Marisa Isabel da Silva Gomes

# BIRDS IN INTERFACE RIPARIAN VEGETATION-WOODLAND MATRIX: THEIR HABITAT USE AND ROLE IN ECOSYSTEM PROCESSES AND ECOLOGICAL SERVICES

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UNIVERSIDADE DE COIMBRA

# Birds in interface riparian vegetation-woodland matrix: their habitat use and role in ecosystem processes and ecological services

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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 Prof. Dr. João Eduardo Rabaça

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# Summary

Riparian ecosystems are critical in maintaining biodiversity on a regional scale, which is particularly important for open agroforestry systems. These ecosystems, among the most important and vulnerable habitats, have relatively high biodiversity offering refuge and source areas for prey and predators and consequently providing corridors for migration. These areas provide many fruit resources and attract many animals, such as frugivorous birds, which are the main seed dispersers in the Mediterranean basin. The importance of riparian galleries is well known for the most specialized riparian bird species, but the interface riparian galleries vs. surrounding matrix in terms of importance for passerine bird communities is understudied. This thesis compares the bird composition, diet and feeding ecology and the dynamics of seed dispersal between passerine birds inhabiting the riparian gallery and the surrounding woodland matrix (montado). We also gave the first step in attempting to evaluate the economic value of passerines in seed dispersal.

This thesis comprises four data chapters.

In the first chapter we analyze bird communities at different distances from the stream in order to describe seasonal and daily variations in the use of riparian galleries and woodland adjacent areas (montado). Furthermore, we assess whether birds move actively from the surrounding matrix into the riparian gallery and their flight direction in three different seasons. Species richness and bird abundance (total number of individuals) in Mediterranean riparian galleries of southern Portugal were strongly influenced by distance to stream and season, and were significantly higher in the riparian gallery than in the adjacent matrix. Species richness was significantly higher during the summer-autumn migration period, and bird abundance significantly lower during the breeding season. There were a significant higher percentage of birds moving from the surrounding matrix into the riparian gallery in mid-summer, but not during the autumn migration and winter.

In the second chapter we analyzed the diet of passerines using fecal samples, and trophic ecology using carbon and nitrogen stable isotopes of blood samples of 10 species (5 riparian passerines and 5 surrounding matrix passerine species). We assessed also food availability in two riparian forest areas of Southern Portugal (Évora) during four seasons (spring, summer, autumn and winter). We report consistent differences in the diet and trophic ecology

between passerines that inhabit the riparian gallery and the adjacent matrix among seasons, and in relation to the abundance of food resources, particularly during periods with higher species density.

In the third chapter we studied seed dispersal patterns by birds in the riparian gallery and in the surrounding forest matrix using a specific type of fruit marking and the conventional seed traps. Seed dispersal was strongly influenced by the abundance of fruits, distance to stream, and seed dimensions. The results of this study present some implications for the colonization of fleshy fruit plants from the riparian gallery into the adjacent matrix, meaning that smaller sized seeds may be dispersed at larger distances, and suggesting that the abundance of each species producing fruits will influence strongly the vegetation composition of the adjacent matrix.

In the fourth chapter we set an example and create a precedent using Replacement Cost (RC) analysis to estimate the economic value of the environmental service of seed dispersal performed by the Blackcap (*Sylvia atricapilla*) dispersing blackberries (*Rubus ulmifolius*) and wild olives (*Olea europaea* var. *sylvestris*) in the riparian gallery and in the immediate adjacent areas of southern Portugal.
We discuss that RC varies according to the replacement method used, spreading seeds or planting saplings. A compromise has to be made to replace the service using the most similar method of replacement to seed dispersal performed by birds, however he complexity of factors that affect germination and sapling survival probably resulted in an underestimation of the environmental service provided by blackcap in this study. Taking into consideration that blackcap performs this process freely, this kind of approach can constitute an important tool to achieve better conservation measures and management strategies.

# Keywords

Riparian gallery, Montado, passerines, diet, seed dispersal, ecosystem services.

# Resumo

Os ecossistemas ripícolas são fundamentais para manter a biodiversidade à escala regional, sendo particulamente importantes em sistemas agroflorestais abertos. Estes ecossistemas estão entre os mais importantes e vulneráveis, e apresentam uma biodiversidade relativamente elevada, oferecendo refúgio e áreas de alimentação para presas e predadores e consequentemente constituem corredores de migração. Estas áreas fornecem muitos recursos e atraem muitos animais, como aves frugívoras, que são os principais dispersores de sementes na bacia do mediterrâneo. A importância das galerias ripícolas para as comunidades de aves é reconhecida para as espécies ripícolas mas, a interface entre as galerias ripícolas e a matrix envolvente tem sido pouco estudada. Esta tese compara a comunidade de aves em termos de composição, dieta, ecologia alimentar e a dinâmica da dispersão de sementes entre aves que habitam a galeria ripícola e a matriz florestal envolvente (montado). Demos também um primeiro passo na tentativa de estimar o valor económico do serviço de ecossistema "dispersão de sementes" fornecido pelos passeriformes.

Esta tese compreende quatro capítulos.

No primeiro capítulo analisamos as comunidades de aves a diferentes distâncias da ribeira no sentido de descrever variações sazonais e diárias no uso das galerias ripícolas e das áreas florestais adjacentes (montado). Para além disso, avaliamos se as aves se movimentam activamente da matriz envolvente para a galeria ripícola e a sua direcção de voo em três diferentes estações do ano. A riqueza específica e a abundância de aves (número total de indivíduos) nas galerias ripícolas do sul de Portugal foram fortemente influenciadas pela distância à ribeira e pela estação do ano, e foram significativamente mais elevadas na galeria ripícola do que na matriz adjacente. A riqueza específica foi significativamente mais elevada na galeria ripícola durante a o período da migração (verão-outono), e a abundância de aves foi significativamente menor do que durante o período reprodutor. Verificou-se uma percentagem significativa elevada de movimentos de aves da matriz envolvente para a galeria ripícola no meio do verão mas, não durante a migração outonal e no inverno.

No segundo capítulo analisámos a dieta de Passeriformes usando amostras fecais e amostras de sangue, analisadas através de isótopos estáveis de carbono, de 10 espécies de aves; 5 passeriformes característicos da zona ripícola e 5 passeriformes característicos da matriz florestal envolvente. Avaliámos também a disponibilidade de alimento em duas área ripícolas-florestais do sul de Portugal (Évora) em quatro estações do ano (primavera, verão, outono e inverno). Constatámos que a dieta e a ecologia trófica entre passeriformes da galeria ripícola e da matriz adjacente variam entre si de acordo com a estação do ano e com a disponibilidade alimentar, particularmente durante períodos com elevada densidade de aves.

No terceiro capítulo estudámos os padrões de dispersão de sementes pelas aves na galeria ripícola e na matriz florestal envolvente usando um tipo específico de marcação de frutos e as convencionais "seed-traps". A dispersão de sementes foi fortemente influenciada pela abundância de frutos, a distância à ribeira e as dimensões das sementes. Os resultados deste estudo têm implicações na colonização da matriz adjacente pelas plantas de frutos carnudos da galeria ripícola, uma vez que sementes de menores dimensões podem ser dispersadas a maiores distâncias e que a abundância dessas espécies produtoras de frutos vai influenciar fortemente a composição da comunidade de plantas da matriz envolvente.

No quarto capítulo demos um primeiro passo no uso do análise do custo de substituição para estimar o valor económico do serviço de ecossistema "dispersão de sementes" levado a cabo pela Toutinegra-de-barrete-preto (*Sylvia atricapilla*) ao dispersar sementes de amoras silvestres (*Rubus ulmifolius*) e de zambujeiro (*Olea europaea* var. *sylvestris*) na galeria ripícola e na matriz adjacente numa área do sul de Portugal. Discute-se que o custo de substituição da dispersão de sementes varia de acordo com o método de substituição usado, seja ele espalhar sementes ou a plantação de plântulas (alvéolos florestais). Tem de haver um compromisso de forma a substituir este serviço usando o método mais aproximado às dinâmicas de dispersão de sementes pelas aves mas, ainda assim, a complexidade de factores que afectam a germinação e a sobrevivência das plântulas resultou provavelmente numa subestimativa do serviço de ecossitema desempenhado pela toutinegra-de-barrete-preto neste estudo. Tendo em conta que a toutinegra-de-barrete-preto leva a cabo este processo de dispersão de sementes sem qualquer custo económico associado, este tipo de abordagem pode constituir uma importância ferramenta no sentido de desenvolver medidas de conservação e gestão da biodiversidade mais eficientes.

Palavras-chave: Galeria ripícola, Montado, passeriformes, dieta, dispersão de sementes, serviços de ecossistema.

# General Introduction

# The importance of Riparian Galleries

Riparian areas, described as the land adjacent to streams and rivers that interact with the aquatic environments, present high heterogeneity and biodiversity providing critical habitat for rare and threatened species, provides refuge and resource areas for prey and predators (Tabacchi *et al.* 1998, Rodewald & Bakermans 2006, Rosalino & Santos-Reis 2008, Santos *et al.* 2011), and act as corridors for migrating species (Naiman *et al.* 1988, Risser 1990). Riparian galleries are very important for ecosystem functioning, and are particularly relevant in dry areas such as savannah-type habitats of the Mediterranean region, maintaining high biodiversity on a regional scale (Johnson *et al.* 1977, Rottenborn 1999, Godinho *et al.* 2010). The riparian galleries constitute biodiversity-rich ecosystems, which are important for many environmental processes (Nilsson & Svedmark 2002, Salinas & Casas 2007) and are among the richest, dynamic and complex terrestrial ecosystems (Jansson *et al.* 2000, Naiman *et al.* 1993). The riparian galleries function as key landscapes in the maintenance of biological connections through environmental gradients, and provide many ecosystems services to humans, particularly regulating services. The vegetation is an essential component of the riparian galleries, depending mostly from nutrients transported in the water current that allow a structurally complex plant community with large biomass productivity, and a wide variety of species, comparatively to the surrounding woodland matrix (Lavorel 1999, Naiman *et al.* 1993). Of particular interest in the riparian forest are the species of trees and shrubs that produce fleshy fruits, an important food source for many frugivorous species especially in the Mediterranean region (Ferreira & Aguiar, 2006). As a result, during summer, the riparian gallery presents lower temperatures and high humidity, in contrast to the surrounding matrix, and thus provide favourable environmental conditions for many animal communities that may use the riparian forest to escape the heat of the surrounding matrix (Fabião & Fabião 2007, Saab 1999). Due to intensive alterations in the vegetation cover during centuries, the Mediterranean region now presents highly fragmented woodlands and a strong reduction in riparian galleries (Ferreira 2001, Pereira *et al.* 2015), which are in some areas the only vegetation cover important for animals to breed, feed and shelter (e.g. Deschênes *et al.* 2003, Pereira *et al.* 2014). In Mediterranean environments the riparian gallery plant community is more complex and diverse than that of the surrounding woodland matrix (Aguiar *et al.* 2000, Herrera & García 2008), which contributes to explain

the greater avian species richness in riparian galleries (Bub *et al.* 2004). Furthermore, the biodiversity of the riparian galleries influences strongly the surrounding matrix (Herrera & García 2008, Saab 1999); for instance by providing an important source of seeds for plant colonization in the surrounding matrix (Herrera & García, 2008). The surrounding matrix is often profoundly altered and the riparian gallery can be important for matrix functioning and ecological rehabilitation (Aguiar *et al.* 2000, Herrera & García 2008).

# The importance of the riparian gallery for bird communities

Throughout the year the riparian gallery is essential for many species of birds: for example as a nesting site for aquatic species (e.g. Herons); source of food supplies like berries for frugivorous species (e.g. Blackcap) and insects for insectivorous species, and shelter for migrant species (e.g. flycatchers). The Riparian gallery attracts many seed dispersers, particularly frugivorous birds that are the major seed dispersers in the Mediterranean basin (Machtans *et al.* 1996), which by feeding on fruits increase the germination rate of seeds that pass through the digestive tract (Debussche & Isenmann 1992, Martínez del Rio & Restrepo 1993). At the end of the summer/winter, riparian galleries present a large fleshy fruit production that constitutes an important food supply for many animal species, including frugivorous birds and mammals (Espírito-Santo *et al.* 2000, Ferreira & Aguiar 2006, Fabião & Fabião 2007, Rosalino & Santos-Reis 2008, Santos *et al.* 2011). A large production of fleshy fruits contributes to explain the higher numbers of resident and migrant birds' along riparian galleries in the Iberian Peninsula, particularly during autumn migration (Pereira *et al.* 2014), and higher species richness due to the influx of migrating and wintering birds.

Few studies have so far described the importance of riparian galleries vs. the surrounding matrix taking into account seasonal variations in bird species diversity (e.g. Leal *et al.* 2011), although several studies suggest that riparian forest may provide higher quality habitat for birds than the surrounding matrix (Kinley & Newhouse 1997, Frochot *et al.* 1999; Bub *et al.* 2004, Staicer 2005). Riparian forests allow more shade and wet conditions, thus greater microclimatic stability for fauna than adjacent areas, but this prediction has rarely been

addressed (Bub *et al.* 2004). Furthermore, thermal variation between riparian galleries and the surrounding matrix is markedly different (Brosofske, 1996) and linked to light intensity, as understory light tends to be highest at the riparian forest edge, but decreases rapidly towards the riparian forest interior (MacDougall & Kellman, 1992). This thermal variation should favour, particularly during the summer, the movement of birds from the surrounding matrix into the riparian gallery. Although, particularly important for resident and migrating songbirds during the summer hot periods, and for wintering and resident passerines during the cold season, the role of microclimatic conditions to explain seasonal differences in bird diversity between riparian areas and the surrounding matrix has not been considered explicitly.

The composition of bird communities are determined not only by the regional pool of species, but also by landscape and patch features like the matrix type, patch width, size and shape, habitat configuration, floristic and physiognomic vegetation structure (e.g. Davis 2004, Gil-Tena *et al.* 2007). Therefore, the riparian galleries and the surrounding matrix have different bird communities. In a study in central Alentejo, southern Portugal, it was possible to identify three main groups of birds in the system riparian gallery-adjacent woodland matrix (Montado ecosystem): 8 species of birds typical of the riparian gallery (for example *Sylvia atricapilla* and *Luscinia megarhynchos*), 6 species of birds typical of the woodland matrix (for example *Cyanistes caeruleus* and *Parus major*) and 5 species of birds dwelling on the interface riparian gallery-woodland matrix (for example *Sylvia melanocephala* and *Emberiza calandra*) (Pereira *et al.* 2014); it was also found that species richness is higher in the riparian gallery than in the surrounding woodland matrix (Pereira *et al.* 2014, Pereira *et al.* 2015). Riparian galleries might be particularly important for surrounding matrix bird communities in the summer, providing shelter during hot periods, and throughout the year because riparian vegetation may be richer in food sources such as insects and fruits than the surrounding matrix (Brinson *et al.* 1981). Although the importance of riparian galleries is well known for the most specialized riparian bird species (Godinho *et al* 2010, Bryce *et al.* 2002), few studies were developed to compare the importance of riparian galleries vs. surrounding matrix for passerine bird communities.

# Bird Diet and Seed Dispersal

A species diet and factors that affect food availability are essential for understanding their ecological requirements, and this is true for both passerines foraging in the riparian gallery and in the adjacent matrix. According to Whitaker *et al.* (2000), flying insects are more abundant in riparian buffer strips because they offer them shelter from greater wind speeds; therefore riparian buffers accumulate flying insects and might represent high-quality food patches for insectivorous bird species. In temperate climate regions most plant species flower in spring and present ripe fruits in summer, autumn, or early winter (Herrera, 1984a) and, in general, the availability and diversity of fruits are greater in riparian galleries than in the surrounding matrix (Thompson & Willson 1978, 1979). However, there are very few studies that explicitly compared resources such as the abundance of insects and fruits between the riparian gallery and the adjacent matrix. Therefore, it is expected that surrounding matrix bird species use riparian galleries throughout the year, particularly for shelter during hot summer periods, and to feed on insects and fruits that are particularly abundant in late summer and autumn (Brinson *et al.* 1981, Blake & Hoppes 1986).

The analysis of regurgitations and fecal samples as a mean to assess diet allow great taxonomic detail in discrete samples; particularly for small passerines fecal samples they rely on the ability to identify hard parts of arthropod remains but underestimates soft-bodied or very small arthropods. However, identification is relatively easy in terms of seeds. Stable isotopes have become increasingly used to study the diet of predators because they overcome some limitations associated with conventional methods, although under-used in ecological studies of small passerines. Stable-carbon and nitrogen isotope analysis are now increasingly used as a tool to identify dietary patterns in terrestrial ecosystems (Peterson & Fry 1987, Rundel *et al.* 1989, Hobson & Clark 1992, Kelly 2000, Inger & Bearshop 2008). In our case study, stable isotope analysis is particularly useful to differentiate two isotopically distinct dietary sources available for birds in the interface riparian gallery and the adjacent matrix, insects and berries. Isotope ratios pass from prey to consumer tissues in a predictable manner (Hobson & Clark, 1992) due to a selective retention of the heavy isotope and excretion of the light isotope in metabolic reactions (Inger & Bearshop 2008, Masello 2013). In dietary studies the most used stable isotopes are nitrogen (N) and carbon (C)

(Forero & Hobson, 2003), which provide information about the trophic level and foraging habitats, respectively.

Birds use all the area covered by the riparian gallery and the woodland matrix and, especially woodland matrix birds might have a role in seed dispersion, given their movements to the riparian gallery to feed on berries. Upon returning to the woodland matrix they will defecate and promote plant colonization in the matrix (Herrera 1984b, Jordano *et al.* 2007, Grünewald *et al.* 2010, Cruz *et al.* 2013, Fleming & Kress 2013). Seed dispersing bird species in temperate areas disperse seeds almost continuously throughout the year, with an accentuated peak in autumn which, in Europe, can be extended until winter (Debussche & Isenmann, 1992). Seed dispersion is an important process that connects successive plant generations and influences vegetation dynamics (Nathan & Muller-Landau 2000, Heleno *et al.* 2011).

# Seed dispersal as an Ecosystem Service

Biodiversity plays a key role in ecosystems structure and dynamics, and is essential for maintaining basic ecosystem processes and supporting ecosystem functions (Cardinale *et al.* 2012, Naeem *et al.* 2012). Ecosystem services can be defined as ecosystem functions that are important for human activities and human well-being (Barbier *et al.* 1994) receiving direct and indirect benefits (MA, 2003), or as conditions and processes through which natural ecosystems, and the species that they contain, support human life (Daily, 1997). The benefits provided by natural ecosystems are both now widely recognized but still poorly understood (Pagiola *et al.* 2004). Economic valuation of ecosystem services can provide a useful tool to policymakers, in  raising awareness regarding the substantial benefits that ecosystems provide, targeting resources to provide most efficient protection of ecosystems and their services and contributing for the rational decision-making process (Glenk *et al.* 2013; Bateman *et al.* 2014; Laurans & Mermet, 2014). Nevertheless, ecosystem services are often criticized for excluding the idea of biodiversity as an inherent value, beyond human needs (Reyers *et al.* 2012, Deliège & Neuteleers 2014, Schröter *et al.* 2014). Focusing our attention on ecosystem services benefits often implies economic valuation. Economic valuation has a role to play, but it must be considered alongside other types of value, like

socio-cultural, health and nature conservation values, reflecting also its intrinsic value of moral concretion and happiness (Hougner *et al.* 2006).

