Luís Fernando Pascoal da Silva

A COMMUNITY-LEVEL APPROACH TO FOREST BIODIVERSITY AND AVIAN DISPERSAL SERVICES

Tese de Doutoramento em Biociências, especialização em Ecologia,
orientada pelo Professor Doutor Jaime Albino Ramos e pelo Doutor Rúben Hüttel Heleno
e apresentada ao Departamento de Ciências da Vida da Faculdade de Ciências e Tecnologia da Universidade de Coimbra

Setembro de 2016

• U C •

UNIVERSIDADE DE COIMBRA

A community-level approach to forest biodiversity and avian dispersal services

· U C ·

Universidade de Coimbra

Doctoral thesis in Biosciences (Scientific area of
Ecology) presented to the University of Coimbra for the
degree of Doctor of Philosophy supervised by Prof. Dr. Jaime
Albino Ramos and co-supervised by Dr. Rúben Hüttel Heleno

Tese doutoral em Biociências (especialidade em Ecologia)
apresentada à Universidade de Coimbra para obtenção do
grau de Doutor, orientada pelo Prof. Dr. Jaime Albino Ramos
e co-orientada pelo Dr. Rúben Hüttel Heleno

Luís Fernando Pascoal da Silva
Department of Life Sciences
University of Coimbra
Coimbra | 2016

This thesis was supported by:

FCT – Fundação para a Ciência e Tecnologia
PhD grant attributed to
Luís Fernando Pascoal da Silva
SFRH/BD/77746/2011

MARE – Marine and Environmental Sciences Centre
Department of Life Sciences
Faculty of Sciences and Technology
University of Coimbra (FCTUC)

CEF – Centre for Functional Ecology
Department of Life Sciences
Faculty of Sciences and Technology
University of Coimbra (FCTUC)

This thesis is based on the following manuscripts:

Chapter I

da Silva, LP; Heleno, RH; Costa, J; Valente, M; da Silva, AA; Alves, J; Ramos, JA. Submitted. A multi-taxa assessment reveals the negative impacts of novel forests on biodiversity.

Chapter II

da Silva, LP; Ramos, JA; Olesen, JM; Traveset, A; Heleno, RH. 2014. Flower visitation by birds in Europe. OIKOS 123 (11): 1377-1383. DOI: 10.1111/oik.01347

Chapter III

da Silva, LP; Ramos, JA; Coutinho, AP; Tenreiro, PQ; Heleno, RH. Under review. Flower visitation by European birds offers the first evidence of Interaction Release in continents.

Chapter IV

da Silva, LP; Coutinho, AP; Heleno, RH; Tenreiro, PQ; Ramos, JA. 2016. Dispersal of fungi spores by non-specialized flower-visiting birds. Journal of Avian Biology 47(3): 438-442. DOI: 10.1111/jav.00806

This thesis should be cited as:

da Silva, L.P. 2016. A community-level approach to forest biodiversity and avian dispersal services. PhD Thesis, University of Coimbra, Coimbra, Portugal.

Affiliations and addresses of co-authors:

Anna Traveset [1]

António Alves da Silva [2]

António Pereira Coutinho [2]

Jaime A. Ramos [3]

Jens Mogens Olesen [4]

Joana Alves [2]

José Costa [2;3]

Mariana Valente [2;3]

Paulo Quadros Tenreiro [5]

Rúben H. Helleno [2]

[1] IMEDEA – Mediterranean Institute for Advanced Studies, Terrestrial Ecology Group, Mallorca, Balearic Islands, Spain.

[2] CEF – Centre for Functional Ecology, Department of Life Sciences, University of Coimbra, Portugal.

[3] MARE – Marine and Environmental Sciences Centre, Department of Life Sciences, University of Coimbra, Portugal.

[4] Department of Bioscience, Aarhus University, Denmark.

[5] ICNF – Instituto da Conservação da Natureza e das Florestas, Departamento de Conservação da Natureza e Florestas do Centro, Divisão de Gestão Operacional e Valorização, Mata Nacional do Choupal, Coimbra, Portugal

Contents

List of Tables

List of Figures

Acknowledgements

I am thankful to my supervisors, Professor Dr. Jaime Ramos and Dr. Ruben Heleno for their support during the four years of this thesis. During this period they have provided important guidance and encouragement on the several tasks of this challenge. I am indebted for their patience and time spent with this work.

My family that has always supported me and was always present.

To Vanessa for everything…mainly patience.

Joana and Toni for all your help planning everything, for your friendship, my sincere thanks.

I want to acknowledge José Costa for his help identifying plants. Mariana Valente for her work with the pitfall arthropods. To Professor Dr. António Coutinho for his invaluable help in the pollen slides preparation and respective identification.

To all the people from the office and borrowed from the lab. A special reference to Andreia, Daniela, Helena, Ines and Paco for the companionship and company in all that lunches, snacks and others. See all of you around.

To all from the gymn, specially Pi.

A sincere thanks to Claudia, Julio, Miguel, Paulos (PJF and PQT), Pedro and Ricardo that often watched and ringed birds with me. Thank all of you for the teachings, experiences and well spent time.

To the ‘guys’ from Grada (and nearby), with a special reference to Carlos and Luís, for the coffees, parties and all other similar relaxation moments. Thank you very much for getting me out of the little work world.

I am very grateful to several people not mentioned before, for the help and constructive comments on the several manuscripts in which the chapters of the thesis are based on. I cannot fail to mention: Anna Traveset, Jens Mogens Olesen, Nicklas Wase, Pablo Vargas and of course all the anonymous referees during the manuscripts revision processes.

The great majority of the financial support for this thesis was provided by the ‘Fundação para a Ciência e Tecnologia – (FCT)’ through the grant SFRH/BD/77746/2011.

I want to acknowledge the ‘Instituto da Conservação da Natureza e das Florestas – ICNF’ for providing all the authorization needed to legally perform the fieldwork.

The two research centres of the Department of Life Sciences on the University of Coimbra were I was during the past years, the Marine and Environmental Sciences Centre – MARE and the Centre for Functional Ecology – CEF. They have provided me the space were I developed most of my laboratory work and a great part of the data analysis and writing.

A final and cliché mention to the birds that were often my personal seclusion, especially the ‘white tail’.

Summary

Natural ecosystems are formed by diverse species assemblages permanently interacting with each other to survive and reproduce. These ecosystems provide humans several essential services. However, due to human population growth and its consequent demand for space and raw materials, man has been changing their surroundings for a long time. These caused alterations in many ecosystems, heavily affecting their biodiversity and threatening their long-term persistence and capacity to provide essential ecosystem services. Efforts have been made to halt biodiversity loss and maintain human well-being and a sustainable human growth, often with meagre success. To understand entirely the impacts of environmental changes on long-term persistence of ecosystems is vital to evaluate explicitly their impact across the different taxa and on biological interactions. This thesis explores the impact of anthropogenic land-use changes on entire biological communities and expands the current knowledge about interactions between birds, plants and fungi. The thesis comprises four data chapters.

In the first chapter, I explore the impact of novel, i.e. anthropogenic, forests on the diversity of trees, shrubs, herbs, macrofungi, ground arthropods, night-flying arthropods, reptiles, birds, small mammals, carnivores and bats. The abundance, species richness and community composition of these groups was compared between native oak *Quercus* spp. woodlands, plantations of the native pine *Pinus pinaster*, plantations of the exotic *Eucalyptus globulus* and woodlands of the invasive acacia *Acacia dealbata*. In most groups the abundance and species richness was significantly higher in native woodlands, followed by pine plantations and in exotic woodlands. Community composition differed between all woodlands, with pinewoods being the most similar to native woodlands. The different study groups presented distinct responses to the different woodland types. Ground arthropods were similar in all woodlands, while trees, shrubs, herbs and birds were the groups that were most affected by habitat transformation.

In the second chapter, I performed a literature review assembling all available information on flower visitation by birds in Europe. The mutualisms between non-specialized nectarivorous bird families and flowers has been largely neglected. I found records of at least 45 bird species visiting 95 plant species in Europe. The most visited flowers belong to the genus *Brassica* sp., *Citrus* sp. and *Eucalyptus* sp., which were visited mainly by warblers of the genus *Sylvia* sp. and *Phylloscopus* sp. and tits, mainly the blue tit *Cyanistes caeruleus*. Birds seem to visit flowers more often during winter and spring, and mainly in the Mediterranean basin, suggesting that birds may have a relevant role in the long distance dispersal of pollen.

In the third chapter, I reconstructed an empirical ecological network quantifying the pollen transport by birds in a native forest in central Portugal. This work not only empirically confirmed most of the results from the previous chapter, but also showed for the first time an *ecological release*, i.e. the broadening of the trophic niche of an entire guild to include underexplored resources in the environment, in a continent when it was only known from oceanic islands. The *ecological release* appears to be less pronounced in Europe than in oceanic islands likely due to the higher diversity of the continent. The ecological network of this chapter has many similar properties to other bird-flower networks including networks of specialized nectarivorous birds' families.

In the fourth chapter, I explored the co-dispersal of fungi spores by flower-visiting birds in two forests in central Portugal. The pollen accumulations found on birds often contained fungi spores. The occurrence of fungi spores in the birds' pollen accumulations was strongly associated with the amount of pollen, suggesting that birds acquire the two propagules simultaneously. It was shown that birds that visit flowers actively transport fungi spores between flowers, in a direct dispersal of the spores, i.e. to particularly suitable recruitment sites (flowers). This interaction has been largely unnoticed until now.

The current thesis increases the knowledge about the biodiversity of European forests and how they are negatively affected by anthropogenic changes associated with the plantation and expansion of new forest species. A literature review and original empirical data confirmed that pollen transport by non-specialized nectarivorous birds is a common and widespread phenomenon in Europe, reflecting an interaction release of generalist birds to explore underexplored flower resources. Many of these flower visiting birds act as direct co-dispersers of fungi spores between flowers. This thesis shows the importance of not studying single and isolated taxon, because by only studying several taxa and their interactions in a community level approach allows a better understanding of the ecosystems. Interestingly, many interactions detected between birds and plants were with exotic plant species brought to Europe and now forming novel forest ecosystems. Such novel interactions should be important in shaping and re-structuring these novel forest ecosystems throughout Europe.

Key-words: bird transport; ecological network; exotic; Interaction release; multi-taxa; mutualism; plantations; pollen.

Resumo

Os ecossistemas naturais são formados por diversos conjuntos de espécies que interagem permanentemente umas com as outras para sobreviver e se reproduzir. Estes ecossistemas fornecem ao homem diversos serviços essenciais. Contudo, devido ao crescimento da população humana e a sua consequente necessidade por espaço e matérias-primas, o homem tem modificado o espaço que o rodeia ao longo do tempo. Estas alterações causadas em muitos ecossistemas têm afetado fortemente a biodiversidade, ameaçando a sua persistência ao longo do tempo e a sua capacidade em fornecer serviços do ecossistema essenciais. Têm sido desenvolvidos esforços para travar a perda de biodiversidade, manter o bem-estar e a sustentabilidade do crescimento do homem, muitas vezes com sucesso reduzido. Para compreender inteiramente os impactos das alterações ambientais na persistência a longo-termo dos ecossistemas é fundamental avaliar explicitamente os impactos em diferentes taxa e nas interações biológicas. Esta tese explora o impacto antropogénico das alterações do uso de solo sobre toda a comunidade biológica e expande o conhecimento existente sobre as interações entre aves, plantas e fungos. Esta tese é constituída por quatro capítulos.

No primeiro capítulo estudei o impacto das novas, i.e. antropogénicos, florestas na diversidade de árvores, arbustos, herbáceas, macrofungos, artrópodes terrestres, artrópodes voadores noturnos, repteis, aves, pequenos mamíferos terrestres, carnívoros e morcegos. A abundância, riqueza específica, e composição da comunidade destes grupos foram comparados entre bosques nativos de carvalhos *Quercus* spp., plantações de pinheiro nativo *Pinus pinaster*, plantações da espécie exótica *Eucalyptus globulus* e bosques da espécie invasora *Acacia dealbata*. Para a maioria dos grupos a abundância e riqueza específica foram significativamente maiores nos bosques nativos, seguidos das plantações de pinheiro e finalmente dos bosques de espécies exóticas. A composição da comunidade diferiu entre todos os bosques, com os pinhais sendo os mais parecidos com os bosques nativos. Os diferentes grupos estudados apresentaram respostas distintas aos diferentes tipos de bosque. Os artrópodes terrestres foram semelhantes entre todos os bosques, enquanto árvores, arbustos, herbáceas e aves foram os grupos mais afetados pelas alterações do habitat.

No segundo capítulo efetuei uma revisão bibliográfica, recolhendo toda a informação sobre visitas de flores por aves na Europa. Os mutualismos entre famílias de aves não especializadas e flores têm sido amplamente negligenciados. Eu encontrei registos de pelo menos 45 espécies de aves a visitar 95 espécies de plantas na Europa. As flores mais visitadas pertencem aos géneros *Brassica* sp., *Citrus* sp. e *Eucalyptus* sp. sendo visitados principalmente por felosas dos géneros *Sylvia* sp. e *Phylloscopus* sp. e chapins, principalmente o chapim-azul *Cyanistes caeruleus*. As aves parecem visitar mais frequentemente as flores durante o inverno e a primavera, e especialmente na bacia do Mediterrâneo, sugerindo que as aves podem ter um papel pertinente na dispersão do pólen a longa distância.

No terceiro capítulo construí uma rede ecológica empírica que quantifica o transporte de pólen por aves numa floresta nativa no centro de Portugal. Este trabalho não só confirmou empiricamente a maioria dos resultados do capítulo anterior, mas demostrou também pela primeira vez, num continente, uma *libertação ecológica*, i.e. o aumento do nicho trófico de uma guilda inteira para incluir recursos pouco explorados do ambiente, enquanto anteriormente isto apenas era conhecido em ilhas oceânicas. A *libertação ecológica* aparenta ser menos intensa na Europa do que nas ilhas oceânicas provavelmente devido à maior diversidade biológica dos continentes. A rede ecológica deste capítulo apresenta muitas propriedades semelhantes a outras redes de ave-flor incluindo redes de famílias de aves nectarívoras especializadas.

No quarto capítulo abordei a co-dispersão de esporos de fungos por aves que visitam flores em duas florestas em Portugal. As acumulações de pólen encontradas nas aves contêm frequentemente esporos de fungos. A ocorrência dos esporos de fungos nas acumulações de pólen das aves está fortemente associada à quantidade de pólen, sugerindo que as aves adquirem os dois propágulos em simultâneo. Foi demonstrado que as aves que visitam flores transportam ativamente os esporos de fungos entre flores, numa dispersão direta dos esporos, i.e. para locais especificamente adequados para o seu desenvolvimento (flores). Esta interação permaneceu praticamente desconhecida até agora.

A presente tese aumentou o conhecimento existente sobre a biodiversidade nas florestas Europeias e como esta é negativamente afetada pelas modificações antropogénicas associadas à plantação e expansão de novas espécies florestais. Uma revisão bibliográfica e dados empíricos e originais confirmaram que o transporte de pólen por aves nectarívoras não especializadas é um fenómeno comum na Europa, refletindo um *libertação ecológica* de aves generalistas que utilizam recursos florais pouco explorados. Muitas das aves que visitam flores agem como co-dispersores de esporos de fungos entre flores. Esta tese demonstra a importância de não estudar cada táxon isoladamente, porque apenas estudando vários taxa e as suas interações numa abordagem ao nível da comunidade é possível uma melhor compreensão dos ecossistemas. Curiosamente, muitas das interações detetadas entre aves e plantas envolveram plantas exóticas, que formam atualmente ecossistemas florestais novos na Europa. Estas novas interações serão importantes na formação e re-estruturação destes novos ecossistemas florestais europeus.

Palavras-chave: exótico; *libertação ecológica*; multi-taxa; mutualismo; plantações; pólen; redes ecológicas; transporte por aves.

General Introduction

Biodiversity

Biodiversity was coined by W. G. Rosen of the National [North American] Research Council in 1985 as the abbreviation of 'biological diversity', and used as the title word in a seminar to discuss biological diversity (Wilson 1988). Biodiversity was later defined by the United Nations in 1992, as "(…) *the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems.*" (*in* Harper and Hawksworth 1994). This definition divided biodiversity in 3 hierarchical levels of biological organization: *"diversity within species"* that represents the genetic variation of individuals or populations of the same species; *"diversity between species"* represent the variety of species including their abundances, distributions and interactions; and the *"diversity of ecosystems"* which includes biological communities that exist in the same space and all the variation they have in response to biotic and abiotic factors. Although some authors have divided biodiversity in more categories than these three levels (e.g. Noss 1990), these are the most widely accepted and the commonly used. Each of these levels of biodiversity can be further considered under three attributes, applicable to all the biodiversity levels: composition, structure and function (Franklin et al. 1981). The composition describes the diversity or number of members within a group, e.g. number of species present. The structure of biodiversity refers to the organization of each group, e.g. trees varying in height creating different canopies or the structure of animal populations due to differences in sex or age classes within individuals. Finally, the function of biodiversity is the variation in the ecological processes in which each group participates, such as predator-prey relationships and mutualistic interactions (Noss 1990). Functional biodiversity is thus a key attribute to understand the ecological and evolutionary mechanisms that shape biological communities.

Only c. 1.2 million species have been described to science out of the 8.7 million estimated to inhabit our planet, (Mora et al. 2011), but why is it important to understand and preserve such species diversity and all the biodiversity they represent? It is long known that natural communities and their biodiversity provide fundamental ecosystems services to humans, i.e. processes that benefit the human society (Ehrlich and Mooney 1983, Bengtsson et al. 2003, Mace et al. 2012). These ecosystem services can be grouped in four main classes (Millenium Ecosystem Assessment 2005): provisioning services (e.g. food, pharmaceutical products, wood, fuel, and other raw materials); regulating services (e.g. climate and water disturbance and regulation, detoxification and decomposition of wastes, carbon sequestration); supporting services (e.g. soil formation, nutrient cycling, seed dispersal, pollination); and cultural services (e.g. recreational opportunities, inspiration for various types of art, spiritual value) (Costanza et al. 1997, Daily et al. 2000, Mace et al. 2012).

Natural communities and their complex web of interactions among organisms have coevolved temporally and spatially influenced by several natural factors such as climate cycles and catastrophes (Martin 1993, Errikarta-Imanol et al. 1997, Pitelka 1997, Allen and Breshears 1998). However, since prehistoric times human activities have drastically affected several ecosystems (Errikarta-Imanol et al. 1997, Anderson 2002, Delcourt and Delcourt 2004). The continuous growth of the human population led to an increasing demand of natural resources either for food, wood and other raw materials, or simply for space to create settlements and agricultural areas. These are some of the reasons why man has wittingly changed natural landscapes, often overexploiting biological resources with a direct negative effect on biodiversity (Foley et al. 2005). Habitat loss and degradation, invasive species, climate change, overexploitation of populations, pollution, and disease spreading are among the major anthropogenic causes threatening biodiversity (Kingsford et al. 2009). Land use modifications and other anthropogenic related pressures have severely impacted biodiversity (Foley et al. 2005, Fischer and Lindenmayer 2007, Newbold et al. 2016). On the last century, protected areas have been created to reduce human related biodiversity loss and have since been regarded as essential for biodiversity conservation (Margules and Pressey 2000). In 2003, the global network of protected areas covered 11.5% of the planet's land surface (Rodrigues et al. 2004a, b). These protected areas have positive effects worldwide, as they sustain particularly high levels of biodiversity (Gray et al. 2016). However, the network of protected areas is not a sufficient safeguard to the whole biodiversity on Earth (Margules and Pressey 2000, Rodrigues et al. 2004b), and an increase of the network is needed (Margules and Pressey 2000, Bengtsson et al. 2003, Rodrigues et al. 2004b) alongside with better planning strategies, more research, management and well defined conservation priorities (Margules and Pressey 2000, Rodrigues et al. 2004a, Araújo et al. 2007, Fischer and Lindenmayer 2007). Moreover, the global loss of diversity in the 21st century shows no signs of slowing down (Pereira et al. 2010), and will most likely continue to decline (Butchart et al. 2010), despite the conservation efforts and some local success stories (Butchart et al. 2010, Pereira et al. 2010). If we fail to halt biodiversity loss, we will likely jeopardize the global efforts towards a long-term sustainable development (Newbold et al. 2016). The present situation is so critical that some authors consider that we are on the edge of, if not already in, the sixth global extinction event, this one attributed to humans (Ceballos et al. 2015).

In this scenario, understanding how different ecological drivers affect populations and species has been a research priority. Single taxon studies have been very popular in ecology (e.g. da Silva et al. 2008, Calviño-Cancela et al. 2013, Cruz et al. 2015a). However, the intricate interdependence of species, forming complex biological communities (Tylianakis 2008, Mougi and Kondoh 2012) render such single taxa centred studies inefficient to understand community changes and functioning. Moreover, different taxa are known to have distinct responses to the same forms of environmental perturbation (Barlow et al. 2007, Irwin et al. 2014, Ewers et al. 2015). Therefore, to fully understand the length of the anthropogenic impacts on biodiversity and how it might affect the long-term ecosystem functions, multi-taxa studies are increasingly needed, and specifically those that explicitly consider species interactions (Jordano 2016).

Anthropogenic disturbances might affect the several biodiversity levels asymmetrically, i.e. the composition may not be affected in the same proportion as the function (Flynn et al. 2009). The interactions between taxa within the communities, are one of the most important factors on ecosystem stability and maintenance (Thébault and Fontaine 2010, Mougi and Kondoh 2012, de Mazancourt et al. 2013, Loreau and de Mazancourt 2013). It is important to focus on biodiversity function and the interactions across taxa and not only on biodiversity composition (Díaz and Cabido 2001). This is fundamental to fully understand the response to human induced changes in biodiversity across all its levels (Hooper et al. 2005, Urban et al. 2013).

However, to fully understand how natural ecosystems function is not an easy task. In recent years ecological network analysis have gained popularity among ecologists to study relationships among community composition and function (Heleno et al. 2014). Specifically, ecological networks allow ecologists to “see simultaneously the forest and the tree” by allowing the accurate description of interaction patterns at the level of species, functional groups or emerging properties of whole communities. Many of these holistic properties of the ecosystems are otherwise hard to detected within traditional frameworks (Fath et al. 2007) and are particularly relevant for guiding applied conservation efforts (Zhang and Wang 2006, Kaiser-Bunbury and Blüthgen 2015). Several metrics that characterize ecological networks properties have helped to consolidate our understanding of the ecological communities and their relations, as the connectance (the proportion of detected interactions from all possible considered the found species (Jordano 1987a)), nestedness (the degree to which the interaction of less connected (specialist) species are a subset of more connected (generalists) species (Almeida-Neto and Ulrich 2011)), network specialization (evaluate the specificity of the species in the network (Blüthgen et al. 2006)) and modularity (a measure of the presence of groups of strongly interacting species (Dormann and Strauss 2014)).

For example the study of bird-plant mutualisms through networks has evidenced a general pattern of high heterogeneity (a few species are highly connected and many species have few interactions), nested (specialists species interact with subsets of species with whom generalists interact) and an asymmetric relationship between groups (García 2016). The use of ecological networks has led to the appearance of new ecological hypothesis that explain better the interaction of species, as the interaction release. The interaction release hypothesis states that entire communities can broad their trophic niche to take advantage of underexplored resources in their environment (Traveset et al. 2015). The formulation and understanding of new ecological hypothesis are essential to a better knowledge of the ecosystems biodiversity, how they react to anthropogenic changes, and crucial to known how to preserve and protect it, and ultimately to continue to benefit from its services.

Forests

Forests support more than half of the world’s terrestrial taxa, having the highest species diversity for many taxonomic groups, such as birds and invertebrates (Lindenmayer et al.

2006 and references therein). Forests deliver a wide range of ecosystem services (Thompson et al. 2011, Mace et al. 2012), and are one of the most valuable ecosystems worldwide (Costanza et al. 1997). Therefore preserving and conserving forests is of critical importance (Lindenmayer et al. 2003, 2006, Thompson et al. 2011).

Worldwide, the area of natural forest has been continuously decreasing (FAO 2016). This reduction is mainly due to the deforestation in developing countries and in tropical regions (Millenium Ecosystem Assessment 2005, FAO 2016), where natural forests are rapidly being replaced by agricultural areas or monospecific plantations (Foley et al. 2005, FAO 2016). The growing human demand for raw materials led to a higher valorisation of provisioning ecosystem services with a direct market price, such as wood or pulp mill. These materials are usually more valued than the other services, even if their global value is lower (Costanza et al. 1997, Bremer and Farley 2010). This search for immediate valorization, led to the optimization of forests for the production of the desired raw material, usually the plantation of monospecific stands (Carnus et al. 2006). Worldwide, these plantations are often constituted by fast growing species, mainly *Acacia* spp., *Eucalyptus* spp. and *Pinus* spp. (Carnus et al. 2006, Paquette and Messier 2010) which are frequently planted outside their native ranges. Eucalyptus plantations deserve a special attention since they cover more than 20 million ha, are present in more than 90 countries (Booth 2013, Laclau et al. 2013), and are a major source of biomass for paper pulp, fibreboard, industrial charcoal and fuelwood (Turnbull 1999).

In Europe and in North America the area of forest is currently increasing in opposition to the rest of the world, due to agricultural abandonment and the expansion of production forests (Millenium Ecosystem Assessment 2005, Forest Europe 2015). Natural forests have been altered for centuries throughout Europe (Amo et al. 2007, Brockerhoff et al. 2008), and presently only 4% of the forest area in Europe can be considered undisturbed by man while approximately 80% is available for raw material supply (Forest Europe 2015). Forest plantations are usually considered to have a low biodiversity and poor niche diversity (e.g. Hartley 2002, Carnus et al. 2006, Stephens and Wagner 2007, Bremer and Farley 2010). Many studies have identified several taxa that present lower diversity in forestry plantations than in native or semi-natural forests, noticeably within plants and birds (e.g. Barlow et al. 2007, Paillet et al. 2010, Proença et al. 2010, Calviño-Cancela et al. 2012, Calviño-Cancela 2013), but also in fungi, lichens, several arthropod groups, amphibians, reptiles and mammals (Amo et al. 2007, Gardner et al. 2007, Umetsu and Pardini 2007, da Silva et al. 2008, Zahn et al. 2009, Calviño-Cancela et al. 2013, Gainsbury and Colli 2014, Cruz et al. 2016). The low biodiversity in plantations, especially in eucalyptus plantations, have led some authors to use the expression ‘biological deserts’ (Gardner et al. 2007) or ‘green deserts’ (Bremer and Farley 2010) do describe them. However, biodiversity is not always significantly lower in plantations as reviewed by Carnus et al. (2006) and Stephens and Wagner (2007). Plantations can actually be used for the restauration and conservation of other human degraded habitats, especially if near remnant natural forests (Hartley 2002, Lindenmayer et al. 2003, Kanowski et al. 2005, Carnus et al. 2006), but will not replace native habitats (Brockerhoff et al. 2008).

Nowadays it is crucial to understand the impacts on global biodiversity of the expanding novel forests created by anthropogenic interference. These ‘novel ecosystems’ as coined by Hobbs result in new species mixtures and abundances that have a great potential to perform changes in the ecosystems (Hobbs et al. 2006). Understanding the impact of novel forest is especially relevant in the world’s biodiversity hotspots such as the Mediterranean basin (Myers et al. 2000), where more species are likely to be affected by a replacement from natural forest to forestry plantations. The European Mediterranean region has three times more tree species in a quarter of the area than temperate Europe (Fady-Welterlen 2005), and presents a high risk of extinction of native species (Malcolm et al. 2006). However, despite its higher diversity, biodiversity assessments are relatively scarce when compared to temperate Europe (Paillet et al. 2010). Even inside the Mediterranean basin it is important to highlight the biodiversity of specific areas such as the Iberian Peninsula, that harbours 50% of the European plant and terrestrial vertebrate species and presents around 31% of the European endemism (approximately 900) within these groups (Williams et al. 2000).

Birds as mobile links

Birds colonized all types of habitats and are the most studied class of animals (Sekercioglu 2006, Wenny et al. 2011). Birds have long attracted man because of their elaborated songs, appealing colours and the ability to fly. These factors likely make birds the animal group with more sympathizers. Nevertheless, birds do not provide only important cultural and recreational ecosystem services, they are also very relevant for several ecosystem functions (Sullivan 2012). Wild birds provide important ecosystem services, mainly supporting and regulating services (Sekercioglu 2006, Wenny et al. 2011). The most important services that birds provide are seed dispersion, pollination, pest control, scavenging, nutrient cycling and ecosystem engineering (Sekercioglu 2006, Whelan et al. 2008, Wenny et al. 2011). Birds are highly mobile organisms (Wenny et al. 2011), which makes them very important long distance dispersers and genetic linkers for plants (Sekercioglu 2006). The bird-plant mutualisms (birds feed on seeds, fruits or nectar and disperse their seeds or pollen) are among the most studied interactions. Almost one third of the birds species disperse seeds (Wenny et al. 2011), mainly through the consumption of fleshy fruits (Wenny et al. 2011, Costa et al. 2014). Birds also disperse seeds through scatter-hoarding of nuts and conifer seed crops (Vander Wall 2001, Sekercioglu 2006), and sometimes also disperse seeds attached to their feathers (Choi et al. 2010, Costa et al. 2014) and feet (Brochet et al. 2010). The high bird mobility allows seeds to cross oceans and colonize remote territories (Viana et al. 2015). Birds are also known to have an important role on the long distance transport of other propagules such as moss spores (Lewis et al. 2014) and aquatic organisms (Viana et al. 2013). Even if the prevalence of a given propagule is very low (e.g. Costa et al. 2014, Viana et al. 2015) the enormous number of birds that annually migrate between continents (Hahn et al. 2009) made birds critical long distance dispersers.

There are around 352 000 flowering plant species and they constitute the base of most terrestrial ecosystems. Proximally 90% of these plants rely on animal pollinators, as insects and birds, to transport pollen grains from anthers to the stigma of the flowers (Knight et al. 2005, Sargent and Ackerly 2008, Ollerton et al. 2011). Regarding bird pollination, at least 500 plant genera are known to be pollinated by over 900 bird species (Sekercioglu 2006) but there are more bird species visiting flowers (Carstensen and Olesen 2009). The number of species involved in bird pollination is lower than in bird seed dispersion, but the mutualism in pollination systems tends to be more specialized (Kelly et al. 2010, Wenny et al. 2011, Sekercioglu 2011). The co-evolution between flowering plants and pollinating birds mean that the disappearance of certain bird species, and consequently its functional extinction, leads to reduced pollination, seed production, and plant density (Sekercioğlu et al. 2004, Anderson et al. 2011).

In Europe, there is a good amount of knowledge about seed dispersal by birds (e.g. Jordano and Herrera 1981, Jordano 1987b, Costa et al. 2014, Viana et al. 2015). On the other hand, studies about pollen dispersal and the potential of bird pollination are almost anecdotal, although birds are known to pollinate flowers in Europe (Búrquez 1989, Peters et al. 1995, Ortega-Olivencia et al. 2005). Despite the absence of specialized nectarivorous bird species in Europe, the new assemblage of exotic plant species throughout Europe means that, the role of birds as pollinators might be important in these novel ecosystems. Moreover, there are *circum*-Mediterranean native plants as the Fabaceae *Anagyris foetida* (Ortega-olivencia and Catalán 2009), in which the main pollinators are European birds (Ortega-Olivencia et al. 2005).

