pollinators of our cultivated crops and wild flowers. • The nests are generally constructed within large burrows in wood, cavities in old walls and also occasionally in soil.	Native	

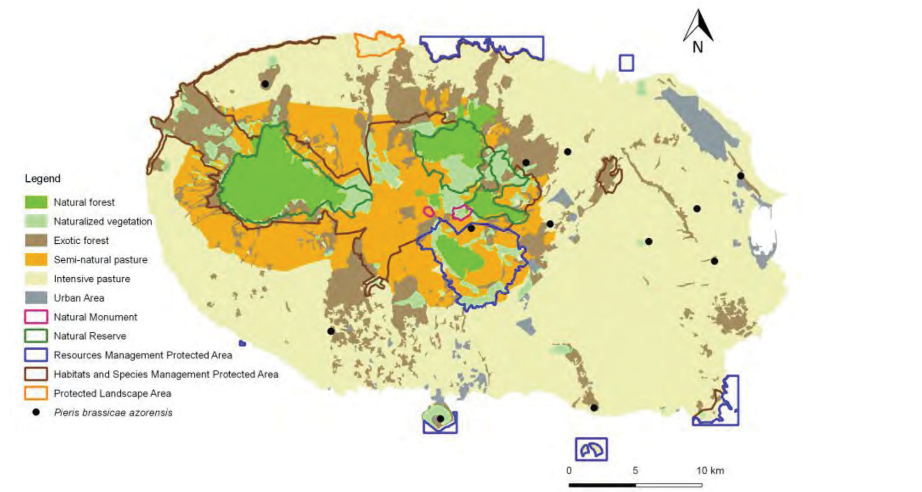
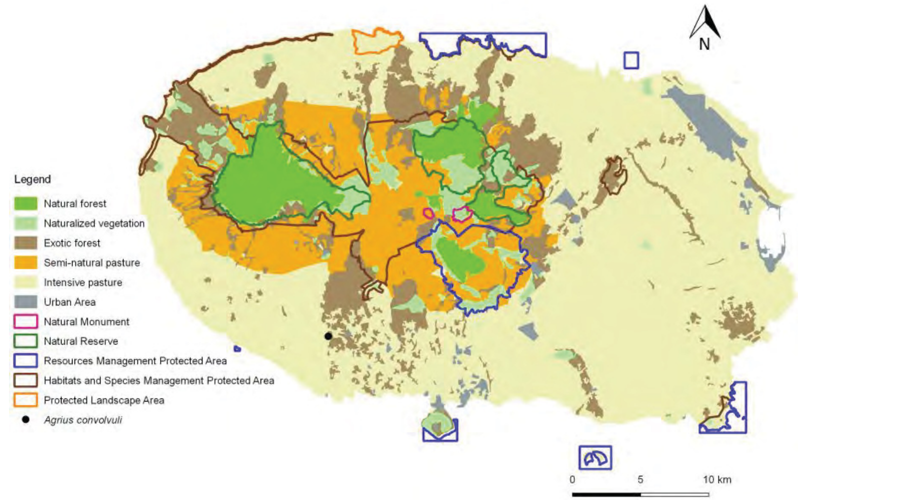
Chrysis ignita ignita Linnaeus, 1758	Order Hymenoptera Suborder Apocrita – Aculeata Superfamily Chrysidoidea Family Chrysididae	• Known as “cuckoo wasps”. • They are kleptoparasites. • Have metallic, armored bodies, and can roll up into balls to protect themselves from harm when infiltrating the nests of host bees and wasps.	Native	
Lasius grandis Forel, 1909	Order Hymenoptera Suborder Apocrita – Aculeata Superfamily Vespoidea Family Formicidae	• Also known like *Lasius niger* (Linnaeus, 1758). • The common garden black ant, is a small brown to dark brownish black ant. • Scapes and tibia have erect hairs. • The clypeus has dense pubescence. • Most species nest in the soil.	Native	

Ancistrocerus parietum Linnaeus, 1758	Order Hymenoptera Suborder Apocrita – Aculeata Superfamily Vespoidea Family Vespidae Subfamily Eumeninae	• Known as “wall mason wasp”. • Females vary from 10 to 13mm, males are slightly smaller and reach a bodily length of 8 to 11mm. • The basic colour is black, with yellow bands, and they have a very narrow waist.	Exotic	

Vespula germanica Fabricius, 1793	Order Hymenoptera Suborder Apocrita – Aculeata Superfamily Vespoidea Family Vespidae Subfamily Vespinae	• The German wasp is about 13 mm long. • Has typical wasp colours of black and yellow. • It is very similar to the common wasp (*Vespula vulgaris*), but unlike the common wasp, has three tiny black dots on the clypeus. • German wasps also have black dots on their abdomens, while the common wasp's analogous markings are fused with the black rings above them, forming a different pattern. • German yellowjackets are known to be especially successful and destructive invaders of new territories. • These wasps are polyphagous predators which feed on native arthropods.	Native	

Hipparchia azorina azorina Strecker, 1899	Order Lepidoptera Suborder Glossata Superfamily Papilionoidea Family Nymphalidae Subfamily Satyrinae	• Common name Azores Grayling. • This species is listed in the IUCN Red list of Threatened Species under the least concern criteria, due mostly to the loss of habitat. • Different pattern on the underside of the wings, usually cryptic. • The Azores Grayling is a butterfly of sheltered places on grassy slopes on the Azores. • The butterflies are often observed on flowers where they come for nectar. • The Azores Grayling has one generation a year. • Occurs mostly in the higher altitudes of the islands above 500m asl where heathland with dwarf shrubs, mosses, lichens and Festuca francoi dominate. • The butterflies and larvae also occur in sunny embankments in open woodland. • The larvae prefer sunny and a bit more dry places. • Penetrates extensively managed cattle pastures along broad embankments and grassy walls, but generally lacks	Endemic	

Colias croceus Fourcroy, 1785	Order Lepidoptera Suborder Glossata Superfamily Papilionoidea Family Pieridae Subfamily Coliadinae	• It is known as the clouded yellow small butterfly. • The upp erside is golden to orange yellow with a broad black margin on all four wings and a black spot near the centre forewing. The underside lacks the black borders and is lighter, with a more greenish tint, particularly on the forewings. In the forewing underside is the same dark spot as on the upperside, but often with a light centre; the hindwing underside has a white centre spot, often with a smaller white or dark dot immediately above it. Sometimes, a row of black dots occurs on the underwings' outer margins, corresponding to where the black border ends on the upperside. • In flight, it is easily identifiable by the intense yellow colouring, much brighter than that of the lemon-yellow male common brimstone which also lacks black colour. • They feed on brassica plants and can become pests	Native	

Pieris brassicae azorensis Rebel, 1917	Order Lepidoptera Suborder Glossata Superfamily Papilionoidea Family Pieridae	• Known as Azorean “cabbage white” is a subspecies of insect with 2 observations.	Endemic	
Agrius convolvuli Linnaeus, 1758	Family Sphingidae	• Commonly known as hawkmoths. They are moderate to large in size, and easily distinguished due to their rapid and sustained flying ability. Body very robust; abdomen usually tapering to a sharp point. Proboscis well developed.	Native	

Tebenna micalis Mann, 1857	Family Choreutidae	• Small moths often with metallic scales and are mostly day-flying. • The mothswith 19 genera in three subfamilies defined by structural characteristics of immature stages.	Exotic