People value species' existence from an aesthetic and ethical perspective, but it is important that wild populations are also valued by their functional roles. With a deeper knowledge of those roles, there will be more opportunities to analyze the economic significance of populations and to value the ecosystem services that they provide, such as the case of seed dispersal by avian frugivores (Hougner *et al.* 2006), pollination by insects or insect pest control by invertebrate and vertebrate predators (Östman *et al.* 2003). Another way to illustrate the economic significance of the services is to measure the cost of replacing them by man-made substitutes; for example, replacing pollination services performed by native bees by human artificial means (Hougner *et al.* 2006). The valuation methods follow either of two strategies: (1) to reveal people's trade-offs with respect to ecosystem services from their behaviour on markets for related goods (revealed preferences (RP) methods), and (2) to ask people directly about what trade-offs they are willing to make through survey instruments such as face-to-face interviews and mail questionnaires (stated preferences (SP) methods, such as contingent valuation) (Freeman III, 2003). The RP methods includes the Production Function (PF) approach because economic values are measured from changes in producer and consumer surpluses at the market for the product for which the ecosystem service serves as an input, giving focus to the species functional roles in terms of species' provision of ecosystem services. SP methods, on the contrary, take functional roles into account only if people are aware of them. An alternative way to value species functional roles is to follow the replacement cost (RC) method. This method focuses on the costs of programs providing man-made substitutes for ecosystem services. Because society would not have to pay such costs if the ecosystem service is available, the idea is that such cost savings indicate the economic value of the service. However, three conditions have to be assured so that the method results in valid estimates of economic values (Shabman & Batie, 1978; Bockstael, Freeman, Kopp, Portney, & Smith, 2000; Freeman III, 2003): 1) The man-made substitute provides functions that are equivalent in quality and magnitude to the ecosystem service; 2) The man-made substitute is the least cost alternative way of replacing the ecosystem service; 3) Individuals in aggregate would be willing to incur the replacement costs if the ecosystem service was no longer available.

In temperate and Mediterranean European areas fleshy-fruited plants commonly produce mature fruit crops in late summer and autumn, and some species also in winter,

when flocks of wintering migrant birds are abundant in those areas (Thompson & Willson, 1979; Willson & Thompson, 1982; Herrera C. M., 1984a; Herrera C., 1995; Skeate, 1987; Snow & Snow, Birds and Berries, 1988; Willson & Traveset, 2000). Fruit consumption among temperate birds has been repeatedly documented (e.g., McAtee 1947, Turček 1961). For example Blackcaps' tendency to frugivory is well known (e.g. Turček 1961, Tutman 1969) and according to Jordano & Herrera (1981) this species ingests olive fruits more frequently for their high fat and protein values (Tutman, 1969). Hougner *et al.* (Economic valuation of a seed dispersal service in the Stockholm National Urban Park, Sweden, 2006) estimated the number of seed-dispersed oak trees that resulted from jays and determined the costs of replacing this service in an artificial way, using PF and RC approaches, which can be particularly invoked in cases of known functional ecological relationships. Applying production function and replacement cost approaches to estimate the economic value of ecosystem services provided by individual species requires a detailed ecological knowledge of the species (Hougner, Colding, & Söderqvist, Economic valuation of a seed dispersal service in the Stockholm National Urban Park, Sweden, 2006). Most economic valuation studies of species derive from stated preferences methods. These methods fail to take into account biodiversity values that the general public does not know about. Hence, production function (PF) and replacement cost (RC) approaches to valuation may be preferable in situations where species perform key life support services in ecosystems, such as seed dispersal, pollination, or pest regulation (Hougner, Colding, & Söderqvist, Economic valuation of a seed dispersal service in the Stockholm National Urban Park, Sweden, 2006).

# Objectives and outline

This thesis has two main goals. Firstly, it intends to examine seasonal variations in activity, movements and diet of birds inhabiting the riparian gallery and the adjacent matrix to provide a better understanding of the importance of the riparian gallery for birds, and evaluate their role in seed dispersal and potential vegetation dynamics in the riparian gallery and the woodland matrix. Secondly, it uses quantitative information of seed dispersal, in these two habitats, to assess the economic value of this ecosystem service.

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

Chapter I – Examines the seasonal variation in songbird species richness and abundance in the riparian gallery and in the adjacent matrix.

Chapter II – Characterizes the diet of riparian gallery specialists and woodland matrix birds throughout the year using two different methods, fecal analysis and stable isotopes.

Chapter III – Characterizes and analyses the pattern of seed dispersal by frugivorous bird species between the riparian gallery and the woodland matrix.

Chapter IV – Addresses the replacement costs of seed dispersal in the riparian gallery/adjacent matrix as an ecosystem service.

# Chapter I

## Seasonal variation in the bird species richness and abundance in riparian galleries in Southern Portugal

# Abstract

Riparian ecosystems are critical in maintaining biodiversity on a regional scale, which is particularly important for open agroforestry systems. We evaluated bird species richness and abundance in three different distances from the stream (0, 125 and 250 m) in Cork and Holm oak forest systems (Montado) in southern Portugal. We used 5 minutes point-counts to survey birds in two daily periods (morning and afternoon) of three different seasons (breeding season, summer-autumn migration and winter), to describe seasonal and daily variations in the use of riparian galleries and adjacent areas by birds. To assess whether birds move actively from the surrounding matrix into the riparian gallery we installed mist-nets in mid-summer, autumn migration and winter, in two sites adjacent to streams, and recorded flight direction of all passerines trapped in the mist-nets. Both, species richness and bird abundance, were significantly higher in the riparian gallery than in the adjacent matrix. Species richness was significantly higher during the summer-autumn migration period, and bird abundance significantly lower during the breeding season. Apart from the Short-toed treecreeper *Certhia brachydactyla*, Nuthatch *Sitta europaea* and Chaffinch *Fringilla coelebs*, all other species were generally more abundant close to the stream than at 250 m away. There were a significant higher percentage of birds moving from the surrounding matrix into the riparian gallery in mid-summer, but not during the autumn migration and winter periods. This suggests that microclimatic conditions are important to explain seasonal differences in bird abundance in the interface riparian gallery and surrounding matrix. This study shows the importance of considering seasonal variation for the management of passerine bird populations in riparian galleries of Mediterranean areas. A well conserved riparian gallery appears to be a keystone structure exerting a strong influence on the number of bird species associated with surrounding agro-forestry systems such as the Montado.

# Keywords

Riparian gallery, surrounding matrix, passerine, census, Montado, summer, winter.

# Introduction

Riparian areas are described as the land adjacent to streams, rivers, and nearshore environments that interact with the aquatic environments (Naiman & Decamps 1997, Ferreira *et al.* 2005). Riparian galleries present greater heterogeneity, have relatively high biodiversity, provide critical habitat for rare and threatened species, are refuge and resource areas for prey and predators, and can act as corridors for migrating species (Naiman *et al.* 1988, Risser 1990). The importance of riparian galleries for the functioning of ecosystems is particularly relevant for relatively dry areas such as savannah-type habitats of the Mediterranean region. In arid regions in particular, riparian ecosystems are critical in maintaining high biodiversity on a regional scale (Johnson *et al.* 1977, Rottenborn 1999, Godinho *et al.* 2010). This is noticeable when riparian galleries provide the only breeding and feeding forest habitat in otherwise open landscapes (e.g. Deschênes *et al.* 2003, Pereira *et al.* 2014). Bird species richness in Mediterranean riparian galleries varies throughout the year as a result of seasonal habitat changes, and particularly due to the influx of migrating and wintering birds. For example, during autumn migration both resident and migrant birds are present at higher numbers in the Iberian Peninsula particularly along riparian galleries (Pereira *et al.* 2014).

However, few studies have so far described the importance of riparian galleries vs. the surrounding matrix taking into account seasonal variations in bird species diversity (e.g. Leal *et al.* 2011). In Mediterranean-type ecosystems the vegetation cover and habitat heterogeneity is usually higher for riparian galleries than for the surrounding matrix, which leads to greater avian species richness in riparian galleries (Bub *et al.* 2004). The higher vegetation cover of riparian galleries provides more shade and wet conditions, and thus greater microclimatic stability for fauna  than adjacent areas, but this prediction has rarely been addressed (Bub *et al.* 2004). Thermal variation between riparian galleries and the surrounding matrix is markedly different (Brosofske 1996) and linked to light intensity, as understory light tends to be highest at the riparian forest edge, but decreases rapidly towards the riparian forest interior. (MacDougall & Kellman 1992). This thermal variation should favour the movement of birds from the surrounding matrix into the riparian gallery, particularly during the hot summer months and especially in the afternoon when the thermal variation should be even more markedly different. Overall, the role of microclimatic

conditions to explain seasonal differences in bird diversity between riparian areas and the surrounding matrix has not been considered explicitly. This is likely to be of particular importance for resident and migrating songbirds during the summer hot periods, and for wintering and resident passerines during the cold season. In this study we examined the seasonal variation in songbird species richness and diversity in the riparian gallery and in the adjacent matrix, to answer the following questions: 1) How important are the riparian galleries vs. adjacent areas for songbirds? 2) Does this importance vary throughout the year? 3) Does the abundance of each species vary between the morning and the afternoon? 4) Do birds show active seasonal movements from the surrounding matrix into the riparian gallery and vice versa? Results are discussed taking into consideration the empirical microclimate conditions and food resources of the riparian gallery and the surrounding matrix.

# Methods

**Study area**

Bird surveys were conducted in 2013 and 2014 on 30 sites of riparian corridors and adjacent matrix located in an approximated 34 km radius around the city of Évora (Évora, Montemor-o-Novo, Redondo and Arraiolos municipalities), Central Alentejo, Portugal. All sites were selected to present a relatively similar habitat structure in terms of vegetation and stream width. The climate is Mediterranean with an annual rainfall that varies between 500-800mm (Instituto do Ambiente, 1999). Temperature varies from 9˚C in January to 24˚C in July, with daily mean temperature records ranging from 7˚C to 43˚C, and annual insolation ranging from 2900 to 3000h/year (Instituto do Ambiente 1999). Altitude ranges from 200 to 300m a.s.l. (Instituto do Ambiente 1999). Cork oak *Quercus suber* and Holm oak *Q. rotundifolia* agro-forestry systems, locally known as 'Montados', are the dominant element of the landscape. Our riparian areas were dominated by Blackberry *Rubus* spp*.*, Ash *Fraxinus angustifolia* and Willow *Salix spp.*, and the dominant vegetation of our adjacent matrix areas were Holm oak and Cork oak with a shrub layer of Rockrose (*Cistus crispus, Cistus salviifolius* and *Cistus ladanifer*) and Thistle *Cynara* spp*..* All the riparian galleries sampled had relatively similar stream width, ranging from 5 to 10 m with a torrential character.

## Sampling sites and bird surveys

We evaluated bird communities in each of the 30 sampling units (stretches of streams) in watercourses from the Tejo, Sado and Guadiana basins. In all sampling units the surrounding matrix of 'montado' was relatively similar in terms of arboreal and shrub percentage cover, with ca. 30 mature trees/ha. In each unit we followed the procedure used by Pereira *et al.* (2014) and sampled one point in the riparian gallery (P1) followed by two points in the surrounding matrix: P2, 125 m perpendicular from P1 and P3, 250 m from P1, thus comprising 90 sampling points. We used fixed 5 min point-count stations (Fleishman *et al.* 2003) and counted birds, located visually and by sound, within a 50 m radius for point-counts located in the matrix (P2 and P3), and within a band of 100 length x 25 m width (including both sides of the stream) in the riparian gallery, due to its linear structure. To better visualize differences in bird composition among the three points, we represented graphically the seasonal variation in species richness and bird density within the area surveyed for each point P1, P2 and P3. All sites were surveyed during the breeding season (from 6 May to 8 June 2013), summer-autumn migration period (from 29 August to 27 September 2013) and in winter (from 10 December 2013 to 22 January 2014) both in the morning and in the afternoon. For each sampling unit, P1, P2 and P3 were surveyed in the same morning and in the same afternoon. Surveys were carried out in the morning during the first 4 hours after sunrise and in the afternoon 4 hours before sunset, in order to understand daily and seasonal variations of how surrounding matrix bird species use riparian galleries. Species detected more often in the riparian gallery were classified as Riparian birds (RP) and species detected more often in the adjacent matrix were classified as Matrix birds (MT), similarly to data provided by Pereira *et al.* (2014).

To assess whether birds move actively from the surrounding matrix into the riparian gallery we installed mist-nets parallel to the stream, at about 3 m from the riparian gallery, and along a 300 m stretch, and registered the flight direction of each individual. We recorded all passerine trapped in the mist-nets, i.e. flying from the surrounding matrix into the riparian gallery and vice-versa. The height of the mist nets, approximately 3m, was slightly smaller than the forest height. Therefore, it is possible that some birds flew above the mist nets but in either way the birds captured should show or not a movement trend. Data were collected at the Constant Effort Site of Mitra (University of Évora, near Valverde village) and in a patch of Degebe River just outside Évora (near Canaviais), in mid-summer

(June and July 2013), autumn migration (September and October 2013) and winter (January and February 2014).

**Temperature in the riparian area and the adjacent matrix**

Data loggers (CEM DT-171 USB temperature and humidity data loggers) were set to collect data in a pairwise design every hour during a 24h period, simultaneously for 16 P1 and P3 sampling units during September 2013 (autumn migration), and 8 P1 and P3 sampling units during December 2013 (winter season). P2 temperature values were not measured because the difference between P1 and P2 should be small given the fact that P2 was still relatively closer to the stream. For each day we retrieved the minimum and the maximum daily temperature for analysis. We recorded daily temperatures only in late summer and winter because they represent the periods with more extreme temperatures, and thus could be used to evaluate the importance of the riparian galleries as a source of shelter.

**Statistical analyses**

We used bird species recorded in our morning 90 sampling units to compare overall species richness, diversity and evenness for the three distances to stream (P1, P2 and P3) among seasons (breeding, autumn migration and winter), using the Simpson reciprocal index of diversity (D = 1 / $\sum P_i^2$; $P_i$ = the proportion of all individuals in the community that belong to species i, and evenness:  E = D / S; S = species richness). Like Pereira *et al.* (2014) we excluded from our initial bird dataset (1) species with a wider spatial use of the census area, i.e., insectivorous aerial flyers such as swifts and swallows, (2) flocks of birds flying above and (3) species recorded in less than 15 % of all sampling sites. This last criterion was used because some species occurred in very lower abundances. After analyzing data with the 10, 15 and 20% threshold we decided for the 15% because this percentage excluded some less abundant species that were not statistically important, but ecologically relevant species for the study such as Nightingale (*Luscinia megarhynchos*) were not excluded. In all, 21 bird species satisfied our criteria and were included in subsequent analyses.

Generalized Linear Mixed Models (GLMM) with a Poisson distribution and a log link function were conducted to compare the effects of distance to stream (0m, 125m and 250m), season and their interaction on:  a) species richness (using the total number of species recorded in each point) and b) total bird abundance (the number of individuals of all species that occurred at least in 15% of the sampling units). The survey effort entered the model as an offset variable (as it differed between P1 and P2, P3; see above) and the sampling unit as a random factor. For

these two models we used only data from morning census, when a higher number of species was detected. To assess differences in the abundance of each species in relation to distance to stream and period of the day (morning and afternoon) we used Generalized Linear Models (GLM) with a Poisson distribution and a log link function. Because the detectability of each species is likely to differ among seasons we analyzed each season separately. To evaluate the null hypothesis that birds would fly in an equal proportion from the matrix into the riparian gallery in mid-summer, autumn migration and winter we used a binomial GLMM, in which the response variable was 0 (when a bird flew out of the riparian gallery) and 1 (when a bird flew into the riparian gallery), season was a fixed effect and sampling site a random factor. Likelihood-ratio tests and the analyses of individual standardized residuals were used to assess the fit of all GLMM models (Zuur *et al.* 2007). Finally, we used a paired t-test to compare the minimum and the maximum temperature between P1 and P3, both for the autumn migration and the wintering seasons. All statistical analyses were carried out using SPSS version 19.

# Results

**Seasonal variations in bird species richness and abundance**

Overall we recorded 57 bird species in the morning census (no further species were recorded in the afternoon census), 34 in the breeding season, 42 in autumn migration and 39 in winter. It is clear that species richness was higher during the autumn migration, particularly at the stream (P1 station, Table 1). There was a significant effect of season (Wald $X^2_2$ = 40.2, p < 0.001) and distance to stream (Wald $X^2_2$ = 108.1, p < 0.001) on species richness but no interaction between these two factors (Wald $X^2_4$ = 0.9, p = 0.93). When compared to the wintering season, species richness was significantly higher for summer-autumn migration (Estimate ± SE = 0.35 ± 0.11, p = 0.001), but not for the breeding season (Estimate ± SE = 0.001 ± 0.11, p = 1; Fig. 1). When compared to P1, species richness was significantly lower for both P2 (Estimate ± SE = -0.51 ± 0.12, p < 0.001) and P3 (Estimate ± SE = -0.55 ± 0.12, p < 0.001; Fig. 1). The Likelihood-ratio test indicated a good fit of the model ($X^2_8$ = 143.6, p < 0.001) and the analysis of the residuals indicated no cases of concern.

**Table 1** - Comparison of diversity measures among seasons for the three distances to stream (P1 = 0m, P2 = 125m and P3 = 250m).

| Distance from stream (m) | Breeding season | | | Summer-autumn migration | | | Winter season | | |
|---|---|---|---|---|---|---|---|---|---|
| | P1 | P2 | P3 | P1 | P2 | P3 | P1 | P2 | P3 |
| Overall species richness | 21 | 23 | 23 | 30 | 23 | 23 | 22 | 24 | 23 |
| Simpson reciprocal index of diversity | 8.85 | 7.70 | 7.19 | 12.06 | 9.62 | 10.55 | 11.92 | 10.70 | 10.49 |
| Evenness | 0.42 | 0.33 | 0.31 | 0.52 | 0.42 | 0.46 | 0.52 | 0.47 | 0.46 |
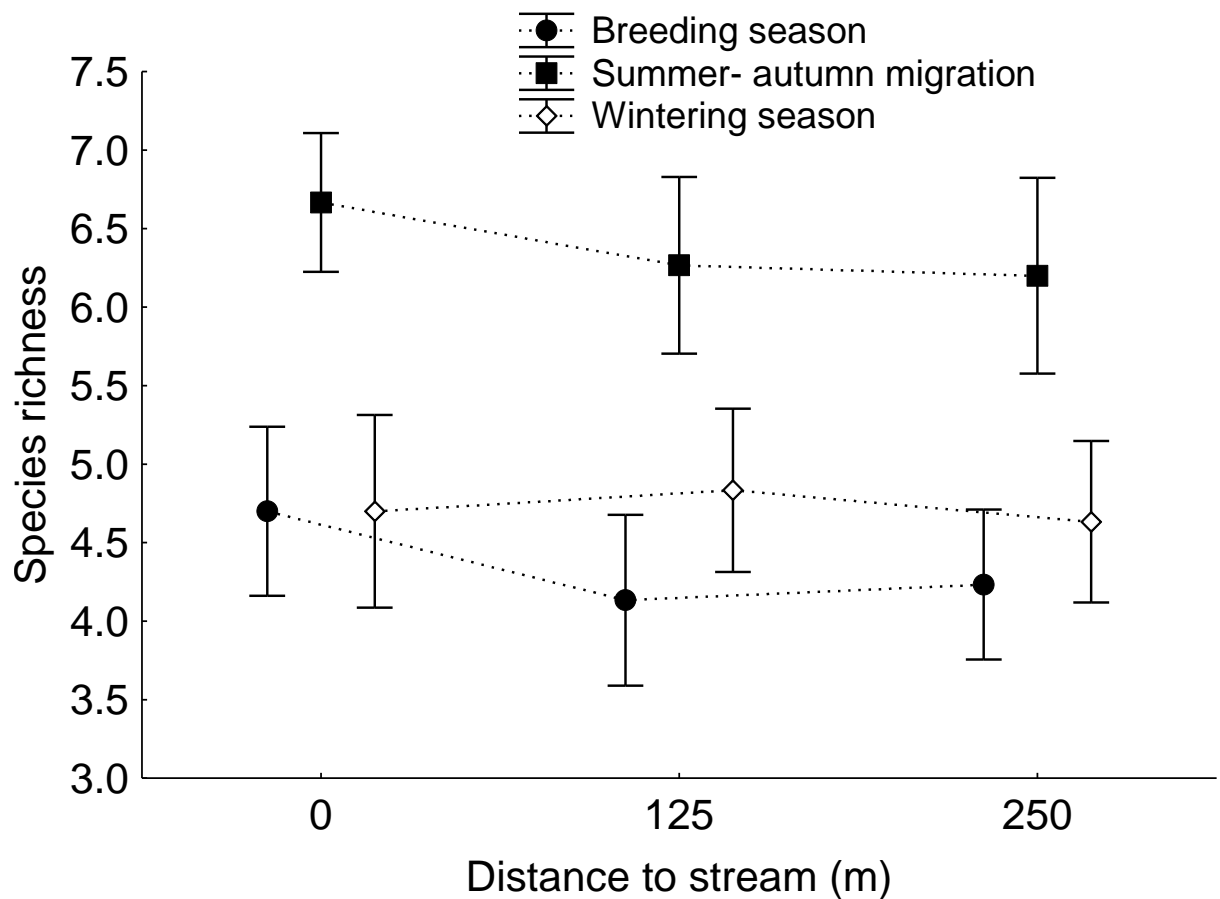


**Figure 1** – Seasonal comparison of species richness per sampling station (mean ±SE) in relation with distance to stream (P1 = 0m, P2 = 125m and P3 = 250m).