There is a general need to attribute a marked value to supporting and regulating ecosystem services, that are usually assumed as free (Costanza et al. 1997, Daily et al. 2000, Wenny et al. 2011). However, even our knowledge about the different ecosystem services provided by a well-known taxa such as birds, is very unbalanced and there is an urgent need to have a better understanding of all ecosystem processes and their potentially associated services. There are many bird species threatened, and projections show that by 2100, 6-15% of bird species will be extinct and 7-25% will be functionally extinct, i.e. their contribution to ecosystem services will be negligible (Sekercioğlu et al. 2004). This means that it is very important that we correctly evaluate all potential ecosystems services provided by birds, in order to focus conservation efforts not only in single species but also on their ecosystem functions.

Objectives and outline

This thesis has two main goals. Firstly, it intends to provide a better understanding of the impact of novel forest ecosystems on forest biodiversity. Secondly, it uses biological interactions to explore the magnitude and diversity of diaspore dispersal by European birds, in particularly of pollen grains and fungi spores.

To achieve the two main aims, the present thesis is organized into four data chapters, each of them exploring a specific objective:

Chapter I – Understand how the continuous replacement of native forests by novel forest resulting from plant invasions and from the plantation of production forests affect multiple taxa, including plants, fungi and animals.

Chapter II – Evaluate the existing knowledge and potential importance of pollen dispersal by birds in Europe, by providing a comprehensive literature review and discussing emerging patterns and knowledge gaps.

Chapter III – Characterize pollen transport interactions at the community level in Europe and evaluate how these interactions differ from those established by specialized nectarivorous birds and from those reported from oceanic islands.

Chapter IV – Evaluate annual patterns of pollen and yeasts dispersal by birds in Europe.

Chapter I

A multi-taxa assessment reveals the negative impacts of novel forests on biodiversity

Abstract

The biodiversity sustained by natural habitats, particularly forests, provide ecosystem services that are essential to human well-being. However, natural forests have been largely transformed mainly via monospecific plantations and the spread of invasive species. Given the extension of these “novel forests”, it is critical to find out how they affects forest biodiversity, especially in biodiversity hotspots with high anthropogenic pressure such as the southwest Europe. As different taxa are likely to be affected differently, such assessment requires a multi-taxa approach. We compared the biodiversity in natural Oak woodlands, native Pine plantations, exotic Eucalyptus plantations, and invasive Acacia woodlands in Central Portugal. We sampled 11 taxa: trees, shrubs, herbs, macrofungi, ground and night-flying arthropods, reptiles, birds, small mammals, carnivores, and bats. We evaluated the relative abundance, Shannon diversity index, species richness and composition of each taxon among woodland types. Natural oak woodlands sustain higher diversity, abundance and a unique species composition compared to “novel forests” for most taxa, especially when compared to both exotic woodlands. The greater differences were recorded for shrubs, herbs and birds. Only the diversity of ground arthropod did not differ significantly among the four woodland types. The abundance and diversity in the Acacia woodlands of macrofungi and carnivores were surprisingly similar to the Oak woodland. Our results reveal that, distinct taxa respond differently to habitat chances, while ground arthropods were similar in all woodland types others such as shrubs and birds were very different. The large-scale replacement of natural forests by anthropogenic novel forests has significant negative impacts on the biodiversity of several groups. The consequences of these changes for long-term forest dynamics and particularly for the resilience of the services we derive from forests require further evaluation.

Keywords

Acacia dealbata; *Eucalyptus globulus*; *Quercus* spp.; Mediterranean; monospecific forests; *Pinus pinaster.*

Introduction

Biodiversity has a crucial role in supporting ecosystem functioning, promoting ecosystem resilience, and delivering important ecosystem services (Mace et al. 2012). Humans gained the capacity to severely change their surroundings, shaping natural landscape and its biodiversity (Foley et al. 2005). Most terrestrial taxa are found on forests (Lindenmayer et al. 2006 and references therein), which deliver a wide range of supporting, provisioning, regulating, and cultural ecosystem services (Thompson et al. 2011, Mace et al. 2012). For this reason, forests are one of the most valuable ecosystems worldwide both in natural and economic terms (Costanza et al. 1997). However, short-term market needs, such as the demand for raw materials (e.g. wood), tend to be more valued due to its direct market price (Costanza et al. 1997, Bremer and Farley 2010), therefore raw material production has been often optimized by the plantation of monospecific stands (Carnus et al. 2006). These plantations are often of exotic species (mainly *Pinus* spp. and *Eucalyptus* spp.) due to their fast growing rates (Carnus et al. 2006, Paquette and Messier 2010). Similarly, invasive species are frequently fast growing species that benefit from high disturbance levels such as fires, and are able to form monoculture copses (Royo and Carson 2006, Thompson et al. 2011). Given the high human alteration of native forests (Foley et al. 2005) and their replacement by fast growing tree plantations and invasive stands worldwide, it is critical to understand the possible consequences of this large-scale land-use change from natural to novel forests (*sensu* Hobbs et al. 2006) on biodiversity.

Natural forests in Europe were profoundly altered for centuries (Brockerhoff et al. 2008). Presently one third of Europe is covered by forests, but around 80% of them are novel forestry ecosystems available for raw material supply, and intensively managed forest as plantations are increasing in Europe (Forest Europe 2015). The Mediterranean basin, one of the world's biodiversity hotspots (Myers et al. 2000) presents many threatened and endemic species (Malcolm et al. 2006) under high anthropogenic influences. Given the present extension of novel forests in the Mediterranean region and worldwide, their effect in the conservation of biodiversity cannot be ignored (Carnus et al. 2006). Several studies suggest that in the Southwest Europe, monospecific plantations and forests dominated by exotic species sustain lower biodiversity than original natural forests, but these studies focused exclusively in one or two taxonomical group, typically plants and birds (e.g. Tellería and Galarza 1990, Proença et al. 2010, Calviño-Cancela et al. 2012, Calviño-Cancela 2013). However, different taxa might respond very differently to land use changes: for example, while birds tend to be less diverse in exotic forests, several arthropods might not be affected or even benefit from this disturbance (Barlow et al. 2007, Irwin et al. 2014). Therefore, a holistic multi-taxa approach is critical if we are to fully understand the impact of novel forest on ecosystems.

We evaluated the compositional biodiversity of vascular plants (trees, shrubs and herbs), macrofungi, ground and night-flying arthropods, birds, small mammals, carnivores, and bats in four common types of native and exotic woodlands in the southwestern Europe, namely: natural oak woodlands, *Pinus pinaster* plantations (native species), *Eucalyptus globulus* plantations (exotic species), and woodlands of *Acacia dealbata* (exotic invasive species). We expected to find an overall higher biodiversity in native than in exotic woodlands, but also that not all groups are equally affected.

Material and methods

Study area

The study was performed in a strongly anthropogenic region near Coimbra, Central Portugal (Figure 1). The landscape is fragmented and covered mainly with urban, agricultural, and forest areas, typical of many regions of the Southwest Europe (Mediterranean basin) where native woodlands dominated by oaks (*Quercus* spp.) represent the native forests. In Portugal, most of the forested area is increasingly occupied by plantations of the exotic *Eucalyptus globulus*, which already represent 26% of the country' forested area and plantations of native *Pinus pinaster* also occupy 23% of the Portuguese forest (ICNF 2013). *Acacia dealbata* is likely the most aggressive exotic tree species in Portugal and its occupancy area is expected to increase rapidly (Correia et al. 2014). We selected 40 plots of mature forest representative of the study area, 10 of each type, randomly distributed in the study area (Figure 1). The selected plots had an area of at least 100x100m of the same forest type, and were at least 1km apart. Sampling was planned to avoid edge effects as much as possible.

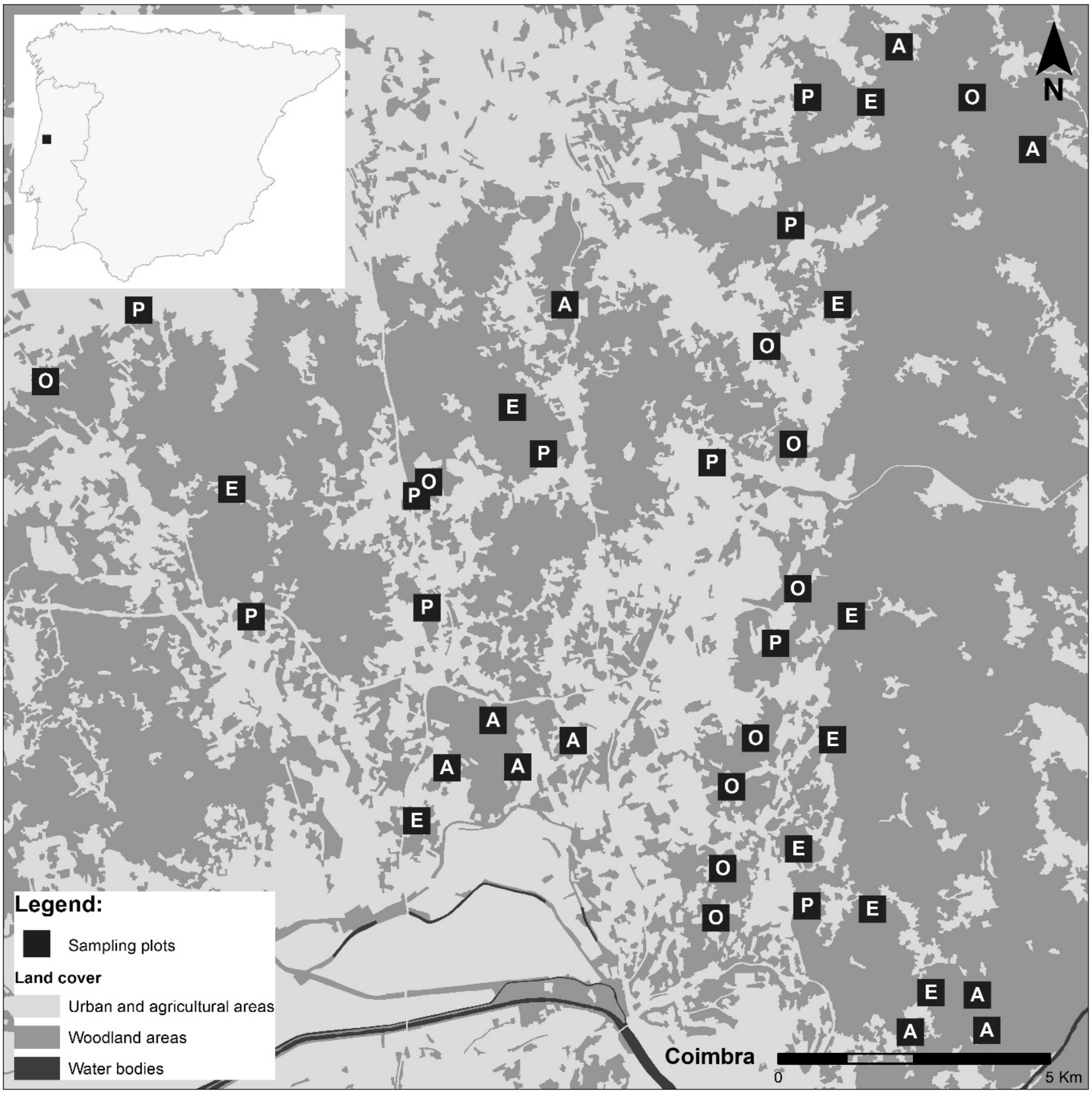

Figure 1 – Study area in Central Portugal, Southwest Europe. O – natural oak woodlands, P – native *Pinus pinaster* plantations, E – exotic non-invasive *Eucalyptus globulus* plantations, and A – exotic invasive *Acacia dealbata* woodlands.

Sampling was conducted regularly between June 2013 and May 2014 (see below), with the exception of two *A. dealbata* plots that were only sampled until December 2013, when they were cut. Hereafter we refer to the four different woodland habitats as Oak, Pine, Eucalyptus and Acacia. To rule out the effect of potential confounding landscape spatial variables, we measured the following five variables using digital models of terrain and orthophotos: distance to the nearest riparian gallery, urban area, agricultural field and to any edge type, and altitude. We compared these variables among the four woodland types and found no significant differences (Table 1).

Table 1 – Statistics summary of the comparisons of five landscape variables that may affect biodiversity, between the four different woodlands.

Variable	F value (df=3,36)	p-value
Distance to riparian gallery	1.777	0.169
Distance to urban area	1.613	0.203
Distance to agricultural field	0.280	0.839
Distance to any edge	0.569	0.640
Altitude	1.041	0.386

Sampling methodology

Plants – We divided plants in three different groups: trees, shrubs and herbaceous plants (hereafter herbs). All plants were sampled from June to August 2013. Trees and shrubs were sampled in five squares of 10x10m, one in the center of the plot and the remaining with their center at 25m from the center, one in each quadrant. The relative abundance of each tree and shrub species were estimated from 1 to 10, according to the visual percentage of area covered by each species. Herbs were sampled in 4 squares of 1x1m equally spaced, inside each of the five squares of 10x10m, and its relative abundance was assessed according to the visual percentage cover of each species from 1 to 100.

Macrofungi – We sampled this group by running three transects inside each plot, during November and December of 2013. Transects were 60m long and crossed each other in the middle of the plot (30m to each side) in a star-like design. We used the number of spore-bearing fruiting bodies (i.e. mushrooms) for the relative abundance of the macrofungi. When we were unable to identify the macrofungi species, we classified it as a morphospecies of the lowest possible taxa.

Arthropods – Sampling of arthropods was divided in two groups, the ground arthropods and night-flying arthropods. Ground arthropods were sampled in each plot with five pitfall traps placed in the center of the 10*10m squares used in the vegetation sampling. The pitfalls were placed during seven consecutive days in each sampling season, having 7cm of diameter and filled with ethylene glycol. Ground arthropods were sampled in three seasons, from July to August 2013, January to February, and April to May 2014 to assess their global biodiversity. Night-flying arthropods were captured with an UV light funnel trap during an entire night, from April to May of 2014. For this group we only considered insects belonging to the following orders: coleoptera, diptera, leptidoptera, hymenoptera (family ichneumonidae), psocoptera, and trichoptera. In both arthropod groups, when we were unable to identify individuals at the species level, they were classified into morphospecies.

Vertebrates – The sampling was performed in more than one season for most of these taxa to assess their global diversity. Sampling of vertebrates was done with distinct methodologies for the five groups: reptiles, birds, small mammals, carnivores and bats. Birds, small mammals and carnivores were sampled in three seasons, from July to August 2013, January to February, and April to May 2014; bats in two seasons, July to August 2013 and April to May 2014; and reptiles from July to August 2013. Reptiles were visually sampled during sunny afternoons along the same transects used for macrofungi. We were only able to identify with certainty 45% of the lizards detected, but these were all *Psammodromus algirus* except one individual of the unmistakable limbless lizard (*Anguis fragilis*). Therefore, we assumed that all unidentified lizards were *P. algirus*. Birds were sampled with point counts in the center of each plot using a radius of 30m. We performed two point counts in each sampling season. Point counts lasted 10 minutes, and were performed during the first 2.5 hours after sunrise without strong winds or rain, and all birds seen or heard within this period were counted. Small mammals were captured using 21 Sherman traps in each plot, baited with cereals and sardines, during three consecutive nights, in all sampling seasons. The Sherman traps were placed in a web design along the previously described transects, 10m apart (the central point had 3 traps). All small mammals captured were marked with cuts in the fur. Medium-size carnivores (order carnivora) were sampled with camera traps placed in the center of each plot, for four consecutive nights, in each season. The relative abundance of carnivores was determined as the number of photos taken of each species with a minimum of one hour of interval, to avoid multiple photos of the same individual foraging around the camera. Bats were recorded with a real time bat detector, in a 10-minute duration point recording in the center of each plot, twice per season. The recording period occurred between 30 minutes and 2.5 hours after nightfall, in nights with no or light wind, no full moon and without rain. The relative abundance was defined as the duration (in seconds) of the recordings of each species. Bat species identification was based in the identification of their ultra-sound pulses and only species known to occur in the study area were considered (Rainho et al. 2013). The exception was the *Miniopterus schreibersii* exclude from the identifications because its pulses are very similar to the much more abundant *Pipistrellus pygmaeus* (all possible *M. schreibersii* were classified as *P. pygameus*), and *Plecotus* sp. were only identified to genus.

Data analysis

We compared mean species richness (number of species), relative abundance (hereafter only abundance), and Shannon diversity index of all sampled groups between the four woodland types. The Shannon index was not calculated for groups with an average number of species <5. We also compared the overall species richness between all woodland types, using the number of all species recorded in each plot. All comparisons were made using Generalized linear models (GzLM) assuming either a Gaussian or Poisson distribution of the residuals, and when necessary, using a power transformation to meet the test assumptions. Post-hoc Tukey HSD tests were used to identify differing groups. We also computed the species accumulation curves using 1000 Mao Tau randomizations of the data obtained on each plot (Colwell et al. 2012) to evaluate the significance of the differences in the total number of observed species across woodland types. We considered that the observed number of species (for a given group) differed if the 95% confidence intervals of both woodland types did not overlap. To compare the species composition of each group among the four woodland types, we used an analysis of dissimilarity matrices (PerMANOVA-function adonis with 1000 permutations) with Bray-Curtis distances, and to represent it we used Non-metric Multidimensional Scaling ordination (NMDS). Whenever a species group differed between woodland types, we performed multiple comparisons with subsets of that groups' data to verify which woodland types differed significantly. All statistical analysis were performed with packages MASS (Venables and Ripley 2002), lme4 (Bates et al. 2015) and vegan (Oksanen et al. 2016) in R (R Core Team 2016) with the exception of rarefaction curves that were calculated in EstimateS (Colwell 2013). A significance level of α<0.05 was considered for all analysis.

Results

Species richness, diversity and abundance

Oak woodlands had approximately 40% more species than the other three woodland types, which did not differ significantly from each other (Figure 2). Trees had approximately 1.5 more species and were more abundant in Oak and Acacia woodlands than Pine and Eucalyptus woodlands (Figure 2). Although the four woodland types had the same number of observed shrub species, shrubs were significantly more abundant and more diverse in Oak woodlands, followed by Pine and Eucalyptus woodlands and less common and less diverse in Acacia woodlands. Herbs were on average twice more abundant in Pine woodlands than in the other woodlands, but its diversity was significantly higher in Oak woodlands than in Eucalyptus and Acacia woodlands. Macrofungi were on average approximately twice more abundant and diverse in Oak and Acacia woodlands than in Pine and Eucalyptus woodlands. Pine woodlands had particularly low richness and abundance of macrofungi. Ground and night-flying arthropods presented similar abundances and diversity in all woodland types, with the exception of the number of observed night-flying species, which were significantly higher in Oak woodlands than in the other woodland types (Figure 2).

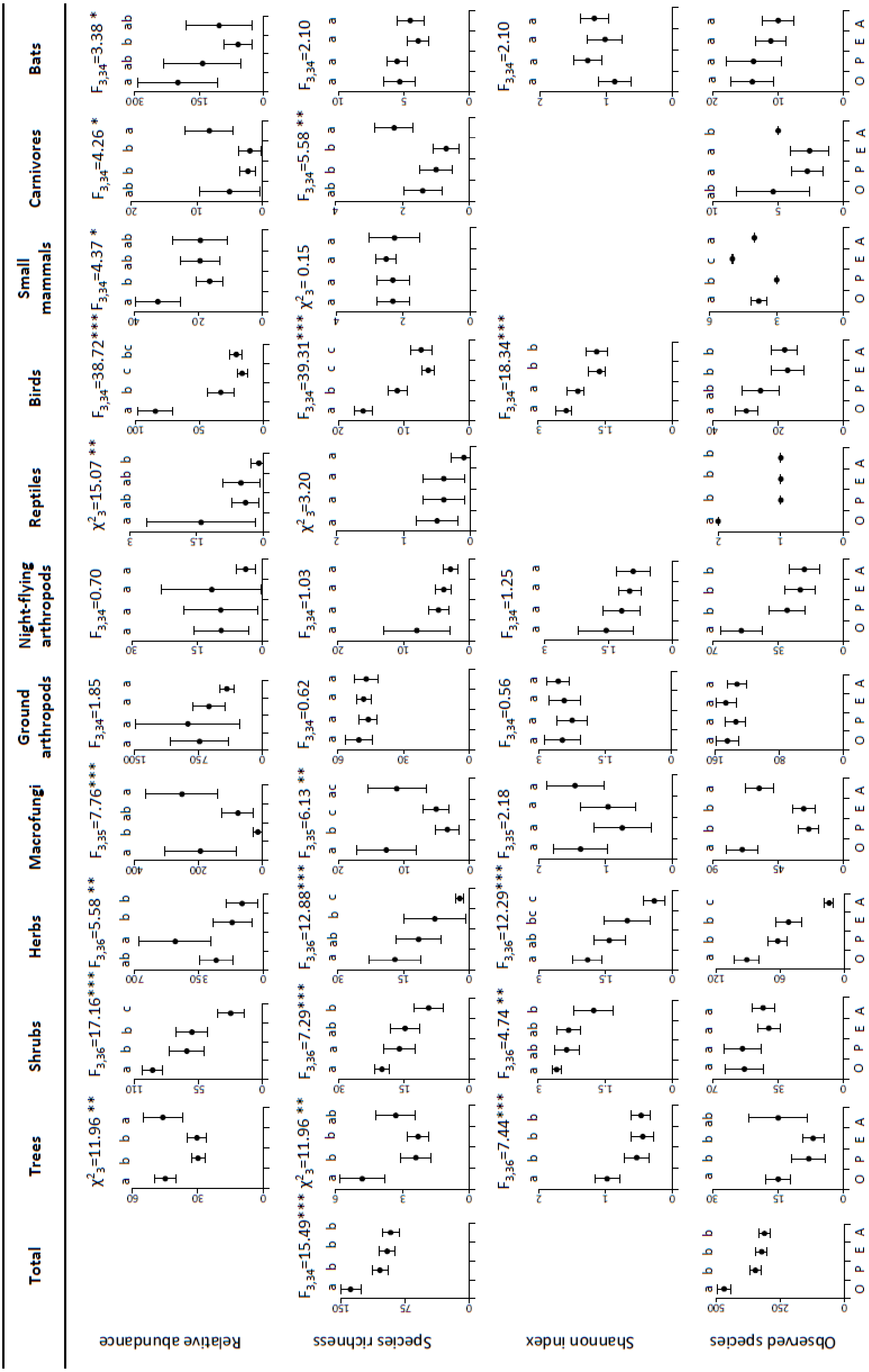
Total
Trees
Shrubs
Herbs
Macrofungi
Ground arthropods
Night-flying arthropods
Reptiles
Birds
Small mammals
Carnivores
Bats
Relative abundance
Species richness
Shannon index
Observed species
χ^2_3=11.96 **
$F_{3,36}$=17.16***
$F_{3,36}$=5.58 **
$F_{3,35}$=7.76***
$F_{3,34}$=1.85
$F_{3,34}$=0.70
χ^2_3=15.07 **
$F_{3,34}$=38.72***
$F_{3,34}$=4.37 *
$F_{3,34}$=4.26 *
$F_{3,34}$=3.38 *
$F_{3,34}$=15.49***
χ^2_3=11.96 **
$F_{3,36}$=7.29***
$F_{3,36}$=12.88***
$F_{3,35}$=6.13 **
$F_{3,34}$=0.62
$F_{3,34}$=1.03
χ^2_3=3.20
$F_{3,34}$=39.31***
χ^2_3= 0.15
$F_{3,34}$=5.58 **
$F_{3,34}$=2.10
$F_{3,36}$=7.44***
$F_{3,36}$=4.74 **
$F_{3,36}$=12.29***
$F_{3,35}$=2.18
$F_{3,34}$=0.56
$F_{3,34}$=1.25
$F_{3,34}$=18.34***
$F_{3,34}$=2.10
O P E A

Figure 2 – Comparisons of the relative abundance, species richness, Shannon diversity index and observed species with confidence intervals estimated using Mao Tau accumulation curves. The central point represents the average for each level and the error bars the respective 95% confidence interval. P-values are represented by * = 0.05 to 0.01; ** = 0.01 to 0.001; *** <0.001. Different letters on the top of each woodland type denote significant differences found between habitats: O –natural oak woodlands, P – native *Pinus pinaster* plantations, E – exotic *Eucalyptus globulus* plantations, and A – exotic and invasive *Acacia dealbata* woodlands.

Finally, all vertebrate groups tend to be more abundant in Oak woodlands, but only birds presented a significantly higher abundance in Oak woodlands than in the other three woodland types. Carnivores were equally abundant in Oak and Acacia woodlands, and were significantly more abundant in Acacia woodlands than in Pine and Eucalyptus woodlands. The number of vertebrate species in each group was usually very low: two reptile, five small mammal, six carnivore, and 17 bat species. Birds were the richest vertebrate group, with 38 species detected, and were significantly more diverse in Oak woodlands than in the other three woodland types (Figure 2).

Community composition

Community composition differed significantly among the four woodland types for all studied taxa except ground arthropods and reptiles (Figure 3). Pine woodlands presented the more similar community composition to that of native Oak woodlands. However, the highest overlap in community composition was between Pine and Eucalyptus woodlands (Figure 3). As expected, tree composition was very different between the four woodland types, while differences on the shrub community were less pronounced and were not significantly different between Pine and Eucalyptus woodlands (Figure 3; Table 2). Herb composition was similar between Eucalyptus and Acacia woodlands, but differed significantly between these two woodland types and Oak and Pine woodlands (Figure 3; Table 2). Regarding macrofungi, Oak woodlands and Acacia woodlands were strikingly different, while there was some overlap between Eucalyptus and Pine woodlands (Figure 3; Table 2). Night-flying arthropod composition in Oak woodlands was more heterogeneous and significantly distinct from the other three woodland types (Figure 3; Table 2). Birds' composition differed significantly among the four woodland types (Figure 3). The community of small mammals and bat species showed a large overlap (Figure 3), but the community composition of small mammals in the oak woodlands differed from the Eucalyptus and Acacia woodlands, while that of bats differed between the Oak woodlands and both Pine and Eucalyptus woodlands (Table 2). Finally, the community of carnivores overlapped among woodlands, except between Acacia woodlands and both Pine and Eucalyptus woodlands (Table 2).

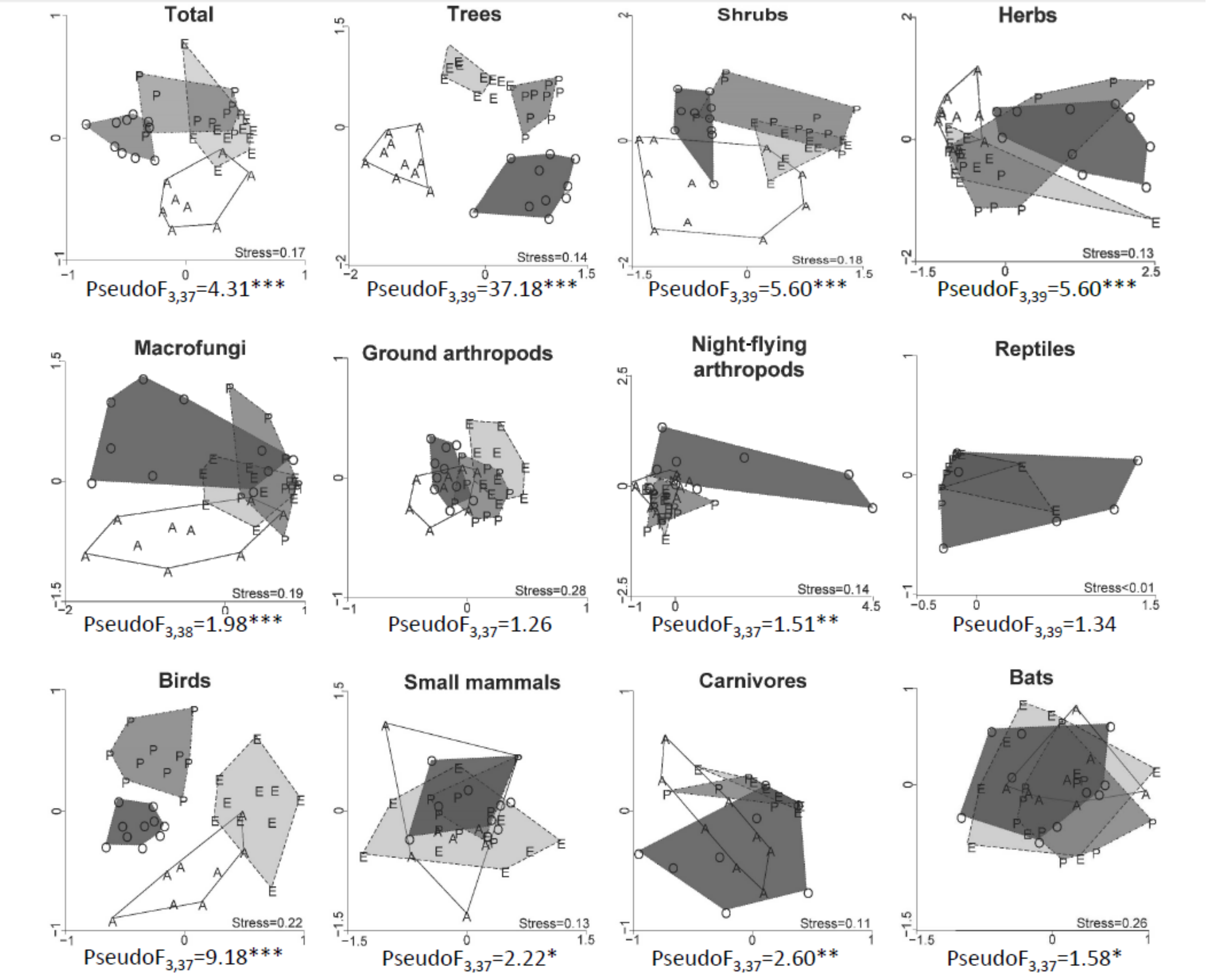

Figure 3 – Non-metric Multidimensional Scaling ordinations (NMDS) representing the differences of the compositional diversity between the different woodlands, on the several groups sampled. The letters represent individual plots of each woodland (O-Oak; P-Pine; E-Eucalyptus; A-Acacia) and each woodland is connected by the maximum polygon of its points. The dark grey polygon represents the oak wood, the mid grey the pine plantation, the light grey the eucalyptus plantation and the white polygon the acacia wood. Below each graphic is the statistics summary of the PerMANOVA in the different groups. P-values are represented by * = 0.05 to 0.01; ** = 0.01 to 0.001; *** <0.001.

Table 2 – Statistics summary of multiple comparison using subsets of the PerMANOVA. Oak – Oak woodland; Pin – Pine Woodland; Pin – Pine woodland; Aca – Acacia woodland. Significant values are at bold.

Group		**Oak woodland**				**Pine woodland**				**Eucalyptus woodland**				**Acacia woodland**			
		PseudoF	df	R^2	p	PseudoF	df	R^2	p	PseudoF	df	R^2	p	PseudoF	df	R^2	p
Total	Oak					3.546	1,19	0.165	**0.001**	5.667	1,19	0.239	**0.001**	3.935	1,17	0.197	**0.001**
	Pin	3.546	1,19	0.165	**0.001**					2.081	1,19	0.104	**0.001**	3.767	1,17	0.191	**0.001**
	Euc	5.667	1,19	0.239	**0.001**	2.081	1,19	0.104	**0.001**					3.373	1,17	0.174	**0.001**
	Aca	3.935	1,17	0.197	**0.001**	3.767	1,17	0.191	**0.001**	3.373	1,17	0.174	**0.001**				
Trees	Oak					21.131	1,19	0.540	**0.001**	30.143	1,19	0.626	**0.001**	24.898	1,19	0.580	**0.001**
	Pin	21.131	1,19	0.540	**0.001**					73.178	1,19	0.803	**0.001**	59.355	1,19	0.767	**0.001**
	Euc	30.143	1,19	0.626	**0.001**	73.178	1,19	0.803	**0.001**					59.295	1,19	0.767	**0.001**
	Aca	24.898	1,19	0.580	**0.001**	59.355	1,19	0.767	**0.001**	59.295	1,19	0.767	**0.001**				
Bushes	Oak					6.026	1,19	0.251	**0.001**	11.086	1,19	0.381	**0.001**	6.585	1,19	0.268	**0.001**
	Pin	6.026	1,19	0.251	**0.001**					1.601	1,19	0.082	0.111	4.460	1,19	0.199	**0.001**
	Euc	11.086	1,19	0.381	**0.001**	1.601	1,19	0.082	0.111					5.426	1,19	0.232	**0.001**
	Aca	6.585	1,19	0.268	**0.001**	4.460	1,19	0.199	**0.001**	5.426	1,19	0.232	**0.001**				
Herbs	Oak					2.672	1,19	0.129	**0.004**	2.900	1,19	0.139	**0.003**	2.740	1,19	0.132	**0.001**
	Pin	2.672	1,19	0.129	**0.004**					1.933	1,19	0.097	**0.036**	2.528	1,19	0.123	**0.004**
	Euc	2.900	1,19	0.139	**0.003**	1.933	1,19	0.097	**0.036**					1.849	1,19	0.093	0.062
	Aca	2.740	1,19	0.132	**0.001**	2.528	1,19	0.123	**0.004**	1.849	1,19	0.093	0.062				
Macrofungi	Oak					2.375	1,19	0.117	**0.004**	1.566	1,19	0.080	**0.037**	1.518	1,18	0.082	**0.034**
	Pin	2.375	1,19	0.117	**0.004**					1.395	1,19	0.072	0.013	3.167	1,18	0.157	**0.002**
	Euc	1.566	1,19	0.080	**0.037**	1.395	1,19	0.072	0.135					2.020	1,18	0.106	**0.008**
	Aca	1.518	1,18	0.082	**0.034**	3.167	1,18	0.157	**0.002**	2.020	1,18	0.106	**0.008**				
Night-flying arthropods	Oak					1.899	1,19	0.095	**0.005**	1.977	1,19	0.099	**0.005**	1.065	1,17	0.062	0.347
	Pin	1.899	1,19	0.095	**0.005**					0.933	1,19	0.049	0.518	1.387	1,17	0.080	0.093
	Euc	1.977	1,19	0.099	**0.005**	0.933	1,19	0.049	0.518					1.748	1,17	0.099	**0.023**
	Aca	1.065	1,17	0.062	0.347	1.387	1,17	0.080	0.093	1.748	1,17	0.099	**0.023**				
Birds	Oak					11.108	1,19	0.382	**0.001**	17.705	1,19	0.496	**0.001**	13.892	1,17	0.465	**0.001**
	Pin	11.108	1,19	0.382	**0.001**					5.311	1,19	0.228	**0.001**	7.049	1,17	0.306	**0.001**
	Euc	17.705	1,19	0.496	**0.001**	5.311	1,19	0.228	**0.001**					3.573	1,17	0.183	**0.004**
	Aca	13.892	1,17	0.465	**0.001**	7.049	1,17	0.306	**0.001**	3.573	1,17	0.183	**0.004**				
Small mammals	Oak					5.004	1,19	0.218	**0.007**	1.981	1,19	0.099	0.077	3.182	1,17	0.166	**0.007**
	Pin	5.004	1,19	0.218	**0.007**					0.794	1,19	0.042	0.574	2.201	1,17	0.121	0.057
	Euc	1.981	1,19	0.099	0.077	0.794	1,19	0.042	0.574					1.193	1,17	0.069	0.356
	Aca	3.182	1,17	0.166	**0.007**	2.201	1,17	0.121	0.057	1.193	1,17	0.069	0.356				
Carnivores	Oak					1.948	1,19	0.098	0.083	1.816	1,19	0.092	0.112	1.716	1,17	0.097	0.137
	Pin	1.948	1,19	0.098	0.083					0.461	1,19	0.025	0.672	4.638	1,17	0.225	**0.002**
	Euc	1.816	1,19	0.092	0.112	0.461	1,19	0.025	0.672					5.110	1,17	0.242	**0.002**
	Aca	1.716	1,17	0.097	0.137	4.638	1,17	0.225	**0.002**	5.110	1,17	0.242	**0.002**				
Bats	Oak					2.015	1,19	0.101	**0.037**	2.529	1,19	0.123	**0.015**	1.707	1,17	0.096	0.087
	Pin	2.015	1,19	0.101	**0.037**					1.550	1,19	0.079	0.105	0.483	1,17	0.029	0.927
	Euc	2.529	1,19	0.123	**0.015**	1.550	1,19	0.079	0.105					1.062	1,17	0.062	0.382
	Aca	1.707	1,17	0.096	0.087	0.483	1,17	0.029	0.927	1.062	1,17	0.062	0.382				

Discussion

We provided the first multi-taxa comparison assessment of biodiversity for novel forest ecosystems in southwestern Europe using representative woodlands of the most common woodland types in the region: natural Oak woodlands, native Pine plantations, exotic Eucalyptus plantations and invasive Acacia woodlands. There are very few multi-taxa studies comparing the biodiversity of different forests, although some work was carried out in Brazil (Barlow et al. 2007, Pardini et al. 2009), USA (Sax 2002) and United Kingdom (Quine and Humphrey 2010, Irwin et al. 2014). Previous studies recorded biodiversity declines in southwest Europe from Oak and Pine forests to Eucalyptus and Acacia forests, but these were only focused in only one or two taxa (Lorenzo et al. 2012, Calviño-Cancela et al. 2012, Calviño-Cancela 2013, Cruz et al. 2015b, 2016). We performed the first truly holistic, multi-taxa study from native to novel forest ecosystem and show that the impact of the different woodlands on biodiversity depends on the taxa studied.

As expected, we found an overall decreasing trend in species richness, species abundance and diversity from Oak to Pine, Eucalytus and Acacia woodlands, respectively. The global biodiversity composition was distinct in the four woodlands, but Pine woodlands (native tree plantations) were the most similar to natural Oak woodlands. In our study, differences in tree abundance, diversity, and community composition reflect an expected pattern since the plantations are optimized to be monospecific production stands (Carnus et al. 2006), and the position and number of planted trees is optimized to obtain the maximum productivity of a single species (Paquette and Messier 2010). The known biodiversity patterns for the understory in southwest Europe shows a lower diversity in Eucalyptus woodlands than in Oak and Pine woodlands (Proença et al. 2010, Calviño-Cancela et al. 2012). Our results indicate a lower abundance, but a similar diversity, of shrubs in both plantations when compared to Oak woodlands. Herbs abundance differed between Pine and Eucalyptus woodlands, and Oak woodlands presented intermediate values, showing however significantly higher herb diversity in Oak woodlands than in Eucalyptus woodlands, as shown by previous studies (Proença et al. 2010, Calviño-Cancela et al. 2012). The effect of Acacia woodlands on biodiversity were virtually unknown in the study region; previously only Lorenzo et al. (2012) showed a lower understory diversity in Acacia woodlands than in Oak woodlands and Pine woodlands (Lorenzo et al. 2012). Our study shows that Acacia woodlands are even poorer than Eucalyptus plantations regarding shrubs and herbs, and these biodiversity declines extended to other taxa such as reptiles, birds and bats.

The macrofungi also seldom evaluated in similar studies, and therefore we remain largely ignorant on how they might be affected by the spread of novel forest ecosystems. We found that macrofungi richness and abundance was lower in planted woodlands, both Pine and Eucalyptus. This is likely related to an almost lack of propitious microhabitats for this group, such as dead wood and root plates in the managed plantations (Paillet et al. 2010). It may also reflect the lower tree abundance and diversity in these monospecific stands, given the close intimacy between plant and macrofungi (Nguyen et al. 2016) and close canopies (Twieg et al. 2007). The lack of differences in the abundance and composition of ground arthropods between Eucalyptus and Oak woodlands was already described for leaf litter arthropods (Bara Temes et al. 1985). However, other taxa as Carabidae and Arachnida were more diverse and abundant in oak woodlands than in Eucalyptus woodlands (da Silva et al. 2008, Zahn et al. 2009), while Collembola only differ in the number of species (Barrocas et al. 1998), and for Isopoda, the abundance was even larger in Eucalyptus woodlands than in Oak woodlands (Zahn et al. 2009). The higher species richness on Oak woodlands for some arthropod taxa is related to the higher heterogeneity of microhabitats (Paillet et al. 2010), however species that are able to efficiently colonize the new available and more homogeneous woodlands can reach larger densities (Barrocas et al. 1998). Regarding ground-arthropods, the lack of differences we obtained among the four woodland types could be related to the low taxonomic resolution, but is more likely due to the higher landscape heterogeneity in our study region and to the extirpation of specialists' species of this taxon due to the long-standing anthropogenic pressures (Hau et al. 2005). The differences in the total number of species and its composition for night-flying arthropods were likely related to the greater diversity of plants in the native Oak woodlands, which provided a greater food diversity for specialized species, as reported in Brazil when comparing native forests and Eucalyptus plantations (Bragança et al. 1998, Zanuncio et al. 1998). Vertebrates showed a general trend of higher abundances in Oak woodlands, likely related to the higher plant diversity that offer better shelter quality and additional food sources. However, with the low number of species in most vertebrate groups in our study area, it was difficult to find significant differences among the four woodland types. Reptiles are known to be negatively affected by Pine plantations in southwest Europe (Amo et al. 2007) and Eucalyptus plantations are also known to have a similar effect in other parts of the world (Gainsbury and Colli 2014). The higher reptile abundance in the Oak woodlands suggest that reptiles were strongly influenced by the structure of the plant community that provide shelter, independent of the availability of their main prey, the ground arthropods. Birds are one of the most studied groups and are often used as indicator species (Gregory and Strien 2010). We showed that the diversity and abundance of birds in Acacia woodlands was similar to that of Eucalyptus plantations, and both were much lower than in Oak woodlands. Pine plantations showed intermediate bird diversity and abundance between native Oak and exotic woodlands, as previously shown by Tellería and Galarza (1990), Proença et al. (2010), da Silva et al. (2012) and Calviño-Cancela 2013). Small mammals' diversity is known to be higher in native forest than in both Eucalyptus (Sax 2002, Umetsu and Pardini 2007) and Pine plantations (Gonçalves et al. 2012). We were not able to find this difference probably due to the lower species richness in our study area, but we were able to detect some trends and found differences in the species composition between Oak woodlands and Pine and Acacia woodlands. Both bird and small mammal diversity, abundance, and composition are likely explained by the diversity of food sources and shelter provided by the different vascular plants present in each woodland type. Most southwest European carnivore species seem to avoid Eucalyptus plantations (Pereira et al. 2012, Cruz et al. 2015b), which is in accordance with our results. Our results suggest that carnivore species tend to avoid both plantations and are more common in Oak and Acacia woodlands. The heavy presence of carnivores in Acacia woodlands was the most unexpected result in this study. This result can be a direct effect of human disturbance (anecdotal in Acacia woodlands), since they were not more common in Oak woodlands where food abundance should be higher, either from animal or plant sources, and apparently better shelter conditions. Finally, bat diversity and activity is known to be higher in Oak woodlands than in Eucalyptus plantations (Cruz et al. 2016), and we were able to find differences in their abundance and species composition between these two woodland types. Many bat species are known to be woodland specialists and usually there are more species in heterogeneous woodlands (Russo et al. 2016). However, our highly fragmented study area associated with bats' high mobility and large home ranges should be important to explain our results. Most bat species were detected on all woodland types, but they spent more time in Oak woodlands, where species of night-flying arthropods were more diverse and its composition more heterogeneous.

Conclusions

Our results highlight the importance of truly holistic multi-taxa studies. Focusing on only a few indicator taxa can often lead to misleading conclusions, because the impact of the different woodlands on biodiversity depends greatly on the taxa studied. We showed that the biodiversity in exotic woodlands, either plantations or copses of an invasive species, was particularly low, and native tree plantations had an intermediate level of biodiversity between the exotic and native woodlands, in southwest Europe. The low biodiversity in novel woodlands is associated with simpler ecosystems and causes a significant reduction in their capacity to deliver other ecosystem services other than provisioning raw materials (Mace et al. 2012). The abundance and richness of animals from higher trophic levels did not seem to be directly related with the abundance and richness of their feeding resources. This suggests that higher trophic levels are more susceptible to habitat structure and anthropogenic pressures other than land use modifications. Our results also highlight the importance of maintaining native patches, even in highly fragmented landscapes, where they can function as biodiversity islands and support not only a broad number of species but also sustain them in considerable densities. Forest plantations are important for the local economy, particularly given the high fragmentation of forest ecosystems in the southwestern Europe region. However, as these novel forest ecosystems occupy very large areas and are continuously increasing, their specific biodiversity needs to be actively considered during conservation planning. Meanwhile it is clear that the remaining native forest fragments are crucial reservoirs to maintain high levels of biodiversity in this highly disturbed hotspot.

Chapter II

Flower visitation by birds in Europe

Abstract

Most flowering plants depend on animal pollination. Several animal groups, including many birds, have specialized in exploiting floral nectar, while simultaneously pollinating the flowers they visit. These specialized pollinators are present in all continents except Europe and Antarctica, and thus, insects are often considered the only ecologically relevant pollinators in Europe. Nevertheless, generalist birds are also known to visit flowers, and several reports of flower visitation by birds in this continent prompted us to review available information in order to estimate its prevalence. We retrieved reports of flower-bird interactions from 62 publications. Forty-six bird species visited the flowers of 95 plant species, 26 of these being exotic to Europe, yielding a total of 243 specific interactions. The ecological importance of bird-flower visitation in Europe is still unknown, particularly in terms of plant reproductive output, but effective pollination has been confirmed for several native and exotic plant species. We suggest nectar and pollen to be important food resources for several bird species, especially tits (*Cyanistes*), and *Sylvia* and *Phylloscopus* warblers during winter and spring. The prevalence of bird flower-visitation, and thus potential bird pollination, is slightly more common in the Mediterranean basin, which is a stopover to many migrant bird species, which might actually increase their effectiveness as pollinators by promoting long-distance pollen flow. We argue that research on bird pollination in Europe deserves further attention to explore its ecological and evolutionary relevance.

Keywords

Animal-plant interaction; bird pollination; nectarivory; passerine; pollen transport.

Introduction

Animal pollination is a key process in the reproduction of almost 90% of the 352 000 flowering plant species that form the foundation of most terrestrial ecosystems (Knight et al. 2005, Sargent and Ackerly 2008, Ollerton et al. 2011).

Together with insects, birds are prominent pollinators of many plant species. Globally, at least 500 plant genera are known to be pollinated by over 900 bird species (Sekercioglu 2006), and the actual number of flower-visiting birds may reach 1100 (Carstensen and Olesen 2009). The main pollinating bird families are the Trochilidae, Nectariniidae and Meliphagidae, but there are other important bird pollinators such as Icteridae, Thraupidae, Drepanidini, Promeropidae, Zosteropidae, Dicaeidae and Loriini, being present in all continents except Europe and Antarctica (Olesen and Valido 2003, Ortega-Olivencia et al. 2005, Carstensen and Olesen 2009).

Although there are no specialized nectarivorous bird species in Europe (Ortega-Olivencia et al. 2005, Cramp 2006), fossil records from the Eocene and the Oligocene suggest that birds close to the Trochilidae once lived in Central Europe (Mayr 2004, 2005, Louchart et al. 2008). The reason why these birds disappeared from Eurasia is still unclear (Mayr 2005). Given that flowers are such an ubiquitous and abundant resource, the apparent paucity of flower-bird visitation records in the literature suggests that it is an uncommon phenomenon (Ford 1985). However, a confirmation bias may also play a role, i.e. people see what they expect to see, and that goes for ornithologists as well. When a bird visits a flower an ornithologist expects it to be foraging for insects and does not value or report the interaction; botanists, by contrast, are those reporting most bird-flower interactions as they are focused on the plants (Straka 1989). Nectar is the major floral reward for most flower visitors, but pollen, floral oil, petals, water and flower-visiting arthropods may also attract birds and other potential pollinators (Grant 1996, Cecere et al. 2011b). Indeed, non-specialized nectarivorous birds are known to efficiently pollinate plants around the world (Fang et al. 2012). Bird flower visitation has also been reported in Europe, including some confirmation of effective pollination (Ortega-Olivencia et al. 2005), although its actual extent, richness and ecological relevance is still unknown (Ford 1985). Here we make an exhaustive review on the use of flowers as food source by birds in Europe and discuss their role as pollinators. We expect a low number of generalist and non-hovering bird species interacting with flowers (Fleming and Muchhala 2008) and consequently a relatively low number of interactions. However, this might be more common in the Mediterranean region where biodiversity is higher. Finally, we foresee a higher use of floral resources in winter and early spring, i.e. in periods with low numbers of invertebrates, plant pollinators and food source for birds (Cronk and Ojeda 2008, Cecere et al. 2011b).

Methods

We reviewed the literature to assemble all records of flower visitation by birds in Europe, using all information available until the end of 2013. Searches were conducted in www.scholar.google.com, www.isiknowledge.com, and “grey” publications, i.e. informally published, written material. In addition, we included unpublished personal observations. We limited the geographic extent of the searches to Europe, i.e. east to the Ural Mountains, including continental islands, but excluding any territories outside the European continental shelf. We compiled all records of birds feeding on open flowers or parts of open flowers (i.e. excluding flower buds), and also records of pollen attached to bird feathers or being present in faeces. Whenever available, the following information was retrieved: species or higher taxon of birds and plants, country or region and month of the observation, and type of interaction, i.e. nectar drinking, damaging the flower to access the nectar, nectarivory or florivory respectively. We included all bird species with persistent populations in Europe, including introduced species with self-sustained populations (Cramp 2006, Crochet and Joynt 2012). Plant taxonomy followed Angiosperm Phylogeny Group III system (Stevens 2001). When plant taxonomy was only available to supra-specific levels (most often genus), we considered the plant as native if there was any native European member of the taxon.

Evidence for bird flower visitation in Europe

Our search revealed 62 publications describing flower visitation by wild European birds. These came from general ecology journals (e.g. Oikos), specific botanical (e.g. Annals of Botany) and ornithological literature (e.g. Ardea, Ibis), including regional publications (e.g. Avocetta, British Birds).

Following some initial information from the end of the XVIII century on European bird-flower visitation (White 1789, Darwin 1791), there was no new information on this subject until 1874, when Charles Darwin noticed the particular way that some flowers were bitten, suggesting that this resulted from the behaviour of birds searching for nectar (Darwin 1874). Until 1959 all records originated from direct feeding observations. J. S. Ash was the first to record interactions based on the identification of pollen grains on bird feathers (Ash 1959, Ash et al. 1961). The first suggestions that European birds could be actively mediating pollination date to 1969 when *Turdus merula* was recorded visiting the flowers of the exotic *Puya chilensis*, which is pollinated by hummingbirds in its natural range in South America (Ebbels 1969). Twenty years later, the native *Rhamnus alaternus* was also reported to be potentially pollinated by *Sylvia atricapilla* and *S. borin* (Calvario et al. 1989). However, these studies did not evaluate the efficiency of birds as pollen vectors. In 1989, bird pollination was finally confirmed in Europe: *Cyanistes caeruleus* was shown to be a pollinator of the ornithophilous *Fritillaria imperialis*, introduced from Turkey and Asia (Búrquez 1989), and later other tit species were also suggested to pollinate this plant species (Peters et al. 1995). Recently, the native legume *Anagyris foetida* was observed to be pollinated by *Phylloscopus collybita*, *Sylvia melanocephala* and *S. atricapilla* (Ortega-Olivencia et al. 2005). Several continental species of *Scrophularia* also have a mixed pollination system consisting mainly of insects, but also birds (Ortega-Olivencia et al. 2012a). On the Italian Ventotene Island, the agriculturally important *Brassica oleracea* group (e.g. cabbage, broccoli, cauliflower) is more often visited by birds than insects and the exclusion of birds reduces fruit-set (Cecere et al. 2011a).

A quantitative analysis of bird-flower visitation in Europe

Our data compilation of bird-flower interactions (Table 3) includes 46 bird species, all but one belonging to the Passeriformes order (here we consider *Passer italiae* as a true species), feeding on flowers of 95 plant species in Europe, 66 native and 29 exotic (including cultivated and invasive plants; see Supplementary material, Table A1). This represents 9% of the total European avifauna, 22% of passerine species (Cramp 2006, Crochet and Joynt 2012), and 0.76% and 0.61% of the total European and native floras, respectively (Winter et al. 2009). These are certainly underestimates, considering the low taxonomic resolution of many records and that few European plants have been surveyed for bird visits. Overall, these reports document 243 different interactions between birds and plants. Of this, only six plant species are known to be effectively pollinated by birds (Búrquez 1989, Ortega-Olivencia et al. 2005, 2012a, Cecere et al. 2011a).

We further searched in our dataset for records of European bird or plant species with flower visitation obtained outside Europe (Table 3). We detected four bird species, two native passerines (*Iduna pallida*/*I. opaca*, formerly regarded as a single species, and *Sylvia crassirostris*) and two exotic species, *Estrilda astrild* and *Psittacula krameri* without any record of flower visitation in Europe and also at least 12 different plant species (see Supplementary material, Table A1). Furthermore, some long-distance migratory European passerine species show a regular nectarivorous behaviour in their African stopover sites during spring migration (Salewski et al. 2006, Cecere et al. 2010). Moreover, some Mediterranean-West European plant species, such as *Arbutus* sp. and *Ulex* sp., were found to be visited and possibly pollinated by birds in their exotic ranges, for example by honeyeaters in Australia (Ford 1985).

Table 3 – Number of bird and plant species and bird-flower interactions recorded, in all data, and data with geographic and temporal information.

			Bird species	**Plant species**	**Interactions**
All records	Europe	Total	46	95	343
		Native	46	66	220
		Exotic	0	29	98
	Outside Europe		13	14	30
Records with geographical information		Total	31	56	160
		Mediterranean	22	25	88
		North and Central Europe	20	32	72
Records with temporal information		Total	27	40	108
		Winter and Spring	26	36	100
		Summer and Autumn	8	5	8

Geographic and temporal patterns

We evaluated the geographical and temporal distributions of the interactions for which such information was available. Records based exclusively on pollen attached to feathers or bills were not included in this analysis, as the interaction might have occurred several months before and on a different region from where it was recorded (e.g. pollen found in feathers of Sylvia and Phylloscopus warblers (thereafter: warblers) in Denmark contained pollen from Mediterranean plant species, and one bird carried pollen from spring flowering plants in August (Laursen et al. 1997)).

Eighty-eight interactions (55%) were from the Mediterranean region (Table 3). Thus, as expected, flower visitation seems slightly more common in the Mediterranean basin where biodiversity is higher. Moreover, many interactions were recorded at the end of winter and beginning of spring making it difficult to separate both seasons. This led us to group both seasons, and as hypothesized most records were obtained during winter and spring (93%).

Ecological relevance of bird-flower interactions

As expected, the majority of the 50 flower-visiting bird species (46 in Europe and four from outside Europe) were trophic generalists, with flexible or opportunistic feeding habits that change throughout the year depending upon food availability (Cramp 2006). The most recorded bird flower visitors are included in Table 4, and belong mostly to the genus *Sylvia* (almost all European species visit flowers, but especially *S. atricapilla*, *S. borin*, *S. melanocephala*, *S. communis* and *S. curruca*), genus *Phylloscopus* (*P. collybita* and *P. trochilus*) and former genus *Parus* (particularly *Cyanistes caeruleus*). Most of these birds are mainly insectivorous or frugivorous, depending on the season. Typical granivorous bird species, particularly finches and sparrows, also visit flowers (for the complete list of interactions see the Supplementary material, Table A1). The number of flower-visiting birds is certainly underestimated and the scarce information from some regions may reflect a paucity of studies rather than of flower visitation. For example, Sylvia and Phylloscopus are prominent flower visitors in Western Europe, and it is most likely that ecologically/morphologically related taxa play a similar role in Eastern Europe. We also found bird species that rarely visit flowers, such as *Muscicapa striata*, *Hippolais icterina*, *Erithacus rubecula* and *Saxicola rubetra*. Many studies have analysed several samples of feathers and faeces of these species and rarely found pollen in them (Schwilch et al. 2001, Cecere et al. 2011b). In these publications, several other passerine species were also inspected for pollen, but showed no evidence of flower visitation, including, for instance, *Phoenicurus phoenicurus*, *Luscinia megarhynchos, Anthus trivialis, Oenanthe oenanthe, Ficedula hypoleuca, Acrocephalus scirpaceus and Acrocephalus schoenobaenus* (Schwilch et al. 2001).

Table 4 – Recorded interactions between the most common flower visitors and plants, the complete interaction matrix (x interactions) is available in Supplementary material Table A1 due to space constraints. **f** - pollen observed on feathers, forehead, bill or breast; **o** -feeding observation; **ns** - not stated; **fe** - pollen in faecal sample; **st** - stomach content; ? - most likely plant taxa; bold - exotic species; ( ) - record outside Europe; * - pollination confirmed.

Order	**Family**	**lower taxa**	*Cyanistes caeruleus*	*Phylloscopus collybita*	*Phylloscopus trochilus*	*Sylvia atricapilla*	*Sylvia borin*	*Sylvia. communis*	*Sylvia curruca*	*Sylvia melanocephala*
Apiales	Apiaceae	*Ferula communis*		o	o	o; fe	o; fe	o; fe	o	o
		Oenanthe sp.			o					
	Araliaceae	*Hedera helix*		f						
	Pittosporaceae	***Pittosporum tobira***					o	o		
Asparagales	Asparagaceae	***Agave Americana***			o					
		***Yucca* sp.**				o				
	Iridaceae	***Chasmanthe aethiopica***					(o)			
		Freesia laxa		o						
	Xanthorrhoeaceae	***Aloe arborescens***	O	o		o				o
		***Aloe* sp.**					ns	f?		
		***Kniphofia* sp.**	o							
Asterales	Asteraceae	tribe Anthemideae		f						
		sub-family Cichorioideae				f				
Brassicales	Brassicaceae	*Brassica fruticulosa*				o; fe	o; fe	o		
		Brassica incana		o		o	o	o		o
		*Brassica oleracea**					o	o		
		Family Brassicaceae		f	f	f	f		f	
	Capparaceae	***Maerua crassifolia***		(o)	(o)			(o)		
Buxales	Buxaceae	*Buxus* sp.		f		f				
Caryophyllales	Caryophyllaceae	Family Caryophyllaceae		f						
Dipsacales	Adoxaceae	*Sambucus* sp.		f						
		Viburnum sp.		f		f				
Ericales	Theaceae	***Camellia* sp.**	o							
Fabales	Fabaceae	***Acacia* sp.**		f						
		*Anagyris foetida**	f	f; o; fe		f; o; fe				f; o; fe
		Erythrina tomentosa					(o)			
		Parkia biglobosa			(o)					
Fagales	Betulaceae	*Betula* sp.	o	f	f	f	f		f	
	Fagaceae	*Quercus* sp.		f	f	f	f		f	
	Myricaceae	*Myrica faya*		f						
		Myrica gale		f						
Lamiales	Bignoniaceae	***Tecoma capensis***	o							
		***Tecoma* sp.**				(o)			(o)	
	Oleaceae	*Fraxinus excelsior*	o							
		Fraxinus sp.		f	f	f				
		Jasminum nudiflorum				o				
	Plantaginaceae	*Plantago lanceolate*		f						
	Scrophulariaceae	*Scrophularia grandiflora**				o				o
		*Scrophularia sambucifolia**		o		o				o
		*Scrophularia trifoliata**				o				o
Liliales	Liliaceae	***Fritillaria imperialis****	o		o	o	o		o	
Malpighiales	Euphorbiaceae	***Euphorbia pulcherrima***		o						
	Salicaceae	*Populus* sp.		f		f				
		Salix caprea	o	o		o				
		Salix cinerea	o							
		Salix sp.	o	f	f	f				
Malvales	Malvaceae	***Abutilon* sp.**				(o)				
		***Hibiscus* sp.**	o							
		Lavatera arborea				o	o	o		o
		Malva sylvestris					o			
Myrtales	Myrtaceae	***Callistemon* sp.**				(o)				
		Eucalyptus globulus		o						
		***Eucalyptus* sp.**		f; o	f	f; (o)	f		f; (o)	
	Onagraceae	***Fuchsia sp.***				o	o			
Pinales	Cupressaceae	*Juniperus phoenicea*			f?					
	Pinaceae	*Pinus* sp.		f	f	f	f		f	
Proteales	Proteaceae	***Grevillea robusta***			(o)		(o)			
Ranunculales	Berberidaceae	***Mahonia japonica***	o			o				
Rosales	Cannabaceae	***Cannabis* spp.**		f					f	
	Rhamnaceae	*Rhamnus alaternus*				o	o			
	Rosaceae	*Crataegus* sp.			st	f; st	ns; st	st	st	
		Eriobotrya japonica	o	o		o				o
		Prunus dulcis	o			o				
		Prunus sp. or *Sorbus* sp.		f	f	f				
		sub-family Amygdalaceae		f	f	f	f		f	
	Ulmaceae	*Ulmus glabra*	o							
	Urticaceae	*Urtica* sp.		f		f	f		f	
Sapindales	Rutaceae	***Citrus aurantium***						f?		
		Citrus sinensis				(o)				
		***Citrus* sp. (not *C. aurantium*)**						f		
		***Citrus* sp.**		f	f	f	f	f	f	
	Sapindaceae	*Acer pseudoplatanus*						f?		
		Acer platanoides				o	o			
		Acer sp.		f					ns	
Saxifragales	Grossulariaceae	***Ribes sanguineum***	o						o	
		Ribes uva-crispa	o							
Solanales	Convolvulaceae	*Calystegia* sp.		f; o						

Most bird-flower visitation in Europe occurs while birds are perching, as opposed to specialized nectarivory birds, which normally hover in front of flowers (Fleming and Muchhala 2008). The only exceptions are the genus *Phylloscopus* and *Regulus* that can feed either while perched or hovering (Rodríguez-Rodríguez and Valido 2008, Ortega-Olivencia et al. 2012a). While some species, such as warblers, mainly drink floral nectar and act as legitimate pollinators (Ortega-Olivencia et al. 2012a), others such as finches and sparrows are mostly nectar robbers, often damaging flowers by tearing parts off the perianth or piercing holes to reach the nectar, without touching the flower reproductive structures (Búrquez 1989). Finally, some species as *Cyanistes caeruleus*, can be both legitimate and illegitimate visitors depending on the flower structure and position (Búrquez 1989, Fitzpatrick 1994). Even when flowers are damaged during a visit, many of them may still produce fruits (Swynnerton 1917). Other bird species, such as the *Phyrrula phyrrula*, are well known to eat flower buds. During this process, they may touch nearby open flowers and potentially transfer pollen between plants (these cases, however, were not included in our dataset).