Table 2 shows the 21 species that occurred in at least 15% of our sampling units and their respective percentage of occurrence. Among them there are species characteristic of the riparian gallery, such as the Nightingale, and species that occurred more frequently in the riparian gallery than in the surrounding matrix: Blackcap *Sylvia atricapilla*, Wren *Troglodytes troglodytes*, Blackbird *Turdus merula* and Song thrush *Turdus philomelos.* All the other species occurred more frequently in the surrounding matrix, particularly Corn bunting *Emberiza calandra*, Wood lark *Lullula arborea* and Stonechat *Saxicola torquatus*. The majority of species are resident (15 out of 21). Based on the number of times we recorded each species in each habitat type, the majority of the species recorded were species characteristic of the matrix (16 out of 21). There was a significant effect of season (Wald $X^2_2$ = 15.5, p = 0.02) and distance to stream (Wald $X^2_2$ = 40.4, p < 0.001), but no interaction between these two factors (Wald $X^2_4$ = 2.7, p =0.61) on the total number of individuals recorded. When compared to the wintering season, bird abundance was significantly lower for the breeding season (Estimate ± SE = -0.37 ± 0.12, p = 0.002) but similar for the summer-autumn migration (Estimate ± SE = -0.15 ± 0.11, p = 0.183; Fig. 2). When compared to P1, bird abundance was significantly lower for both P2 (Estimate ± SE = -0.48 ± 0.11, p < 0.001) and P3 (Estimate ± SE = -0.42 ± 0.10, p < 0.001; Fig. 2). The Likelihood-ratio test indicated a good fit of the model ($X^2_8$= 55.5, p < 0.001) and the analysis of the residuals indicated no cases of concern.

Both in the morning and the afternoon aural detections were around 90% for all seasons (n varied from 241 to 334). From the species that differed in density during each season, it is clear that, apart from hole nesters (Short-toed treecreeper and Nuthatch) and Chaffinch, all other species were significantly more abundant close to the stream (P1) than 250 m away (Table 3). There were only three species with a significantly different density between P2 and P3: 1) during the breeding season, chaffinches were more abundant in P2 than in P3, 2) during the autumn migration nuthatches were more abundant in P2 than in P3, and 3) Sardinian warbler *Sylvia melanocephala* were less abundant in P2 than in P3 (Table 3). In relation to density differences between the morning and the afternoon census, only the Blue tit *Cyanistes caeruleus*, Sardinian warbler and the chaffinch showed differences: the first two species were more abundant in the morning and the third species in the afternoon (Table 3).

**Table 2** – Typology and phenology of bird species, and comparison of the percentage of occurrence (%) of the 21 species (that occurred at least in 15% of the 90 sampling units) among seasons for the three distances to stream (P1 = 0m, P2 = 125m and P3 = 250m), using data for the morning census only. Typology: MT – Matrix; RP – Riparian (This classification was made based on the number of times that we recorded the species in each habitat type, according to our records). Phenology (in the study area): R – Resident; TM – Trans-Saharan migrant; SV – Summer visitor; W – Wintering (phenology according to Catry *et al.* 2010).

| Species | Typology | Phenology | Percentage of occurrence (%) | | | | | | | | |
| | | | Breeding season | | | Summer migration | | | Wintering season | | |
| | | | P1 | P2 | P3 | P1 | P2 | P3 | P1 | P2 | P3 |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| *Luscinia megarhynchos* | RP | SV | 83.3 | 3.3 | 0 | 3.3 | 0 | 0 | 0 | 0 | 0 |
| *Troglodytes troglodytes* | RP | R | 83.3 | 6.7 | 0 | 16.7 | 3.3 | 0 | 20 | 3.3 | 3.3 |
| *Erithacus rubecula* | MT | W | 26.7 | 0 | 0 | 3.3 | 0 | 0 | 83.3 | 70 | 63.3 |
| *Sylvia melanocephala* | MT | R | 46.7 | 30 | 20 | 60 | 46.7 | 36.7 | 36.7 | 30 | 13.3 |
| *Turdus merula* | RP | R | 46.7 | 16.7 | 20 | 53.3 | 3.3 | 3.3 | 33.3 | 0 | 3.3 |
| *Sylvia atricapilla* | RP | R | 26.7 | 3.3 | 3.3 | 60 | 10 | 0 | 46.7 | 20 | 16.7 |
| *Serinus serinus* | MT | R | 26.7 | 16.7 | 16.7 | 0 | 0 | 3.3 | 23.3 | 20 | 30 |
| *Carduelis chloris* | MT | R | 23.3 | 6.7 | 20 | 3.3 | 0 | 10 | 6.7 | 0 | 0 |
| *Cyanistes caeruleus* | MT | R | 26.7 | 63.3 | 63.3 | 46.7 | 80 | 53.3 | 46.7 | 80 | 73.3 |
| *Fringilla coelebs* | MT | R | 23.3 | 93.3 | 90 | 23.3 | 20 | 10 | 23.3 | 56.7 | 40 |
| *Certhia brachydactyla* | MT | R | 16.7 | 46.7 | 73.3 | 16.7 | 36.7 | 50 | 10 | 30 | 36.7 |
| *Emberiza calandra* | MT | R | 6.7 | 30 | 23.3 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Parus major* | MT | R | 6.7 | 10 | 13.3 | 23.3 | 36.7 | 40 | 26.7 | 33.3 | 46.7 |
| *Phylloscopus ibericus* | MT | MB | 3.3 | 13.3 | 3.3 | 16.7 | 20 | 6.7 | 0 | 0 | 0 |
| *Saxicola torquatus* | MT | R | 3.3 | 3.3 | 3.3 | 16.7 | 10 | 13.3 | 0 | 0 | 3.3 |
| *Lullula arborea* | MT | R | 0 | 13.3 | 6.7 | 6.7 | 13.3 | 10 | 0 | 3.3 | 3.3 |
| *Sitta europaea* | MT | R | 0 | 13.3 | 16.7 | 6.7 | 66.7 | 60 | 0 | 30 | 26.7 |
| *Lophophanes cristatus* | MT | R | 0 | 10 | 6.7 | 3.3 | 16.7 | 16.7 | 13.3 | 30 | 30 |
| *Ficedula hypoleuca* | MT | TM | 0 | 0 | 0 | 46.7 | 53.3 | 46.7 | 0 | 0 | 0 |
| *Phylloscopus collybita* | MT | W | 0 | 0 | 0 | 3.3 | 0 | 0 | 40 | 36.7 | 33.3 |
| *Turdus philomelos* | RP | W | 0 | 0 | 0 | 0 | 0 | 0 | 20 | 3.3 | 6.7 |
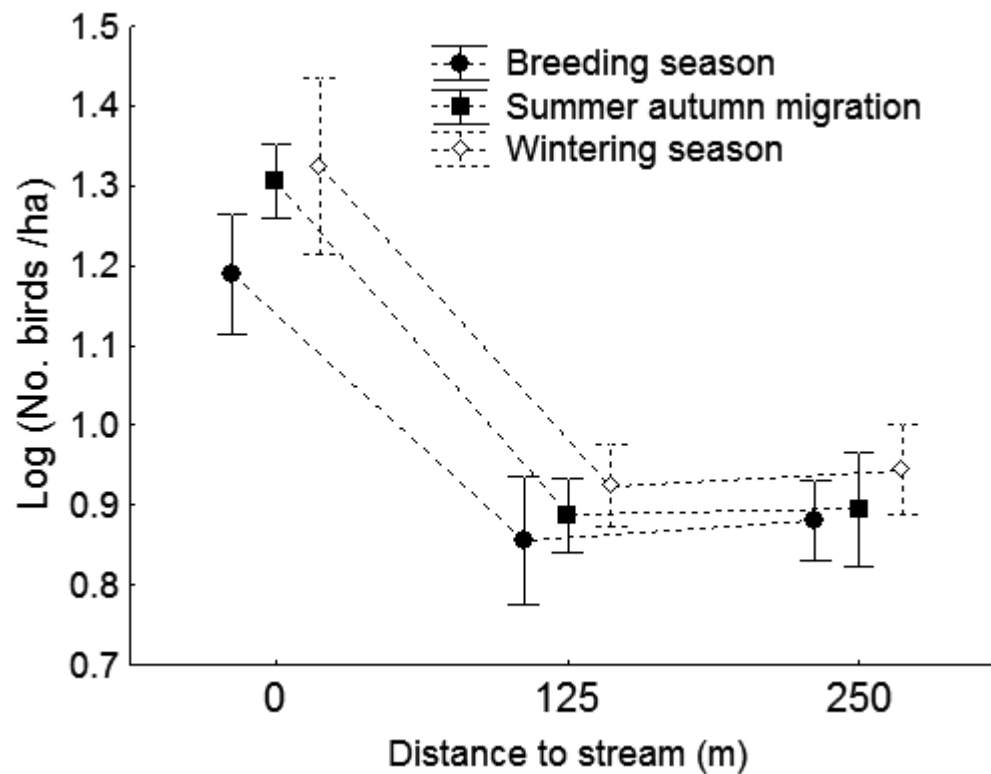
**Figure 2** – Variation in bird density (Log of No. birds/ha) of the 21 species (mean ± SE) that occurred in at least 15% of the point-counts in relation with distance to stream (P1 = 0m, P2 = 125m and P3 = 250m). To calculate bird density we used the number of individuals detected within a 50 m radius for point-counts located in the matrix (P2 and P3), and within a band of 100 length x 25 m width (including both sides of the stream) in the riparian gallery, due to its linear structure.

**Table 3** – GLM analysis results, with a Poisson distribution to assess the influence of distance to stream (P1 = 0 m, P2 = 125 m and P3 = 250 m) and period (morning and afternoon) on the density of each species per season. Statistics (Wald statistic, P value and estimate ± SE) are presented in relation to the reference category (P3 for distance to stream and afternoon for period), and only significant results are shown.

| Season | Species | Distance to stream (Reference = P3) | Period (Reference = Afternoon) |
|---|---|---|---|
| Breeding | Certhia brachydactyla | Wald Stat = 6.11, p = 0.013<br>Estimate: P1 = -0.42 ± 0.171 | |
| | Cyanistes caeruleus | | Wald Stat = 9.27, p = 0.002<br>Estimate: Morning = 0.37 ± 0.123 |
| | Fringilla coelebs | Wald Stat = 38.62, p < 0.001<br>Estimate: P1 = -0.85 ± 0.141<br>P2 = 0.34 ± 1.03 | |
| | Turdus merula | Wald Stat = 36.31, p < 0.001<br>Estimate: P1 = 1.02 ± 0.170 | |
| Summer migration | Certhia brachydactyla | Wald Stat = 5.85, p = 0.016<br>Estimate: P1 = -0.41 ± 0.168 | |
| | Cyanistes caeruleus | | Wald Stat = 5.83, p = 0.016<br>Estimate: Morning = 0.25 ± 0.105 |
| | Fringilla coelebs | Wald Stat = 12.8, p < 0.001<br>Estimate: P1 = -0.99 ± 0.277<br>P2 = 0.48 ± 0.176 | Wald Stat = 5.07, P = 0.024<br>Estimate: Morning = -0.43 ± 0.192 |
| | Sitta europaea | Wald Stat = 15.5, p < 0.001<br>Estimate: P1 = 0.73 ± 0.187<br>P2 = -0.63 ± 0.275 | |
| | Sylvia melanocephala | | Wald Stat = 13.78, p < 0.001<br>Estimate: Morning = 0.60 ± 0.161 |
| Wintering | Erithacus rubecula | Wald Stat = 24.79, p < 0.001<br>Estimate: P1 = 0.49 ± 0.098 | |
| | Fringilla coelebs | | Wald Stat = 3.94, p = 0.047<br>Estimate: Morning = -0.21 ± 0.107 |
| | Sylvia atricapilla | Wald Stat = 18.03, p < 0.001<br>Estimate: P1 = 1.25 ± 0.295 | |
| | Sylvia melanocephala | Wald Stat = 10.12, p = 0.001<br>Estimate: P1 = 0.76 ± 0.238 | |
| | Turdus philomelos | Wald Stat = 11.43, p < 0.001<br>Estimate: P1 = 1.36 ± 0.402 | |

**Bird movements and shelter conditions**

The binomial GLMM used to assess the records of movement directions of passerines captured in mist-nests revealed a significant effect of season on the proportion of bird movements from the matrix into the riparian gallery (Wald $X^2_2$ = 8.2, p = 0.016). Compared to the wintering period, significantly more birds flew into the riparian gallery than out of the riparian gallery in mid-summer (61.5% vs. 38.5%, n = 130 birds, Estimate ± SE = 1.16 ± 0.43, p = 0.006), but not in autumn (Estimate ± SE = 0.18 ± 0.41, p = 0.67). The Likelihood-ratio test indicated a good fit of the model ($X^2_2$ = 8.9, p = 0.012) and the analysis of the residuals indicated no cases of concern.

The minimum and the maximum temperature did not differ significantly between P1 and P3, for both the autumn migration (P1: 12.3°C ± 3.11, 14.4°C ± 5.4; P3: 33.8°C ± 4.2, 32.7°C ± 6.7, n = 16) and the wintering season (P1: 6.1°C ± 2.56, 6.6°C ± 2.64; P3: 15.8°C ± 1.49, 15.8°C ± 2.03, n = 8; all paired t-test, t < 1.74, p> 0.10).

# Discussion

**Seasonal variations in bird species richness and abundance**

Our study shows that bird density in Mediterranean riparian galleries of southern Portugal was strongly influenced by season and distance to the stream, with a higher species richness and bird abundance in the riparian gallery than in the surrounding Cork oak and Holm oak forest, particularly during the summer-autumn migration period. Furthermore, we observed a significant higher percentage of birds moving from the surrounding matrix into the riparian gallery in summer. The importance of the riparian gallery for birds is well known, and our study provides a first step to understand seasonal variations in the patterns of bird species richness and abundance of riparian vs. adjacent matrix passerines.

In relation to the abundance of each species during each season, our results showed a significantly higher abundance at the riparian gallery than at 250m away for all bird species, except those that are characteristic of the surrounding woodland matrix: Short-toed treecreeper, Nuthatch and Chaffinch (Cramp 1994, Snow & Perrins 1998, Hoyo *et al.* 2014). Other studies (Woinarski *et al.* 2000, Palmer & Bennett 2006) obtained similar results showing that species richness and the total abundance of birds is significantly greater in

riparian areas than in matched non-riparian areas. It was also noticeable that the density of very few bird species in our study differed between 125m and 250m distant from the stream.  A similar result was obtained by Pereira *et al.* (2014) in their study carried out in the same geographic area. Therefore our data suggests that the effect of the riparian gallery is noticeable at a distance below 125m. Such a small scale effect should be a result of the riparian gallery's small width in our study area as verified by Shirley & Smith (2005). In fact, in this study, higher species richness occurred only in the widest buffers of vegetation and abundances dropped dramatically between wide (125m) and medium (41m) width buffers. In Keller *et al.* (1993), several area-sensitive neotropical migrants were encountered more frequently in wider riparian forests, and their probabilities of occurrence increased most rapidly between 25m and 100m. Therefore, it seems that a wider riparian gallery supports a richer bird community.

The majority of the species recorded in the riparian gallery and in the surrounding matrix of 'montado' were resident birds, as in Pereira *et al.* (2014) and Godinho *et al.* (2010), and the bird community composition that we registered was similar to that of these two studies, except for Woodlark and European crested tit *Lophophanes cristatus*. A greater percentage of residents occur in riparian forests (e.g. Larsen *et al.* 2010, Godinho *et al.* 2010, Roché *et al.* 2010) and in mature woodlands in Europe (Rabaça 1990, Brotons *et al.* 2004, Gil-Tena *et al.* 2007), which is associated to a tendency to converge in the composition of bird communities in the last stages of different successional habitat gradients (Blondel & Farré, 1988).

We cannot rule out the possibility that differences in the detectability of species between the riparian gallery and the adjacent matrix might underestimate bird abundance in the more closed riparian gallery forest than in the more open adjacent matrix areas (Bibby *et al.* 2000, Paquet *et al.* 2006). However, we think that this would include a small bias in our results because the riparian gallery forests had a relatively small width, and visibility and aural conditions were good. Nevertheless, if differential detectability conditions were importance they would increase even more the importance of the riparian gallery for birds. The high percentage of aural detections registered (around 90%) during the surveys is consistent with other studies that registered 80-90% (Best 1981, Scott & Kepler 1981) in northern temperate forested habitats. Also, aural detections percentages were similar between the three different seasons surveyed, similarly to the results of other studies that compared summer with winter (Richards 1981, Scott & Kepler 1981, Hamel 1984. The fact

that species richness was higher during the summer-autumn migration should be attributed to the fact that in this period both resident and migrant birds are present in the area particularly along riparian galleries (Pereira *et al.* 2014). This fact may be explained with the possible use of riparian galleries as migration corridors by birds (e.g. Machtans *et al.* 1996, Naiman & Decamps 1997, Beier & Noss 1998, Burbrink *et al.* 1998) because they provide shelter and abundant food supplies (Gray 1989, Saab 1999, Fabião & Fabião 2007, Jacobs *et al.* 2007, Pereira *et al.* 2014). The autumn migration overlaps with the fructification period of most plant species producing berries throughout Europe (Snow & Snow 1988), and riparian galleries are recognized as rich habitats (Naiman & Decamps 1997, Palmer & Bennett 2006) providing abundant foraging resources for birds (Sanders, 1998). Temperate frugivory is a strongly seasonal phenomenon among migrant birds (Thompson & Willson 1978, Stiles 1980, Herrera 1982, Herrera, 1998, Snow & Snow 1988) and riparian galleries are very important for that, particularly given the high abundance of fruits provided by generalist plant species. Season and distance to stream had also a strong influence on bird abundance, which was significantly higher in the riparian gallery than in the matrix, particularly during winter. Such pattern of a much higher abundance of individuals and species of birds in riparian habitats than in adjacent areas was previously reported in a revision paper by Naiman & Decamps (1997); mostly notably it is stated that 82% of the breeding birds of northern Colorado, USA, occur in riparian areas (Knopf & Samson, 1994). Again, the higher bird densities in the riparian gallery during winter may be due to better shelter conditions and higher food resources than in the surrounding matrix. Similarly, previous studies suggested a higher abundance of insects and fruits in the riparian vegetation than in the surrounding matrix, although data presented is scarce (Brinson *et al.* 1981, Whitaker *et al.* 2000, Leal *et al.* 2011, Pereira *et al.* 2015).