In most flower-visiting birds, pollen is adhered to the bill and feathers around upper mandible and on forehead, face, chin, and sometimes even on breast feathers (Ash et al. 1961, Laursen et al. 1997, Schwilch et al. 2001). However, in finches they often occur half-way out on the mandibles and sometimes only on the lower mandible (Ash et al. 1961). If pollen loads are large and humidity is high, birds may accumulate a hornlike structure on the forehead known as a pollen horn (Laursen et al. 1997). Pollen horns can persist on the birds for several weeks or even months, storing information on bird-flower visits until feathers get shed.

Flower visitation seems to be more common during the early stages of an ecological succession, when annual plants and flowers are more abundant (Cecere et al. 2010). During their spring migration, at least *S. borin* and *S. communis* seem to prefer nectar to insects (Schwilch et al. 2001). This choice might be explained by the chemical content of nectar, i.e. water and simple sugars, being readily absorbed by the digestive tract of the birds, which is reduced during migration (Schwilch et al. 2001, Cecere et al. 2011b). Finally, handling time of flowers is shorter than that of insects, and flowers may also be easier to locate (Cecere et al. 2010, 2011b). Although *Cyanistes caeruleus* does not prefer nectar as its major food source, it is even able to select the most productive flowers (Fitzpatrick 1994). Finally, the low insect availability during winter and cold springs may force birds to feed on flowers.

The most common pollen grains found on European birds belong to the genera *Brassica*, *Citrus* and *Eucalyptus* (Ash et al. 1961, Laursen et al. 1997, Schwilch et al. 2001, Cecere et al. 2011c, Provost et al. 2012). Their flowers are certainly among the most important to nectar-foraging birds. However, their importance for bird populations cannot be easily estimated, due to regional variation in flower, arthropod and seed abundances and in the incomplete sampling of this interaction type. While some bird-visited flowers have bird-pollination characteristics such as *Fritillaria imperialis* (Búrquez 1989, Peters et al. 1995), most have insect-pollination traits such as *Brassica* or wind-pollination traits such as *Quercus* sp. (Cecere et al. 2011a, c). Most plants reported do not require bird pollination, so it is expected that birds are the most benefitted in the interactions. The fact that almost one third of bird-visited plants are exotic and involved in approximately one third of the recorded interactions (Table 3) raises interesting ecological questions such as which is the role of these exotic plants to wintering and migrating bird populations, and how important birds may be for the pollination and subsequent expansion of these exotic plants. On the other hand, native plants visited by birds offer an equally stimulating research topic with evolutionary implications. It would be particularly interesting to know not only how many plant species are benefitting from birds, but also to what extent, and how important their flowers are to birds. Studies using a combination of methods, as direct observations and pollen load in birds, should be able to answer these and other ecological and evolutionary questions.

General remarks

Records of flower-visiting birds in Europe have been frequently considered to be rare and with reduced ecological relevance. This work shows that the relationship between birds and flowers is richer and more widespread than hitherto thought. European flower-visiting birds are mainly food generalists that may expand their food niche and explore flowers for nectar and other floral resources. Floral resources may be crucial to winter and spring migration survival, and the early reproductive phase of many bird species. Nearly one third of the plant species visited are exotic, and are involved in almost the same proportion of the total interactions, which might have important ecological implications. On the other hand, the bird-flower interaction with native flora is still poorly understood and likely has evolutionary and ecological implications, opening two promising research topics. Due to their high mobility, birds may fulfil an important function as long–distance pollen vectors (Yates et al. 2007). However, our understanding of the ecological relevance of bird-flower interactions in Europe is still in its infancy.

Chapter III

Flower visitation by European birds offers the first evidence of interaction release in continents

Abstract

Aim - All species are imbedded on a network of interactions with other species, which define an important component of their ecological niche. These interactions are dynamic and can change the emergence of vacant niches in the environment. Niche adjustments have been predicted to be particularly common on insular communities as a response to the poor and disharmonic biota of oceanic island – the Interaction Release Hypothesis, however the phenomena has not yet been reported on continents. Specialized nectarivorous birds are present on all continents except in Europe where they became extinct in the Oligocene, likely leaving behind underexplored flower resources. We performed the first community level assessment of flower visitation by European birds to evaluate if insectivorous and granivorous birds show an interaction release towards consuming flower resources in Europe.

Location - Larçã - Coimbra, Portugal, Europe

Methods - During one year, we collected pollen loads from 634 birds. Pollen loads were prepared by acetolysis and all pollen grains were identified under a microscope. All interactions were compiled into a quantitative interaction matrix describing the first pollen-transport network by European birds.

Results - One fifth of the birds sampled, corresponding to 21 species, carried 45 pollen types. The vast majority of the plant species found were native but the alien *Eucalyptus globulus* was by far the most common. Overall, the structure of the pollen transport network from Europe shared many attributes of other networks that include specialized nectarivorous birds.

Main conclusions - We show that the interaction release hypothesis is not exclusive to insular communities but can also be observed in continents, greatly increasing the potential geographic distribution of this phenomenon. However, it seems considerably less pronounced in Europe than in the Galápagos, where it was first described, probably due to the much stronger selective pressures on the simplified ecosystems of oceanic islands.

Keywords

Bird-flower network; mutualistic networks; ecological niche; resource opportunity; ecological release; pollen transport; rewiring; trophic niche.

Introduction

All species are imbedded in an intricate web of interactions upon which they depend to survive and reproduce (Tylianakis 2008). These inter-specific interactions form a fundamental component of each species ecological niche – the Eltonian niche (Elton 1927). Obviously, these interactions are not static but they constantly change in response to environmental alterations, such as the colonization of remote sites, the arrival of new competitors or the local extinction of co-occurring species (Cox and Ricklefs 1977, Keane and Crawley 2002, Refsnider et al. 2015). Specifically, when a species experiences a reduction in the pressure from competitors, predators or parasites, it frequently expands its niche by increasing its population size, expand its distribution area, and including new items in its diet, a phenomena known as ecological release (Cox and Ricklefs 1977, Bolnick et al. 2010, Refsnider et al. 2015). A particular case of ecological release has been documented on oceanic islands, which are characterized by disharmonic biotas and overall low species richness, as a result of long distance dispersal limitations (Whittaker and Fernández-Palacios 2007, Heleno and Vargas 2015). On the other hand, the few species that successfully colonize islands, free from their continental natural competitors often sustain large population densities (Cox and Ricklefs 1977). The interaction release hypothesis postulates that in this particular conditions of high intraspecific competition and available empty niches due to dispersal filtering, insular animals can expand their classic trophic niche in order to include underexplored resources (Traveset et al. 2015). A remarkable example is the massive shift of Galápagos land bird species that expanded their initially insectivorous and granivorous diets in order to consume nectar and pollen from flowers, as a response to low insect abundance in these islands (Traveset et al. 2015). While this hypothesis was developed considering the typical biological disharmony of oceanic islands, comparable high-quality datasets accessing pollen transport by birds on continental communities are still lacking, and therefore it is still not clear if this is strictly an island phenomena (Traveset et al. 2015).

Specialized nectarivorous birds are present on all continents except Europe, namely: hummingbirds (Trochilidae Vigors, 1825) and tanagers (Thraupidae Cabanis, 1847) in the Americas, sunbirds (Nectariniidae Vigors, 1825) in Africa and southern Asia, honeyeaters (Meliphagidae Vigors, 1825) in Oceania, sugar-birds (Promeropidae Vigors, 1825) in southern Africa, honeycreepers (Drepanidini James, 2004) in Hawaii, flowerpeckers (Dicaeidae Bonaparte, 1853) and lories (Loriini Selby, 1836) in south-eastern Asia and Oceania (del Hoyo et al. 2016). Nevertheless, the fossil record indicates the presence of nectarivorous birds in Europe, at least until the early Oligocene, i.e. 30 million years ago (Mayr 2004, Louchart et al. 2008). These birds very likely fed actively on flowers (Mayr and Wilde 2014) and their extinction likely left an ecological opportunity of available flower resources that could be explored by other non-specialized nectarivorous birds. Flowers, and particularly nectar, represent an abundant and valuable resource in many regions of the world, and therefore it is no surprise that even birds without specific adaptations for nectar consumption try to explore flower resources when they are available (da Silva et al. 2014). Indeed, several studies report this opportunistic behaviour on insectivorous and granivorous birds (e.g. Ortega-Olivencia et al., 2005; da Silva et al., 2014; Calviño-Cancela & Neumann, 2015). However, these records come from taxonomically or temporal restricted studies not encompassing whole communities (Cecere et al. 2011b, Ortega-Olivencia et al. 2012b, Wood et al. 2014, Calviño-Cancela and Neumann 2015). Therefore, we are still largely ignorant of the extent of this phenomenon at the community level, which is the appropriate organizational level to detect an interaction release (Traveset et al. 2015), and thus unable to understand if the phenomenon is geographically restricted to island communities or if it can also occur on the more complex continental communities. Ecological networks provide a powerful tool to explore community level patterns, by considering simultaneously community composition, structure and function (Heleno et al. 2014), however they require an intensive field sampling, which practically hinders large scale replication (Heleno et al.

2014). Here we built the first year-round and community wide, bird-flower interaction network on a continent to look for evidence of an interaction release of a European bird community as a response to the absence of specialized nectarivorous birds. Given the alternative food sources provided by the complex habitat structure in Europe and the competition for flowers from insects, we expect some consumption of flower resources by insectivorous and granivorous birds, mainly during periods of main food shortage e.g. winter, but not as high as that reported for the Galápagos Islands, where the phenomenon was first described (Traveset et al. 2015).

Material and methods

Study area

The study was performed in a secondary native forest in Larçã (40°19’N; 8°24’W) near Coimbra, central Portugal, under a Mediterranean climate influence, with hot and dry summers and mild winters. The forest in Larçã resulted from the gradual replacement of an old *Pinus pinaster* Aiton plantation by autochthonous vegetation, forming a dense Mediterranean scrubland, dominated by *Arbutus unedo* L. and *Quercus faginea* Lam., with some pines left.

Data collection

From June 2013 to May 2014, we captured birds twice per month using Ecotone mist nets (Gdynia, Poland) and released them after collecting pollen loads from their head. Pollen loads were collected by cutting a few feathers from the forehead of captured birds, which were individually marked so that they were not resampled on the same day. The feathers were directly stored in sterile Eppendorf tubes and latter prepared by acetolysis (Erdtman 1960) and mounted in glycerine jelly on three microscope slides. Due to the high viscosity of the mounting solution, approximately 20% of the solution was lost by adherence to walls of the tubes during preparation of the samples (da Silva et al. 2016). All slides were scanned under a light microscope to identify and quantify all pollen grains. Pollen was identified to the lowest possible taxa, most frequently to species or genus, but sometimes to a morphopollinic group. Identification was performed at 1000x magnification, based on its morphology (shape, exine sculpture, number and types of apertures, etc.) based on a reference collection and specialized bibliography (Kapp 1969, Moore and Webb 1978, Belmonte et al. 1986, Valdés et al. 1987, Mateus 1989, Reille 1992, Queiroz 2012).

Data analysis

All interactions between bird species and pollen types have been compiled into a single, quantitative interaction matrix. No direct observations of feeding birds were performed during this study. We considered an interaction when intact pollen was found in a sample (Traveset et al. 2015). In the cases where a plant was not identified to the species level but to a higher taxonomic level, it was considered native if any representative of those taxa occurs naturally in the region. Bird trophic guilds were determined according to del Hoyo et al. (2016) as insectivores, granivores and omnivores. The dataset was sorted into four main seasons: summer (from June to August), autumn (September to November), winter (December to February), and spring (March to May). An evaluation of the level of sampling completeness for species was performed by implementing the Chao asymptotic richness estimator (Chao 1987) in package `vegan´ (Oksanen et al. 2016) for R 3.2.2 (R Core Team 2016). To analyse the importance of each bird feeding trophic guild and plant origin in the network structure, the following species-level descriptors were calculated: linkage level, i.e. the number of species in the network with which a focal species interacts; species strength, a measure of a species' importance across all its partners (Bascompte et al. 2006); and specialization index (d'), describing the level of selectiveness for partners of each species (Blüthgen et al. 2006). In order to evaluate how the structure of the assembled bird-flower network is related to other previously described bird-flower networks, the following network structure descriptors were calculated: connectance, i.e. the proportion of realized links from all possible links (Jordano 1987a); weighted nestedness (WNODF), indicating the degree to which the interactions of the most specialist species are nested within the partners of the most generalists (Almeida-Neto and Ulrich 2011); interaction evenness, measuring the Shannon's evenness of interaction frequencies (Bersier et al. 2002); network specialization index (H_2'), i.e. the degree of network selectiveness as the departure from a theoretical non-discrimination of interactions (Blüthgen et al. 2006); and modularity (Q), evaluating the presence of clusters of strongly interacting species using the QuanBiMo algorithm (Dormann and Strauss 2014). As the QuanBiMo can produce slightly different modularity estimates between runs, we performed 100 independents runs set to 10^8 swaps of the network and selected the highest modularity (Valverde et al. 2016). Network analyses were performed using package `bipartite´ (Dormann et al. 2008) in R 3.2.2.

We compared our European bird-flower network with the only other available network of pollen transport by non-specialized nectarivorous birds, that of Galápagos (Traveset et al. 2015), and also with other bird-flower networks which include both specialized and non-specialized nectarivorous birds. Because the majority of bird-flower network metrics available in the literature had qualitative descriptors (Traveset et al. 2015, Vizentin-Bugoni et al. 2016) we also calculate the qualitative versions of nestedness (NODF) and modularity (M), with software ANINHADO 3.0.3 (Guimarães Jr and Guimarães 2006) and Netcarto (Guimerà and Amaral 2005), respectively. The level of network specialization (H_2') was further compared with that of the networks described in Dalsgaard et al. (2011), Maruyama et al. (2014) and Vizentin-Bugoni et al. (2016). The significance of the network metrics was assessed by comparing the observed values to those from 1000 networks assembled under null model *vaznull* in package bipartite and model *Ce* in Aninhado. Comparisons of species-level network descriptors between bird guilds (insectivores, granivores and omnivores), plant's origin (native or alien), and season (summer, autumn, winter and spring) were performed with general linear models (GLMs), with a significance level of $\alpha<0.05$ with the package `lme4´ (Bates et al. 2015) in R 3.2.2. Undetermined pollen types, i.e. types without identification of the plant family, representing 3% of all interactions, are shown in table 1, but were excluded from the comparisons. Data are presented as mean ± SD.

Results

Overall, 634 individual birds from 31 species were sampled and pollen grains were found on 129 of these birds (20%) from 21 species (68%; Figure 4). A total of 45 different pollen types were found, of which half (51%) were identified to the genus or species level and the remaining were identified to the family or to a morphopollinic group, that in most cases represent groups from known plant families (Table 5). Therefore, the resulting network quantifies 105 links between birds and plant species (Figure 5). Our sampling detected 84% of the bird species and 63% of the pollen types estimated by the Chao asymptotic richness estimator. Most interactions were detected in winter (GLM: t=2.176, P=0.042) and there were no significant differences on the presence of pollen throughout the other three seasons.

The most frequently captured bird species, *Sylvia atricapilla* Linnaeus, 1758, was also the species that most frequently carried pollen, representing 49% of the individuals with pollen (Figure 4).

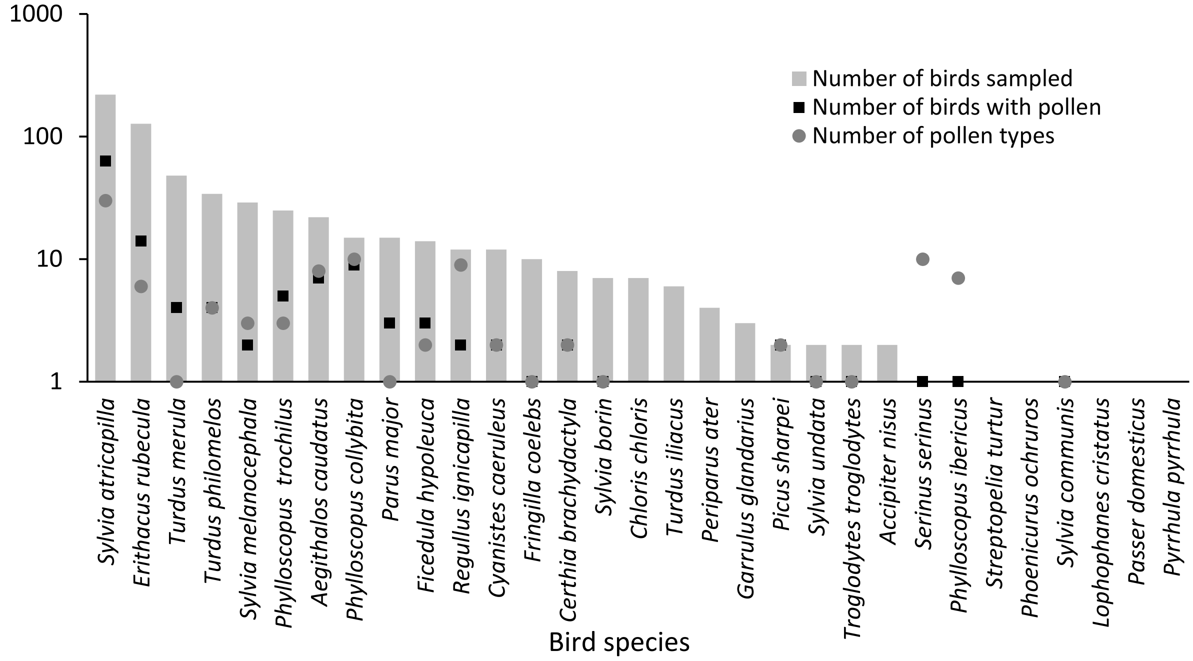

Figure 4 – Number of birds captured and presence and diversity of pollen grains found on each bird species in the Larçã – Portugal network. Notice the logarithmic scale. Bird species are ordered by abundance.

Pollen loads had an average of 568 pollen grains (SD =1 980; Min.=1, Max.=13 008). Approximately one third of the pollen loads (30%) were mixed, i.e. had pollen of more than one type (1.7±1.5, Min.=1, Max.=10 pollen types per sample). Native plants species represented most of the interactions (57%). Nevertheless, approximately half (53%) of the samples with pollen contained pollen of the alien tree species, *Eucalyptus globulus* Labill., which alone represented 31% of all detected interactions (Table 5). On average each bird species carried pollen of five different types (Min.=1; Max.=30) and each pollen type was dispersed by 2.3 bird species (Min.=1; Max.=12).

Table 5 – Origin, family and number of interactions for each plant taxa or pollen type transported by birds in the Larçã - Portugal network.

Origin	Family	Lower taxa or pollen type	Number of samples
Alien	Cupressaceae Bartlett	*Cupressus* sp.	2
	Myrtaceae Juss.	*Eucalyptus globulus* Labill.	68
	Pinaceae Lindley	*Cedrus* sp.	18
Native	Adoxaceae E.Mey.	*Viburnum* sp.	1
	Amaranthaceae Juss.	Amaranthaceae Juss.	2
	Anacardiaceae (R.Br.) Lindl.	*Pistacia* sp.	1
	Araliaceae Juss.	*Hedera* sp.	1
	Asparagaceae Juss./Amaryllidaceae J.St.-Hil.	Asparagaceae/Amaryllidaceae	1
	Asteraceae Bercht. & J.Presl	Anthemideae Cass.	3
		Cichorieae Cassini	3
		Cynareae Lam. & DC.	2
	Betulaceae Gray	*Alnus* sp.	1
		Betula sp.	1
	Brassicaceae Burnett	type *Capsella bursa-pastoris* (L.) Medik.	5
		type *Raphanus raphanistrum* L.	7
		type *Sinapis arvensis* L.	5
	Caryophyllaceae Juss.	Caryophyllaceae	1
	Cistaceae Juss.	type *Cistus ladanifer* L.	1
		type *Halimium halimifolium* (L.) Willk.	2
	Ericaceae Juss.	*Arbutus unedo* L.	1
		Calluna vulgaris (L.) Hull	2
		Erica arborea L.	4
		Erica lusitanica Rudolphi	3
		Erica scoparia L.	2
	Fabaceae Lindl.	*Cytisus* sp.	1
	Fagaceae Dumort	*Quercus* sp.	12
	Lamiaceae Martynov	type *Mentha aquatica* L.	1
		type *Salvia verbenaca* L.	1
	Oleaceae Hoffmanns. & Link	*Olea europaea* L.	1
		Phillyrea latifolia L.	2
	Pinaceae Lindley	*Pinus* sp.	30
	Plantaginaceae Juss.	*Plantago* sp.	1
	Poaceae Barnhart	Poaceae	7
	Rhamnaceae Juss.	*Rhamnus alaternos* L.	6
	Rosaceae Juss.	*Prunus* sp.	5
		Rubus sp.	3
		Rosaceae type 1	1
		Rosaceae type 2	2
	Salicaceae Mirb.	*Salix* sp.	4
Unkno	Unknown	Type 1	2
		Type 2	1
		Type 3	1
		Type 4	1
		Type 5	1
		Type 6	1

We found no differences on the interaction patterns established by the three bird guilds. On average, alien plant species were present on more samples (GLM: *t*=-2.401, *P*=0.021), were dispersed by more bird species (GLM: *t*=-2.449, P=0.019) and had a higher species strength (GLM: *t*=-2.731, *P*=0.010) than native plants, but they did not differ in their specialization level d’ (GLM: *t*=-0.532, *P*=0.598). Network specialization (H_2’) was low but not significantly different from the null model expectation (H_2’=0.21, *P*=0.146), while interaction evenness was significantly lower than that of the null models (IE=0.58, *P*=0.001). Connectance was generally low (11.1%) and was not confronted to a null model expectation (which assumes fixed connectance). The qualitative (unweighted/binary links) network was significantly nested (NODF=37.8, p<0.001) and was not modular (*M*=0.46, *P*=0.333), while the quantitative network (weighted links) was not significantly nested (WNODF=21.45, P=0.414) but was significantly modular (*Q*=0.33, p<0.016). When comparing the structure of the European network described here, with the structure of other bird-flower networks available in the literature, including that from the Galápagos Islands, we observe that for nearly all descriptors, the structure of the our bird-flower network lay within the range of the values found for the others networks (Figure 6). The only exception was connectance that is slightly lower in our network.

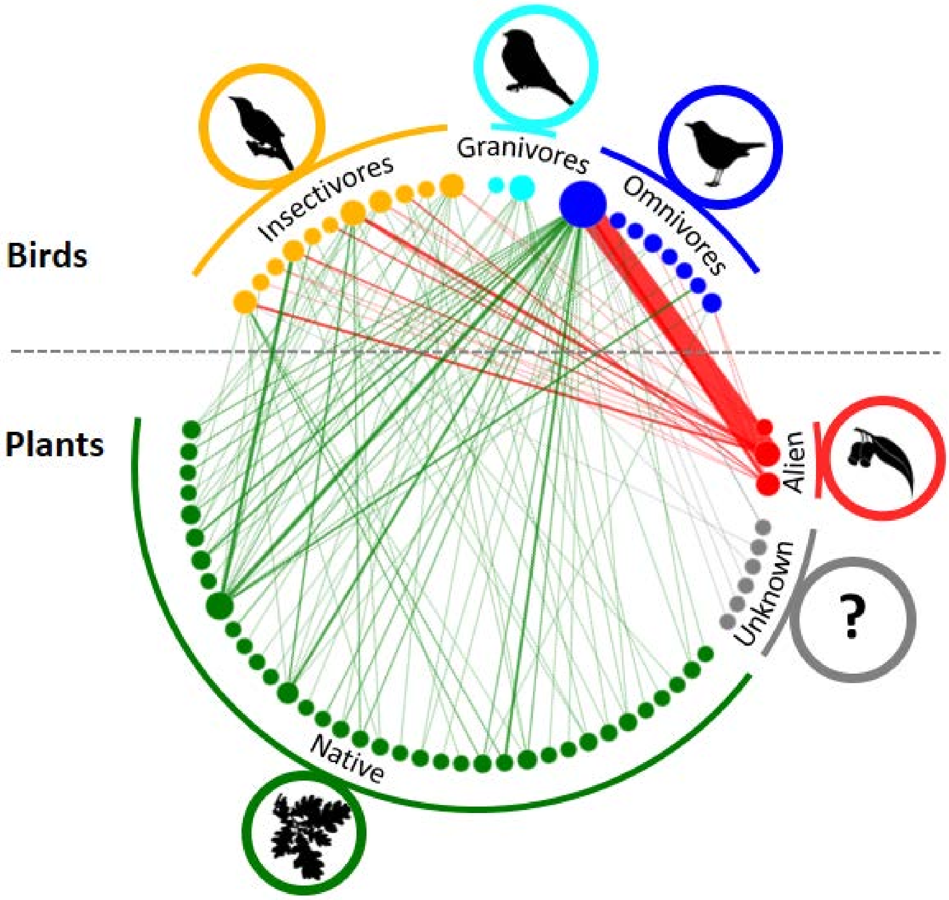

Figure 5 – Quantitative pollen transport network by non-nectarivorous birds in Larçã, Portugal, representing the interactions between 21 bird species and 45 pollen types (morphospecies). The size of each nodes is proportional to the number of links (i.e. linkage level), and the width of the links is proportional to the frequency of the interaction (i.e. number of bird samples containing pollen grains of each type).

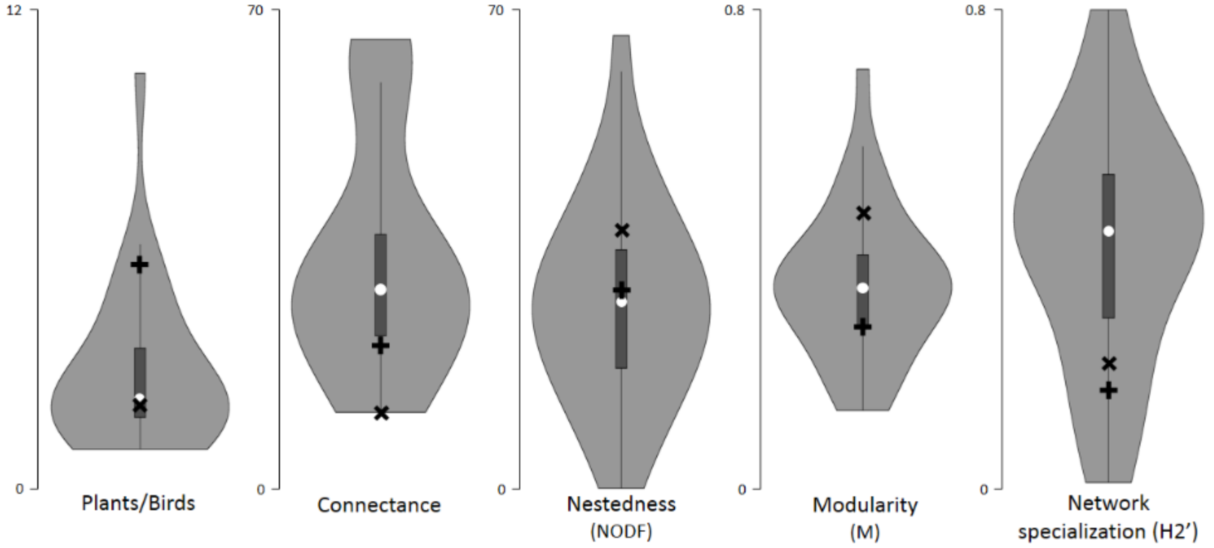

Figure 6 – Violin plots showing how the structure of the pollen transport network by non-nectarivorous birds reported here (represented by an X), relates with similar networks by specialized nectarivorous birds reported around the world and also with the Galápagos network of non-nectarivorous birds (represented with a +). The white circle represents the median, the dark grey box represents the 25th and 75th percentiles, the middle line the upper and lower adjacent values and the light grey represents the kernel density of all data points (Hintze and Nelson 1998). The plants/birds ratio, connectance, nestedness (NODF) and qualitative modularity (M) were based on the data provided in Traveset et al. (2015) and Vizentin-Bugoni et al. (2016), while network specialization (H_2’) also included the data provided in Dalsgaard et al. (2011) and Maruyama et al. (2014).

Discussion

The relatively high frequency of birds carrying pollen grains on their foreheads, and the high abundance and richness of pollen grains found, suggests that many birds, up to one fifth, have been actively feeding on flowers. Although there is no absolute threshold based on which interaction release can be considered to occur or not, the number of European non-specialized birds that likely fed on flowers does not seem to be rare or anecdotal, suggesting the general occurrence of this phenomenon. We cannot rule out the possibility that some pollen grains detected in very small numbers, might have been loaded indirectly from airborne pollen, bird handling, or when birds forage on food sources, other than flowers, resulting in contaminations. In order to facilitate the comparison with previous studies, we considered the presence of any pollen grain found in a sample as evidence that an interaction occurred, similarly to the approach of the Galápagos study (Traveset et al. 2015). If we apply a more conservative approach, and exclude all interactions with fewer than five pollen grains of a specific type, as did Banza et al. (2015) in a study on pollen transport by moths, the resulting network would quantify 31 links between 18 pollen types and nine bird species (Figure 7). This approach will remove approximately 85% of the interactions with typical wind-pollinated plants, which are potential contaminations. The alternative of removing the typical wind-pollinated plants from our network would probably be over-conservative since some birds species (*e.g. Cyanistes caeruleus* (Linnaeus, 1758), *Phylloscopus collybita* (Vieillot, 1817) and *Regulus ignicapilla* (Temminck, 1820)) were seen on several occasions actively foraging on flowers of *Q. faginea*, a typical wind-pollinated plant. Moreover, *Quercus* spp. pollen loads reach as much as 732 pollen grains in a single sample from a *R. ignicapilla*. Nevertheless, as we collected a small proportion, i.e. only a few feathers, from each bird, and only 80% of the mounting solution was used in the microscopic slides, the pollen grains identified in the slides represent only part of the total number of pollen grains transported by each bird at the time it was sampled.

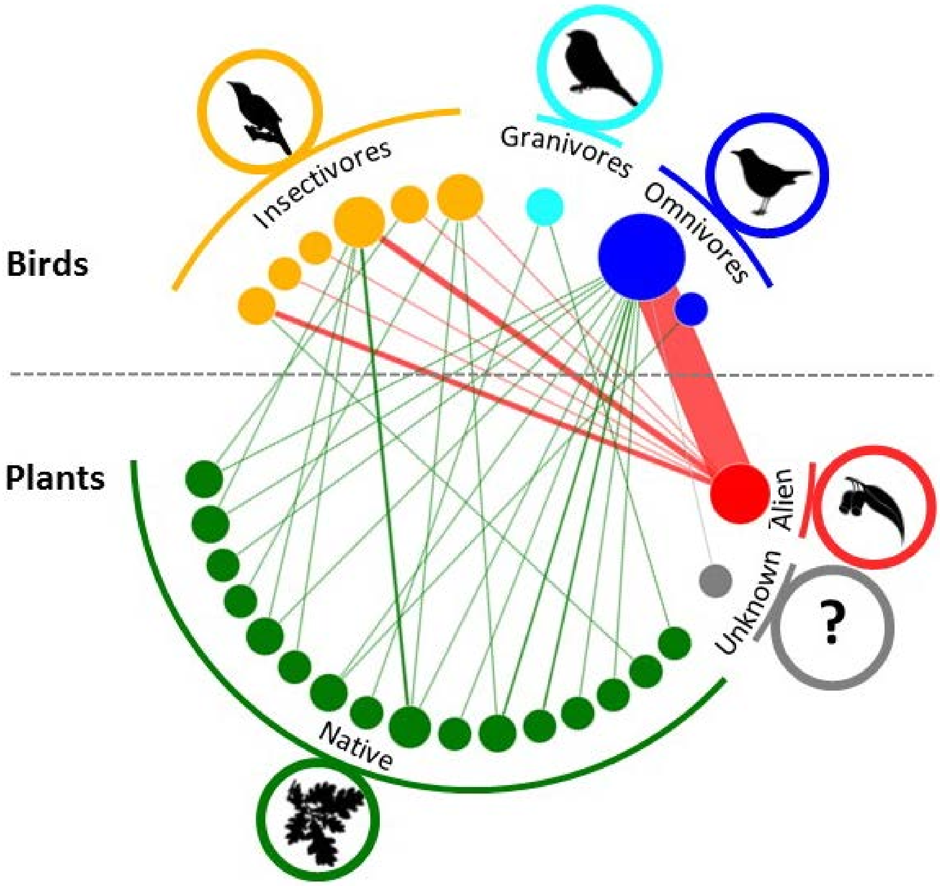

Figure 7 – Quantitative pollen transport network by non-nectarivorous birds in Larçã, Portugal, where samples with less than five pollen grains were truncated to exclude potential sources of contamination. The network represents the interactions between nine bird species and 18 pollen types (morphospecies). The size of each node is proportional to the number of links (i.e. linkage level), and the width of the links is proportional to the frequency of the interaction (i.e. number of bird samples containing pollen grains of each type).

At least 61 bird species are known to visit flowers or transport pollen in Europe (da Silva et al. 2014, Calviño-Cancela and Neumann 2015). However, these records result from anecdotal observations (see da Silva et al., 2014) or from studies either focused on specific time periods or taxonomically restricted groups (Cecere et al. 2011b, Ortega-Olivencia et al. 2012b, Wood et al. 2014, Calviño-Cancela and Neumann 2015), and this is the first community level assessment quantifying pollen transport by birds in Europe. Our study confirms that pollen transport by European birds is not a rare or anecdotal event but that it is frequent and generalised. Birds tended to expand their diet niche to consume flower resources particularly when the availability of their typical food sources is low, such as insects during the winter (Wolda 1988), confirming the prediction of da Silva et al. (2014). It has been shown that non-specialized European birds can act as legitimate pollinators of both, native (Ortega-Olivencia et al. 2005) and alien plants (Búrquez 1989). Although the most common pollen found was from the alien *E. globulus*, the vast majority of the pollen types dispersed were native (Figure 5). Our dataset suggest that European birds visit the flowers of very few exotic plant species (Table 5), nevertheless they can be important for their establishment if they mitigate the loss of their native pollinators (Traveset and Richardson 2014). This may occur for example for *E. globulus* which has a mixed pollination system by insects and birds on its native range (Hingston et al. 2004), or for typical ornithophilous plants such as *Fritillaria imperialis* L. introduced in Europe from Asia (Búrquez 1989) or *Aloe arborescens* Mill. from Africa (da Silva et al. 2014).

The comparison of network structure descriptors across multiple studies should be interpreted carefully (Traveset et al. 2016). Nonetheless, it is clear that for most network structure descriptors, the pollen transport network by non-specialized European birds falls within the range of values reported for networks including specialized nectarivorous birds and for the Galápagos network, which is also formed by non-specialized nectarivorous (Figure 6). The diet shift observed in all Galápagos bird species, when compared to the shift observed in 68% of the bird species in this study suggests that the ecological release is more intense in the Galápagos. This might be explained by the overall lower insect abundance and the most extreme biotic and abiotic environment in the Galápagos, resulting in stronger intra-specific competition for resources and stronger selective pressure to explore alternative resources (Traveset et al. 2015). Alternatively, European birds have a greater diversity of alternative food sources and also have a richer insect community competing for flower resources. Both European and Galápagos networks are less specialized (H_2') than most nectarivorous bird networks (Figure 6), however the Galápagos presents particularly low levels of specialization, reflecting the stronger interaction release.

The contrasting results of nestedness and modularity between quantitative or binary matrices were also reported for hummingbird networks in Brazil (Vizentin-Bugoni et al. 2016) and highlight the problem of extracting network structure descriptors from binary (presence/absence) interaction data (Banašek-Richter et al. 2004, Blüthgen et al. 2006, Vizentin-Bugoni et al. 2016).

The first pollen transport network by a community of non-nectarivorous continental birds, reveals that interaction release is not an exclusively island phenomena, but it occurs on a much wider geographical area. Nevertheless, European birds show a less pronounced response than the Galápagos bird community to the presence of underexplored flower resources, suggesting that interaction release is stronger on oceanic islands given their poor and disharmonic biota. We detected interaction release in the absence of a specialized nectarivorous bird community in Europe. This work represents an important step into quantifying pollen dispersal by European birds, however much work is still needed in order to fully evaluate the amplitude and ecological relevance of this process. Finally, testing the interaction release hypothesis on other types of mutualistic and antagonistic interactions, and on other communities around the world, will provide us a much better picture about the geographical and ecological relevance of community-level diet shifts.

Chapter IV

Dispersal of fungi spores by non-specialized flower-visiting birds

Abstract

Birds are important biotic dispersers of a wide range of propagules. Fungi spores are mainly dispersed by wind. Nevertheless there are several animals known to disperse fungi spores, which might be particularly important if spores are delivered to particularly favourable sites i.e. directed dispersal. This may be especially important for fungi that require specific microsites such as flowers. We sampled birds for the presence of fungi spores and pollen grains during one year at two forest sites in central Portugal. We found that out of the 894 birds sampled, 131 individuals from 11 species carried spores from at least 6 morphological types, mainly during winter. The great majority of birds found to carry fungi spores was also found to carry pollen grains, suggesting that they were feeding on flowers, which are the main origin of the spores. This co-dispersion of pollen and fungi spores suggest that the latter are not randomly dispersed on the environment, but are likely to have an increased probability of being deposited on flowers propitious to fungi development. Our results suggest that directed dispersal of fungi by flower-visiting birds might be a common and under-appreciated phenomenon with potentially important ecological, biogeographic and even economic outcomes.

Keywords

Fungi dispersal; directed dispersal; flower visitation; Europe; plant animal interactions.

Introduction

Due to their ubiquity and mobility, birds are very important animal dispersal vectors for a vast array of propagules, from microorganisms as bacteria (Elfving et al. 2010) and fungi (Suthers 1985, Cafarchia et al. 2006, Belisle et al. 2014), to plants (Brochet et al. 2010, Costa et al. 2014) and even small aquatic invertebrates (Sánchez et al. 2012).

Fungi spores are mainly dispersed by wind (Aylor 2003, Viljanen-Rollinson et al. 2007) but animal dispersion may also play an important role on spore dissemination (Suthers 1985, Nagarajan and Singh 1990, Viljanen-Rollinson et al. 2007). In wind dispersal, the deposition of spores is mostly random, being affected by general wind patterns regardless of the biological characteristics of the deposition microsite. Conversely, dispersal by animals is dependent on their behaviour and has the potential to be specifically directed at suitable deposition sites - directed dispersal (Wenny and Levey 1998). For example, flowers are habitat for several microfungi (Brysch-Herzberg 2004, Ngugi and Scherm 2006, Herrera et al. 2010, Belisle et al. 2012). Several typical pollinators are known to inadvertently transport fungi between flowers, such as bees (Brysch-Herzberg 2004, Herrera et al. 2010), ants (de Vega and Herrera 2013) and even specialized nectarivorous vertebrates, as hummingbirds (Belisle et al. 2012, 2014) and bats (Belisle et al. 2014). While insects are likely to play an important role in a range of up to 10km (Goddard et al. 2010), birds might be more relevant at larger spatial scales (Alfonzo et al. 2013), maybe even globally, as in liverworts - Bryopsida (Lewis et al. 2014). Birds might move fungi spores in their beaks and mouth parts (Belisle et al. 2012, 2014) that will be exposed to other flowers by directed dispersal. By contrast, spores attached to birds' body feathers or ingested (Warner and French 1970, Francesca et al. 2010, Valera et al. 2011), will tend to have lower probability of deposition on a favourable microenvironment.

In this study we used data from two different sites to describe the directed fungi dispersal by an European bird community without specialized nectarivorous birds. Specifically, we evaluated if generalist birds can be relevant dispersers of fungi spores, the relevance of the phenomena throughout the year and whether spore dispersal is correlated with pollen dispersal in flower feeding birds.

Methods

We sampled fungal spores and pollen loads on birds during an entire year, from June 2013 to May 2014, at two sites in Portugal: Vale Soeiro (40°19’N; 8°24’W) and Antuzede (40°16’N; 8°29W). Both sites were old maritime pine *Pinus pinaster* plantations where old decaying trees have been mostly replaced by dense high Mediterranean scrubland dominated by strawberry tree *Arbutus unedo* and Portuguese oak *Quercus faginea*. While Vale Soeiro is surrounded by small agricultural land (mostly vineyards), Antuzede is adjacent to blue gum *Eucalyptus globulus* plantations and disturbed land dominated by the invasive silver wattle *Acacia dealbata*.

Sampling - Birds were captured every half month (minimal interval of 8 days) using Ecotone mist nets (Gdynia, Poland). From each bird, a small sample of feathers (3/4 mm) around the beak was cut and stored in a sterile Eppendorf at 4°C until further processing. Birds were individually marked so that the same individual was not sampled twice on the same session. The samples were prepared by acetolysis (Erdtman 1960), dissolving most tissues, lipids, and debris and leaving mainly fungi spores (and other spores if present, such as Pteridophytes) and pollen grains. Each sample was mounted in glycerine jelly, in three microscope slides (approx. 80% of the solution). All slides (n=2682) were scanned under a light microscope at a 400 magnification, to quantify spores and pollen. Fungal spores were classified into known spores morphotypes according to their main morphological traits: size, shape and degree of separation between cells, according to Saccardo et al. (1882).

Statistical analysis - In order to explore which variables influenced the presence of fungi spores on birds we used generalized linear models (GLM) with a binominal distribution (logit link function). We tested the effect of bird species; abundance of pollen (log number pollen grains+1; an indirect measure of bird-flower visitation), site and sampling period, on the probability of a bird carrying fungi spores (only presence/absence data was used due to the overdispersion of the data). The model was built by comparing the relative support of all possible candidate models (all variables and their possible interactions) using Akaike’s information criterion (AIC). Candidate models were built using all variables and their possible interactions. An average model was calculated, using the models with ΔAIC<2, and the selection probability of each variable was estimated as a measure of its relative importance in the model (Burnham and Anderson 2002). All statistical analyses were carried with package MuMIn (Barton 2014) in R v3.1.3 (R Core Team 2016).

Results

We sampled 894 birds of 34 species, of which 131 individuals of 11 species transported fungi spores, while 229 individuals of 23 species transported pollen (Table 6, Supplementary material, Table A2). Remarkably, the vast majority (93.9%) of the birds with fungi also had pollen, while half (53.7%) of the birds with pollen had fungi. Most birds with fungi spores (71.8%) transported more than five spores (Mean=163; Min=1; Max= 2148). All birds with more than 16 pollen grains also transported spores. Birds transported fungi spores almost all year round, with a pronounced peak in winter (Figure 8). Six morphological spore types were identified: the most common were the Amerosporae and the Scolecosporae present in 119 and 95 birds respectively, while Didymosporae, Phragmosporae, Dictyosporae and Staurosporae, were detected less often (39, 16, 2 and 1, respectively; Supplementary material, Table A2).

The most common and abundant fungi disperser on this study was the blackcap *Sylvia atricapilla*, with spores present in 76 out of 270 sampled individuals (36%), however, chiffchaff *Phylloscopus collybita* was the most frequent disperser with spores on 71.1% of the 38 sampled bird species (Table 6).

Table 6 – Number of birds sampled and prevalence of pollen and fungi spores per bird species. Only bird species with more than 10 individuals sampled are present (for the complete list see Supplementary material Table A2).

Bird species	**Birds sampled**	**Birds with pollen (%)**	**Birds with fungi (%)**
Aegithalos caudatus	25	10 (40.0)	8 (32.0)
Certhia brachydactyla	11	3 (27.3)	0 (0.0)
Cyanistes caeruleus	16	4 (25.0)	3 (18.8)
Erithacus rubecula	215	29 (13.5)	6 (2.8)
Ficedula hypoleuca	14	3 (21.4)	0 (0.0)
Fringilla coelebs	13	1 (7.7)	0 (0.0)
Garrulus glandarius	10	0 (0.0)	0 (0.0)
Parus major	18	4 (22.2)	2 (11.1)
Phylloscopus collybita	38	30 (78.9)	27 (71.1)
Phylloscopus trochilus	27	6 (22.2)	0 (0.0)
Regulus ignicapillus	22	4 (18.2)	2 (9.1)
Sylvia atricapilla	270	104 (38.5)	76 (28.1)
Sylvia borin	10	3 (30.0)	0 (0.0)
Sylvia melanocephala	37	4 (10.8)	2 (5.4)
Troglodytes troglodytes	16	3 (18.8)	0 (0.0)
Turdus merula	74	7 (9.5)	0 (0.0)
Turdus philomelos	38	4 (10.5)	0 (0.0)
Other species	40	10 (25.0)	5 (12.5)
Total	**894**	**229 (25.6)**	**131 (14.7)**

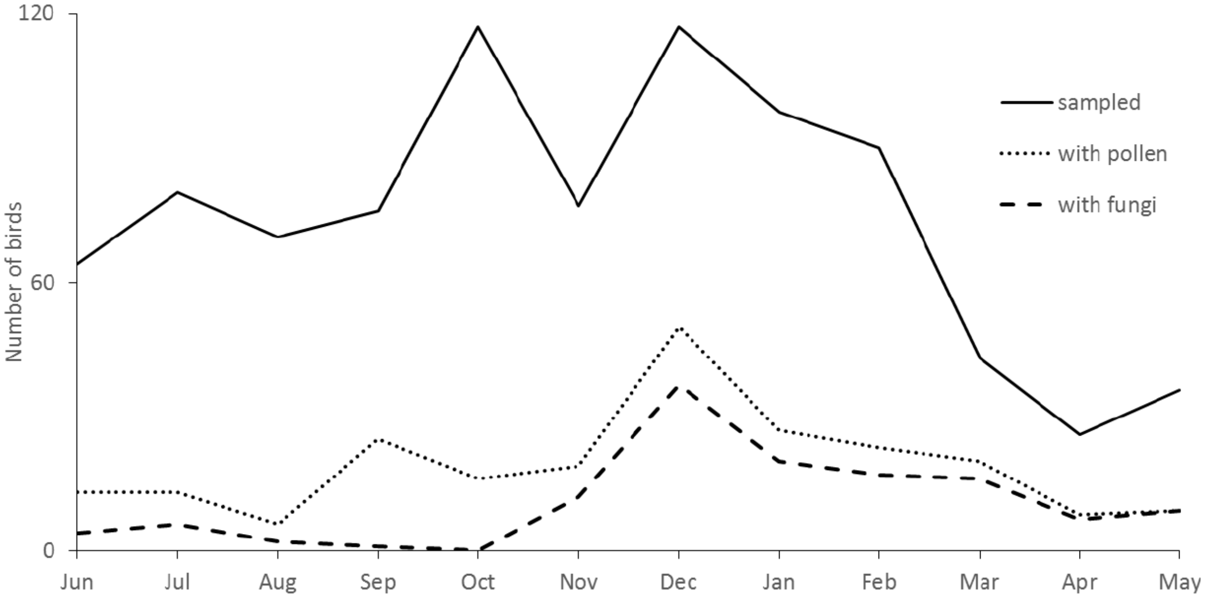

Figure 8 – Monthly variation of the number of sampled birds, birds with pollen and fungi.

The most important variable explaining the presence of fungi spores on sampled birds, according to the coefficient estimate, is the amount of pollen grains (Z=3.857, P<0.001) (Figure 9), followed by the sampling period (Z= 3.109, P=0.002). Neither site, bird species nor any interactions were important or significant in the averaged model (Table 7; Supplementary material, Table A3).

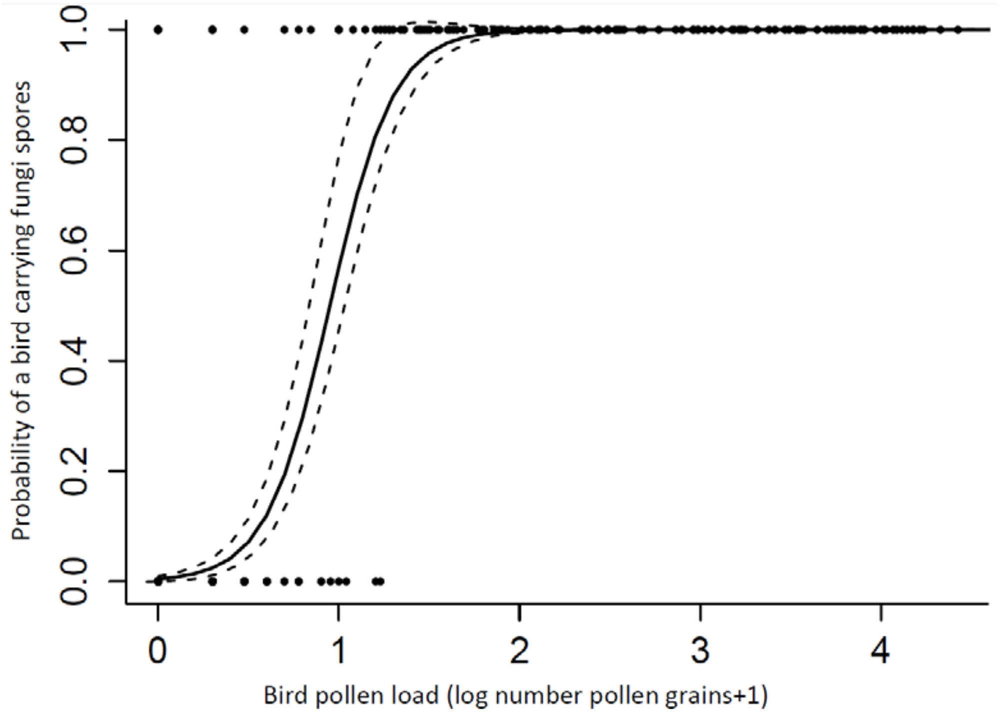

Figure 9 – Predictive curve based on the averaged GLM model of the probability of a bird carrying fungi spores according to its pollen load (log number pollen grains+1). Dotted lines represent the 95% confidence intervals and dots the raw data.

Table 7 – Summary of the average model including the importance of each variable and the number of models were they are present. Significant values are at bold.

	Coefficient Estimate	**Standard Error (SE)**	**Adjusted SE**	**z value**	**p value**	**Selection probability**	**N models present**
(Intercept)	-8.264	1.484	1.486	5.564	**<0.001**		
Pollen abundance	7.514	1.946	1.949	3.857	**<0.001**	1.00	4
Sampling period	0.245	0.079	0.079	3.109	**0.002**	1.00	4
Pollen abundance * Sampling period	-0.199	0.102	0.102	1.947	0.051	0.83	3
Site	0.156	1.451	1.452	0.108	0.914	0.41	2
Site* Sampling period	0.106	0.099	0.099	1.070	0.284	0.16	1

Discussion

Our results confirm that the presence of fungi around the birds' beak is highly constrained to individuals that also carry pollen and thus likely to feed on flowers. This suggests that birds feeding more often on flowers are more likely to carry fungi spores, and are also more likely to disperse them to other flowers. This confirms previous anecdotal observations of 18 birds (individuals) transporting pollen and spores (Ash et al. 1961). While we cannot completely discard some airborne spore contamination, the high number of spores found suggest that most spores likely originate from a common specific source, i.e. flowers. Airborne contamination could probably explain the very few (n=8) records of fungi spores in samples with no pollen, especially since 7 of these samples have a single spore. Although our spore identification does not allow a taxonomical assignment of fungi species, most fungi that are able to grow on flowers typically have Amerosporae spores (Brysch-Herzberg 2004, Ngugi and Scherm 2006, Herrera et al. 2010), which were the most common and abundant in our samples. We were only able to identify a small proportion of spores as belonging to the family Aspergillaceae. Furthermore, fungi species as *Alternaria alternate*, *Aureobasidium pullulans*, *Cladosporium cladosporioides* and *Fusicoccum eucalypti* usually found on flowers of *Eucalyptus globulus* (Lupo et al. 2001), which are commonly visited by birds (da Silva et al. 2014) were possibly present in our samples.

The prevalence of spores and pollen followed a similar pattern along the year except during September and October, when flowers were almost absent from the study area, and therefore a likely explanation is that spores detach from feathers earlier than pollen grains. The prevalence of fungi spores did not differ significantly between the two sampled sites. This is in line with the results from truly nectarivorous birds (hummingbirds) in Costa Rica, where the composition of fungi on the birds' beaks were not correlated with spatial distance or habitat type (Belisle et al. 2014). Our results indicate that the dispersal of fungi spores by birds is mainly influenced by their foraging behaviour (i.e. whether they feed or not on flowers) and by the season, which influences the flower availability. Typical flower visitors, including nectar feeding insects, hummingbirds and bats, can disperse fungi spores between flowers (Brysch-Herzberg 2004, Herrera et al. 2010, Belisle et al. 2012, 2014, de Vega and

Herrera 2013), sometimes quite frequently, e.g. c.80% of the hummingbirds, from January to March, have been reported to transport fungi (Belisle et al. 2014).

European birds are known to disperse fungi between fruits (Francesca et al. 2010) and insects (Valera et al. 2011) through their faeces. Here, we show for the first time that European birds, although not specialized on flower resources, can be relevant vectors for fungi dispersion between flowers. Moreover, the quality of the dispersal for fungi spores around the beak is probably much greater than wind dispersal or than dispersal by other body parts (e.g. wings, abdomen). Birds will tend to use their beaks to forage on similar substrates, likely appropriate for fungi development. Some fungi are known to produce pseudoflowers, that mimic true flowers in shape, size, colour, scent, and nectar production (Roy 1994, Kaiser 2006). This happens for example on several crucifers species (Roy 1993, 2001), which are frequently visited by European birds (da Silva et al. 2014). While pseudoflowers are known to be highly effective attracting insects (Roy 1993) there is no information regarding its effects on birds, but since some of these pseudoflowers produce nectar (Roy 1993, Roy and Widmer 1999), it is also likely that they effectively attract birds. Furthermore bird-pollinated flowers in South Africa had more spores in nectar than did flowers pollinated by other animals (de Vega et al. 2009).

The dispersion of fungi between flowers is highly relevant, as several fungi are plant pathogens that can lead to large economic losses, due to abrupt losses of fruit sets (Ngugi and Scherm 2006). Flowers, including important cultivars, are known to be important for European birds, particularly during the spring migration (da Silva et al. 2014). During their migrations, birds can easily spread spores (Lewis et al. 2014). Fungi can remain viable on the birds' feathers for over 45 days (Warner and French 1970), during which period birds can travel thousands of kilometres between continents (from Africa to Europe, Asia and vice-versa) and isolated islands, therefore spore dispersal by birds is likely to have biogeographic, ecological and economic repercussions.

General Discussion

In the face of the accelerated biodiversity declines associated with the Anthropocene, there is a pressing need to understand how ecosystems respond to environmental changes. Focusing ecological research on individual species or taxa can lead to important advances but does not give a broad overview about the resilience of complex biological communities. Therefore it is critical to complement such taxa-focused approaches with community level approaches that can simultaneously detect chances on concurring species and on the biological interactions that keep these communities together (Barlow et al. 2007, Ewers et al. 2015, Jordano 2016). Such community-level approaches form the backbone of this thesis.

Biodiversity in novel forest ecosystems

This thesis shows the importance of multi-taxa studies in the assessment of biodiversity. As expected an overall higher diversity and abundance was present in native oak woodlands, which present a unique species composition for most taxa evaluated. The woodland plantations of the native Pine were the most similar to the native woodlands, while the woodlands dominated by exotic tree species were the most dissimilar. The groups most often used in the literature to compare differences between habitat types are birds, shrubs and herbs (Tellería and Galarza 1990, Proença et al. 2010, Calviño-Cancela et al. 2012, Calviño-Cancela 2013), and here we show that these were the groups where the differences between woodlands were more notorious. On the other hand, the abundance, species richness and composition of ground arthropods were similar across the four studied woodland types. The reptiles, small mammals and bats had higher abundances in Oak woodlands. While small mammals can directly benefit from the higher plant diversity and the food resources it provides; reptiles and bats likely benefit indirectly from the habitat complexity caused by these plant diversity. The habitat complexity provide better shelter conditions and more available niches at least for night-flying arthropods that were very abundant in Oak woodlands. The diversity and abundance of macrofungi and carnivores in the exotic and invasive Acacia woodlands was not significantly lower to that of native Oak woodlands. Macrofungi richness and abundance is likely related to the greater availability of microhabitats in woodlands with non-intensive management, i.e. outside forestry tree plantations (Paillet et al. 2010) and to their close intimacy relation with tree abundance

(Twieg et al. 2007) and diversity, as many macrofungi depend on the symbiotic interaction with tree roots (Nguyen et al. 2016). The carnivores' abundance and richness in Acacia forests was even more puzzling, as their abundance is likely related to the availability of feeding resources, which is greater in Oak woodlands than in Acacia woodland. This suggests that carnivores are possibly affected by other anthropogenic factors and possible by factors at larger spatial scales as the habitat fragmentation. The different taxa had distinctive responses to the anthropogenic novel forests, similarly to what has been documented in Brazil (Barlow et al. 2007, Pardini et al. 2009), USA (Sax 2002) and United Kingdom (Quine and Humphrey 2010, Irwin et al. 2014). Even the global biodiversity response differed between the study regions, while in some multi-taxa studies the number of species in exotic and native woodlands was similar (e.g. Sax 2002, Quine and Humphrey 2010) in others, as in this thesis, the number of species was lower in the exotic woodlands (Barlow et al. 2007). The most common response between multi-taxa studies is the fact that community composition changes strongly from native to exotic woodlands.

Overall, this thesis showed that in southwestern Europe, the novel anthropogenic forests have a lower abundance and richness of species when compared to native forests and they change the species present in the forest communities. Therefore, it is important to know how this biodiversity change affects the ecosystem services that woodland ecosystems provide. The novel forests represent an increase in provisioning services with direct market value (Carnus et al. 2006, Paquette and Messier 2010). Nevertheless, the loss of species also entails a decline in the ecosystems functions performed by those species, and therefore of the natural resilience to perturbations, such as forest fires, biological invasions and pests (Mace et al. 2012). This makes the protection of native areas an essential conservation tool. However, we cannot neglect that the vast majority of the territory has been altered and that these anthropogenic habitats, such as the novel forest plantations, agricultural fields, and urban areas can be important to sustain at least partially, some ecological functions (Carnus et al. 2006, Bremer and Farley 2010, Brockerhoff et al. 2013). Therefore, it is increasingly important to understand to what extent they can mitigate some of the impacts associated with the loss of natural forests and if they can be better managed in order to hinder further biodiversity declines.

Birds as mobile links

Most of this thesis was focused on the dispersal services provided by birds. More precisely, it evaluated the role of birds in the dispersal of pollen and as potential pollinators in Europe, as well as co-dispersers of fungi spores that inhabit flowers. Birds live in all habitats types and can easily travel great distances which makes them important mobile links for sessile life forms, such as plants, and are often responsible for the maintenance of connectivity between isolated populations (Sekercioglu 2006, Whelan et al. 2008).

I found 62 publications referring to bird flower visitation in Europe between 1789 and 2013 and a few more have been publish more recently (e.g. Wood et al. 2014, Calviño-Cancela and Neumann 2015). Bird flower visitation in Europe was firstly noticed in the end of the 18th century (White 1789). However only nearly 100 years later there were new references to European bird flower visitation (Darwin 1874) and once again, several decades have passed without any significant contributions to the subject. Only after the mid XX century there were new insights about the subject (Ash 1959, Ash et al. 1961). The time interval between reports shows that although bird flower visitation in Europe was noticed centuries ago, it has been largely overlooked.

The literature review revealed that 46 bird species were known to visit flowers of at least 95 plant species of which 26 have been introduced in Europe. There is an overall lack of knowledge regarding the ecological importance of bird flower visitation in Europe. However effective pollination has already been confirmed in native (Ortega-Olivencia et al. 2005, 2012a) and introduced plant species (Búrquez 1989, Peters et al. 1995). The most visited flowers in Europe are from the genera *Brassica*, *Citrus* and *Eucalyptus* (Ash et al. 1961, Laursen et al. 1997, Schwilch et al. 2001, Cecere et al. 2011c, Provost et al. 2012). While most bird-visited flowers have animal pollination traits, such as nectar production, surprisingly some bird species appear to visit frequently flowers that are typically wind pollinated and do not produce nectar, the usual animal flower reward (de la Barrera and Nobel 2004). This suggests that birds seek flowers not only for nectar as suggested by Schwilch et al. (2001) but also for pollen. The birds that most often forage on flowers appear to be warblers *Sylvia* spp. and *Phylloscopus* spp. and tits, especially *Cyanistes caeruleus*. The foraging on flowers by birds is slightly more common in the Mediterranean basin and during the winter and spring. These periods are associated with the migration of many bird species (including warblers) that make stopovers in the Mediterranean area. This may actually increase birds' effectiveness as long distance pollinators. Obviously, to say that European birds regularly visit flowers for pollen or nectar does not imply that they are important and effective pollinators. The efficiency of a pollinator will vary from plant to plant. Until now, it is only known that European birds can effectively pollinate six plant species, one exotic and five native. In these six European bird pollinated plants, birds can be the main pollinators species (Ortega-Olivencia et al. 2005) or they may act as a complement to the insect pollination (Ortega-Olivencia et al. 2012a). However, for the great majority of European plant species the importance of birds as pollinators as never been evaluated.

When species undergo a reduction in ecological pressures from competitors, predators or parasites, they frequently expand their ecological niche in a phenomena known as ecological release (Cox and Ricklefs 1977, Bolnick et al. 2010, Refsnider et al. 2015). Recently, a particular case of ecological release has been described, where entire communities broaden their trophic niche in order to take advantage of underexplored resources in the environment, a process coined as interaction release (Traveset et al. 2015). This phenomenon was first described in Galápagos where an originally insectivorous and granivorous bird community widened its diet to regularly include flower resources, forced by high intra-specific competition and low inter-specific competition for food (Traveset et al. 2015). Such empty niches are characteristic of oceanic islands, where limitations to the dispersal and colonization of organisms are known to promote disharmonic communities (Whittaker and Fernández-Palacios 2007, Heleno and Vargas 2015), and therefore interaction release was assumed to be chiefly an island phenomenon (Traveset et al. 2015). However, specialized nectar feeding birds are also absent from Europe but there are several birds known to visit flowers, as showed in chapter II. In the third chapter of this thesis, I show that around 20% and 70% of the birds' individuals and species, respectively, carried pollen on their heads, suggesting that they actively fed on flowers. This pollen belonged to at least 45 different pollen types that likely represent a higher number of plant species. These results offer the first evidence that continental species, in this case European birds', can also broaden their typical feeding niche in order to take advantage of underexplored resources in the environment, i.e. to show an interaction release. The interaction release in Europe appears to be considerably less pronounced than in the Galapagos, likely due to a higher abundance of alternative food resources in Europe when compared to the simplified Galapagos ecosystems. This work empirically confirmed that the bird species that more often explore flower resources are *Sylvia* spp. and *Phylloscopus* spp., represented in the study area mainly by *S. atricapilla* and *P. collybita*, and that bird-flower interactions occur more often during winter, when other typical food sources are usually scarcer. Similarly, the most common pollen type found was from *Eucalyptus globulus*, also confirming the results of the literature review presented in chapter II. In the first chapter, I showed that Eucalyptus plantations negatively affect bird abundance, species richness and composition. Nevertheless, here I show that Eucalyptus and other introduced species are not isolated compartments of the ecosystems, but that they can be strongly integrated in interaction networks with the native fauna, particularly by European flower-visiting birds. We are now only beginning to understand the long-term ecological relevance of these novel interactions.