**Bird movements and shelter conditions**

Our afternoon census did not add more bird species to the morning census community composition. Nally (1994) obtained similar results, since there was little difference in either numbers of species or numbers of individuals between morning and afternoon censuses. Therefore, and contrary to our expectation the afternoon census were inconclusive in showing the importance of shelter offered to birds by riparian galleries in summer. The differences detected between the two day periods were species-specific: Blue tit and Sardinian warbler were more abundant in the morning and the Chaffinch appeared to be

more abundant in the afternoon.  Given the fact that the vocal activity of birds is lower in the afternoon then in the morning (Robbins, 1981), and that each species has own daily activity pattern, these differences may not represent true abundances because in habitats like riparian galleries the contacts are more aural than visual, so these results suggest that only the Blue tit and the Sardinian warbler are possibly more abundant in the riparian gallery in the morning or just vocalize more than in the afternoon period. The same can be said for the Chaffinch, but this species apparently vocalizes more in the afternoon period (personal observations). The Chaffinch presented higher densities in P2 than in P3 for the breeding season, and the nuthatch had a similar pattern for the autumn migration period and, that should be explained by a higher foraging frequency closer to the riparian gallery (Gregory *et al.* 1991), where insects should be more abundant than in adjacent matrix areas. During the breeding season the presumably higher abundance of insects along the riparian gallery should be important to feed nestlings (Newton, Finches. Vol. 55., 1972).

Our temperature data did not support a significant difference in thermal shelter conditions between the riparian gallery and the adjacent area, but it should be noted that our sample size was small, and continuous temperature readings in different microhabitats should be needed to clarify this aspect. Other studies report that riparian microclimates are generally characterized by cooler air temperature, lower daily maximum air temperature, and higher relative humidity than the microclimates of adjacent areas (Brosofske *et al.* 1997, Danehy & Kirpes 2000). Nevertheless, our study showed a significant higher percentage of birds moving from the surrounding matrix into the riparian gallery only in mid-summer. This is an interesting result that points out for possible evidence that surrounding matrix birds do move into the riparian gallery in the summer for thermal shelter reasons. These movements into the riparian gallery were described by Woinarski *et al.* (2000), Gillies *et al.* (2011) and Levey *et al.* (2005), but these authors have linked them to exploitation of shifting in resource availability and shelter from predators; however these factors were not examined in our study.

**Conservation and Management considerations**

The overall higher bird diversity and abundance in the riparian gallery than in the adjacent Montado matrix may be explained by several factors including better shelter conditions (this study) and a higher abundance of food resources (Brinson *et al.* 1981, Naiman *et al.* 1988, Risser 1990) in the riparian gallery, particularly in Mediterranean areas where the surrounding matrix is fairly open. Insects use riparian habitats for feeding, resting, refuge and reproduction and in turn they provide a critical and concentrated resource base for many wildlife species (Motroni 1984, Gray 1993, Doyle 1990), including insectivorous birds (Gray 1989, Gray 1993). As a result of a higher vegetation complexity in riparian areas, the abundance of fruits in autumn and winter throughout the Mediterranean is also higher in riparian areas than in surrounding open forest such as the montado, particularly for highly abundant and consumed fleshy fruits such as blackberries *Rubus* spp. (Santos *et al.* 2011, Costa *et al.* 2014), which have a generally positive effect in determining the presence of birds in riparian galleries (Nur *et al.* 2008).

Overall, riparian ecosystems have high and frequently unique biodiversity (Sabo *et al.* 2005), despite their small land area. They also serve multiple roles, including water provision, nutrient retention (Jacobs *et al.* 2007), refuge for unique species (Sabo *et al.* 2005), and as movement and dispersal corridors (Machtans *et al.* 1996, Beier & Noss 1998, Burbrink *et al.* 1998). Our data shows that these ecosystems attract insectivorous and frugivorous birds throughout the year. Therefore, the preservation of riparian galleries is particularly important to maintain healthy bird communities in Mediterranean areas, which are crucial for key ecosystems functions such as seed dispersal (e.g. Naiman & Decamps 1997, Herrera 1998, Jordano 2000), and key ecosystems services such as pest control (Ceia & Ramos, 2014).

In summary, our results strengthen the importance of riparian galleries in Mediterranean areas for bird species richness and abundance in the summer-autumn migration and winter periods. Therefore, the management of passerine bird populations and their habitats should consider the importance of these areas outside the breeding season. Furthermore, a well conserved riparian natural plant community potentiates the number of bird species associated with the surrounding agro-forestry habitats (Woinarski *et al.* 2000, Palmer & Bennet 2006), and should be a keystone structure for the conservation of montado agro-forestry systems at a large scale (Leal *et al.* 2011, Pereira *et al.* 2015).

# Chapter II

Diet and feeding ecology of passerines in the riparian gallery and adjacent habitat matrix

# Abstract

The bird community of riparian galleries and the surrounding matrix are different, but riparian galleries should be particularly important for surrounding matrix bird communities throughout the year, providing shelter and food resources (insects and fruits). The importance of riparian galleries is well known for the most specialized riparian bird species, but the interface riparian galleries vs. surrounding matrix in terms of importance for passerine bird communities has been little studied. We used fecal samples to compare diet, and blood samples to compare carbon and nitrogen stable isotopes between passerines of the riparian gallery and the adjacent matrix, and assessed seasonal variations in food abundance in two areas of Southern Portugal (Évora). The riparian passerine species were nightingale *Luscinia megarhynchos*, Cetti's warbler *Cettia cetti,* wren *Troglodytes troglodytes,* blackcap *Sylvia atricapilla* and blackbird *Turdus merula*; and the surrounding matrix passerine species were: robin *Erithacus rubecula*, sardinian warbler *Sylvia melanocephala*, chaffinch *Fringilla coelebs*, great tit *Parus major* and blue tit *Cyanistes caeruleus*.

This study shows consistent differences in the diet and feeding ecology between passerines that inhabit the riparian gallery and the adjacent matrix: a) woodland passerines fed more on *Araneae* and fruits than riparian passerines, b) riparian species fed at a consistently higher trophic level in spring, summer and autumn but in winter they fed on lower trophic level food items. Our results show that food resources for passerines are more abundant in the riparian gallery, particularly during periods of higher species density, such as the summer-autumn migration period. This should be important in explaining the much higher density of birds in the riparian gallery (chapter 1), particularly in autumn when the food resources are also higher at the riparian gallery (this study).

# Keywords

# Introduction

Riparian areas have relatively high biodiversity, maintain critical habitat for rare and threatened species, are refuge and source areas for prey and predators and provide corridors for migration (Naiman *et al.* 1988, Risser 1993). The composition of bird communities are determined not only by the regional pool of species, but also by landscape and patch features like the matrix type, patch width, size and shape, habitat configuration, floristic and physiognomic vegetation structure (e.g. Davis 2004, Gil-Tena *et al.* 2007). Therefore, the bird community of riparian galleries is different from that in the surrounding matrix. Riparian galleries might be particularly important for surrounding matrix bird communities in the summer, providing shelter during very hot periods (chapter 1), and throughout the year because riparian vegetation may be richer in food sources such as insects and fruits than the surrounding matrix (Brinson *et al.* 1981). The importance of riparian galleries is well known for the most specialized riparian bird species (Godinho *et al.* 2010; Bryce *et al.* 2002), but there are few studies developed to compare the importance of riparian galleries vs. surrounding matrix for passerine bird communities. Passerines are one of the most important vertebrate communities of riparian forests and adjacent habitats with very important functional roles such as seed dispersal and pest control (Frochot et al 1999). Several studies suggest that riparian forest may provide higher quality habitat for birds than that provided by the surrounding matrix (Kinley & Newhouse 1997, Frochot *et al.* 1999, Bub *et al.* 2004, Staicer 2005).

In temperate climate regions most plant species flower in spring and present ripe fruits in summer, autumn, or early winter (Herrera, 1984a) and, in general, the availability and diversity of fruits are greater in riparian galleries than in the surrounding matrix (Thompson & Willson 1978, 1979). However, there are very few studies that explicitly compare resources such as the abundance of insects and fruits between the riparian gallery and the adjacent matrix. According to Pereira (2007) observations on Alentejo, southern Portugal, birds from the adjacent matrix do use the riparian gallery, so there are movements between the two habitats. Therefore, we expect that the surrounding matrix bird communities use riparian galleries throughout the year, but in particular as a shelter during very hot periods and whenever food resources are very abundant (Brinson *et al.* 1981), such

as in autumn when berries are very abundant for frugivorous birds along riparian galleries (Blake & Hoppes, 1986).

Fundamental to understanding the ecological requirements of a species is knowledge of its diet and the factors that affect food availability (Newton, 1998). Diet studies deal with fundamental aspect of the biology of organisms and provide important information for a given set of evolutionary, ecological, and conservation questions (Turshak & Mwansat, 2011). Such studies identify the food resources that provide the necessary nutrient and energy requirements of organisms (Turshak & Mwansat, 2011). According to Whitaker *et al.* (2000), flying insects are more abundant in riparian buffer strips because they offer them shelter from greater wind speeds; therefore riparian buffers accumulate flying insects and might represent high-quality food patches for insectivorous bird species. These authors found also that small-bodied insects were more abundant early in the season, whereas large insects became more prevalent as the season progressed. Food sources such as berries, that are very important for resident birds in late summer/autumn, for migrating birds in autumn and spring, and for wintering birds in autumn and spring, are likely to be abundant within the riparian gallery (Johnsgard 2009, Leal *et al.* 2011).

Conventional methods to assess diet such as regurgitations and fecal samples may allow great taxonomic detail, but reflect ingested prey in discrete samples and, in the case of fecal samples for small passerines, rely on the ability to identify hard parts of arthropod remains, and underestimate soft-bodied or very small arthropods. However, identification is relatively easy in terms of seeds. Intrinsic markers, such as stable isotopes, have become increasingly used to study the diet of predators because they overcome some limitations associated with conventional methods, but this technique has been under-used in ecological studies of small passerines. Stable-carbon and nitrogen isotope analysis is being used increasingly as a tool to delineate dietary patterns in terrestrial ecosystems (reviewed by Peterson & Fry 1987, Rundel *et al.* 1989, Kelly 2000, Inger & Bearshop 2008) and is a useful technique in situations where two isotopically distinct dietary sources are available to consumers (Hobson & Clark, 1992), which in our case are insects and berries for birds in the interface riparian gallery and the adjacent matrix. Naturally occurring stable isotopes provide an integrative view on assimilated diets, and their use is based on the fact that isotope ratios pass from prey to consumer tissues in a predictable manner (Hobson & Clark, 1992). During ingestion, digestion, and assimilation of prey, isotopic concentrations change

mainly due to a selective retention of the heavy isotope and excretion of the light isotope in metabolic reactions (Inger & Bearshop 2008, Masello 2013). The difference between isotopes ratios of consumers and their prey is a consequence of this discrimination against heavy isotopes (Fry, 2006). In dietary studies the most used stable isotopes are nitrogen (N) and carbon (C) (Forero & Hobson, 2003), which are discriminated differently. Primary producers at the base of food webs often differ in carbon and nitrogen isotopic composition (Farquhar *et al.* 1989, Martínez del Rio *et al.* 2009, Robinson 2001).

In this study fecal and blood samples were collected to evaluate, respectively, diet and trophic ecology of passerine birds in the interface riparian gallery adjacent matrix. The bird species selected to assess this topic were the riparian passerines: nightingale *Luscinia megarhynchos*, Cetti's warbler *Cettia cetti,* wren *Troglodytes troglodytes,* blackcap *Sylvia atricapilla* and blackbird *Turdus merula*; and the surrounding matrix passerine species: robin *Erithacus rubecula*, sardinian warbler *Sylvia melanocephala*, chaffinch *Fringilla coelebs*, great tit *Parus major* and blue tit *Cyanistes caeruleus.* Those were the species more frequently captured in the mist-nests, more than 8-10 times in the study area in the last two years before the study (Godinho, *et al.*, 2014; Godinho, *et al.*, 2016). We compared seasonal variations in the diet and stable isotopic values of bird species characteristic from the riparian gallery and the surrounding matrix among seasons, and evaluated seasonal variation in the abundance of fruits and insects in the riparian gallery and in the surrounding matrix to answer the following questions: 1) Does diet of birds from the riparian gallery differ from that of birds from the surrounding matrix?, 2) Is the use of the riparian gallery by birds from the surrounding matrix related with higher food abundance (insects and fruits) in the riparian gallery than in the surrounding matrix? 3) How does abundance of insects and fruits in the riparian gallery vary throughout the year? 4) Do diet and trophic niche (using stable isotopes of Carbon and Nitrogen) differ between riparian bird species and surrounding matrix birds throughout the year?

# Methods

**Study area**

Samples were collected in 2013 and 2014 on 2 sites of riparian corridors and adjacent matrix located in an approximated 20 km radius around the city of Évora (Évora and Montemor-o-Novo municipalities), Central Alentejo, Portugal. Both sample sites are in a riparian gallery – Montado (surrounding matrix) interface. One of the sites was in Valverde Stream in Herdade da Mitra (Valverde) and the other site was the Degebe River affluent (Canaviais). The climate is tipically Mediterranean with an annual rainfall that varies between 500-800mm (Instituto do Ambiente 1999). Temperature varies from 9°C in January to 24°C in July, with daily mean temperature records ranging from 7°C to 43°C, and annual insolation ranging from 2900 to 3000h/year (Instituto do Ambiente 1999). Altitude ranges from 200 to 300m a.s.l. (Instituto do Ambiente 1999). Cork oak *Quercus suber* and Holm oak *Q. rotundifolia* agro-forestry systems, locally known as 'montados', are the dominant element of the landscape. Our riparian areas were dominated by Blackberry *Rubus* spp*.*, Ash *Fraxinus angustifolia* and Willow *Salix spp.*, and the dominant vegetation of our adjacent matrix areas were Holm oak and Cork oak with a shrub layer of Rockrose (*C. crispus, C. salviifolius* and *C. ladanifer*) and Thistle *Cynara* spp.

**Bird trapping**

Ringing sessions were performed during four seasons: spring (between April 4th 2013 and May 29th 2013 and between March 27th and May 28th 2014), summer (between June 6th and July 18th 2013 and between June 4th and July 21th 2014), autumn (between September 4th and October 10th 2013) and winter (between January 23th and February 26th 2014) for both sampling sites Degebe and Mitra next to the riparian gallery and approximately 100m from the stream in the surrounding matrix (sub-sampling sites).

In Degebe we used five 15 m long mist nets in both sub-sampling sites. In Mitra, in the Spring and Summer we set 14 mist nets (198m) in both sub-sampling sites; in Winter we set 8 mist nets (87m) parallel to the riparian gallery; and in autumn we set 9 mist nets (108m) next to the riparian gallery. The mist nets were set up in the morning between 0630 hours and 1000 hours and intermittently checked for possible catch every 30 minutes.

**Fecal sample collection and analysis**

Birds captured in the ringing sessions were kept in clean bags for up to 30 minutes to defecate and droppings were preserved in eppendorf tubes with 70% ethanol until processing in the laboratory. All hard remains in fecal samples (mostly fragmented arthropod parts and seeds) were separated using a binocular microscope. Due to the difficulty in identifying arthropod parts, prey items were typically identified only to the taxonomic level of Order (Barrientos 2004, Ring et al 2013) using several reference sources (Shiel *et al.* 1997, Chinery 1993). A total of 399 fecal samples were collected between April 4th 2013 and July 21th 2014 during ringing sessions.

**Blood sample collection and stable isotope analysis**

The blood samples were collected only in the Degebe site from birds captured in the ringing sessions during the four seasons: spring (April 2013), summer (July 2013), autumn (October 2013) and winter (January 2014). We only sampled the birds from Degebe to assess the utility of this method to distinguish the diet of riparian and surrounding matrix birds. A blood sample (ca 75 µl) was taken into heparinized capillary tubes from the brachial vein of birds from Degebe. The blood was transported to the laboratory and frozen. The blood was used to give information on the current trophic niche of the birds from Degebe, a few days to several weeks prior to sample collection (Bearshop *et al.* 2002). The isotopic signature of metabolically active tissues such as blood will change over time according to switches among isotopically distinct diets or movement between isotopically distinct habitats (Hobson & Clark 1992, Bearshop *et al.* 2002).

In the laboratory blood was dried at 55 °C for a minimum of 24 hours. Pieces of dried blood were weighed (0.3 – 0.4 mg) and encapsulated. The samples were analysed in a continuous-flow isotope-ratio spectrometry, using an Isotope Ratio Mass Spectrometer (Delta V Plus, Thermo Electron) (Inger & Bearshop, 2008). The isotope ratio is calculated as $\delta X = [(R_{SAMPLE} / R_{STANDARD})-1] \times 1000$, where $X$ (‰) is $^{13}C$ or $^{15}N$ and R is $^{13}C / ^{12}C$ or $^{15}N / ^{14}N$ (Kelly 2000, Inger and Bearhop 2008). For carbon, $R_{STANDARD}$ is the Vienna-Peedee Belemnite marine fossil limestone formation from South Carolina. For nitrogen, $R_{STANDARD}$ is the atmospheric nitrogen (Kelly, 2000). We measured stable-nitrogen isotope ratios ($^{15}N{:}^{14}N$, expressed as $\delta^{15}N$) and stable-carbon isotope ratios ($^{13}C{:}^{12}C$, expressed as $\delta^{13}C$) in blood. Nitrogen is enriched at

each successive trophic level by 2 to 5‰ (DeNiro & Epstein 1978, Hobson & Clark *et al.* 1992, Kelly 2000), whereas carbon stable isotope ratios ($\delta^{13}C$) are enriched only $0 - 1$‰ per trophic level (Inger & Bearshop, 2008). Thus, carbon isotope ratios of consumers reflect the source of carbon at the base of the food web (Kelly, 2000) and can be used to evaluate foraging habitats. This is because isotopic differences in the tissues of producers, caused by the different photosynthetic pathways used by terrestrial plants (C3, C4 and CAM), macrophytes, or phytoplankton (Farquhar *et al.* 1989), are passed throughout the food web to the consumers (Cherel & Hobson 2007; Hobson *et al.* 1994).

**Insect abundance**

In order to evaluate the seasonal variation in the abundance of arthropods we used the beat-sheet method (Boyer & Dumas 1969, Shepard *et al.* 1974) (half of a pyramid; a triangle with 60x60x65cm with 75 cm deep) to sample the accessible branches of trees and bushes with a total of 10 beats/sample. We collected 15 samples at the riparian gallery and 15 samples in the surrounding matrix chosen randomly in both study areas, Mitra and Degebe. Sampling occurred in summer and autumn of 2013, Winter 2013/2014, spring 2014 and Winter 2014/2015 with a total of 285 samples collected. Collected specimens where classified taxonomically to order (Barrientos, 2004; Chinery, 1993; Ring, Häuser, Hagedorn, & Wetzel, 2013), dried in the oven (50ºc during 4 days) and weighted to obtain dry weight by sample.

**Fruit abundance**

We marked plots (whole individuals or branches) of plants with fruits and performed monthly counts to document fruit-removal between August 2013 – April 2014 and August 2014 – March 2015 in Degebe and Mitra. The plots were visited until no fruits remained, and new plots were established when new fruits appeared, such as *Hedera* spp. which fructifies in winter. The plots were established 1.5 m from the ground to exclude the removal of fruits by non-flying animals. We evaluated the seasonal decline in the abundance of the most common fleshy fruit producing species in the area: blackberry *Rubus ulmifolius*, common smilax *Smilax aspera*, myrtle *Myrtus communis*, wild olive *Olea europaea* var. *sylvestris*, black bryony *Tamus communis*, mastic *Pistacia lentiscus*, strawberry tree *Arbutus unedo*, flax-leaved daphne *Daphne gnidium*, butcher's-broom *Ruscus aculeatus*, asparagus *Asparagus aphyllus*, grapevine *Vitis* spp., ivy *Hedera* spp., dog-rose *Rosa canina* and common hawthorn *Crataegus monogyna*. These were marked according to presence and abundance in each sampling unit and in the study areas. For the most abundant plant species we marked 15-20 plots and about 10 plots for the less common plant species depending on the number of individuals with berries in each sampling season, because not all plants fructified all years. In very abundant species, and/or with many fruits like *Rubus* spp. or *Smilax aspera*, each sampling unit was constituted by a branch with many fruits to simplify the fruit counting. We marked plots in the riparian gallery (between 0 and 50m from the stream) and in the surrounding matrix (more than 50m from the stream) to evaluate if the consumption of fruits is different in both habitats.