When birds forage on flowers, they may transport pollen grain between conspecific flowers. However, not only pollen attach to the bird's feathers. In chapter III I show that fungi spore are very often loaded and transported among the pollen grains. Indeed, more than half of the birds that carried pollen grains also carried fungi spores, and the amount of pollen transported was a highly reliable predictor of its probability to carry fungi spores. As many of these fungi find perfect development conditions in the humid and warm habitat provided by flowers, the co-transport of fungi spores by flower visiting birds is a form of direct dispersal to a particularly suitable recruitment site. The direct dispersal of flower-growing fungi spores by birds is one that can have relevant ecological, biogeographic and economic impacts. Birds can act as disseminators of fungi spores within and between continents, as they do with seeds (Viana et al. 2015) and moss spores (Lewis et al. 2014). This movement can rapidly disperse fungi related to plant diseases resulting in reduced fruit sets (Ngugi and Scherm 2006).

Novel interactions, such as those reported in this thesis will likely play a relevant role in shaping and re-structuring anthropogenic habitats throughout Europe. In the first chapter I showed that exotic woodlands have a negative impact on general biodiversity and birds may facilitate the spread of introduced species that are well integrated in bird-plant interaction networks (Traveset and Richardson 2014). Moreover, exotic plants may bring associated fungi from their native areas and birds can assist their spread in Europe. In accordance to the hypothesis denoted as enemy release, these exotic species can easily become invasive by experiencing a lower regulation than native species, once they will be free of their natural enemies or competitors in the new habitats (Keane and Crawley 2002). On the other hand, birds can be spreading native fungi that can minimize the spreading of invasive plant species if they had a higher negative effect on the exotic plants, in a biotic resistance (Levine et al. 2004).

Future research

While it is critical to understand and halt global biodiversity loss, there is enough evidence suggesting that the concomitant loss of ecological functions can be even more worrying (Flynn et al. 2009). Even more so as species may cease to provide their usual functions in the ecosystems long before they are actually extinct (Sekercioğlu et al. 2004, McConkey and Drake 2006, Jordano 2016). It is now vital to evaluate how novel habitats influence the ecosystems functions. It is important that assessments of biological function are performed at the community-level and preferably using a multi-taxa approach. Only such holistic analysis can accurately evaluate the net effect of the transformations inflicted in the ecosystems on their likely to self-perpetuate and continue to deliver the ecosystem services we depend on (Ewers et al. 2015).

The next critical step to assess the ecological relevance of pollen transport by European birds is to evaluate their pollination effectiveness. To know the pollination effectiveness it is necessary to evaluate the impact of bird flower visitation on fruit- and seed-set and on plant recruitment (Rodríguez-Rodríguez and Valido 2008, Cecere et al. 2011a, Rodríguez-Rodríguez et al. 2013). The impacts of superabundant exotic pollen grains in birds also deserve further investigation, particularly as it may cause pollen clogging of native plants negatively affecting their seed-set (Wilcock and Neiland 2002).

Due to their great mobility, birds are the most important vector connecting population including at the inter-continental level (Lewis et al. 2014). Understanding how birds interact with other species in their environment is thus essential to understand the ecology and evolution of most ecosystems.

The use of new techniques, such as next generation sequencing (NGS) as meta-barcoding, is likely to rapidly become a central tool in community-level studies, including on pollen dispersal. These methodologies allow a higher taxonomic resolution and are frequently less time consuming (Wilson et al. 2010, Richardson et al. 2015, Sickel et al. 2015). Moreover, NGS techniques allow the simultaneous identification of fungi spores and other diaspores transported by birds (Schwarzott and Schüßler 2001, Tonge et al. 2014). The identification of the fungal species transported by birds between flowers is essential to correctly evaluate the ecological implications of their dispersal. Given the amount of information resulting from meta-genomic studies, their combination with ecological networks analysis seems particularly valuable to increase our understanding of the biological communities and their response to natural and anthropogenic changes. This understanding is fundamental in the current period of rapid biodiversity decline where it is critical to understand what will actually be lost when a species becomes extinct. Community ecology is more relevant today than ever, and the conservation of species alongside with species interactions is critical if we want to maintain functional ecosystems and the services we derive from them.

References

Alfonzo, A. et al. 2013. Filamentous fungi transported by birds during migration across the mediterranean sea. - Curr. Microbiol. 66: 236–42.

Allen, C. D. and Breshears, D. D. 1998. Drought-induced shift of a forest-woodland ecotone: rapid landscape response to climate variation. - Proc. Natl. Acad. Sci. USA 95: 14839–14842.

Almeida-Neto, M. and Ulrich, W. 2011. A straightforward computational approach for measuring nestedness using quantitative matrices. - Environ. Model. Softw. 26: 173–178.

Amo, L. et al. 2007. Natural oak forest vs. ancient pine plantations: lizard microhabitat use may explain the effects of ancient reforestations on distribution and conservation of Iberian lizards. - Biodivers. Conserv. 16: 3409–3422.

Anderson, A. 2002. Faunal collapse, landscape change and settlement history in remote Ocenania. - World Archaeol. 33: 375–390.

Anderson, S. et al. 2011. Cascading effects of bird functional extinction reduce pollination and plant density. - Science. 331: 1068–1071.

Araújo, M. B. et al. 2007. The effectiveness of Iberian protected areas in conserving terrestrial biodiversity. - Conserv. Biol. 21: 1423–1432.

Ash, J. S. 1959. Pollen contamination of birds. - Br. Birds 52: 424–425.

Ash, B. J. S. et al. 1961. The contamination of birds with pollen and other substances. - Br. Birds 54: 93–100.

Aylor, D. E. 2003. Spread of plant disease on a continental scale: role of aerial dispersal of pathogens. - Ecology 84: 1989–1997.

Banašek-Richter, C. et al. 2004. Sampling effects and the robustness of quantitative and qualitative food-web descriptors. - J. Theor. Biol. 226: 23–32.

Banza, P. et al. 2015. The structure and robustness of nocturnal lepidopteran pollen-transfer networks in a biodiversity Hotspot. - Insect Conserv. Divers. 8: 538–546.

Bara Temes, S. et al. 1985. Efectos ecologicos del *Eucalyptus globulus* en Galacia: estudio comparativo con *Pinus pinaster* y *Quercus robur*. - Instituto Nacional de Investigaciones Agrarias.

Barlow, J. et al. 2007. Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. - Proc. Natl. Acad. Sci. U. S. A. 104: 18555–18560.

Barrocas, H. M. et al. 1998. lmpact of reafforestation with *Eucalyptus globulus* Labill. on the edaphic collembolan fauna of Serra de Monchique (Algarve, Portugal). - Miscellània Zooogica 21: 9–23.

Barton, K. 2014. MuMIn: Multi-Model Inference.

Bascompte, J. et al. 2006. Asymetric coevolutionary networks facilitate biodiversity maintenance. - Science. 312: 431–433.

Bates, D. et al. 2015. Fitting linear mixed-effects models using lme4. - J. Stat. Softw. 67: 1–48.

Belisle, M. et al. 2012. Flowers as islands: spatial distribution of nectar-inhabiting microfungi among plants of *Mimulus aurantiacus*, a hummingbird-pollinated shrub. - Microb. Ecol. 63: 711–718.

Belisle, M. et al. 2014. Temporal variation in fungal communities associated with tropical hummingbirds and nectarivorous bats. - Fungal Ecol.: 1–7.

Belmonte, J. et al. 1986. Claves para la determinación de los pólenes de las principales especies melíferas de la Peninsula Ibérica. - Orsis 2: 27–54.

Bengtsson, J. et al. 2003. Reserves, resilience and dynamic landscapes. - AMBIO A J. Hum. Environ. 32: 389–396.

Bersier, L. F. et al. 2002. Quantitative descriptors of food-web matrices. - Ecology 83: 2394–2407.

Blüthgen, N. et al. 2006. Measuring specialization in species interaction networks. - BMC Ecol. 6: 9.

Bolnick, D. I. et al. 2010. Ecological release from interspecific competition leads to decoupled changes in population and individual niche width. - Proc. R. Soc. B Biol. Sci. 277: 1789–1797.

Booth, T. H. 2013. Eucalypt plantations and climate change. - For. Ecol. Manage. 301: 28–34.

Bragança, M. A. L. et al. 1998. Effects of environmental heterogeneity on Lepidoptera and Hymenoptera populations in *Eucalyptus* plantations in Brazil. - For. Ecol. Manage. 103: 287–292.

Bremer, L. L. and Farley, K. A. 2010. Does plantation forestry restore biodiversity or create green deserts? A synthesis of the effects of land-use transitions on plant species richness. - Biodivers. Conserv. 19: 3893–3915.

Brochet, A. L. et al. 2010. Plant dispersal by teal (*Anas crecca*) in the Camargue: Duck guts are more important than their feet. - Freshw. Biol. 55: 1262–1273.

Brockerhoff, E. G. et al. 2008. Plantation forests and biodiversity: oxymoron or opportunity? - Biodivers. Conserv. 17: 925–951.

Brockerhoff, E. G. et al. 2013. Role of eucalypt and other planted forests in biodiversity conservation and the provision of biodiversity-related ecosystem services. - For. Ecol. Manage. 301: 43–50.

Brysch-Herzberg, M. 2004. Ecology of yeasts in plant-bumblebee mutualism in Central Europe. - FEMS Microbiol. Ecol. 50: 87–100.

Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. - Springer.

Búrquez, A. 1989. Blue Tits, *Parus caeruleus*, as pollinators of the Crown Imperial, *Fritillaria Imperialis*, in Britain. - Oikos 55: 335–340.

Butchart, S. H. M. et al. 2010. Global biodiversity: indicators of recent declines. - Science (80-.). 328: 1164–1168.

Cafarchia, C. et al. 2006. Occurrence of yeasts in cloacae of migratory birds. - Mycopathologia 161: 229–34.

Calvario, E. et al. 1989. The Blackcap *Sylvia atricapilla* and the Garden Warbler *Sylvia borin* as pollinator of *Rhamnus alaternus* (Rhamnaceae). - Avocetta 13: 53–55.

Calviño-Cancela, M. 2013. Effectiveness of eucalypt plantations as a surrogate habitat for birds. - For. Ecol. Manage. 310: 692–699.

Calviño-Cancela, M. and Neumann, M. 2015. Ecological integration of eucalypts in Europe: Interactions with flower-visiting birds. - For. Ecol. Manage. 358: 174–179.

Calviño-Cancela, M. et al. 2012. Do eucalypt plantations provide habitat for native forest biodiversity? - For. Ecol. Manage. 270: 153–162.

Calviño-Cancela, M. et al. 2013. The potential role of tree plantations in providing habitat for lichen epiphytes. - For. Ecol. Manage. 291: 386–395.

Carnus, J. et al. 2006. Planted forests and biodiversity. - J. For. 104: 65–77.

Carstensen, D. W. and Olesen, J. M. 2009. Wallacea and its nectarivorous birds: nestedness and modules. - J. Biogeogr. 36: 1540–1550.

Ceballos, G. et al. 2015. Accelerated modern human – induced species losses: entering the sixth mass extinction. - Sci. Adv. 1: 1–5.

Cecere, J. G. et al. 2010. Nectar exploitation by songbirds at Mediterranean stopover sites. - Ardeola 57: 143–157.

Cecere, J. et al. 2011a. Birds outnumber insects in visiting *Brassica* flowers on Ventotene Island (Central Mediterranean). - Vie milieu 61: 145–150.

Cecere, J. G. et al. 2011b. Nectar: an energy drink used by European songbirds during spring migration. - J. Ornithol. 152: 923–931.

Cecere, J. G. et al. 2011c. Pollen couriers across the Mediterranean: the case of migrating warblers. - Ardea 99: 33–42.

Chao, A. 1987. Estimating the population size for capture-recapture data with unequal catchability. - Biometrics 43: 783–791.

Choi, C. Y. et al. 2010. Exotic seeds on the feathers of migratory birds on a stopover island in Korea. - J. Ecol. F. Biol. 33: 19–22.

Colwell, R. 2013. EstimateS: Statistical estimation of species richness and shared species from samples. Version 9. User’s Guide and application published at: http://purl.oclc.org/estimates.

Colwell, R. K. et al. 2012. Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. - J. Plant Ecol. 5: 3–21.

Correia, M. et al. 2014. Reproductive biology and success of invasive Australian acacias in Portugal. - Bot. J. Linn. Soc. 174: 574–588.

Costa, J. M. et al. 2014. Endozoochory largely outweighs epizoochory in migrating passerines. - J. Avian Biol. 45: 59–64.

Costanza, R. et al. 1997. The value of the world's ecosystem services and natural capital. - Nature 387: 253–260.

Cox, G. and Ricklefs, R. 1977. Species diversity and ecological release in Caribbean land bird faunas. - Oikos 28: 113–122.

Cramp, S. (Eds) 2006. Birds of the Western Palearctic interactive. - Oxford University Press and BirdGuides Ltd.

Crochet, P.-A. and Joynt, G. 2012. AERC list of Western Palearctic birds. - December 2012 version. Available http//www.aerc.eu/tac.html

Cronk, Q. and Ojeda, I. 2008. Bird-pollinated flowers in an evolutionary and molecular context. - J. Exp. Bot. 59: 715–727.

Cruz, J. et al. 2015a. Exotic fish in exotic plantations: a multi-scale approach to understand amphibian occurrence in the Mediterranean region. - PLoS One 10: e0129891.

Cruz, J. et al. 2015b. Influence of exotic forest plantations on occupancy and co-occurrence patterns in a mediterranean carnivore guild. - J. Mammal. 96: 854–865.

Cruz, J. et al. 2016. Bats like vintage: managing exotic eucalypt plantations for bat conservation in a Mediterranean landscape. - Anim. Conserv. 19: 53–64.

da Silva, P. M. et al. 2008. Diversity patterns of ground-beetles (Coleoptera: Carabidae) along a gradient of land-use disturbance. - Agric. Ecosyst. Environ. 124: 270–274.

da Silva, L. P. et al. 2012. Variation in the abundance and reproductive characteristics of Great Tits *Parus major* in forest and monoculture plantations. - Acta Ornithol. 47: 147–155.

da Silva, L. P. et al. 2014. Flower visitation by birds in Europe. - Oikos 123: 1377–1383.

da Silva, L. P. et al. 2016. Dispersal of fungi spores by non-specialized flower-visiting birds. - J. Avian Biol. 47: 438–442.

Daily, G. et al. 2000. The value of nature and the nature of value. - Science. 289: 395–396.

Dalsgaard, B. et al. 2011. Specialization in plant-hummingbird networks is associated with species richness, contemporary precipitation and quaternary climate-change velocity - PLoS One 6: e25891.

Darwin, E. 1791. The botanic garden. - Printed for J. Johnson, St. Paul's Church Yard.

Darwin, C. 1874. Flowers of the primrose destroyed by birds. - Nature 9: 482.

de la Barrera, E. and Nobel, P. S. 2004. Nectar: properties, floral aspects, and speculations on origin. - Trends Plant Sci. 9: 65–69.

de Mazancourt, C. et al. 2013. Predicting ecosystem stability from community composition and biodiversity. - Ecol. Lett. 16: 617–625.

de Vega, C. and Herrera, C. M. 2013. Microorganisms transported by ants induce changes in floral nectar composition of an ant-pollinated plant. - Am. J. Bot. 100: 792–800.

de Vega, C. et al. 2009. Yeasts in floral nectar of some South African plants: quantification and associations with pollinator type and sugar concentration. - South African J. Bot. 75: 798–806.

del Hoyo, J. et al. 2016. Handbook of the birds of the world alive. - Lynx Edicions.

Delcourt, P. A. and Delcourt, H. R. 2004. Pre-historic native americans and ecological change: human ecosystems in eastern north America since the Pleistocene. - Cambridge University Press.

Díaz, S. and Cabido, M. 2001. Vive la différence: plant functional diversity matters to ecosystem processes. - Trends Ecol. Evol. 16: 646–655.

Dormann, C. F. and Strauss, R. 2014. A method for detecting modules in quantitative bipartite networks. - Methods Ecol. Evol. 5: 90–98.

Dormann, C. F. et al. 2008. Introducing the bipartite package: analysing Ecological networks. - R News 8: 8–11.

Ebbels, D. L. 1969. Pollination of *Puya chilensis* by *Turdus merula* in the isles of Scilly. - Ibis 111: 615.

Ehrlich, P. R. and Mooney, H. a. 1983. Extinction, substitution, and ecosystem services. - Bioscience 33: 248–254.

Elfving, K. et al. 2010. Dissemination of spotted fever rickettsia agents in Europe by migrating birds. - PLoS One 5: e8572.

Elton, C. 1927. Animal Ecology. - Sidgwick and Jackson.

Erdtman, G. 1960. The acetolysis method: a revised description. - Sven. Bot. Tidskr. 54: 561–564.

Errikarta-Imanol, Y. et al. 1997. Palynological evidence for climatic change and human activity during the Holocene on Minorca (Balearic Islands). - Quat. Res. 48: 339–347.

Ewers, R. M. et al. 2015. Logging cuts the functional importance of invertebrates in tropical rainforest. - Nat. Commun. 6: 6836.

Fady-Welterlen, B. 2005. Is there really more biodiversity in Mediterranean forest ecosystems? - Taxon 54: 905–9010.

Fang, Q. et al. 2012. Generalist passerine pollination of a winter-flowering fruit tree in central China. - Ann. Bot. 109: 379–84.

FAO 2016. Global forest resources assessment 2015.

Fath, B. D. et al. 2007. Ecological network analysis: network construction. - Ecol. Modell. 208: 49–55.

Fischer, J. and Lindenmayer, D. B. 2007. Landscape modification and habitat fragmentation: a synthesis. - Glob. Ecol. Biogeogr. 16: 265–280.

Fitzpatrick, S. 1994. Nectar-feeding by suburban Blue Tits: contribution to the diet in spring. - Bird Study 41: 136–145.

Fleming, T. H. and Muchhala, N. 2008. Nectar-feeding bird and bat niches in two worlds: pantropical comparisons of vertebrate pollination systems. - J. Biogeogr. 35: 764–780.

Flynn, D. F. B. et al. 2009. Loss of functional diversity under land use intensification across multiple taxa. - Ecol. Lett. 12: 22–33.

Foley, J. A. et al. 2005. Global Consequences of Land use. - Science 309: 570–574.

Ford, H. A. 1985. Nectarivory and pollination by birds in southern Australia and Europe. - Oikos 44: 127–131.

Forest Europe 2015. State of Europe’s Forests 2015.

Francesca, N. et al. 2010. Indigenous yeast communities in the environment of “Rovello bianco” grape variety and their use in commercial white wine fermentation. - World J. Microbiol. Biotechnol. 26: 337–351.

Franklin, J. F. et al. 1981. Ecological characteristics of old-growth Douglas-fir forests. - USDA For. Serv. Gen.Tech. Rep. PNW-118, 48 p. Pac. Northwest For. and Range Exp. Stn.

Gainsbury, A. M. and Colli, G. R. 2014. Effects of abandoned *Eucalyptus* plantations on lizard communities in the Brazilian Cerrado. - Biodivers. Conserv. 23: 3155–3170.

García, D. 2016. Birds in ecological networks: insights from bird-plant mutualistic interactions. - Ardeola 63: 5–34.

Gardner, T. A. et al. 2007. The value of primary, secondary, and plantation forests for a neotropical herpetofauna. - Conserv. Biol. 21: 775–787.

Goddard, M. R. et al. 2010. A distinct population of *Saccharomyces cerevisiae* in New Zealand: Evidence for local dispersal by insects and human-aided global dispersal in oak barrels. - Environ. Microbiol. 12: 63–73.

Gonçalves, P. et al. 2012. Effects of management options on mammal richness in a Mediterranean agro-silvo-pastoral system. - Agrofor. Syst. 85: 383–395.

Grant, B. 1996. Pollen digestion by Darwin’s finches and its importance for early breeding. - Ecology 77: 489–499.

Gray, C. L. et al. 2016. Local biodiversity is higher inside than outside terrestrial protected areas worldwide. - Nat. Commun. 7: 12306.

Gregory, R. D. and Strien, A. Van 2010. Wild bird indicators: using composite population trends of birds as measures of environmental health. - Ornithol. Sci. 9: 3–22.

Guimarães Jr, P. and Guimarães, P. 2006. Improving the analyses of nestedness for large sets of matrices. - Environ. Model. Softw. 21: 1512–1513.

Guimerà, R. and Amaral, L. A. N. 2005. Cartography of complex networks: modules and universal roles. - J. Stat. Mech. Theory Exp. 2005: P02001.

Hahn, S. et al. 2009. The natural link between Europe and Africa - 2.1 billion birds on migration. - Oikos 118: 624–626.

Harper, J. L. and Hawksworth, D. L. 1994. Preface. - Philos. Trans. R. Soc. B Biol. Sci. 345: 5–12.

Hartley, M. J. 2002. Rationale and methods for conserving biodiversity in plantation forests. - For. Ecol. Manage. 155: 81–95.

Hau, B. et al. 2005. Beyond Singapore: Hong Kong and Asian biodiversity. - Trends Ecol. Evol. 20: 281–282.

Heleno, R. H. and Vargas, P. 2015. How do islands become green? - Glob. Ecol. Biogeogr. 24: 518–526.

Heleno, R. et al. 2014. Ecological networks: delving into the architecture of biodiversity. - Biol. Lett. 10: 20131000.

Herrera, C. M. et al. 2010. Inhospitable sweetness: nectar filtering of pollinator-borne inocula leads to impoverished, phylogenetically clustered yeast communities. - Proc. Biol. Sci. 277: 747–754.

Hingston, A. et al. 2004. The swift parrot, *Lathamus discolor* (Psittacidae), social bees (Apidae), and native insects as pollinators of *Eucalyptus globulus* ssp. *globulus* (Myrtaceae). - Aust. J. Bot. 52: 371–379.

Hintze, J. L. and Nelson, R. D. 1998. Violin plots: a box plot-density trace synergism. - Am. Stat. 52: 181–184.

Hobbs, R. J. et al. 2006. Novel ecosystems: theoretical and management aspects of the new ecological world order. - Glob. Ecol. Biogeogr. 15: 1–7.

Hooper, D. U. et al. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. - Ecol. Monogr. 75: 3–35.

ICNF 2013. Áreas dos usos do solo e das espécies florestais de Portugal continental. Resultados preliminares. - Instituto da Conservação da Natureza e das Florestas.

Irwin, S. et al. 2014. The value of plantation forests for plant, invertebrate and bird diversity and the potential for cross-taxon surrogacy. - Biodivers. Conserv. 23: 697–714.

Jordano, P. 1987a. Patterns of mutualistic interactions in pollination and seed dispersal: connectance, dependence asymmetries, and coevolution. - Am. Nat. 129: 657–677.

Jordano, P. 1987b. Frugivory, external morphology and digestive system in mediterranean sylviid warblers *Sylvia* spp. - Ibis. 129: 175–189.

Jordano, P. 2016. Chasing ecological interactions. - PLOS Biol. 14: e1002559.

Jordano, P. and Herrera, C. M. 1981. *Prunus mahaleb* and birds the high - efficiency seed dispersal system of a temperate fruiting tree. - Ecol. Monogr. 51: 203–218.

Kaiser, R. 2006. Flowers and fungi use scents to mimic each other. - Science. 311: 806–807.

Kaiser-Bunbury, C. N. and Blüthgen, N. 2015. Integrating network ecology with applied conservation: a synthesis and guide to implementation. - AoB Plants 7: plv076.

Kanowski, J. et al. 2005. Consequences of broadscale timber plantations for biodiversity in cleared rainforest landscapes of tropical and subtropical Australia. - For. Ecol. Manage. 208: 359–372.

Kapp, R. O. 1969. How to know pollen and spores. - W. C. Brown Co.

Keane, R. M. and Crawley, M. J. 2002. Exotic plant invasions and the enemy release hypothesis. - Trends Ecol. Evol. 17: 164–170.

Kelly, D. et al. 2010. Mutualisms with the wreckage of an avifauna: the status of bird pollination and fruit-dispersal in New Zealand. - N. Z. J. Ecol. 34: 66–85.

Kingsford, R. T. et al. 2009. Major Conservation Policy Issues for Biodiversity in Oceania. - Conserv. Biol. 23: 834–840.

Knight, T. M. et al. 2005. Pollen limitation of plant reproduction: pattern and process. - Annu. Rev. Ecol. Evol. Syst. 36: 467–497.

Laclau, J.-P. et al. 2013. Perspectives for the management of eucalypt plantations under biotic and abiotic stresses. - For. Ecol. Manage. 301: 1–5.

Laursen, K. et al. 1997. Pollen as a marker in migratory warblers, Sylviidae. - Ardea 85: 223–231.

Levine, J. M. et al. 2004. A meta-analysis of biotic resistance to exotic plant invasions. - Ecol. Lett. 7: 975–989.

Lewis, L. et al. 2014. Direct long-distance dispersal shapes a New World amphitropical disjunction in the dispersal-limited dung moss *Tetraplodon* (Bryopsida: Splachnaceae). - J. Biogeogr. 41: 2385–2395.

Lindenmayer, D. B. et al. 2003. Plantation forests and biodiversity conservation. - Aust. For. 66: 62–66.

Lindenmayer, D. B. et al. 2006. General management principles and a checklist of strategies to guide forest biodiversity conservation. - Biol. Conserv. 131: 433–445.

Loreau, M. and de Mazancourt, C. 2013. Biodiversity and ecosystem stability: a synthesis of underlying mechanisms. - Ecol. Lett. 16: 106–115.

Lorenzo, P. et al. 2012. Invasion by the leguminous tree *Acacia dealbata* (Mimosaceae) reduces the native understorey plant species in different communities. - Aust. J. Bot. 60: 669.

Louchart, A. et al. 2008. Hummingbird with modern feathering: an exceptionally well-preserved Oligocene fossil from southern France. - Naturwissenschaften 95: 171–175.

Lupo, S. et al. 2001. Endophytic fungi from flowers, capsules and seeds of *Eucalyptus globulus*. - Rev. Iberoam. Micol. organo la Asoc. Esp. Espec. en Micol. 18: 38–41.

Mace, G. M. et al. 2012. Biodiversity and ecosystem services: a multilayered relationship. - Trends Ecol. Evol. 27: 19–25.

Malcolm, J. R. et al. 2006. Global warming and extinctions of endemic species from biodiversity hotspots. - Conserv. Biol. 20: 538–548.

Margules, C. R. and Pressey, R. L. 2000. Systematic conservation planning. - Nature 405: 243–53.

Martin, P. 1993 1993. Vegetation responses and feedbacks to climate: a review of models and processes. - Clim. Dyn. 8: 201–210.

Maruyama, P. K. et al. 2014. Morphological and spatio-temporal mismatches shape a neotropical savanna plant-hummingbird network. - Biotropica 46: 740–747.

Mateus, J. 1989. Pollen morphology of Portuguese Ericales. - Rev. Biol. 14: 135–208.

Mayr, G. 2004. Old World fossil record of modern-type hummingbirds. - Science. 304: 861–864.

Mayr, G. 2005. Fossil hummingbirds in the Old World. - Biologist 52: 12–16.

Mayr, G. and Wilde, V. 2014. Eocene fossil is earliest evidence of flower-visiting by birds. - Biol. Lett. 10: 1–4.

McConkey, K. R. and Drake, D. R. 2006. Flying foxes cease to function as seed dispersers long before they become rare. - Ecology 87: 271–276.

Millenium Ecosystem Assessment 2005. Ecosystems and human well-being: Synthesis. - Island Press.

Moore, P. D. and Webb, J. A. 1978. An illustrated guide to pollen analysis. - Hodder and Stoughton.

Mora, C. et al. 2011. How many species are there on earth and in the ocean? - PLoS Biol. 9: 1–8.

Mougi, A. and Kondoh, M. 2012. Diversity of interaction types and ecological community stability. - Science. 337: 349–351.

Myers, N. et al. 2000. Biodiversity hotspots for conservation priorities. - Nature 403: 853–858.

Nagarajan, S. and Singh, D. 1990. Long-distance dispersion of rust pathogens. - Annu. Rev. Phytopathol. 28: 139–26.

Newbold, T. et al. 2016. Has land use pushed terrestrial biodiversity beyond the planetary boundary? A global assessment. - Science. 353: 288–291.

Ngugi, H. K. and Scherm, H. 2006. Biology of flower-infecting fungi. - Annu. Rev. Phytopathol. 44: 261–282.

Nguyen, N. H. et al. 2016. Ectomycorrhizal and saprotrophic fungal diversity are linked to different tree community attributes in a field-based tree experiment. - Mol. Ecol.: 4032–4046.

Noss, R. F. 1990. Indicators for Monitoring Biodiversity: A Hierarchical Approach. - Conserv. Biol. 4: 355–364.

Oksanen, J. et al. 2016. Vegan: community ecology package. - R package version 2.4.

Olesen, J. M. and Valido, A. 2003. Bird pollination in Madeira island. - Ardeola 50: 67–69.

Ollerton, J. et al. 2011. How many flowering plants are pollinated by animals? - Oikos 120: 321–326.

Ortega-olivencia, A. and Catalán, P. 2009. Systematics and evolutionary history of the circum-Mediterranean genus *Anagyris* L . (Fabaceae) based on morphological and molecular data. - Taxon 58: 1290–1306.

Ortega-Olivencia, A. et al. 2005. First confirmation of a native bird-pollinated plant in Europe. - Oikos 110: 578–590.

Ortega-Olivencia, A. et al. 2012a. Insects, birds and lizards as pollinators of the largest-flowered *Scrophularia* of Europe and Macaronesia. - Ann. Bot. 109: 153–167.

Ortega-Olivencia, A. et al. 2012b. Insects, birds and lizards as pollinators of the largest-flowered *Scrophularia* of Europe and Macaronesia. - Ann. Bot. 109: 153–167.

Paillet, Y. et al. 2010. Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. - Conserv. Biol. 24: 101–12.

Paquette, A. and Messier, C. 2010. The role of plantations in managing the world's forests in the Anthropocene. - Front. Ecol. Environ. 8: 27–34.

Pardini, R. et al. 2009. The challenge of maintaining Atlantic forest biodiversity: A multi-taxa conservation assessment of specialist and generalist species in an agro-forestry mosaic in southern Bahia. - Biol. Conserv. 142: 1178–1190.

Pereira, H. M. et al. 2010. Scenarios for global biodiversity in the 21st century. - Science 330: 1496–1501.

Pereira, P. et al. 2012. Coexistence of carnivores in a heterogeneous landscape: habitat selection and ecological niches. - Ecol. Res. 27: 745–753.

Peters, W. S. et al. 1995. Pollination of the Crown Imperial *Fritillaria imperialis* by Great Tits *Parus major*. - J. Ornithol. 136: 207–212.

Pitelka, L. F. 1997. Plant migration and climate change. - Am. Sci. 85: 464–473.

Proença, V. M. et al. 2010. Plant and bird diversity in natural forests and in native and exotic plantations in NW Portugal. - Acta Oecologica 36: 219–226.

Provost, S. et al. 2012. Pollen transporté par les pouillots véloces *Phylloscopus collybita* Pendat leur halte migratoire pré-nuptiale. - Alauda 80: 23–32.

Queiroz, P. F. 2012. Morfologia polinica das Cistaceae portuguesas. - Terra Scenica.

Quine, C. P. and Humphrey, J. W. 2010. Plantations of exotic tree species in Britain: Irrelevant for biodiversity or novel habitat for native species? - Biodivers. Conserv. 19: 1503–1512.

R Core Team 2016. R: A language and environment for statistical computing. - R Foundation for Statistical Computing.

Rainho, A. et al. 2013. Atlas dos morcegos de Portugal continental. - Instituto de Conservação da Natureza e Florestas.

Refsnider, J. M. et al. 2015. Evidence for ecological release over a fine spatial scale in a lizard from the White Sands formation. - Oikos 124: 1624–1631.

Reille, M. 1992. Pollen et spores d'Europe et d'Afrique du nord. - Laboratoire de Botanique Historique et Palynologie.

Richardson, R. T. et al. 2015. Application of ITS2 metabarcoding to determine the provenance of pollen collected by honey bees in an agroecosystem. - Appl. Plant Sci. 3: 1400066.

Rodrigues, A. S. L. et al. 2004a. Global gap analysis: priority regions for expanding the global protected-area network. - Bioscience 54: 1092–1100.

Rodrigues, A. S. L. et al. 2004b. Effectiveness of the global protected area network in representing species diversity. - Nature 428: 640–643.

Rodríguez-Rodríguez, M. C. and Valido, A. 2008. Opportunistic nectar-feeding birds are effective pollinators of bird-flowers from Canary Islands: experimental evidence from *Isoplexis canariensis* (Scrophulariaceae). - Am. J. Bot. 95: 1408–15.

Rodríguez-Rodríguez, M. C. et al. 2013. Quantity and quality components of effectiveness in insular pollinator assemblages. - Oecologia 173: 179–90.

Roy, B. A. 1993. Floral mimicry by a plant pathogen. - Nature 362: 56–58.

Roy, B. A. 1994. The use and abuse of pollinators by fungi. - Trends Ecol. Evol. 9: 335–339.

Roy, B. A. 2001. Patterns of association between crucifers and their flower-mimic pathogens: host jumps are more common than coevolution or cospeciation. - Evolution 55: 41–53.

Roy, B. A. and Widmer, A. 1999. Floral mimicry: a fascinating yet poorly understood phenomenon. - Trends Plant Sci. 4: 325–330.

Royo, A. and Carson, W. 2006. On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. - Can. J. For. Res. 36: 1345–1362.

Russo, D. et al. 2016. Identifying key research objectives to make European forests greener for bats. - Front. Ecol. Evol. 4: 1–8.

Saccardo, P. A. et al. 1882. Sylloge fungorum omnium hucusque cognitorum. Digessit P. A. Saccardo. - Patavii, sumptibus auctoris.

Salewski, V. et al. 2006. Nectarivory of Palearctic migrants at a stopover site in the Sahara. - Br. Birds 99: 299–305.

Sánchez, M. I. et al. 2012. Comparing the potential for dispersal via waterbirds of a native and an invasive brine shrimp. - Freshw. Biol. 57: 1896–1903.

Sargent, R. D. and Ackerly, D. D. 2008. Plant-pollinator interactions and the assembly of plant communities. - Trends Ecol. Evol. 23: 123–30.

Sax, D. F. 2002. Equal diversty in disparate species assemblages: a comparison of native and exotic woodlands in California. - Glob. Ecol. Biogeogr. 11: 49–57.

Schwarzott, D. and Schüßler, a. 2001. A simple and reliable method for SSU rRNA gene DNA extraction, amplification, and cloning from single AM fungal spores. - Mycorrhiza 10:

203–207.

Schwilch, R. et al. 2001. Nectar consumption of warblers after long-distance flights during spring migration. - Ibis 143: 24–32.

Sekercioglu, C. H. 2006. Increasing awareness of avian ecological function. - Trends Ecol. Evol. 21: 464–71.

Sekercioglu, C. H. 2011. Functional extinctions of bird pollinators cause plant declines. - Science 331: 1019–1020.

Sekercioğlu, C. H. et al. 2004. Ecosystem consequences of bird declines. - Proc. Natl. Acad. Sci. U. S. A. 101: 18042–7.

Sickel, W. et al. 2015. Increased efficiency in identifying mixed pollen samples by meta-barcoding with a dual-indexing approach. - BMC Ecol. 15: 20.

Stephens, S. and Wagner, M. 2007. Forest plantations and biodiversity: a fresh perspective. - J. For. 105: 307–313.

Stevens, P. F. 2001. Angiosperm Phylogeny Website.

Straka, U. 1989. Die Mönchsgrasmücke (*Sylvia atricapilla*) als Blütenbesucher. - Egretta: 22–24.

Sullivan, M. P. M. 2012. Ecosystem services: do we need birds? - Ibis 154: 884–886.

Suthers, H. B. 1985. Ground-feeding migratory songbirds as cellular slime mold distribution vectors. - Oecologia 65: 526–530.

Swynnerton, C. F. M. 1917. Nectar-eating by blue tits and warblers. - Br. Birds 10: 292.

Tellería, J. L. and Galarza, A. 1990. Avifauna and landscape in northern Spain: effects of reafforestations with exotic trees. - Ardeola 37: 229–245.

Thébault, E. and Fontaine, C. 2010. Stability of ecological communities and the architecture of mutualistic and trophic networks. - Science in press.

Thompson, I. D. et al. 2011. Forest biodiversity and the delivery of ecosystem goods and services: translating science into policy. - Bioscience 61: 972–981.

Tonge, D. P. et al. 2014. Amplicon – based metagenomic analysis of mixed fungal aamples using proton release amplicon sequencing. - PLoS One 9: e93849.

Traveset, A. and Richardson, D. M. 2014. Mutualistic interactions and biological invasions. - Annu. Rev. Ecol. Evol. Syst. 45: 89–113.

Traveset, A. et al. 2015. Bird–flower visitation networks in the Galápagos unveil a widespread interaction release. - Nat. Commun. 6: 6376.

Traveset, A. et al. 2016. Global patterns of mainland and insular pollination networks. - Glob. Ecol. Biogeogr. 25: 880–890.

Turnbull, J. W. 1999. Eucalypt plantations. - New For. 17: 37–52.

Twieg, B. D. et al. 2007. Ectomycorrhizal fungal succession in mixed temperate forests.: 437–447.

Tylianakis, J. M. 2008. Understanding the web of life: the birds, the bees, and sex with aliens. - PLoS Biol. 6: 0224–0228.

Umetsu, F. and Pardini, R. 2007. Small mammals in a mosaic of forest remnants and anthropogenic habitats - Evaluating matrix quality in an Atlantic forest landscape. - Landsc. Ecol. 22: 517–530.

Urban, M. C. et al. 2013. Moving forward: dispersal and species interactions determine biotic responses to climate change. - Ann. N. Y. Acad. Sci. 1297: 44–60.

Valdés, B. et al. 1987. Atlas polínico de Andalucía occidental. - Instituto de Desarrollo Regional, Universidad de Sevilla, Excma. Diputación de Cádiz.

Valera, F. et al. 2011. Evaluation of large-scale dissemination of *Nosema ceranae* spores by European bee-eaters *Merops apiaster*. - Environ. Microbiol. Rep. 3: 47–53.

Valverde, J. et al. 2016. The temporal dimension in individual-based plant pollination networks. - Oikos 125: 468–479.

Vander Wall, S. B. 2001. The evolutionary ecology of nut dispersal. - Bot. Rev. 67: 74–117.

Venables, W. N. and Ripley, B. D. 2002. Modern Applied Statistics with S. - Springer.

Viana, D. S. et al. 2013. Migratory strategies of waterbirds shape the continental-scale dispersal of aquatic organisms. - Ecography 36: 430–438.

Viana, D. S. et al. 2015. Overseas seed dispersal by migratory birds. - Proc. R. Soc. B Biol. Sci. 283: 20152406.

Viljanen-Rollinson, S. L. H. et al. 2007. Monitoring long-distance spore dispersal by wind-a review. - New Zeal. Plant Prot. 60: 291–296.

Vizentin-Bugoni, J. et al. 2016. Influences of sampling effort on detected patterns and structuring processes of a Neotropical plant-hummingbird network. - J. Anim. Ecol. 85: 262–272.

Warner, G. M. and French, D. W. 1970. Dissemination of fungi by migratory birds: survival and recovery of fungi from birds. - Can. J. Bot. 48: 907–910.

Wenny, D. G. and Levey, D. J. 1998. Directed seed dispersal by bellbirds in a tropical cloud forest. - Proc. Natl. Acad. Sci. U. S. A. 95: 6204–6207.

Wenny, D. G. et al. 2011. The need to quantify ecosystem services provided by birds. - Auk 128: 1–14.

Whelan, C. J. et al. 2008. Ecosystem services provided by birds. - Ann. N. Y. Acad. Sci. 1134: 25–60.

White, G. 1789. The natural history of Selborne. - B. White and Son.

Whittaker, R. J. and Fernández-Palacios, J. M. 2007. Island Biogeography. - Oxford University Press.

Wilcock, C. and Neiland, R. 2002. Pollination failure in plants: why it happens and when it matters. - Trends Plant Sci. 7: 270–7.

Williams, P. H. et al. 2000. Endemism and important areas for conserving European biodiversity: a preliminary exploration of atlas data for plants and terrestrial vertebrates. - Belgian J. Entomol. 2: 21–46.

Wilson, E. O. (eds.). 1988. Biodiversity. - National Academy Press.

Wilson, E. E. et al. 2010. Pollen foraging behaviour of solitary Hawaiian bees revealed through molecular pollen analysis. - Mol. Ecol. 19: 4823–4829.

Winter, M. et al. 2009. Plant extinctions and introductions lead to phylogenetic and taxonomic homogenization of the European flora. - Proc. Natl. Acad. Sci. U. S. A. 106:

21721–5.

Wolda, H. 1988. Insect seasonality: why? - Annu. Rev. Ecol. Syst. 19: 1–18.

Wood, M. J. et al. 2014. Exploring the prevalence and diversity of pollen carried by four species of migratory Old World warbler (Sylvioidea) on arrival in the UK. - Bird Study: 1–10.

Yates, C. J. et al. 2007. Composition of the pollinator community, pollination and the mating system for a shrub in fragments of species rich kwongan in south-west Western Australia. - Biodivers. Conserv. 16: 1379–1395.

Zahn, A. et al. 2009. Low macro-arthropod abundance in exotic *Eucalyptus* plantations in the Mediterranean. - Appl. Ecol. Environ. Res. 7: 297–301.

Zanuncio, J. C. et al. 1998. Influence of strips of native vegetation on Lepidoptera associated with *Eucalyptus cloeziana* in Brazil. - For. Ecol. Manage. 108: 85–90.

Zhang, L. and Wang, H. 2006. Planning an ecological network of Xiamen Island (China) using landscape metrics and network analysis. - Landsc. Urban Plan. 78: 449–456.

Supplementary Material

Table A1 - All recorded interactions between birds and flowers (x interactions). f - pollen observed on feathers, forehead, bill or breast; o -feeding observation; ns - not stated; fe - pollen in faecal sample; st - stomach content; ? - most likely plant taxa; bold - exotic species; ( ) - record outside Europe; * - pollination confirmed. Information source:1- Alexander 1898; 2- Ash 1959; 3- Ash et al. 1961; 4- Búrquez 1989; 5- Búrquez 1992; 6- Calvario et al. 1989; 7-Campbell 1963; 8- Cecere et al. 2010; 9- Cecere et al. 2011a; 10- Cecere et al. 2011c; 11- Cecere et al. 2011b; 12- Comber 1877; 13- Cortés 1982; 14- Cramp 2006 and references therein; 15- Darwin 1791; 16- Dyer 1874; 17- Ebbels 1969; 18- Feare 1993; 19- Fitzpalrick 1993; 20- Fitzpatrick 1994; 21- Ford 1985 and references therein; 22- Fordham 1875; 23- Foster and Godfrey 1950; 24- Gibb 1954; 25- Hagger 1961; 26- Hardy 1978; 27- Harrup 1998; 28- Holm and Laursen 1982; 29- Holt 1992; 30- Kay 1985; 31- Laursen 1978; 32- Laursen et al. 1997; 33- Lester 1992; 34- Lowe 1896; 35- Merino and Nogueras 2003; 36- Moscrop 1999; 37- Olesen 1985; 38- Ortega-Olivencia et al. 2012; 39- Ortega-Olivencia et al. 2005; 40- Pennington 2006; 41- Peters et al. 1995 and references therein; 42- Pettet 1977; 43- Prinzinger 1988; 44- Provost et al. 2012; 45- Radford 1984; 46- Renshaw 1877; 47- Robertson 1877; 48- Rodríguez-Gironés and Santamaría 2004; 49- Salewski et al. 2006; 50- Schwilch et al. 2001; 51- Straka 1989; 52- Swynnerton 1916a; 53- Swynnerton 1916b; 54- Swynnerton 1917; 55- Tait 1924; 56- Tegetmeier 1877; 57- Thake 1980; 58- Visick 1977; 59- Vogel et al. 1984; 60- White 1789; 61- Yeatman 1978; 62- Yeo 1972 and references therein; 63-da Silva et al unpublished

Order	Family	lower taxa	Ferula communis	Oenanthe sp.	Hedera helix	**Pittosporum tobira**	Galanthus nivalis	**Agave americana**	**Yucca sp.**	**Chasmanthe aethiopica**	Crocus tomasinianus
			Apiales				Asparagales				
			Apiaceae		Araliaceae	Pittosporaceae	Amaryllidaceae	Asparagaceae		Iridaceae	
not applicable	not applicable	unspecified	f 9								
Psittaciformes	Psittaculidae	**Psittacula krameri**									
Piciformes	Picidae	Dendrocopos major									
	Turdidae	Turdus merula									
		Sylvia sarda									
		Sylvia rueppelli									
		Sylvia nisoria									
		Sylvia melanocephala	o 10								
		Sylvia hortensis									
		Sylvia curruca	o 10								
		Sylvia crassirostris									
		Sylvia conspicillata	o 10								
		Sylvia communis	o 10, 50; fe 50			o 10					
		Sylvia cantillans	o 10, 50; fe 50								
		Sylvia borin	o 10, 50; fe 50			o 10				(o) 34	
	Sylviidae	Sylvia atricapilla	o 10, 50; fe 50						o 34		
		Sturnus vulgaris									
	Sturnidae	Sturnus unicolor						o 13			
	Remizidae	Remiz pendulinus									
		Regulus regulus									
	Regulidae	Regulus ignicapilla									
	Prunellidae	Prunella modularis									
		Phylloscopus trochilus	o 10	o 7				o 13			
		Phylloscopus sibilatrix									
		Phylloscopus ibericus									
	Phylloscopidae	Phylloscopus collybita	o 10		f 44						
		Passer sp.									
		Passer montanus									
		Passer italiae	o 10								
	Passeridae	Passer domesticus					o 62	o 37			o 62
		Poecile palustris									
		Poecile montanus									
		Periparus ater									
		Parus major									
	Paridae	Cyanistes caeruleus									
	Oriolidae	Oriolus oriolus									
		Saxicola rubetra									
		Phoenicurus ochruros									
		Muscicapa striata									
	Muscicapidae	Erithacus rubecula									
		Serinus serinus									
		Serinus citrinella									
		Fringilla coelebs									
		Carpodacus									
		Carduelis spinus									
		Carduelis hornemanni									
	Fringillidae	Carduelis carduelis									
	Estrildidae	**Estrilda astrild**									
	Corvidae	Cyanopica cookie									
	Aegithalidae	Aegithalos caudatus									
		Hippolais icterina									
Passeriformes	Acrocephalidae	Iduna pallida/opaca									

Order			Asparagales						
	Family		Iridaceae			Xanthorrhoeaceae			
		lower taxa	Crocus sp.	**Freesia laxa**	Iris reticulata	**Aloe arborescens**	**Aloe maculata**	**Aloe sp.**	**Kniphofia uvaria**
not applicable	not applicable	unspecified							
Psittaciformes	Psittaculidae	**Psittacula krameri**							
Piciformes	Picidae	Dendrocopos major							
	Turdidae	Turdus merula							
		Sylvia sarda				o 13, 21	o 13		
		Sylvia rueppelli							
		Sylvia nisoria							
		Sylvia melanocephala				o 48			
		Sylvia hortensis							
		Sylvia curruca							
		Sylvia crassirostris							
		Sylvia conspicillata							
		Sylvia communis						f? 3	
		Sylvia cantillans							
		Sylvia borin						ns 14	
	Sylviidae	Sylvia atricapilla				o 13, 21			
		Sturnus vulgaris							
	Sturnidae	Sturnus unicolor							
	Remizidae	Remiz pendulinus							
		Regulus regulus							
	Regulidae	Regulus ignicapilla							
	Prunellidae	Prunella modularis							
		Phylloscopus trochilus							
		Phylloscopus sibilatrix							
		Phylloscopus ibericus							
	Phylloscopidae	Phylloscopus collybita		o 57		o 13, 21			
		Passer sp.	o 52						
		Passer montanus							o 59
		Passer italiae							
	Passeridae	Passer domesticus	o 12, 16, 46, 47, 56, 62		o 62	o 13	o 13		
		Poecile palustris							
		Poecile montanus							
		Periparus ater				o 63			
		Parus major							
	Paridae	Cyanistes caeruleus				o 13			
	Oriolidae	Oriolus oriolus							
		Saxicola rubetra							
		Phoenicurus ochruros				o 13			
		Muscicapa striata							
	Muscicapidae	Erithacus rubecula							
		Serinus serinus							
		Serinus citrinella							
		Fringilla coelebs							
		Carpodacus							
		Carduelis spinus							
		Carduelis hornemanni							
	Fringillidae	Carduelis carduelis							
	Estrildidae	**Estrilda astrild**							
	Corvidae	Cyanopica cookie				o 63			
	Aegithalidae	Aegithalos caudatus							
		Hippolais icterina							
Passeriformes	Acrocephalidae	Iduna pallida/opaca							

Order			Asparagales	Asterales					Brassicales			
	Family		Xanthorrhoeaceae	Asteraceae					Brassicaceae			
		lower taxa	**Kniphofia sp.**	tribe Anthemideae	sub-family Asteroideae	Taraxacum officinale	sub-family Cichorioideae	Family Asteraceae	Brassica fruticulosa	Brassica incana	Brassica oleracea*	Brassica sp.
not applicable	not applicable	unspecified						f 9				f 9
Psittaciformes	Psittaculidae	**Psittacula krameri**										
Piciformes	Picidae	Dendrocopos major	o 33									
	Turdidae	Turdus merula										
		Sylvia sarda										
		Sylvia rueppelli										
		Sylvia nisoria										
		Sylvia melanocephala								o 10		
		Sylvia hortensis										
		Sylvia curruca										
		Sylvia crassirostris										
		Sylvia conspicillata										
		Sylvia communis							o 50	o 10	o 11	
		Sylvia cantillans							o 50; fe 50	o 10	o 11	
		Sylvia borin							o 50; fe 50	o 10	o 11	
	Sylviidae	Sylvia atricapilla					f 3		o 50; fe 50	o 10		
		Sturnus vulgaris										
	Sturnidae	Sturnus unicolor										
	Remizidae	Remiz pendulinus										
		Regulus regulus										
	Regulidae	Regulus ignicapilla										
	Prunellidae	Prunella modularis										
		Phylloscopus trochilus										
		Phylloscopus sibilatrix										
		Phylloscopus ibericus										
	Phylloscopidae	Phylloscopus collybita		f 44						o 10		
		Passer sp.										
		Passer montanus										
		Passer italiae								o 10		
	Passeridae	Passer domesticus				o 62						
		Poecile palustris										
		Poecile montanus										
		Periparus ater										
		Parus major										
	Paridae	Cyanistes caeruleus	o 58									
	Oriolidae	Oriolus oriolus										
		Saxicola rubetra										
		Phoenicurus ochruros										
		Muscicapa striata										
	Muscicapidae	Erithacus rubecula										
		Serinus serinus						o 63				
		Serinus citrinella										
		Fringilla coelebs										
		Carpodacus										
		Carduelis spinus			f 3							
		Carduelis hornemanni										
	Fringillidae	Carduelis carduelis										
	Estrildidae	**Estrilda astrild**										
	Corvidae	Cyanopica cookie										
	Aegithalidae	Aegithalos caudatus										
		Hippolais icterina										
Passeriformes	Acrocephalidae	Iduna pallida/opaca										

Order	Family	lower taxa	Brassicales			Buxales	Caryophyllales					Cornales	Dipsacales
			Brassicaceae	Capparaceae		Buxaceae	Aizoaceae	Caryophyllaceae	Chenopodiaceae	Polygonaceae	Tamaricaceae	Hydrangeaceae	Adoxaceae
			Family Brassicaceae	**Capparis decidua**	**Maerua crassifolia**	Buxus sp.	**Carpobrotus sp.**	Family Caryophyllaceae	Family Chenopodiaceae	Rumex sp.	Tamarix sp.	Philadelphus sp.	Sambucus sp.
not applicable	not applicable	unspecified					f 9		f 9	f 9	f 9		
Psittaciformes	Psittaculidae	**Psittacula krameri**											
Piciformes	Picidae	Dendrocopos major											
	Turdidae	Turdus merula										o 29	
		Sylvia sarda											
		Sylvia rueppelli											
		Sylvia nisoria											
		Sylvia melanocephala											
		Sylvia hortensis			(o) 49								
		Sylvia curruca	f 32										
		Sylvia crassirostris		(ns) 14									
		Sylvia conspicillata											
		Sylvia communis			(o) 49								
		Sylvia cantillans		(o) 49	(o) 49								
		Sylvia borin	f 32										
	Sylviidae	Sylvia atricapilla	f 32			f 44							
		Sturnus vulgaris											
	Sturnidae	Sturnus unicolor											
	Remizidae	Remiz pendulinus											
		Regulus regulus											
	Regulidae	Regulus ignicapilla											
	Prunellidae	Prunella modularis											
		Phylloscopus trochilus	f 32		(o) 49								
		Phylloscopus sibilatrix											
		Phylloscopus ibericus											
	Phylloscopidae	Phylloscopus collybita	f 32		(o) 49	f 44		f 44					f 44
		Passer sp.											
		Passer montanus											
		Passer italiae											
	Passeridae	Passer domesticus											
		Poecile palustris											
		Poecile montanus											
		Periparus ater											
		Parus major											
	Paridae	Cyanistes caeruleus											
	Oriolidae	Oriolus oriolus											
		Saxicola rubetra											
		Phoenicurus ochruros											
		Muscicapa striata											
	Muscicapidae	Erithacus rubecula											
		Serinus serinus											
		Serinus citrinella											
		Fringilla coelebs											
		Carpodacus											o 14
		Carduelis spinus											
		Carduelis hornemanni											
	Fringillidae	Carduelis carduelis											
	Estrildidae	**Estrilda astrild**											
	Corvidae	Cyanopica cookie											
	Aegithalidae	Aegithalos caudatus											
		Hippolais icterina											
Passeriformes	Acrocephalidae	Iduna pallida/opaca											

not applicable	not applicable	unspecified		f 9		f 9						f 9
Psittaciformes	Psittaculidae	**Psittacula krameri**										
Piciformes	Picidae	Dendrocopos major			ns 14							
	Turdidae	Turdus merula										
		Sylvia sarda										
		Sylvia rueppelli										
		Sylvia nisoria										
		Sylvia melanocephala										
		Sylvia hortensis										
		Sylvia curruca										
		Sylvia crassirostris										
		Sylvia conspicillata										
		Sylvia communis										
		Sylvia cantillans										
		Sylvia borin										
	Sylviidae	Sylvia atricapilla	f 44									
		Sturnus vulgaris										
	Sturnidae	Sturnus unicolor										
	Remizidae	Remiz pendulinus										
		Regulus regulus										
	Regulidae	Regulus ignicapilla										
	Prunellidae	Prunella modularis										
		Phylloscopus trochilus										
		Phylloscopus sibilatrix										
		Phylloscopus ibericus										
	Phylloscopidae	Phylloscopus collybita	f 44									f 44
		Passer sp.							o 52			
		Passer montanus										
		Passer italiae										
	Passeridae	Passer domesticus					o 62	o 22, 62				
		Poecile palustris										
		Poecile montanus										
		Periparus ater										
		Parus major										
	Paridae	Cyanistes caeruleus								o 58		
	Oriolidae	Oriolus oriolus										
		Saxicola rubetra										
		Phoenicurus ochruros										
		Muscicapa striata										
	Muscicapidae	Erithacus rubecula										
		Serinus serinus										
		Serinus citrinella										
		Fringilla coelebs										
		Carpodacus										
		Carduelis spinus				f 3						
		Carduelis hornemanni										
	Fringillidae	Carduelis carduelis										
	Estrildidae	**Estrilda astrild**										
	Corvidae	Cyanopica cookie										
	Aegithalidae	Aegithalos caudatus										
		Hippolais icterina										
Passeriformes	Acrocephalidae	Iduna pallida/opaca									(f) 49	
		lower taxa	Viburnum sp.	Family Dipsacaceae	Rhododendron sp.	Family Ericaceae	**Primula polyantha**	Primula vulgaris	Primula sp.	**Camellia sp.**	**Acacia raddiana**	**Acacia sp.**
	Family		Adoxaceae	Dipsacaceae	Ericaceae		Primulaceae			Theaceae	Fabaceae	
Order			Dipsacales		Ericales						Fabales	

Order	Family	lower taxa	Anagyris foetida*	**Erythrina tomentosa**	**Erythrina sp.**	**Parkia biglobosa**	**Robinia sp.**	**Wisteria sinensis**	Alnus sp.	Betula sp.
Order			Fabales						Fagales	
	Family		Fabaceae						Betulaceae	
not applicable	not applicable	unspecified					f 9			f 9
Psittaciformes	Psittaculidae	**Psittacula krameri**								
Piciformes	Picidae	Dendrocopos major							ns 14	
	Turdidae	Turdus merula								
		Sylvia sarda								
		Sylvia rueppelli								
		Sylvia nisoria								
		Sylvia melanocephala	f 39; o 39; fe 39							
		Sylvia hortensis								
		Sylvia curruca								f 32
		Sylvia crassirostris								
		Sylvia conspicillata								
		Sylvia communis								
		Sylvia cantillans								
		Sylvia borin		(o) 52						f 32
	Sylviidae	Sylvia atricapilla	f 39; o 39; fe 39							f 32, 44
		Sturnus vulgaris			(o) 18					
	Sturnidae	Sturnus unicolor								
	Remizidae	Remiz pendulinus								
		Regulus regulus								
	Regulidae	Regulus ignicapilla								
	Prunellidae	Prunella modularis								
		Phylloscopus trochilus				(o) 42				f 32, 44
		Phylloscopus sibilatrix								
		Phylloscopus ibericus								
	Phylloscopidae	Phylloscopus collybita	f 39; o 39; fe 39							f 32, 44
		Passer sp.								
		Passer montanus								
		Passer italiae								
	Passeridae	Passer domesticus	f 39; o 39							
		Poecile palustris								o 24
		Poecile montanus							o 14	
		Periparus ater								o 24
		Parus major								
	Paridae	Cyanistes caeruleus	f 39							o 24
	Oriolidae	Oriolus oriolus								
		Saxicola rubetra								
		Phoenicurus ochruros								
		Muscicapa striata						o 45		
	Muscicapidae	Erithacus rubecula								
		Serinus serinus								
		Serinus citrinella								
		Fringilla coelebs								
		Carpodacus								
		Carduelis spinus								
		Carduelis hornemanni								
	Fringillidae	Carduelis carduelis								
	Estrildidae	**Estrilda astrild**		(o) 52						
	Corvidae	Cyanopica cookie								
	Aegithalidae	Aegithalos caudatus								
		Hippolais icterina								
Passeriformes	Acrocephalidae	Iduna pallida/opaca								

not applicable	not applicable	unspecified	f 9	f 9	f 9	f 9				f 9			f 9		f 9
Psittaciformes	Psittaculidae	**Psittacula krameri**													
Piciformes	Picidae	Dendrocopos major													
	Turdidae	Turdus merula													
		Sylvia sarda													
		Sylvia rueppelli													
		Sylvia nisoria													
		Sylvia melanocephala													
		Sylvia hortensis													
		Sylvia curruca					f 32					(o) 43			
		Sylvia crassirostris													
		Sylvia conspicillata													
		Sylvia communis													
		Sylvia cantillans													
		Sylvia borin					f 32								
	Sylviidae	Sylvia atricapilla					f 32					(o) 43			f 44
		Sturnus vulgaris													
	Sturnidae	Sturnus unicolor													
	Remizidae	Remiz pendulinus													
		Regulus regulus													
	Regulidae	Regulus ignicapilla													
	Prunellidae	Prunella modularis													
		Phylloscopus trochilus					f 32, 44								f 44
		Phylloscopus sibilatrix													
		Phylloscopus ibericus													
	Phylloscopidae	Phylloscopus collybita					f 32, 44	f 3	f 3						f 44
		Passer sp.													
		Passer montanus													
		Passer italiae													
	Passeridae	Passer domesticus													
		Poecile palustris													
		Poecile montanus													
		Periparus ater												o 24	
		Parus major													
	Paridae	Cyanistes caeruleus									o 13			o 24	
	Oriolidae	Oriolus oriolus													
		Saxicola rubetra													
		Phoenicurus ochruros													
		Muscicapa striata													
	Muscicapidae	Erithacus rubecula													
		Serinus serinus													
		Serinus citrinella													
		Fringilla coelebs													
		Carpodacus													
		Carduelis spinus													
		Carduelis hornemanni													
	Fringillidae	Carduelis carduelis													
	Estrildidae	**Estrilda astrild**													
	Corvidae	Cyanopica cookie													
	Aegithalidae	Aegithalos caudatus													
		Hippolais icterina													
Passeriformes	Acrocephalidae	Iduna pallida/opaca													
		lower taxa	Ostrya sp.	Castanea sativa	Quercus ilex	Quercus sp. (not Q. ilex)	Quercus sp.	Myrica faya	Myrica gale	**Pelargonium sp.**	**Tecoma capensis**	**Tecoma sp.**	Family Lamiaceae	Fraxinus excelsior	Fraxinus sp.
	Family		Betulaceae	Fagaceae				Myricaceae		Geraniaceae	Bignoniaceae		Lamiaceae	Oleaceae	
Order			Fagales							Geraniales	Lamiales				