**Data analysis**

Diet data is presented as percentage of occurrence (% of fecal samples where a particular arthropod Order was present) per season (spring, summer, autumn and winter), between April 2013 and July 2014. We performed a PCA (Principal Component Analysis) to describe patterns of diet between riparian gallery and surrounding matrix bird species. PCA is a powerful tool for analyzing ecological data because it reduces the number of dimensions graphically, without much loss of information (Zuur *et al.* 2007, Smith 2002). PCA was chosen in order to identify patterns in data, and expressing the data in such a way as to highlight their similarities and differences, as it is not a hypothesis test. In PCA there are no

underlying assumptions except that the relationships between the variables should be linear. We used one-way ANOVAs to test for differences in stable isotope values ($\delta^{13}$C and $\delta^{15}$N) of each species among seasons, after verifying that variance was homogeneous and data was normally distributed. We used Generalized Linear Mixed Models (GLMM) to evaluate the effect of habitat type (riparian gallery vs. surrounding matrix), season (winter, autumn, spring and summer) and their interaction on the abundance of arthropod data. Area (Degebe, Mitra) entered the analysis as a random factor. Results are given as means ± SD with a significance level at $p < 0.05$. All statistical analyses were carried out using the program STATISTICA (Version 7; StatSoft 2004).

# Results

**Insect consumption**

A total of 367 individual passerines were trapped and fecal droppings were collected. A total of 1139 fragments were identified and recorded, 354 in Degebe and 609 in Mitra. Of the total of these fragments, 963 (85%) were arthropod remains, 76 (7%) fleshy fruits seeds and 100 (9%) vegetative plant materials (Fig 3).
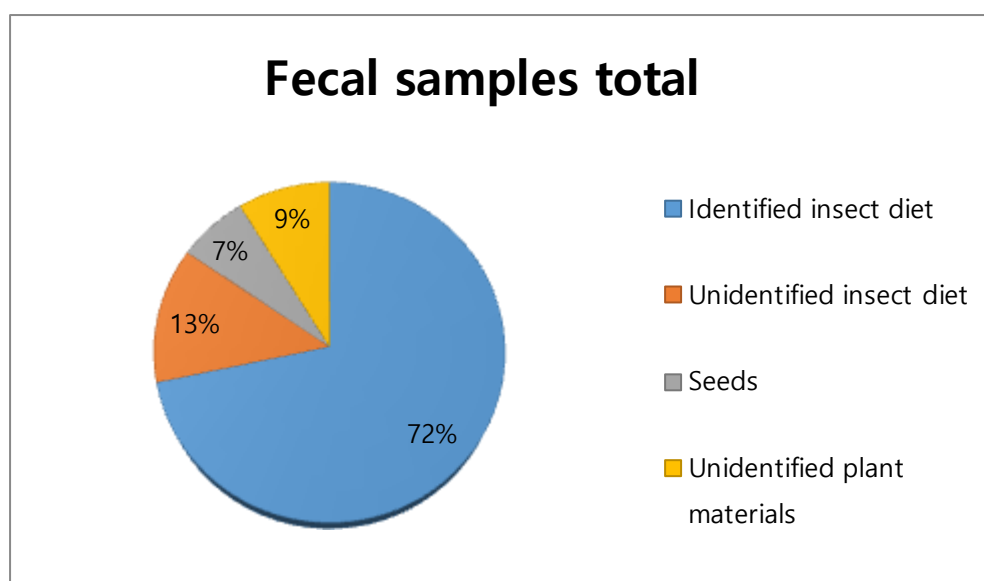


**Figure 3** – Proportion of identified and unidentified arthropods, seeds and other plant material in all fecal samples.

Analysis of fecal droppings of passerines showed that there were 13 Orders and 22 Families recorded. The 22 Families positively identified from fecal droppings of passerines belong to the Orders *Araneae*, *Hymenoptera*, *Coleoptera*, *Hemiptera*, *Diptera*, *Lepidoptera* and *Chilopoda*. The Orders *Hymenoptera*, *Coleoptera*, *Hemiptera* and *Araneae* together constituted 72% of the passerines insect diet, while 12% was made up of other insect orders and 15% of the insect fragments were unidentified at the level of Order (Fig 3). Analysis of fecal droppings of passerines reveals that birds fed primarily on *Hymenoptera* (27%), *Coleoptera* (26%), *Hemiptera* (12%), and *Araneae* (7%) (Fig 4).
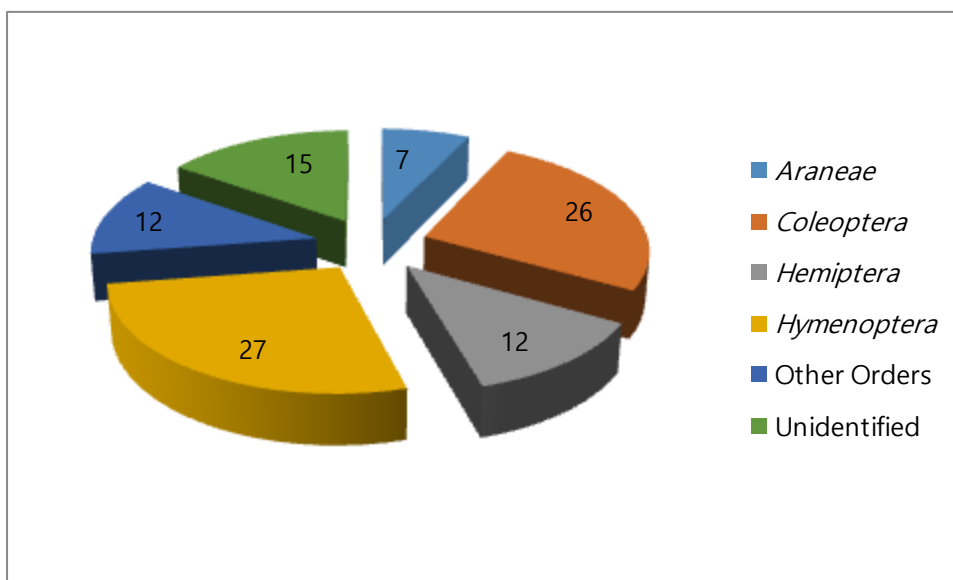


**Figure 4** – Percentage of diet items.

Exploring differences between riparian and woodland bird species we observed that woodland species seem to prey more on arthropds (92%) than riparian species (84%), but seeds were found twice more in the fecal samples of riparian species than in the fecal samples of woodland matrix species (20% and 10%; Fig 5).
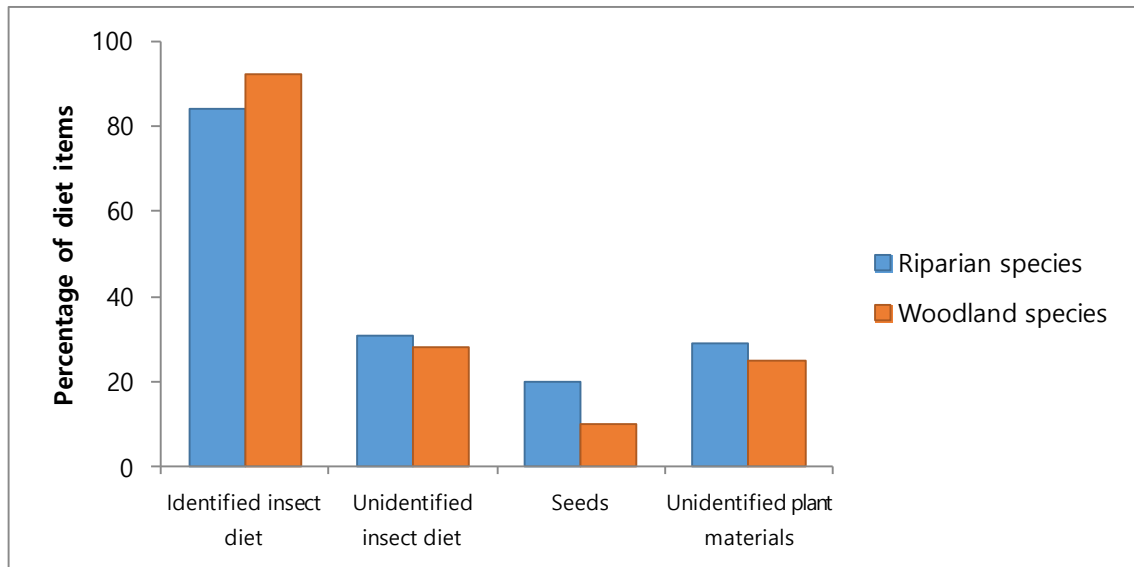
**Figure 5** – Percentage of different items in all fecal samples of riparian and woodland bird species.

Looking more closely to diet in terms of arthropods orders, we observed that woodland passerines seem to fed more on *Araneae* and *Hemiptera,* mainly *Pentatomidae*, than riparian passerines. However, in relation to all the other insect orders the percentage of arthropod remains in fecal samples was higher for the riparian species (Fig 6).
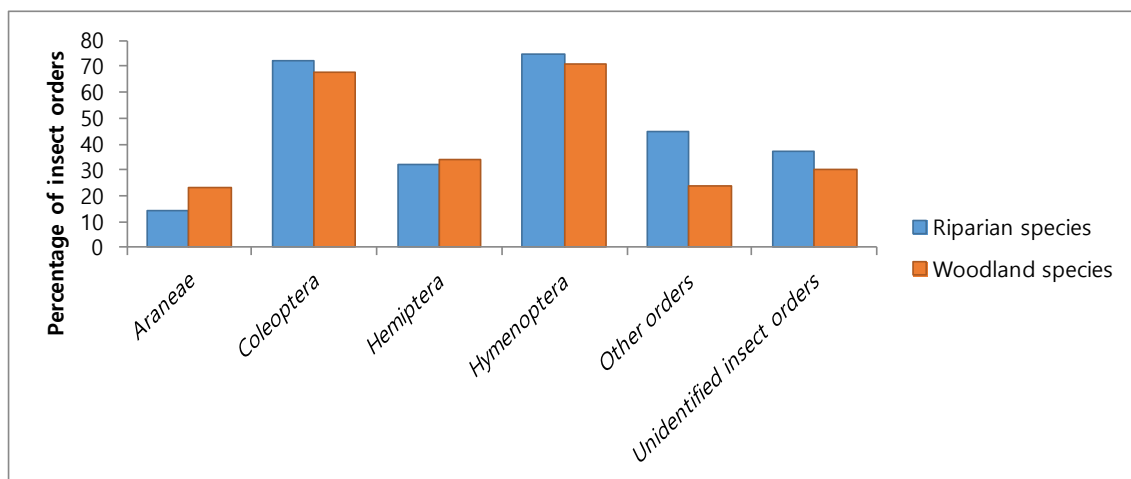


**Figure 6** – Percentage of insect orders in all fecal samples for riparian and woodland bird species.

The more representative insect orders in nightingale's diet were *Coleoptera* and *Hymenoptera*. Blackcap and blue tit fed mostly on *Araneae* in the winter. Blackbirds fed mostly on *Hymenoptera* and other orders (e.g. *Julida*), and the most representative order in Robin's diet was *Hymenoptera* (Table 4).

**Table 4 –** Seasonal comparison in the diet (% of occurrence) of the six bird species with a larger sample size of fecal samples collected between the riparian gallery species (Nightingale *Luscinia megarhynchos*, Blackcap *Sylvia atricapilla*, Blackbird *Turdus merula*) and the woodland matrix species (Blue tit *Cyanistes caeruleus*, Sardinian warbler *Sylvia melanocephala*, Robin *Erithacus rubecula*) in Degebe and Mitra in all seasons: spring (April – May 2013; March – May 2014), summer (June – July 2013 and 2014); autumn (September – October 2013), winter (January – February 2014). We used only the four most important orders in the diet and the category other orders includes all the other less present orders in the fecal samples. Sample size (no. of fecal samples for each period is shown in parentheses).

| Diet items | Degebe | | | | Mitra | | | |
|---|---|---|---|---|---|---|---|---|
| | Spring | Summer | Autumn | Winter | Spring | Summer | Autumn | Winter |
| **Riparian gallery** | | | | | | | | |
| Nightingale | | | | | | | | |
| *Araneae* | 0.0 (1) | 0.0 (4) | 100.0 (1) | 0.0 (0) | 6.7 (15) | 0.0 (15) | 0.0 (1) | 0.0 (0) |
| *Coleoptera* | 0.0 (1) | 50.0 (4) | 100.0 (1) | 0.0 (0) | 60.0 (15) | 73.3 (15) | 100.0 (1) | 0.0 (0) |
| *Hemiptera* | 0.0 (1) | 100.0 (4) | 0.0 (1) | 0.0 (0) | 13.3 (15) | 13.3 (15) | 100.0 (1) | 0.0 (0) |
| *Hymenoptera* | 100.0 (1) | 100.0 (4) | 100.0 (1) | 0.0 (0) | 53.3 (15) | 80.0 (15) | 100.0 (1) | 0.0 (0) |
| Other Orders | 100.0 (1) | 25.0 (4) | 100.0 (1) | 0.0 (0) | 46.7 (15) | 46.7 (15) | 0.0 (1) | 0.0 (0) |
| Unidentified | 100.0 (1) | 0.0 (4) | 0.0 (1) | 0.0 (0) | 46.7 (15) | 26.7 (15) | 0.0 (1) | 0.0 (0) |
| Blackcap | | | | | | | | |
| *Araneae* | 0.0 (6) | 0.0 (4) | 0.0 (4) | 16.7 (6) | 7.1 (14) | 15.4 (13) | 33.3 (3) | 0.0 (5) |
| *Coleoptera* | 50.0 (6) | 25.0 (4) | 75.0 (4) | 50.0 (6) | 57.1 (14) | 76.9 (13) | 33.3 (3) | 40.0 (5) |
| *Hemiptera* | 16.7 (6) | 25.0 (4) | 50.0 (4) | 0.0 (6) | 21.4 (14) | 53.8 (13) | 33.3 (3) | 60.0 (5) |
| *Hymenoptera* | 83.3 (6) | 100.0 (4) | 75.0 (4) | 66.7 (6) | 50.0 (14) | 61.5 (13) | 33.3 (3) | 20.0 (5) |
| Other Orders | 50.0 (6) | 50.0 (4) | 0.0 (4) | 100.0 (6) | 42.9 (14) | 38.5 (13) | 0.0 (3) | 40.0 (5) |
| Unidentified | 16.7 (6) | 75.0 (4) | 25.0 (4) | 100.0 (6) | 42.9 (14) | 23.1 (13) | 0.0 (3) | 100.0 (5) |
| Blackbird | | | | | | | | |
| *Araneae* | 0.0 (4) | 0.0 (1) | 0.0 (1) | 0.0 (0) | 6.7 (15) | 0.0 (11) | 11.1 (9) | 0.0 (0) |
| *Coleoptera* | 0.0 (4) | 0.0 (1) | 0.0 (1) | 0.0 (0) | 86.7 (15) | 63.6 (11) | 33.3 (9) | 0.0 (0) |
| *Hemiptera* | 0.0 (4) | 0.0 (1) | 0.0 (1) | 0.0 (0) | 13.3 (15) | 9.1 (11) | 0.0 (9) | 0.0 (0) |
| *Hymenoptera* | 75.0 (4) | 0.0 (1) | 100.0 (1) | 0.0 (0) | 66.7 (15) | 54.5 (11) | 44.4 (9) | 0.0 (0) |
| Other Orders | 25.0 (4) | 0.0 (1) | 100.0 (1) | 0.0 (0) | 60.0 (15) | 9.1 (11) | 11.1 (9) | 0.0 (0) |
| Unidentified | 50.0 (4) | 0.0 (1) | 0.0 (1) | 0.0 (0) | 33.3 (15) | 63.6 (11) | 22.2 (9) | 0.0 (0) |
| **Woodland matrix** | | | | | | | | |
| Blue tit | | | | | | | | |
| *Araneae* | 50.0 (14) | 40.0 (20) | 0.0 (4) | 40.0 (5) | 20.0 (5) | 53.3 (15) | 5.0 (20) | 40.0 (5) |
| *Coleoptera* | 71.4 (14) | 60.0 (20) | 100.0 (4) | 60.0 (5) | 60.0 (5) | 86.7 (15) | 55.0 (20) | 20.0 (5) |
| *Hemiptera* | 21.4 (14) | 30.0 (20) | 25.0 (4) | 20.0 (5) | 20.0 (5) | 26.7 (15) | 30.0 (20) | 20.0 (5) |
| *Hymenoptera* | 78.6 (14) | 70.0 (20) | 75.0 (4) | 80.0 (5) | 100.0 (5) | 40.0 (15) | 25.0 (20) | 20.0 (5) |
| Other Orders | 21.4 (14) | 15.0 (20) | 0.0 (4) | 20.0 (5) | 60.0 (5) | 33.3 (15) | 10.0 (20) | 0.0 (5) |
| Unidentified | 28.6 (14) | 35.0 (20) | 0.0 (4) | 40.0 (5) | 20.0 (5) | 46.7 (15) | 40.0 (20) | 100.0 (5) |
| Sardinian warbler | | | | | | | | |
| *Araneae* | 14.3 (7) | 20.0 (10) | 0.0 (3) | 0.0 (0) | 22.2 (9) | 14.3 (21) | 0.0 (8) | 0.0 (0) |
| *Coleoptera* | 42.9 (7) | 60.0 (10) | 66.7 (3) | 0.0 (0) | 88.9 (9) | 85.7 (21) | 12.5 (8) | 0.0 (0) |
| *Hemiptera* | 0.0 (7) | 30.0 (10) | 33.3 (3) | 0.0 (0) | 33.3 (9) | 81.0 (21) | 75.0 (8) | 0.0 (0) |
| *Hymenoptera* | 85.7 (7) | 60.0 (10) | 100.0 (3) | 0.0 (0) | 44.4 (9) | 71.4 (21) | 37.5 (8) | 0.0 (0) |
| Other orders | 28.6 (7) | 0.0 (10) | 33.3 (3) | 0.0 (0) | 44.4 (9) | 19.0 (21) | 12.5 (8) | 0.0 (0) |
| Unidentified | 42.9 (7) | 50.0 (10) | 66.7 (3) | 0.0 (0) | 88.9 (9) | 33.3 (21) | 37.5 (8) | 0.0 (0) |
| Robin | | | | | | | | |
| *Araneae* | 0.0 (0) | 0.0 (0) | 0.0 (14) | 14.3 (7) | 0.0 (0) | 0.0 (3) | 0.0 (1) | 0.0 (4) |
| *Coleoptera* | 0.0 (0) | 0.0 (0) | 35.7 (14) | 28.6 (7) | 0.0 (0) | 33.3 (3) | 0.0 (1) | 75.0 (4) |
| *Hemiptera* | 0.0 (0) | 0.0 (0) | 7.1 (14) | 14.3 (7) | 0.0 (0) | 33.3 (3) | 0.0 (1) | 75.0 (4) |
| *Hymenoptera* | 0.0 (0) | 0.0 (0) | 85.7 (14) | 42.9 (7) | 0.0 (0) | 100.0 (3) | 100.0 (1) | 100.0 (4) |
| Other Orders | 0.0 (0) | 0.0 (0) | 28.6 (14) | 14.3 (7) | 0.0 (0) | 0.0 (3) | 0.0 (1) | 50.0 (4) |
| Unidentified | 0.0 (0) | 0.0 (0) | 21.4 (14) | 0.0 (7) | 0.0 (0) | 33.3 (3) | 0.0 (1) | 50.0 (4) |

**Fruit consumption**

In Degebe we found olive seeds in almost 70% of the blackcap's fecal samples during winter, and 75% of blackberry seeds in autumn for both sampling sites Mitra and Degebe. Blackberry seeds were present in 66.7% of the blackbirds' feces in autumn. For woodland birds like Sardinian warbler the blackberry was also the most abundant seed species present in the autumn fecal samples. Finally, it is worth noticing that 66.7% of the autumn feces of blackcap contained seeds of European black nightshade (*Solanum nigrum*) (Table 5).