Order	Family	lower taxa	Lamiales							Liliales		Malpighiales	
			Oleaceae		Plantaginaceae		Scrophulariaceae			Liliaceae		Euphorbiaceae	
			Jasminum nudiflorum	Olea europaea	Plantago lanceolata	Plantago sp.	Scrophularia grandiflora*	Scrophularia sambucifolia*	Scrophularia trifoliata*	**Fritillaria imperialis***	Family Liliaceae	Euphorbia dendroides	**Euphorbia pulcherrima**
not applicable	not applicable	unspecified		f 9		f 9					f 9	f 9	
Psittaciformes	Psittaculidae	**Psittacula krameri**											
Piciformes	Picidae	Dendrocopos major											
	Turdidae	Turdus merula											
		Sylvia sarda											
		Sylvia rueppelli											
		Sylvia nisoria											
		Sylvia melanocephala					o 38	o 38	o 38				
		Sylvia hortensis											
		Sylvia curruca								o 60			
		Sylvia crassirostris											
		Sylvia conspicillata											
		Sylvia communis											
		Sylvia cantillans											
		Sylvia borin								o 28			
	Sylviidae	Sylvia atricapilla	o 26				o 38	o 38	o 38	o 41, 51			
		Sturnus vulgaris											
	Sturnidae	Sturnus unicolor											
	Remizidae	Remiz pendulinus											
		Regulus regulus											
	Regulidae	Regulus ignicapilla											
	Prunellidae	Prunella modularis											
		Phylloscopus trochilus								o 15			
		Phylloscopus sibilatrix											
		Phylloscopus ibericus											
	Phylloscopidae	Phylloscopus collybita			f 44			o 38					o 57
		Passer sp.											
		Passer montanus											
		Passer italiae											
	Passeridae	Passer domesticus											
		Poecile palustris											
		Poecile montanus											
		Periparus ater											
		Parus major								o 41			
	Paridae	Cyanistes caeruleus								o 4, 5			
	Oriolidae	Oriolus oriolus											
		Saxicola rubetra											
		Phoenicurus ochruros											
		Muscicapa striata											
	Muscicapidae	Erithacus rubecula											
		Serinus serinus											
		Serinus citrinella											
		Fringilla coelebs											
		Carpodacus											
		Carduelis spinus											
		Carduelis hornemanni											
	Fringillidae	Carduelis carduelis											
	Estrildidae	**Estrilda astrild**											
	Corvidae	Cyanopica cookie											
	Aegithalidae	Aegithalos caudatus											
		Hippolais icterina											
Passeriformes	Acrocephalidae	Iduna pallida/opaca											

			Malpighiales				Malvales					
			Salicaceae				Cistaceae	Malvaceae				
Order	Family	lower taxa	Populus sp.	Salix caprea	Salix cinerea	Salix sp.	Family Cistaceae	**Abutilon sp.**	**Hibiscus sp.**	Lavatera arborea	Malva sylvestris	Family Malvaceae
not applicable	not applicable	unspecified					f 9					f 9
Psittaciformes	Psittaculidae	**Psittacula krameri**										
Piciformes	Picidae	Dendrocopos major										
	Turdidae	Turdus merula										
		Sylvia sarda										
		Sylvia rueppelli										
		Sylvia nisoria										
		Sylvia melanocephala								o 63		
		Sylvia hortensis										
		Sylvia curruca										
		Sylvia crassirostris										
		Sylvia conspicillata										
		Sylvia communis								o 10		
		Sylvia cantillans								o 10		
		Sylvia borin								o 8, 10	o 10	
	Sylviidae	Sylvia atricapilla	f 44	o 21		f 44		(o) 34		o 10		
		Sturnus vulgaris										
	Sturnidae	Sturnus unicolor										
	Remizidae	Remiz pendulinus				ns 14						
		Regulus regulus										
	Regulidae	Regulus ignicapilla										
	Prunellidae	Prunella modularis										
		Phylloscopus trochilus				f 44						
		Phylloscopus sibilatrix										
		Phylloscopus ibericus										
	Phylloscopidae	Phylloscopus collybita	f 44	o 21		f 44						
		Passer sp.										
		Passer montanus										
		Passer italiae										
	Passeridae	Passer domesticus							o 13			
		Poecile palustris										
		Poecile montanus	o 14			o 14; 23						
		Periparus ater				o 24						
		Parus major				o 24						
	Paridae	Cyanistes caeruleus		o 21, 30	o 30	o 24			o 13			
	Oriolidae	Oriolus oriolus										
		Saxicola rubetra										
		Phoenicurus ochruros										
		Muscicapa striata										
	Muscicapidae	Erithacus rubecula										
		Serinus serinus										
		Serinus citrinella										
		Fringilla coelebs										
		Carpodacus	o 14			o 14						
		Carduelis spinus										
		Carduelis hornemanni										
	Fringillidae	Carduelis carduelis										
	Estrildidae	**Estrilda astrild**										
	Corvidae	Cyanopica cookie										
	Aegithalidae	Aegithalos caudatus										
		Hippolais icterina										
Passeriformes	Acrocephalidae	Iduna pallida/opaca										

Order			Myrtales				Pinales			
	Family		Myrtaceae			Onagraceae	Cupressaceae		Pinaceae	
		lower taxa	**Callistemon sp.**	**Eucalyptus globulus**	**Eucalyptus sp.**	**Fuchsia sp.**	Juniperus phoenicea	Family Cupressaceae	Pinus sp.	Family Pinaceae
not applicable	not applicable	unspecified			f 9			f 9		f 9
Psittaciformes	Psittaculidae	**Psittacula krameri**								
Piciformes	Picidae	Dendrocopos major								
	Turdidae	Turdus merula								
		Sylvia sarda								
		Sylvia rueppelli								
		Sylvia nisoria				o 40				
		Sylvia melanocephala								
		Sylvia hortensis							f 3	
		Sylvia curruca			f 32; (o) 43				f 32	
		Sylvia crassirostris								
		Sylvia conspicillata								
		Sylvia communis								
		Sylvia cantillans								
		Sylvia borin			f 32	o 40			f 32	
	Sylviidae	Sylvia atricapilla	(o) 51		f 32, 44; (o) 43	o 40			f 3, 32	
		Sturnus vulgaris								
	Sturnidae	Sturnus unicolor								
	Remizidae	Remiz pendulinus								
		Regulus regulus								
	Regulidae	Regulus ignicapilla								
	Prunellidae	Prunella modularis								
		Phylloscopus trochilus			f 32, 44		f? 3		f 44	
		Phylloscopus sibilatrix								
		Phylloscopus ibericus								
	Phylloscopidae	Phylloscopus collybita		o 55	f 32, 44; o 61				f 3, 32, 44	
		Passer sp.								
		Passer montanus								
		Passer italiae								
	Passeridae	Passer domesticus								
		Poecile palustris								
		Poecile montanus								
		Periparus ater								
		Parus major		o 63						
	Paridae	Cyanistes caeruleus								
	Oriolidae	Oriolus oriolus								
		Saxicola rubetra								
		Phoenicurus ochruros								
		Muscicapa striata								
	Muscicapidae	Erithacus rubecula							f 3	
		Serinus serinus								
		Serinus citrinella								
		Fringilla coelebs								
		Carpodacus								
		Carduelis spinus								
		Carduelis hornemanni								
	Fringillidae	Carduelis carduelis								
	Estrildidae	**Estrilda astrild**								
	Corvidae	Cyanopica cookie								
	Aegithalidae	Aegithalos caudatus								
		Hippolais icterina								
Passeriformes	Acrocephalidae	Iduna pallida/opaca								

Order	Family	lower taxa	Poales			Proteales	Ranunculales			Rosales			
			Bromeliaceae	Cyperaceae	Poaceae	Proteaceae	Berberidaceae	Ranunculaceae		Cannabaceae	Rhamnaceae		Rosaceae
			Puya chilensis	Family Cyperaceae	Family Poaceae	**Grevillea robusta**	**Mahonia japonica**	Anemone blanda	Ranunculus ficaria	**Cannabis spp.**	Rhamnus alaternus	**Ziziphus mauritiana**	**Cotoneaster horizontalis**
not applicable	not applicable	unspecified		f 9	f 9								
Psittaciformes	Psittaculidae	**Psittacula krameri**											
Piciformes	Picidae	Dendrocopos major											
	Turdidae	Turdus merula	o 17										o 29
		Sylvia sarda											
		Sylvia rueppelli											
		Sylvia nisoria											
		Sylvia melanocephala											
		Sylvia hortensis											
		Sylvia curruca								f 32			
		Sylvia crassirostris											
		Sylvia conspicillata											
		Sylvia communis											
		Sylvia cantillans											
		Sylvia borin				(o) 52					o 6		
	Sylviidae	Sylvia atricapilla					o 27				o 6		
		Sturnus vulgaris											
	Sturnidae	Sturnus unicolor											
	Remizidae	Remiz pendulinus											
		Regulus regulus											
	Regulidae	Regulus ignicapilla											
	Prunellidae	Prunella modularis											
		Phylloscopus trochilus				(o) 53							
		Phylloscopus sibilatrix											
		Phylloscopus ibericus											
	Phylloscopidae	Phylloscopus collybita								f 32			
		Passer sp.											
		Passer montanus											
		Passer italiae											
	Passeridae	Passer domesticus						o 62	o 62				
		Poecile palustris											
		Poecile montanus											
		Periparus ater											
		Parus major											
	Paridae	Cyanistes caeruleus					o 27						
	Oriolidae	Oriolus oriolus											
		Saxicola rubetra											
		Phoenicurus ochruros											
		Muscicapa striata											
	Muscicapidae	Erithacus rubecula											
		Serinus serinus											
		Serinus citrinella											
		Fringilla coelebs											
		Carpodacus											
		Carduelis spinus											
		Carduelis hornemanni											
	Fringillidae	Carduelis carduelis											
	Estrildidae	**Estrilda astrild**											
	Corvidae	Cyanopica cookie											
	Aegithalidae	Aegithalos caudatus											
		Hippolais icterina											
Passeriformes	Acrocephalidae	Iduna pallida/opaca										(o) 49	

			Rosales										
			Rosaceae										Ulmaceae
Order	Family	lower taxa	Crataegus sp.	**Eriobotrya japonica**	Malus sp.	Prunus avium	Prunus domestica	Prunus dulcis	Prunus sp.	Prunus sp. or Sorbus sp.	sub-family Amygdalaceae	Family Rosaceae	Celtis sp.
not applicable	not applicable	unspecified			f 9				f 9			f 9	f 9
Psittaciformes	Psittaculidae	**Psittacula krameri**											
Piciformes	Picidae	Dendrocopos major											
	Turdidae	Turdus merula											
		Sylvia sarda											
		Sylvia rueppelli											
		Sylvia nisoria											
		Sylvia melanocephala		o 35									
		Sylvia hortensis											
		Sylvia curruca	st 31								f 32		
		Sylvia crassirostris											
		Sylvia conspicillata											
		Sylvia communis	st 31										
		Sylvia cantillans				o 10							
		Sylvia borin	ns 14; st 31								f 32		
	Sylviidae	Sylvia atricapilla	f 21; st 31	o 35				o 63		f 44	f 32		
		Sturnus vulgaris								f 44			
	Sturnidae	Sturnus unicolor											
	Remizidae	Remiz pendulinus											
		Regulus regulus											
	Regulidae	Regulus ignicapilla											
	Prunellidae	Prunella modularis					o 25						
		Phylloscopus trochilus	st 31							f 44	f 32		
		Phylloscopus sibilatrix											
		Phylloscopus ibericus											
	Phylloscopidae	Phylloscopus collybita		o 35						f 44	f 32		
		Passer sp.											
		Passer montanus					o 25						
		Passer italiae											
	Passeridae	Passer domesticus					o 25						
		Poecile palustris											
		Poecile montanus											
		Periparus ater											
		Parus major											
	Paridae	Cyanistes caeruleus		o 35				o 62					
	Oriolidae	Oriolus oriolus											
		Saxicola rubetra											
		Phoenicurus ochruros											
		Muscicapa striata											
	Muscicapidae	Erithacus rubecula											
		Serinus serinus											
		Serinus citrinella											
		Fringilla coelebs					o 25						
		Carpodacus											
		Carduelis spinus											
		Carduelis hornemanni											
	Fringillidae	Carduelis carduelis											
	Estrildidae	**Estrilda astrild**											
	Corvidae	Cyanopica cookie											
	Aegithalidae	Aegithalos caudatus											
		Hippolais icterina											
Passeriformes	Acrocephalidae	Iduna pallida/opaca											

not applicable	not applicable	unspecified			f 9	f 9				f 9		
Psittaciformes	Psittaculidae	**Psittacula krameri**										
Piciformes	Picidae	Dendrocopos major										
	Turdidae	Turdus merula										
		Sylvia sarda										
		Sylvia rueppelli										
		Sylvia nisoria										
		Sylvia melanocephala										
		Sylvia hortensis								f 3		
		Sylvia curruca		f 32						f 32		
		Sylvia crassirostris										
		Sylvia conspicillata										
		Sylvia communis					f? 2		f 2	f 3	f? 3	
		Sylvia cantillans										
		Sylvia borin		f 32						f 32		o 28
	Sylviidae	Sylvia atricapilla		f 32				(o) 1		f 2, 3, 32		o 28
		Sturnus vulgaris										
	Sturnidae	Sturnus unicolor										
	Remizidae	Remiz pendulinus										
		Regulus regulus										
	Regulidae	Regulus ignicapilla										
	Prunellidae	Prunella modularis										
		Phylloscopus trochilus								f 3, 32		
		Phylloscopus sibilatrix										
		Phylloscopus ibericus										
	Phylloscopidae	Phylloscopus collybita		f 32						f 32		
		Passer sp.										
		Passer montanus										
		Passer italiae										
	Passeridae	Passer domesticus										
		Poecile palustris	o 24									
		Poecile montanus										
		Periparus ater	o 24									
		Parus major										
	Paridae	Cyanistes caeruleus	o 24									
	Oriolidae	Oriolus oriolus										
		Saxicola rubetra										
		Phoenicurus ochruros										
		Muscicapa striata										
	Muscicapidae	Erithacus rubecula								f 3		
		Serinus serinus										
		Serinus citrinella										
		Fringilla coelebs										
		Carpodacus										
		Carduelis spinus										
		Carduelis hornemanni										
	Fringillidae	Carduelis carduelis								f 3		
	Estrildidae	**Estrilda astrild**										
	Corvidae	Cyanopica cookie										
	Aegithalidae	Aegithalos caudatus										
		Hippolais icterina										
Passeriformes	Acrocephalidae	Iduna pallida/opaca										
		lower taxa	Ulmus glabra	Urtica sp.	Family Urticaceae	Pistacia sp.	**Citrus aurantium**	**Citrus sinensis**	**Citrus sp. (not C. aurantium)**	**Citrus sp.**	Acer pseudoplatanus	Acer platanoides
	Family		Ulmaceae	Urticaceae		Anacardiaceae	Rutaceae				Sapindaceae	
Order			Rosales			Sapindales						

Order	Family	lower taxa	Sapindales	Saxifragales				Solanales	Zygophyllales
			Sapindaceae	Grossulariaceae			Saxifragaceae	Convolvulaceae	Zygophyllaceae
			Acer sp.	**Ribes sanguineum**	Ribes uva-crispa	Ribes sp.	Saxifraga paniculata	Calystegia sp.	**Balanites aegyptiaca**
not applicable	not applicable	unspecified							
Psittaciformes	Psittaculidae	**Psittacula krameri**							
Piciformes	Picidae	Dendrocopos major							
	Turdidae	Turdus merula							
		Sylvia sarda							
		Sylvia rueppelli							
		Sylvia nisoria							
		Sylvia melanocephala							
		Sylvia hortensis							
		Sylvia curruca	ns 14	o 28					
		Sylvia crassirostris							
		Sylvia conspicillata							
		Sylvia communis							
		Sylvia cantillans							(o) 49
		Sylvia borin							
	Sylviidae	Sylvia atricapilla							
		Sturnus vulgaris							
	Sturnidae	Sturnus unicolor							
	Remizidae	Remiz pendulinus							
		Regulus regulus							
	Regulidae	Regulus ignicapilla							
	Prunellidae	Prunella modularis							
		Phylloscopus trochilus							
		Phylloscopus sibilatrix							
		Phylloscopus ibericus							
	Phylloscopidae	Phylloscopus collybita	f 3, 44					f 7; o 7	
		Passer sp.							
		Passer montanus							
		Passer italiae							
	Passeridae	Passer domesticus					o 62		
		Poecile palustris							
		Poecile montanus							
		Periparus ater							
		Parus major				o 14			
	Paridae	Cyanistes caeruleus		o 19, 20, 52, 54	o 52, 54				
	Oriolidae	Oriolus oriolus							
		Saxicola rubetra							
		Phoenicurus ochruros							
		Muscicapa striata							
	Muscicapidae	Erithacus rubecula							
		Serinus serinus							
		Serinus citrinella							
		Fringilla coelebs							
		Carpodacus							
		Carduelis spinus							
		Carduelis hornemanni							
	Fringillidae	Carduelis carduelis							
	Estrildidae	**Estrilda astrild**							
	Corvidae	Cyanopica cookie							
	Aegithalidae	Aegithalos caudatus							
		Hippolais icterina							
Passeriformes	Acrocephalidae	Iduna pallida/opaca							

Order			not applicable	not applicable
	Family		not applicable	not applicable
		lower taxa	unidentified monocotyledon	unknown
Passeriformes	Acrocephalidae	Iduna pallida/opaca		
		Hippolais icterina		f 50
	Aegithalidae	Aegithalos caudatus		f 63
	Corvidae	Cyanopica cookie		
	Estrildidae	**Estrilda astrild**		
	Fringillidae	Carduelis carduelis		
		Carduelis hornemanni		f 14
		Carduelis spinus		
		Carpodacus		
		Fringilla coelebs		
		Serinus citrinella		ns 14
		Serinus serinus		
	Muscicapidae	Erithacus rubecula		
		Muscicapa striata		fe 50
		Phoenicurus ochruros		
		Saxicola rubetra		fe 50
	Oriolidae	Oriolus oriolus		ns 14
	Paridae	Cyanistes caeruleus		
		Parus major		
		Periparus ater		
		Poecile montanus		
		Poecile palustris		
	Passeridae	Passer domesticus		f 36
		Passer italiae		
		Passer montanus		
		Passer sp.		
	Phylloscopidae	Phylloscopus collybita		f 50
		Phylloscopus ibericus		f 63
		Phylloscopus sibilatrix		f 10, 50; fe 50
		Phylloscopus trochilus		f 50; (o) 54
	Prunellidae	Prunella modularis		
	Regulidae	Regulus ignicapilla		f 63
		Regulus regulus		f 63
	Remizidae	Remiz pendulinus		
	Sturnidae	Sturnus unicolor		
		Sturnus vulgaris		o 14
	Sylviidae	Sylvia atricapilla	f 3	f 50; (o) 54
		Sylvia borin		f 50; fe 50; (o) 50
		Sylvia cantillans		f 50; (o) 49
		Sylvia communis	f 3	f 50; fe 50
		Sylvia conspicillata		
		Sylvia crassirostris		
		Sylvia curruca		
		Sylvia hortensis		
		Sylvia melanocephala		f 50
		Sylvia nisoria		
		Sylvia rueppelli		f 10
		Sylvia sarda		
	Turdidae	Turdus merula		
Piciformes	Picidae	Dendrocopos major		
Psittaciformes	Psittaculidae	**Psittacula krameri**		(ns) 14
not applicable	not applicable	unspecified		

References

Alexander, B. 1898. An ornithological expedition to the Cape Verde Islands. - Ibis 40: 74–118.
Ash, J. S. 1959. Pollen contamination of birds. - Br. Birds 52: 424–425.
Ash, B. J. S. et al. 1961. The contamination of birds with pollen and other substances. - Br. Birds 54: 93–100.
Búrquez, A. 1989. Blue Tits, Parus caeruleus, as Pollinators of the Crown Imperial, Fritillaria Imperialis, in Britain. - Oikos 55: 335–340.
Búrquez, A. 1992. Blue Tits as pollinators of the crown imperial. - Br. Birds 85: 41–43.

Calvario, E. et al. 1989. The Blackcap Sylvia atricapilla and the garden Warbler Sylvia borin as pollinator of Rhamnus alaternus (Rhamnaceae). - Avocetta 13: 53–55.

Campbell, W. D. 1963. Warblers as pollinators in Britain. - Br. Birds 56: 111–112.

Cecere, J. G. et al. 2010. Nectar exploitation by songbirds at Mediterranean stopover sites. - Ardeola 57: 143–157.

Cecere, J. et al. 2011a. Pollen couriers across the Mediterranean: the case of migrating warblers. - Ardea 99: 33–42.

Cecere, J. et al. 2011b. Birds outnumber insects in visiting Brassica flowers on Ventotene Island (Central Mediterranean). - Vie milieu 61: 145–150.

Cecere, J. G. et al. 2011c. Nectar: an energy drink used by European songbirds during spring migration. - J. Ornithol. 152: 923–931.

Comber, T. 1877. Yellow Crocuses. - Nature 16: 24.

Cortés, J. 1982. Nectar feeding by European passerines on introduced tropical flowers at Gibraltar. - Alectoris 4: 26–29.

Cramp, S. (Ed) . 2006. Birds of the Western Palearctic interactive. Oxford University Press and BirdGuides Ltd.

Darwin, E. 1791. The Botanic Garden. A Poem in Two Parts. Part I containing The Economy of Vegetation. Part II. The Loves of the Plants. With Philosophical Notes. - Printed for J. Johnson. St. Paul's Church Yard.

Dyer, T. 1874. Flowers of the Primrose Destroyed by Birds. - Nature 9: 509.

Ebbels, D. L. 1969. Pollination of Puya chilensis by Turdus merula in the isles of Scilly. - Ibis (Lond. 1859). 111: 615.

Feare, C. 1993. Nectar feeding by European starlings. - Wilson Bull. 105: 194.

Fitzpalrick, S. 1993. Blue Tits and flowering currants. - Br. Birds 86: 101.

Fitzpatrick, S. 1994. Nectar-feeding by suburban Blue Tits: contribution to the diet in spring. - Bird Study 41: 136–145.

Ford, H. A. 1985. Nectarivory and pollination by birds in southern Australia and Nectarivory Europe. - Oikos 44: 127–131.

Fordham, H. G. 1875. Destruction of Flowers by Birds. - Nature 12: 7.

Foster, J. and Godfrey, C. 1950. A study of the British Willow Tit. - Br. Birds 43: 351–361.

Gibb, J. 1954. The feeding ecology of tits, with notes on the Treecreeper and Goldcrest. - Ibis (Lond. 1859). 96: 513–543.

Hagger, C. H. E. 1961. House Sparrows and other birds drinking nectar from greengage blossoms. - Br. Birds 54: 291.

Hardy, E. 1978. Winter foods of Blackcaps in Britain. - Bird Study 25: 59–61.

Harrup, B. 1998. Wintering blackcaps taking nectar from, and probably pollinating, Mahonia. - Br. Birds 91: 201.

Holm, E. and Laursen, K. 1982. Observations and Experiments on the Oral Apparatus and Its Function in Some Warbler Species (Sylviidae). - Zool. Anzeiger Jena 209: 224–246.

Holt, C. W. 1992. Blackbirds consuming flowers. - Br. Birds 85: 617.

Kay, Q. O. N. 1985. Nectar from willow catkins as a food source for Blue Tits. - Bird Study 32: 40–44.

Laursen, K. 1978. Interspecific relationships between Some Insectivorous Passerine Species, Illustrated by Their Diet during Spring Migration. - Ornis Scand. 9: 178–192.

Laursen, K. et al. 1997. Pollen as a marker in migratory warblers, Sylviidae. - Ardea 85: 223–231.

Lester, D. 1992. Great Spotted Woodpecker apparently feeding on nectar. - Br. Birds 85: 40–41.

Lowe, J. 1896. Notes on a newly discovered habit in the Blackcap warbler and other birds. - Zoologist 20: 1–10.

Merino, S. and Nogueras, I. 2003. Loquat Eriobotrya Japonica as a Winter nectar source of birds in central Spain. - Ardeola 50: 265–267.

Moscrop, C. S. 1999. House sparrows with yellow markings. - Br. Birds 92: 259–260.

Olesen, J. M. 1985. The Macaronesian bird-flower element and its relation to bird and bee opportunists. - Bot. J. Linn. Soc. 91: 395–414.

Ortega-Olivencia, A. et al. 2005. First confirmation of a native bird-pollinated plant in Europe. - Oikos 110: 578–590.

Ortega-Olivencia, A. et al. 2012. Insects, birds and lizards as pollinators of the largest-flowered Scrophularia of Europe and Macaronesia. - Ann. Bot. 109: 153–67.

Pennington, M. G. 2006. Sylvia warblers taking nectar on autumn migration in Shetland. - Br. Birds 99: 579–580.

Peters, W. S. et al. 1995. Pollination of the Crown Imperial Fritillaria imperialis by Great Tits Parus major. - J. Ornithol. 136: 207–212.

Pettet, A. 1977. Seasonal changes in nectar-feeding by birds at Zaria, Nigeria. - Ibis (Lond. 1859). 119: 291–308.

Prinzinger, R. 1988. Nektar als regelmäßige Zugnahrung bei Grasmücken? - J. Ornithol. 129: 475–477.

Provost, S. et al. 2012. Pollen transporté par les pouillots véloces Phylloscopus collybuta Pendat leur halte migratoire pré-nuptiale. - Alauda 80: 23–32.

Radford, A. P. 1984. Spotted Flycatcher eating wisteria petals. - Br. Birds: 245.

Renshaw, A. G. 1877. Yellow Crocuses. - Nature 15: 530.

Robertson, D. 1877. Yellow Crocuses. - Nature 16: 8.

Rodríguez-Gironés, M. A. and Santamaría, L. 2004. Why are so many bird flowers red? - PLoS Biol. 2: e350.

Salewski, V. et al. 2006. Nectarivory of Palearctic migrants at a stopover site in the Sahara. - Br. Birds 99: 299–305.

Schwilch, R. et al. 2001. Nectar consumption of warblers after long-distance flights during spring migration. - Ibis (Lond. 1859). 143: 24–32.

Straka, U. 1989. Die Mönchsgrasmücke (Sylvia atricapilla) als Blütenbesucher. - Egretta: 22–24.

Swynnerton, C. 1916a. Short Cuts by Birds to Nectaries. - J. Linn. Soc. London, Bot. 43: 381–416.

Swynnerton, C. 1916b. Short Cuts to Nectaries by Blue Tits. - J. Linn. Soc. London, Bot. 43: 417–422.

Swynnerton, C. F. M. 1917. Nectar-eating by blue tits and warblers. - Br. Birds 10: 292.

Tait, W. C. 1924. The Birds of Portugal. - H. F. & G. Witherby.

Tegetmeier, W. B. 1877. Colour-Sense in Birds—Blue and Yellow Crocuses. - Nature 16: 163.

Thake, M. A. 1980. Nectar: a supplementary food source for wintering chiffchafs (Phylloscopus collybita). - Riv. Ital. Ornit. Milano 50: 167–168.

Visick, P. 1977. Blue Tits taking nectar. - Br. Birds 70: 548–549.

Vogel, S. et al. 1984. Ornithophilie auf den Canarischen Inseln. - Plant Syst. Evol. 146: 225–248.

White, G. 1789. The Natural History of Selborne. - B. White and Son.

Yeatman, L. 1978. Nouveau type d'alimentation du Pouillot véloce Phylloscopus collybita. - L'Oiseau et R.F.O. 48: 72–73.

Yeo, P. F. 1972. Miscellaneous notes on pollination and pollinators. - J. Nat. Hist. 6: 667–686.

Table A2 - Number of birds sampled, with pollen and fungi with its morphological type by species, site and totals.

	Birds sampled			Birds with pollen			Birds with fungi spores			Morphological spore type																	
										Amerosporae			Dictyosporae			Didymosporae			Phragmosporae			Scolecosporae			Staurosporae		
Bird species	Antuzede	Vale Soeiro	Total	Antuzede	Vale Soeiro	Total	Antuzede	Vale Soeiro	Total	Antuzede	Vale Soeiro	Total	Antuzede	Vale Soeiro	Total	Antuzede	Vale Soeiro	Total	Antuzede	Vale Soeiro	Total	Antuzede	Vale Soeiro	Total	Antuzede	Vale Soeiro	Total
Accipiter nisus	1	2	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acrocephalus scirpaceus	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aegithalos caudatus	3	22	25	3	7	10	3	5	8	3	2	5	0	0	0	2	1	3	0	0	0	3	3	6	0	0	0
Carduelis chloris	0	7	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Certhia brachydactyla	3	8	11	1	2	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Columba palumbus	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cyanistes caeruleus	4	12	16	2	2	4	2	1	3	2	1	3	0	0	0	0	0	0	0	0	0	1	1	2	0	0	0
Dendrocopos major	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Erithacus rubecula	88	127	215	15	14	29	3	3	6	3	1	4	0	0	0	0	0	0	0	0	0	0	2	2	0	0	0
Ficedula hypoleuca	0	14	14	0	3	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fringilla coelebs	3	10	13	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Garrulus glandarius	7	3	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lophophanes cristatus	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Parus major	3	15	18	1	3	4	1	1	2	1	1	2	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0
Passer domesticus	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Periparus ater	1	4	5	1	0	1	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0
Phoenicurus ochruros	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phylloscopus collybita	23	15	38	21	9	30	21	6	27	21	6	27	0	0	0	7	3	10	8	0	8	21	4	25	1	0	1
Phylloscopus ibericus	0	1	1	0	1	1	0	1	1	0	1	1	0	0	0	0	1	1	0	0	0	0	1	1	0	0	0
Phylloscopus trochilus	2	25	27	1	5	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Picus viridis	0	2	2	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pyrrhula pyrrhula	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Regulus ignicapillus	10	12	22	2	2	4	1	1	2	1	1	2	0	0	0	0	1	1	0	0	0	1	1	2	0	0	0
Serinus serinus	2	1	3	2	1	3	2	1	3	2	1	3	0	0	0	2	0	2	0	0	0	2	1	3	0	0	0
Streptopelia turtur	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sylvia atricapilla	50	220	270	41	63	104	37	39	76	36	33	69	2	0	2	19	3	22	6	2	8	29	22	51	0	0	0
Sylvia borin	3	7	10	2	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sylvia communis	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sylvia melanocephala	8	29	37	2	2	4	2	0	2	2	0	2	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0
Sylvia undata	0	2	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Troglodytes troglodytes	14	2	16	2	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Turdus iliacus	1	6	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Turdus merula	26	48	74	3	4	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Turdus philomelos	4	34	38	0	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total	**260**	**634**	**894**	**100**	**129**	**229**	**73**	**58**	**131**	**72**	**47**	**119**	**2**	**0**	**2**	**30**	**9**	**39**	**14**	**2**	**16**	**60**	**35**	**95**	**1**	**0**	**1**

Table A3 - Summary results of information-theoretic model selection for the effects of explanatory variables (and all their interactions) on the presence of fungi on birds. We show the ΔAIC<2 set of best-ranked regression models, and for each one we provide: k - number of variables included in the model; df - degrees of freedom; logLik - maximized log-likelihood value; AIC - Akaike information criteria (AIC); ΔAIC - delta AIC; Akaike weight.

Model	K	df	logLik	AIC	ΔAIC	Akaike weight
Pollen Abundance + Sampling period + Pollen abundance * Sampling period	3	4	-69.53	147.05	0.00	0.43
Site + Pollen abundance + Sampling period + Pollen abundance * Sampling period	4	5	-69.06	148.12	1.07	0.25
Pollen abundance + Sampling period	2	3	-71.47	148.94	1.89	0.17
Site + Pollen abundance + Sampling period + Site* Sampling period + Pollen abundance * Sampling period	5	6	-68.51	149.01	1.96	0.16