**Table 5 –** Seasonal comparison of seeds in the diet (% of Occurrence) between bird species typical of the riparian gallery (Blackcap *Sylvia atricapilla* and Blackbird *Turdus merula*) and  woodland matrix bird species (Blue tit *Cyanistes caeruleus*, Great tit *Parus major*, Sardinian warbler *Sylvia melanocephala* and Robin *Erithacus rubecula*) for Degebe and Mitra in all seasons: spring (April – May 2013, March – May 2014), summer (June – July 2013 and 2014), autumn (September – October 2013), winter (January – February 2014). Sample size (no. of fecal samples for each period is shown in parentheses).

| | Degebe | | | | Mitra | | | |
|---|---|---|---|---|---|---|---|---|
| | Spring | Summer | Autumn | Winter | Spring | Summer | Autumn | Winter |
| **Riparian gallery** | | | | | | | | |
| Blackcap | | | | | | | | |
| *Bryonia dioica* | 0.0 (6) | 25.0 (4) | 0.0 (4) | 0.0 (6) | 7.1 (14) | 23.1 (13) | 0.0 (3) | 0.0 (5) |
| *Hedera* spp. | 0.0 (6) | 0.0 (4) | 0.0 (4) | 0.0 (6) | 7.1 (14) | 0.0 (13) | 0.0 (3) | 0.0 (5) |
| *Olea europaea* var. *sylvestris* | 0.0 (6) | 0.0 (4) | 25.0 (4) | 66.7 (6) | 0.0 (14) | 0.0 (13) | 0.0 (3) | 0.0 (5) |
| *Pistacia lentiscus* | 0.0 (6) | 0.0 (4) | 0.0 (4) | 0.0 (6) | 0.0 (14) | 0.0 (13) | 0.0 (3) | 20.0 (5) |
| *Rubus ulmifolius* | 0.0 (6) | 0.0 (4) | 75.0 (4) | 0.0 (6) | 0.0 (14) | 7.7 (13) | 100.0 (3) | 0.0 (5) |
| *Smilax aspera* | 0.0 (6) | 25.0 (4) | 0.0 (4) | 0.0 (6) | 0.0 (14) | 7.7 (13) | 0.0 (3) | 0.0 (5) |
| *Solanum nigrum* | 0.0 (6) | 0.0 (4) | 0.0 (4) | 0.0 (6) | 0.0 (14) | 7.7 (13) | 66.7 (3) | 0.0 (5) |
| *Tamus communis* | 0.0 (6) | 25.0 (4) | 25.0 (4) | 0.0 (6) | 7.1 (14) | 23.1 (13) | 0.0 (3) | 0.0 (5) |
| *Asparagus aphyllus* | 0.0 (6) | 0.0 (4) | 0.0 (4) | 0.0 (6) | 0.0 (14) | 15.4 (13) | 0.0 (3) | 0.0 (5) |
| Unidentified | 0.0 (6) | 0.0 (4) | 0.0 (4) | 0.0 (6) | 0.0 (14) | 7.7 (13) | 0.0 (3) | 0.0 (5) |
| Blackbird | | | | | | | | |
| *Hedera spp.* | 0.0 (4) | 0.0 (1) | 0.0 (1) | 0.0 (0) | 6.7 (15) | 0.0 (11) | 0.0 (9) | 0.0 (0) |
| *Rubus ulmifolius* | 0.0 (4) | 0.0 (1) | 0.0 (1) | 0.0 (0) | 0.0 (15) | 9.1 (11) | 66.7 (9) | 0.0 (0) |
| *Tamus communis* | 0.0 (4) | 0.0 (1) | 0.0 (1) | 0.0 (0) | 0.0 (15) | 9.1 (11) | 0.0 (9) | 0.0 (0) |
| **Woodland matrix** | | | | | | | | |
| Blue tit | | | | | | | | |
| *Rubus ulmifolius* | 0.0 (14) | 0.0 (20) | 0.0 (4) | 0.0 (5) | 0.0 (5) | 0.0 (15) | 10.0 (20) | 0.0 (5) |
| *Tamus communis* | 0.0 (14) | 5.0 (20) | 25.0 (4) | 0.0 (5) | 0.0 (5) | 0.0 (15) | 0.0 (20) | 0.0 (5) |
| Great tit | | | | | | | | |
| *Daphne gnidium* | 0.0 (3) | 0.0 (19) | 0.0 (0) | 0.0 (0) | 0.0 (3) | 14.3 (7) | 0.0 (1) | 0.0 (1) |
| *Asparagus aphyllus* | 0.0 (3) | 0.0 (19) | 0.0 (0) | 0.0 (0) | 0.0 (3) | 14.3 (7) | 0.0 (1) | 0.0 (1) |
| Sardinian warbler | | | | | | | | |
| *Daphne gnidium* | 0.0 (7) | 10.0 (10) | 0.0 (3) | 0.0 (0) | 0.0 (9) | 0.0 (21) | 0.0 (8) | 0.0 (0) |
| *Myrtus communis* | 0.0 (7) | 0.0 (10) | 0.0 (3) | 0.0 (0) | 11.1 (9) | 0.0 (21) | 0.0 (8) | 0.0 (0) |
| *Rubus ulmifolius* | 0.0 (7) | 0.0 (10) | 66.7 (3) | 0.0 (0) | 0.0 (9) | 4.8 (21) | 75.0 (8) | 0.0 (0) |
| *Asparagus aphyllus* | 0.0 (7) | 20.0 (10) | 0.0 (3) | 0.0 (0) | 0.0 (9) | 4.8 (21) | 0.0 (8) | 0.0 (0) |
| *Tamus communis* | 0.0 (7) | 0.0 (10) | 0.0 (3) | 0.0 (0) | 0.0 (9) | 14.3 (21) | 0.0 (8) | 0.0 (0) |
| Unidentified | 0.0 (7) | 0.0 (10) | 0.0 (3) | 0.0 (0) | 0.0 (9) | 4.8 (21) | 0.0 (8) | 0.0 (0) |
| Robin | | | | | | | | |
| *Bryonia dioica* | 0.0 (0) | 0.0 (0) | 0.0 (14) | 0.0 (7) | 0.0 (0) | 33.3 (3) | 0.0 (1) | 0.0 (4) |
| *Olea europaea* var. *sylvestris* | 0.0 (0) | 0.0 (0) | 0.0 (14) | 0.0 (7) | 0.0 (0) | 0.0 (3) | 0.0 (1) | 25.0 (4) |

**Comparing the diet of Riparian gallery and surrounding matrix passerines**

For Mitra, the Principal Component Analysis of the diet data extracted two axes with an eigenvalue larger than 1, these PC1 and PC2, with eigenvalues of 2.17 and 1.76, explained respectively 31% and 25% of the variance. PC1 was positively related with *Coleoptera*, other insect orders and *Araneae*. PC2 was positively related with other insect orders and fleshy fruits, and negatively related with *Araneae* (Table 6). Birds of the woodland matrix were easier to distinguish from those of the riparian gallery along PC2, which were more related with the consumption of other insect orders, fruits, and very little consumption of *Araneae* (Fig. 7). Apparently woodland matrix birds feed more on other insect orders, mainly Classe Chilopoda - Family *Julida* (millipedes) and Order *Lepidoptera* (butterflies in larval stage) which appeared more frequently in their fecal samples.

**Table 6** – Factor loadings of various food items in the two principal components identified for the diet of riparian bird species and matrix bird species.

|  | PC1 | PC2 |
| --- | --- | --- |
| *Araneae* | 0.51 | -0.70 |
| *Coleoptera* | 0.82 | 0.02 |
| *Hemiptera* | -0.31 | -0.78 |
| *Hymenoptera* | -0.42 | -0.21 |
| Other orders | 0.64 | 0.54 |
| Unidentified insect orders | -0.63 | 0.20 |
| Fruits | -0.40 | 0.53 |
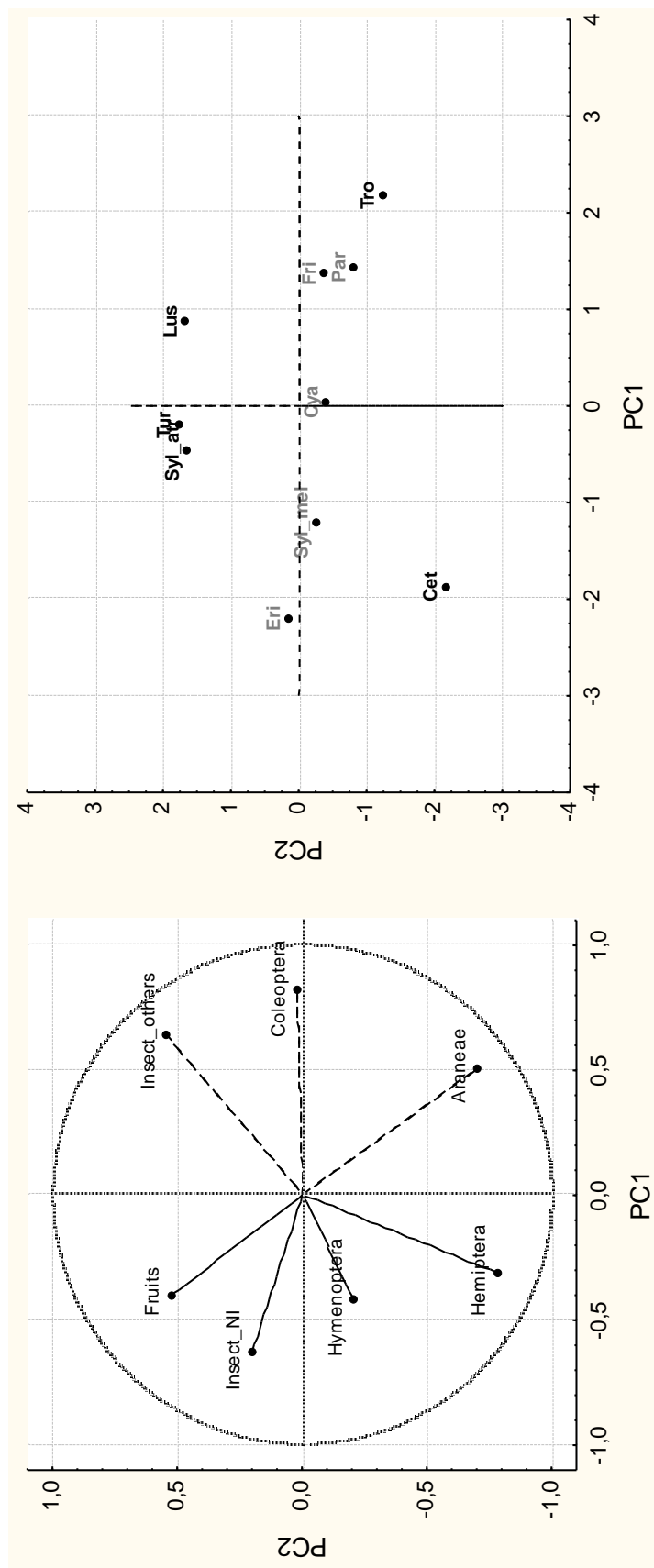
**Figure 7** – Mitra. Factor coordinates of variables and factor scores for each species on the principal components 1 and 2. Birds of the riparian gallery are shown in black and bird species of the woodland matrix in grey. Birds of the woodland matrix are easier to distinguish from those of the riparian gallery along PC2, which is more related with *Hymenoptera*.

For Degebe, the Principal Component Analysis of the diet data extracted three axis with an eigenvalue larger than 1, these PC1, PC2 and PC3, with eigenvalues of 2.58, 1.91 and 1.51, explained respectively 37%, 27% and 22% of the variance. PC1 was positively related with *Araneae* and negatively related with other insect orders. PC2 was positively related with *Hemiptera* and *Hymenoptera*, and PC3 negatively related with *Coleoptera* and fruits (Table 7).

Birds of the woodland matrix were easier to distinguish from those of the riparian gallery along PC2, and fed more on *Hymenoptera*, mainly Family *Formicidae* (ants) which was the more frequent family of the order *Hymenoptera* in our fecal samples. Again it was quite clear that feeding on *Araneae* was a main difference between birds from the riparian gallery and the woodland matrix. Fruits, on the other hand appeared to be less important in separating birds of the riparian gallery from the woodland matrix (Fig. 8).

**Table 7** – Factor loadings of various food items in the three principal components identified (higher loading for *Hymenoptera* is shown in bold) for the diet of riparian bird species and matrix bird species.

|  | PC1 | PC2 | PC3 |
|---|---|---|---|
| *Araneae* | 0.86 | -0.23 | -0.34 |
| *Coleoptera* | 0.60 | 0.04 | -0.71 |
| *Hemiptera* | 0.21 | 0.84 | -0.36 |
| *Hymenoptera* | -0.15 | 0.90 | -0.07 |
| Other orders | -0.81 | 0.33 | -0.08 |
| Unidentified insect orders | -0.67 | -0.47 | -0.48 |
| Fruits | -0.55 | -0.16 | -0.72 |
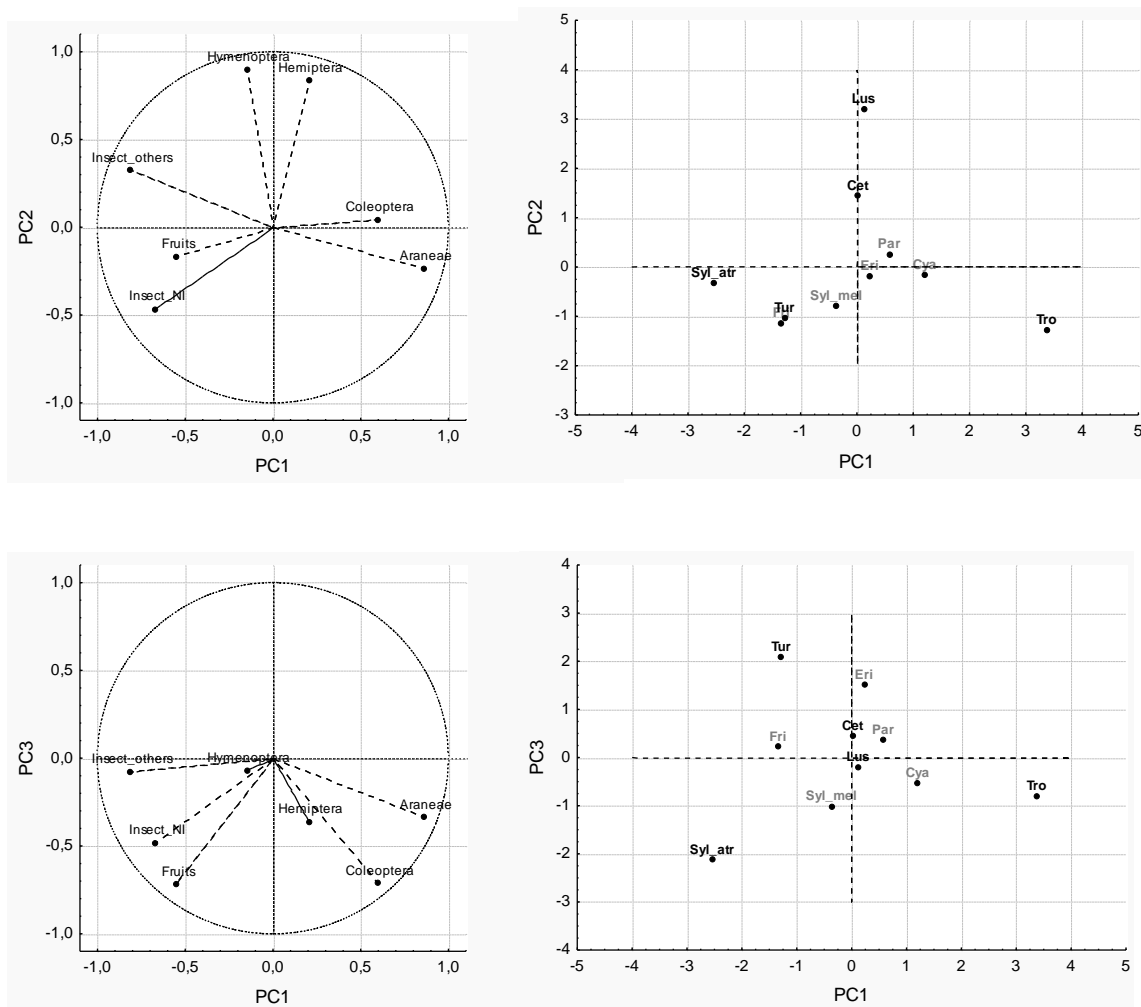
**Figure 8** – Degebe. Factor coordinates of variables and factor scores for each species on the principal components 1, 2 and 3. Birds of the riparian gallery are shown in black and bird species of the woodland matrix in grey. Birds of the woodland matrix are easier to distinguish from those of the riparian gallery along PC2, which is more related with *Hymenoptera*.

**Stable isotopes**

Riparian species fed on a consistently higher trophic level in spring, summer and autumn but in winter they fed on lower trophic level food items. The woodland species fed on lower trophic levels in spring and winter, and we could observe a gradual decrease in their trophic level from summer to winter (Fig. 9).
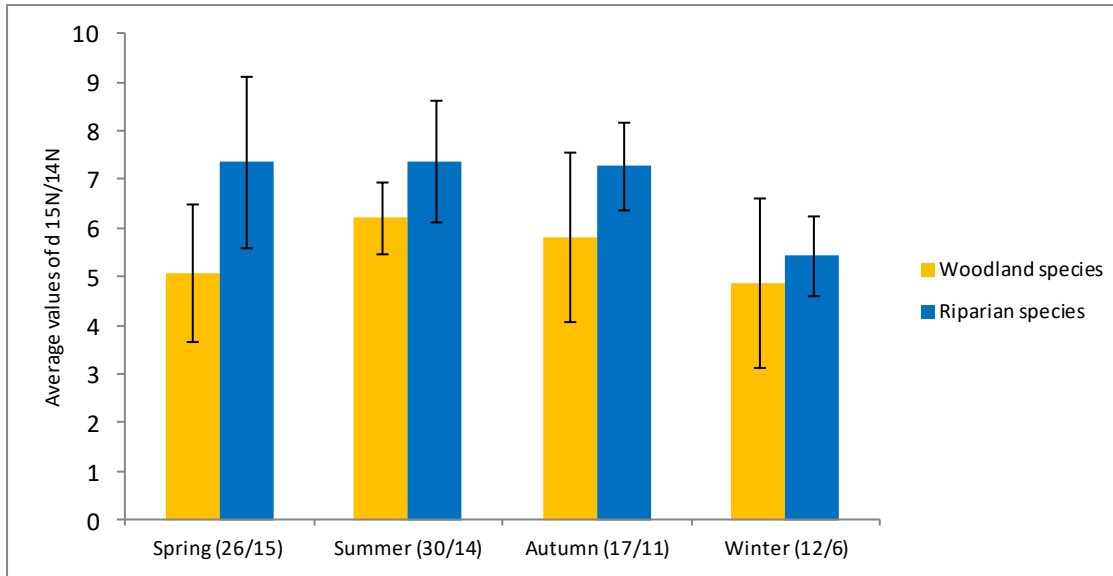
**Figure 9 –** Seasonal variation in trophic level for woodland and riparian bird species, assessed from the $\delta^{15}N$ values in whole blood. Shown is the mean ± SD for all woodland and riparian species in each season. The numbers within parentheses refer to the sample size for each season and habitat.

In the one-way ANOVA performed with $\delta^{15}N$ values there was a statistically significant difference in the diet of blackcap ($F_{3,19}$ = 7.2, p = 0.002), Sardinian warbler ($F_{2,12}$ = 5.0, p = 0.026), blue tit ($F_{3,22}$ = 5.3, p = 0.007) and great tit ($F_{1,16}$ = 39.3, p < 0.001) between seasons, but no statistically significant difference for the diet of robin ($F_{1,17}$ = 0.5, p = 0.476). In the case of $\delta^{13}C$ there was a statistically significant difference in the diet of blackcap ($F_{3,19}$ = 14.3, p < 0.001), Sardinian warbler ($F_{2,12}$ = 7.4, p = 0.008), blue tit ($F_{3,22}$ = 32.7, p < 0.001) and great tit ($F_{1,16}$ = 168.8, p < 0.001) between seasons, but no statistically significant difference for the diet of robin ($F_{1,17}$ = 0.1, p = 0.819) (Table 8).

**Table 8** – One–way ANOVA results for stable isotope in blood samples for the riparian gallery species (Blackcap *Sylvia atricapilla* and Blackbird *Turdus merula*) and the woodland matrix species (Blue tit *Cyanistes caeruleus*, Great tit *Parus major*, Sardinian warbler *Sylvia melanocephala* and Robin *Erithacus rubecula*) in Degebe in all seasons: spring (April 2013), summer (July 2013); autumn (October 2013), winter (January 2014). Sample size (no. of blood samples for each period is shown in parentheses). For each row. Values with different letters were significantly different.

| Species | $\delta^{15}N$ | | | | | $\delta^{13}C$ | | | | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | Breeding | Summer | Autumn migration | Wintering season | Anova | Breeding | Summer | Autumn migration | Wintering season | Anova |
| **Riparian Gallery** | | | | | | | | | | |
| Cetti's warbler | 9.06 ± 0.45 (3) | 8.40 (1) | | | | -25.13 ± 0.43 | -24.93 | | | |
| Nightingale | 5.36 (1) | 5.81 ± 0.33 (3) | 6.82 (1) | | | -23.85 (1) | -24.62 ± 0.19 | -24.86 | | |
| Wren | 3.40 (1) | 8.50 ± 0.21 (2) | 7.88 ± 0.01 (2) | | | -24.43 | 25.54 ± 0.1 | 24.35 ± 0.08 | | |
| Blackcap | 7.84 ± 0.54[a] (6) | 7.91 ± 0.30[a] (5) | 7.28 ± 0.47[a] (6) | 5.45 ± 0.34[b] (6) | $F_{3,19}$ = 7.2, P = 0.002 | -25.46 ± 0.18[a] | -25.56 ± 0.09[a] | -25.06 ± 0.15[b] | -26.34 ± 0.14[c] | $F_{3,19}$ = 14.3, P < 0.001 |
| Blackbird | 6.88 ± 0.52 (4) | 6.95 ± 0.90 (3) | 6.90 ± 0.31 (2) | | | -24.01 ± 0.09 | -25.50 ± 0.12 | -24.72 ± 0.11 | | |
| **Woodland matrix** | | | | | | | | | | |
| Robin | | | 5.11 ± 0.36 (12) | 5.63 ± 0.72 (7) | $F_{1,17}$ = 0.5, P = 0.476 | | | -24.66 ± 0.17 | -24.60 ± 0.15 | $F_{1,17}$ = 0.1, P = 0.819 |
| Sardinian warbler | 5.24 ± 0.39[a] (5) | 5.96 ± 0.22 [b] (8) | 7.04 [b] ± 0.17 (2) | | $F_{2,12}$ = 5.0, P = 0.026 | -25.29 ± 0.16[b] | -25.19 ± 0.10 [b] | -24.35 [a] ± 0.12 | | $F_{2,12}$ = 7.4, P = 0.008 |
| Blue tit | 4.62 ± 0.68[a] (9) | 5.65 ± 0.24[ab] (9) | 7.84 ± 1.26[b] (3) | | $F_{3,22}$ = 5.3, P = 0.007 | -24.93 ± 0.13[a] | -24.42 ± 0.08[b] | -23.35 ± 0.15[c] | | $F_{3,22}$ = 32.7, P < 0.001 |
| Great tit | 5.36 ± 0.24[a] (6) | 6.82 ± 0.11[b] (12) | | 3.82 ± 0.31[a] (5) | $F_{1,16}$ = 39.3, P < 0.001 | -27.72 ± 0.24[b] | -25.17 ± 0.07[a] | | -25.42 ± 0.08[a] | $F_{1,16}$ = 168.8, P < 0.001 |
| Chaffinch | 5.40 ± 0.56 (6) | 5.92 (1) | | | | -27.08 ± 0.22 | -25.29 | | | |

**Insect abundance**

There was a significant effect of habitat on insect biomass ($F_{1,272}$ = 28.42, p < 0.001) but no effect of season ($F_{3,261}$ = 3.96, p = 0.144) or area ($F_{1,272}$ = 1.26, p = 0.364) and the results showed an interaction between area and season ($F_{3,272}$ = 7.69, p < 0.001) (Table 9). In particular, there was a significantly higher insect biomass in riparian gallery (Fig. 10) especially in autumn (Fig. 11).

**Table 9** – Generalized Linear Mixed models results for insect biomass for the riparian gallery and the woodland matrix in Degebe and Mitra in all seasons: winter, autumn, spring and summer. Significant values are shown in bold.

|  | Effect | DF | F | P |
|---|---|---|---|---|
| Intercept |  | 1 | 40.174 | 0.099 |
| area | Random | 1 | 1.265 | 0.364 |
| **habitat** | Fixed | 1 | 28.429 | **<0.001** |
| season | Fixed | 3 | 3.961 | 0.144 |
| area*habitat | Random | 1 | 0.008 | 0.930 |
| **area*season** | Random | 3 | 7.693 | **<0.001** |
| habitat*season | Fixed | 3 | 0.010 | 0.999 |
| Error |  | 272 |  |  |
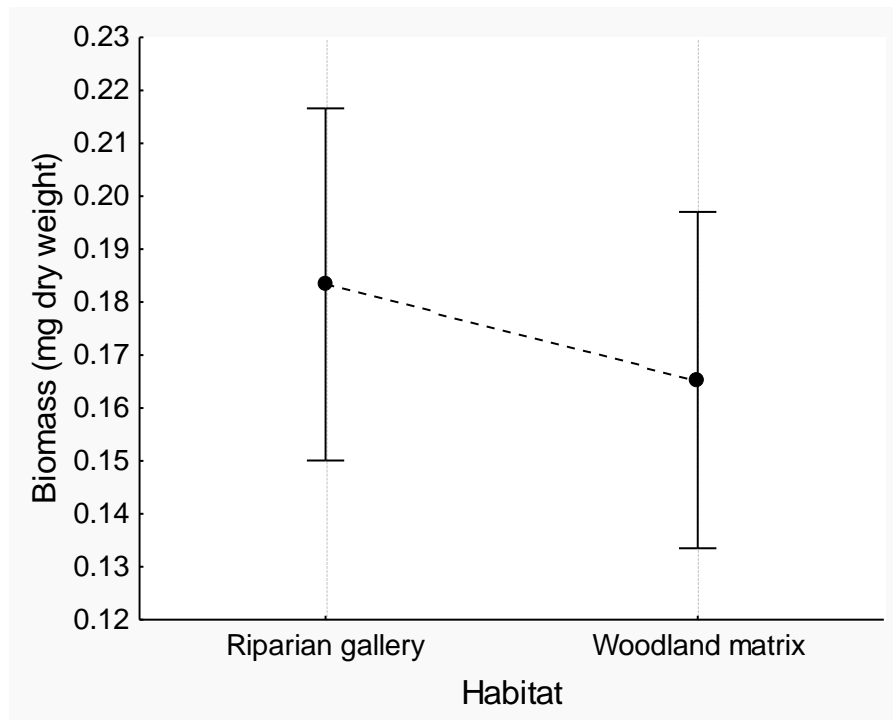
**Figure 10** – Variation in insect biomass (mean ± SE) between the two habitat types.

Insect abundance varied throughout the year in both study areas but the differences in the insect biomass seemed to be more visible in Degebe. Autumn was the season with more insect abundance in Degebe and Mitra, followed by spring, winter and finally summer (Fig. 9).
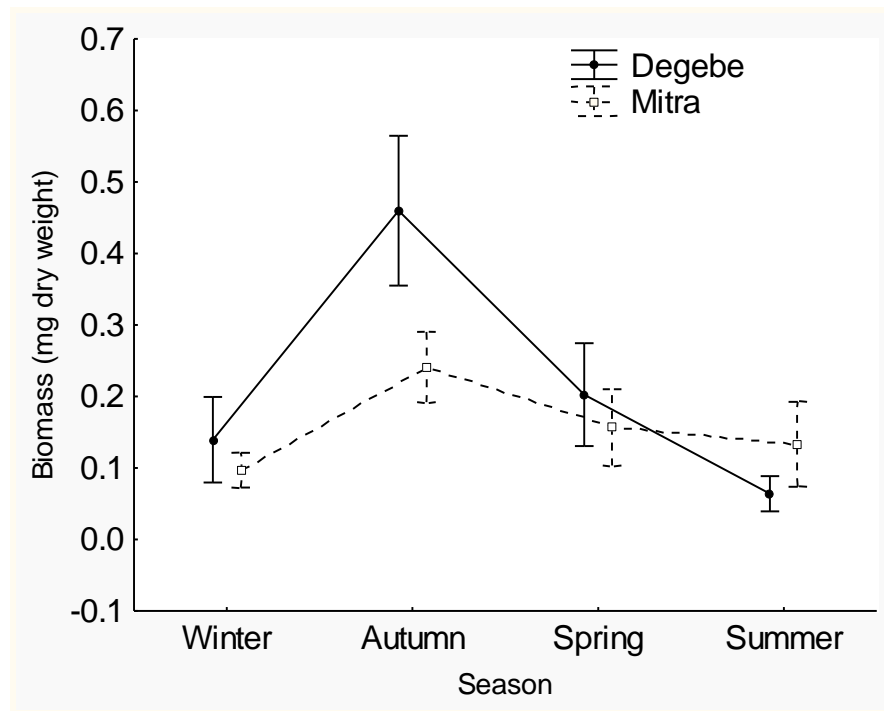
**Figure 11** – Variation in insect biomass (mean ± SE) for the two sampling sites among seasons.

**Fruit abundance**

Analysing fruit abundance for Degebe throughout the two fructification seasons examined, we could observe that blackberries and olives were consumed faster, and fruits lasted for 3 months maximum. Black bryony and common hawthorn fruits lasted from August to January in the 2013-2014 season, and until March in the 2014-2015 fructification season. In the 2014-2015 fructification season the decrease in the number of fruits seemed to be faster than in the 2013-2014 season (Fig. 12).
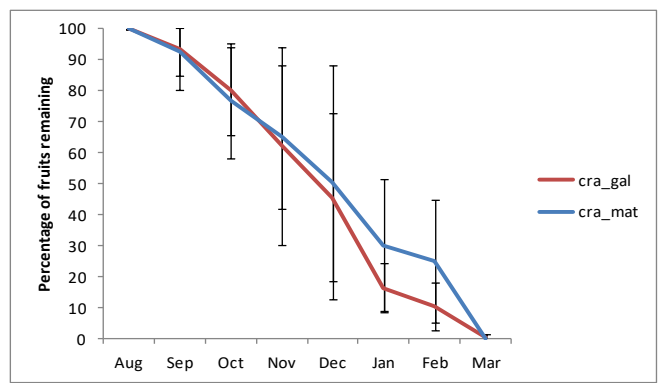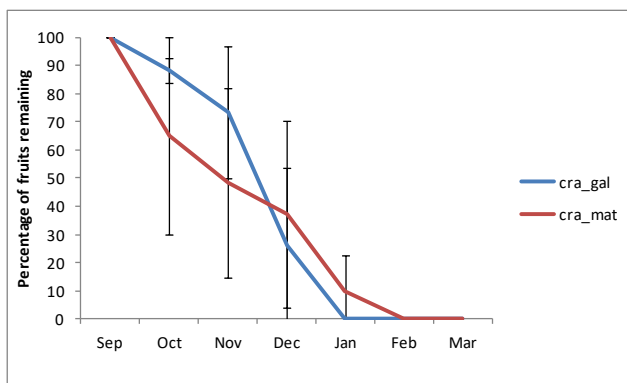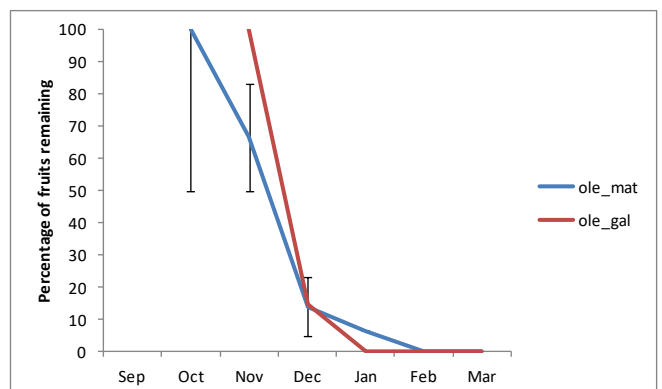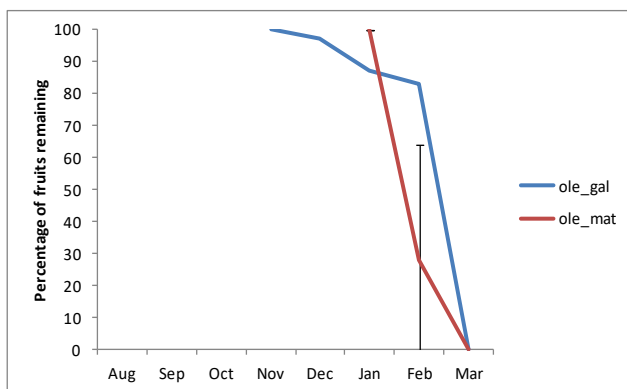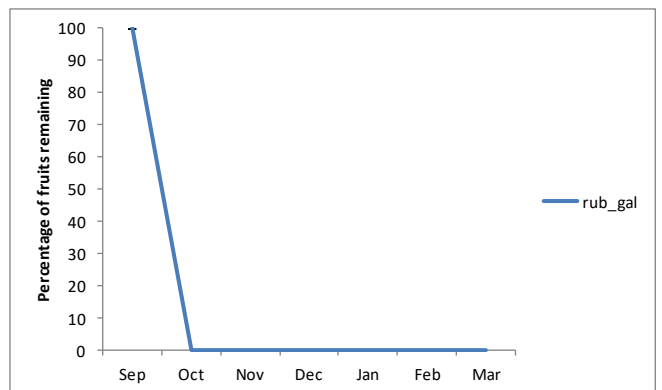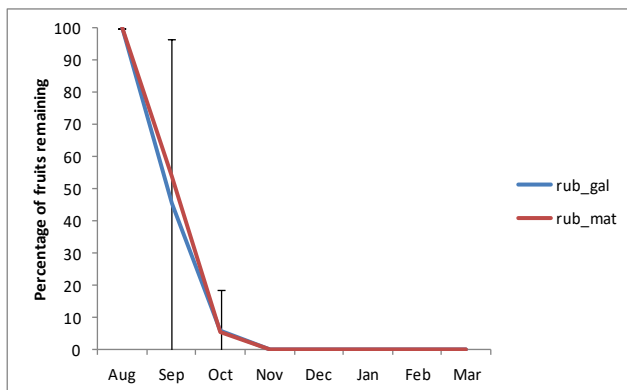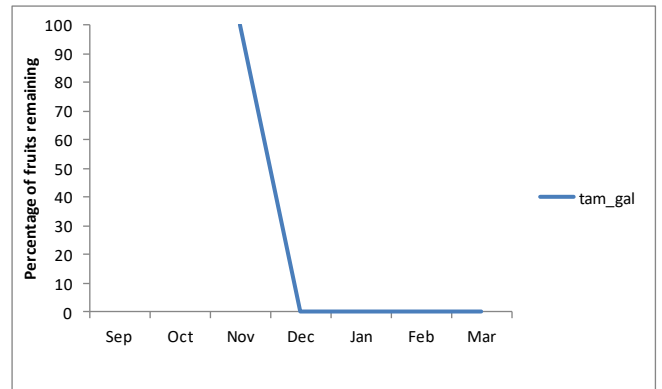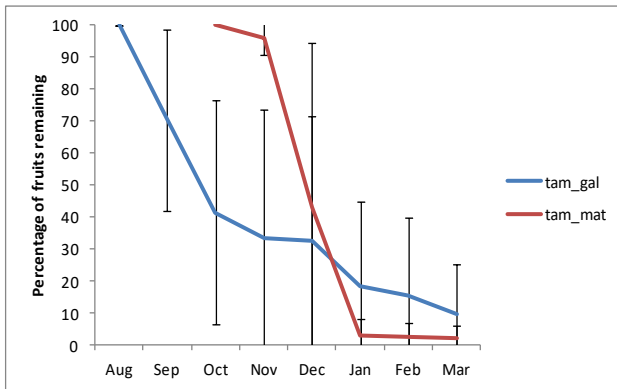
**Figure 12** – Percentage of fruits remaining (mean ±SD) for Degebe in the fructification seasons 2013/2014 (at left) and 2014/2015 (at right) per month for the berries producing species: *Tamus communis* (tam), *Olea europaea* var. *sylvestri*s (ole), *Rubus ulmifolius* (rub) and *Crataegus monogyna* (cra). gal – riparian gallery and mat – woodland matrix.

In relation to fruit abundance for Mitra, we could observe that ivy fruits, myrtles and olives were consumed faster by birds. Ivy fruits lasted only one month, myrtles and olives lasted for 4 months maximum. Black bryony and mastic fruits lasted from August to March in the 2014-2015 fructification season (Fig. 13). In general fruits seemed to be consumed at a faster rate in the woodland matrix than in the riparian gallery (Fig. 12 and Fig. 13).
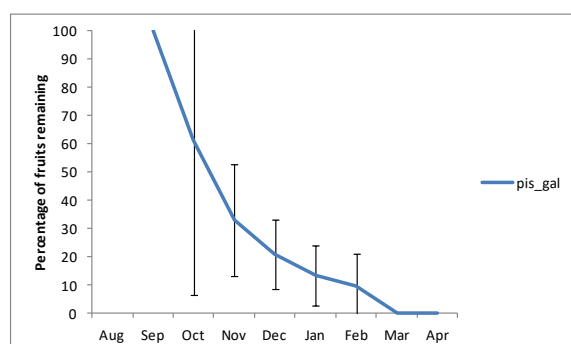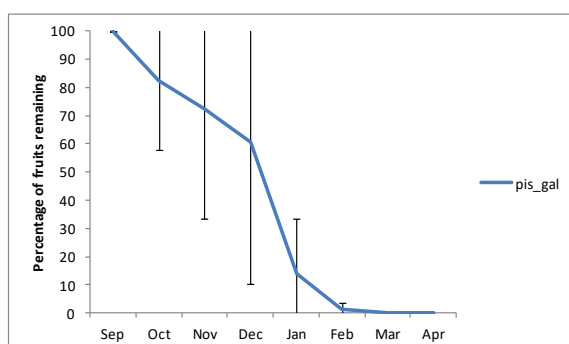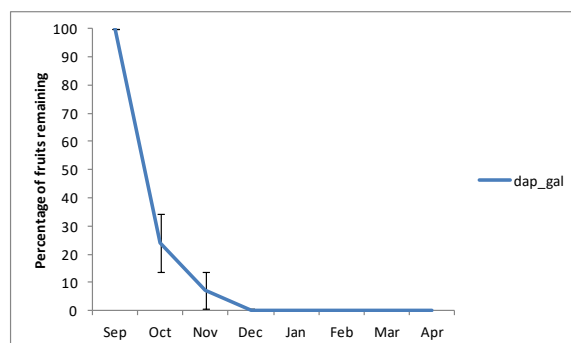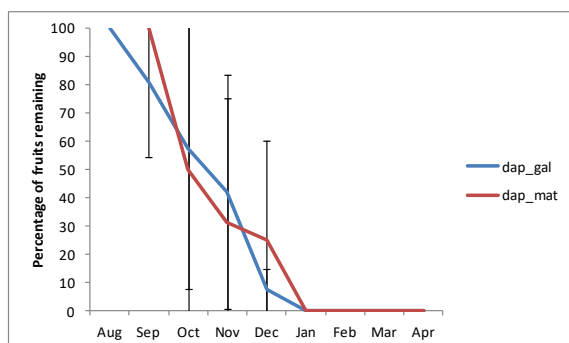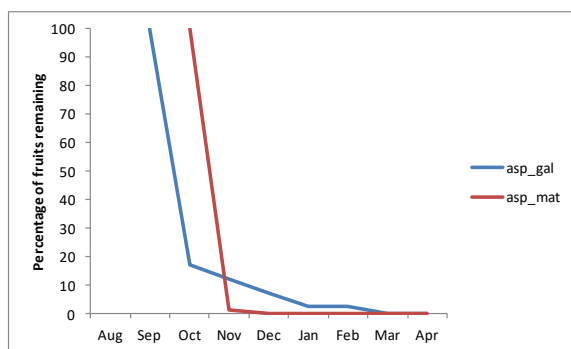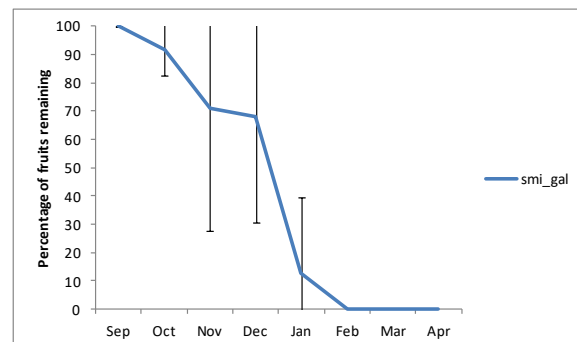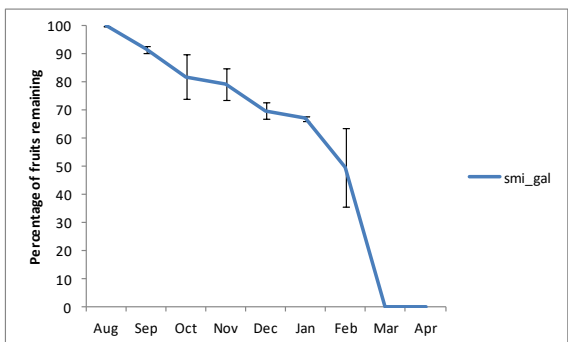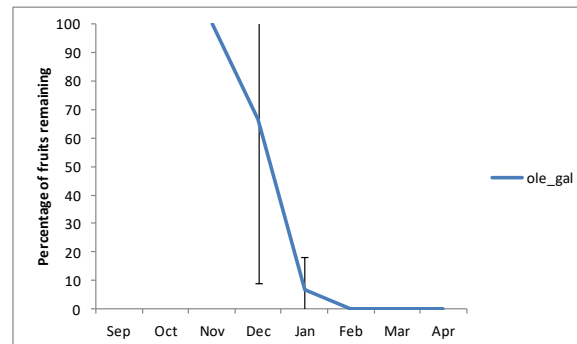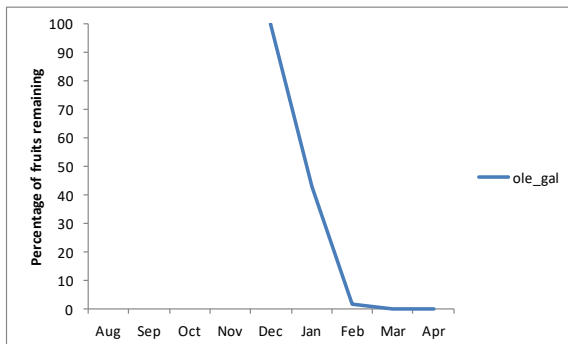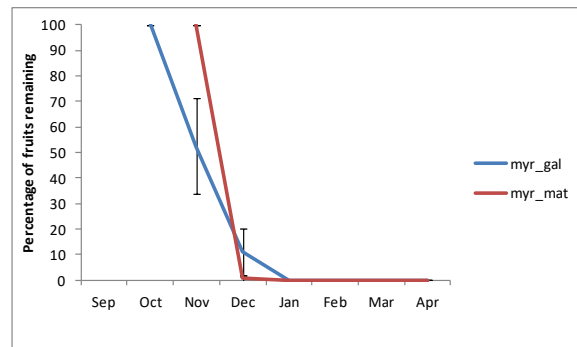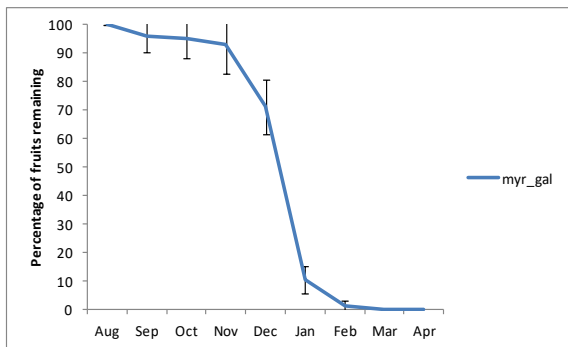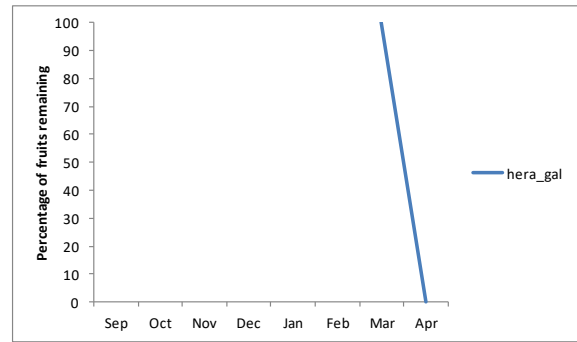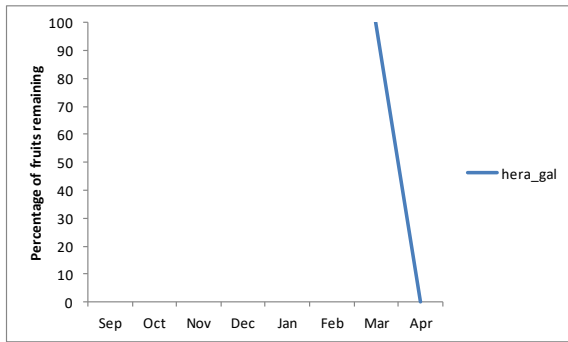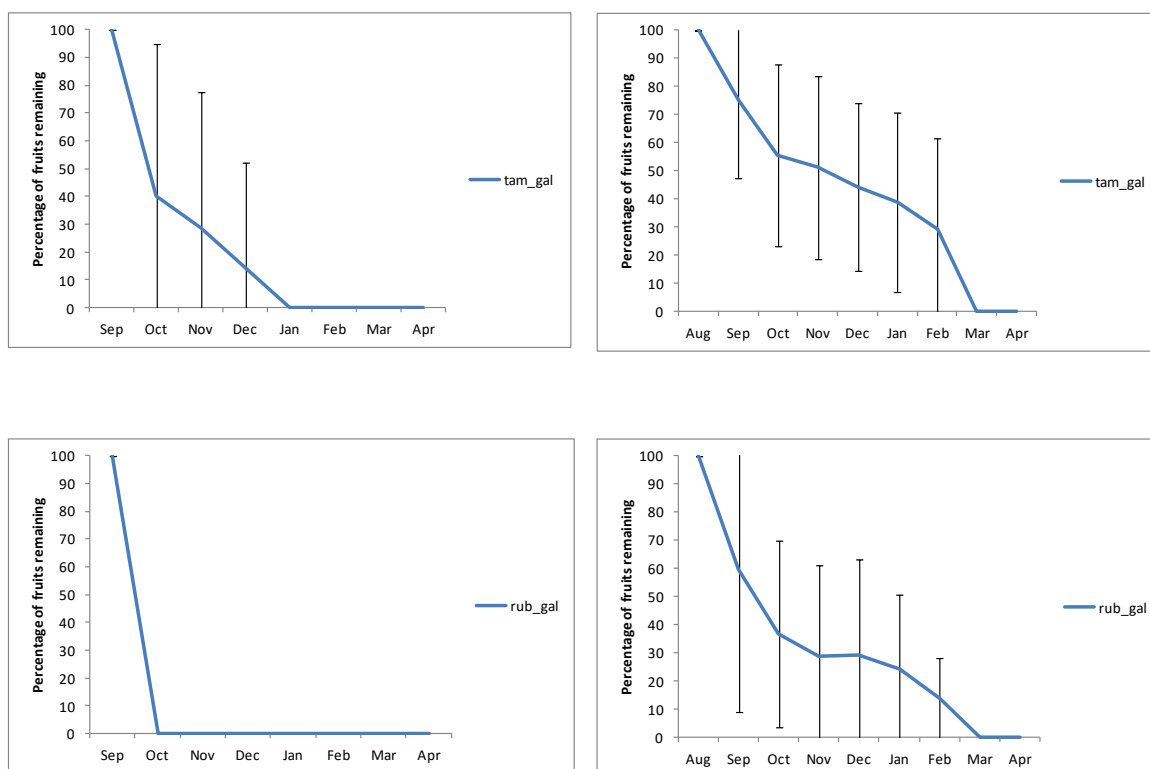
**Figure 13** – Percentage of fruits remaining (mean ± SD) for Mitra in the fructification seasons 2013/2014 (at left) and 2014/2015 (at right) per month for the berries producing species: *Asparagus aphyllus* (asp), *Daphne gnidium* (dap), *Pistacia lentiscus* (pis), *Hera* spp.(hera), *Myrtus communis* (myr), *Olea europaea* var. *sylvestris* (ole), *Smilax aspera* (smi), *Tamus communis* (tam) and *Rubus ulmifolius* (rub). gal – riparian gallery and mat – woodland matrix.

# Discussion

This study shows consistent differences in the diet and feeding ecology between passerines that inhabit the riparian gallery and the adjacent matrix. Our data shows that such differences appear to arise from seasonal differences in the abundance of arthropods and fruits in these two areas. It is important to highlight that arthropods, and to a lower extent fruits, were significantly more abundant in the riparian gallery than in the adjacent matrix. This should be important in explaining the much higher density of birds in the riparian gallery (chapter 1), particularly in autumn when the food resources are also higher at the riparian gallery (this study). Other studies (Jackson & Fisher 1986, Gray 1993, Skagen &

Knopf 1993, Iwata *et al.* 2003, Lecerf *et al.* 2005, Pereira 2007) showed also a higher abundance of food resources for passerines in the riparian gallery. Stevens *et al.* (1977) have also pointed out that riparian habitats may attract over ten times the number of migratory birds in the spring than adjacent upland habitats. Our results showed also that riparian species fed on a consistently higher trophic level in spring, summer and autumn but in winter they fed on lower trophic level food items. This can be explained by the fact that the riparian species in question are mostly insectivorous and by the fact that in winter, a season of lower arthropod abundance (Williams, 1993), bird species such as blackcaps show a change in preference for fruits during autumn and winter when they are superabundant (Berthold, 1976). The woodland matrix species fed on lower trophic levels in spring and winter and we could note a gradual decrease in the trophic level from summer to winter. This decrease in the trophic level from summer to winter may be explained by an increase in fruit consumption, shown by a positive correlation between frugivorous bird abundance and fruit abundance in autumn (Blake & Hoppes, 1986), and by an increase in the consumption of phytofagous insects by insectivorous birds.

In general, the woodland matrix and the riparian gallery differed in terms of insect and fruit abundance for the both areas that we have studied. Although both areas are montados, they present structural differences that allow different insect communities to occur, and suggests that birds feed on the more abundant food resources in each area. For Mitra, birds of the woodland matrix were easier to distinguish from those of the riparian gallery, and apparently feed more on Chilopoda (family *Julida*) and Order *Lepidoptera* (butterflies in larval stage), while for Degebe birds of the woodland matrix were easier to distinguish from those of the riparian gallery because they fed more on *Hymenoptera* (mainly Family *Formicidae*, i.e. ants). We have shown a strong relation between blackcap and blackbird and blackberries in autumn, and between blackcap and olives in winter. We also noticed that blackbirds fed extensively on European black nightshade in autumn; several studies have shown that blackbirds are versatile and opportunistic fruit handlers and consumers (Herrera & Jordano 1981, Snow & Snow 1988). This relation was noted before by McCann (1953). Vegetation should be the key factor to maintain the necessary abundance of fruits and insects as food supplies either for riparian galleries as for surrounding woodland matrix bird communities. Although woody plants dominated riparian habitats, native flowering plants may also provide valuable resources for riparian arthropod populations (Hamilton 1958, Borror *et al.* 1981, Miner 1989, Williams 1993).

This study showed that woodland passerines seemed to feed more on *Araneae* than riparian passerines, but for all other insect orders the proportion of insects remaining in fecal samples was higher than those for the riparian species. Ceia *et al.* (2016) analyzed the diet of three typical bird species from the montado and registered a high presence of *Araneae*, which contributes to explain our results. Bedford & Usher (1994) pointed out that spiders that prefer woodland belong to the family Linyphiidae and are able to disperse by 'ballooning', which is suggestive of the greater mobility of spiders; this characteristic allows them to disperse, occupying for example a sparse montado, and are thus an important food resources for birds. Pinkowski (1978) conducted a passerine diet study in Michigan (USA), during the breeding season and showed that spiders (11.3% of the diet) were particularly important early in the season and for newly-hatched young of Eastern bluebird (*Sialia sialis*). A high density of certain invertebrate groups is thought to be important as food for birds during the breeding season (Hill *et al.* 1990), and insect abundance may be more important than fruit abundance in determining breeding cycles of birds (Levey D. J., 1988). Seasonality is a common phenomenon among insects (Wolda & Wong, 1988), and insect abundance can change over time for a variety of reasons, including macroclimatic and microclimatic changes, and variation in the availability of food resources (Wolda, 1988). Fluctuations in the richness of arthropods are usually much higher in temperate than in tropical regions (Novotny & Basset, 1998). In our study, autumn was the season with more insect abundance for both study areas followed by spring, winter and finally summer. This is contrary to the results obtained by Williams (1993) in a river in San Diego (California) which showed that seasonal variations produced large numbers of arthropods in spring and summer than in autumn and winter.

Razeng & Watson (2015) showed that nutritional quality plays an important role in the selection of prey by insectivorous birds and suggests that micronutrients may be important determinants of prey choice. Our stable isotopic data show clearly that birds typical of the riparian gallery fed at a higher trophic level than birds from the surrounding matrix, which means taking prey of higher quality because higher trophic level prey are likely to be more energetically profitable than lower trophic level prey (Post 2002). Birds during the autumn migration and winter benefit from additional fruit resources provided by the riparian gallery (Leal *et al.* 2011), like olives which are one of the main winter fruiting plants in the Mediterranean shrubland of southern Iberian Peninsula (Herrera 1984a, Jordano 1987). Olives are rich in fatty acids (Ünal & Nergiz 2003, Malheiro *et al.* 2012) that are

important to maintain birds during cold nights and used as fuel for birds' flight (Jenni & Jenni-Eiermann 1998, McWilliams *et al.* 2004, Guglielmo 2010). Fruits appeared to be less important in separating birds of the riparian gallery from the woodland matrix in Degebe contrarily to Mitra, were birds of the woodland matrix were easier to distinguish from those of the riparian gallery by consumption of other insect orders, fruits, and very little consumption of *Araneae*. Once more this can be explained by the fact that the riparian species in question are mostly insectivorous. In general, fruits seemed to be consumed at a faster rate in the woodland matrix than in the riparian gallery, such as shown by (Carlo & Morales, 2008), a fact that is concordant with the high abundance of berries along the riparian gallery for frugivorous birds, especially in autumn (Blake & Hoppes, 1986) and the higher structural complexity of the plant community in the riparian gallery than in the surrounding matrix in Mediterranean environments (Herrera & García 2008, Aguiar et al 2000).

Taken altogether our results show that foraging resources for passerines are more abundant in riparian galleries, particular during periods of higher species density, such as during the summer-autumn migration period. Montados are very important for Mediterranean birds, comprising the habitat with the highest richness for breeding birds in the Iberian Peninsula (Tellería, Passerine bird communities of Iberian dehesas: a review, 2001), which are attracted to certain microhabitats because of higher resource abundance, correlating positively with insect abundance in spring and autumn (Blake & Hoppes, 1986). Riparian galleries are ecosystems with high diversity of plants, animals and environmental processes (Nilsson & Svedmark 2002, Salinas & Casas 2007). They are constituted by very heterogeneous habitats with great availability of food and shelter resources, for the fauna, provided by the vegetation present in the margins of the water course (Rodewald & Bakermans 2006, Tabacchi *et al.* 1998). In the end of summer/autumn riparian galleries are a source of fruit production, providing an important food resource which attracts many animals, specially bird and mammal seed dispersers with fundamental contributions to the dynamics between riparian gallery and surrounding matrix plant communities (Espírito-Santo *et al.* 2000, Fabião & Fabião 2007, Ferreira & Aguiar 2006). Martin *et al.* (2006) suggests that riparian management and restoration to conserve woodland bird assemblages must consider both local habitat condition and landscape context. Overall, riparian galleries function as key landscapes in the maintenance of biological connections through environmental gradients (Klapproth & Johnson 2009, Merritt *et al.* 2010, Naiman &

Décamps 1997) and function as regulation systems between aquatic and terrestrial biotopes (Sabo *et al.* 2005).

# Chapter III


# Seed dispersion by birds in the riparian gallery and the surrounding matrix

## Abstract

Riparian galleries are habitats with a large availability of food resources and shelter for animals, and are among the most important and vulnerable habitats in the world. These areas provide many fruit resources and attract many animals, such as frugivorous birds, which are the main seed dispersers in the Mediterranean basin. The objective of this paper is the study of seed dispersal patterns by birds in the riparian gallery and in the surrounding forest matrix. Fruit abundance was determined in relation to the distance from the stream, and a sub-sample of fruits was marked with fluorescence. Seed traps were used to collect bird droppings and detect fluorescent seeds in those droppings. Fruit abundance and seed dispersal were higher closer to the stream, and decreased rapidly with an increase of distance from the stream. From all species in the study area, the most dispersed was *Smilax aspera.* Plant species with smaller seeds were found at a significantly larger distance from parent plants than species with large seeds. This can be explained by the fact that smaller seed stay longer in the intestinal tract of the birds. The results of this study present some implications for the colonization of fleshy fruit plants from the riparian gallery into the adjacent matrix.

# Keywords

Frugivorous birds, seed dispersal, riparian gallery, forest matrix, parent plant.

## Introduction

The riparian galleries are ecosystems with a great variety of animals, plants and are important for many environmental processes (Nilsson & Svedmark, 2002; Salinas & Casas, 2007). These ecosystems are constituted by heterogeneous habitats with many resources, often derived from the vegetation in the margins which provides food supplies and shelter for the animals (Tabacchi *et al.* 1998, Rodewald & Bakermans 2006). Therefore, they are among the richest, dynamic and complex terrestrial ecosystems (Naiman *et al.* 1993, Jansson *et al.* 2000). The riparian galleries function as key landscapes in the maintenance of biological connections through environmental gradients, and are essential for water availability, landscape architecture and ecological restoration of aquatic environments (Klapproth & Johnson 2009, Merritt *et al.* 2010, Naiman & Décamps 1997). These characteristics suggest that riparian galleries function as regulation systems between aquatic and terrestrial biotopes (Sabo *et al.* 2005), being indicators of the existing functional biodiversity (Borsato & Feiden 2011) and providing the first signs of environmental changes (Gregory *et al.* 1991). The vegetation is an essential component of riparian galleries, depending mostly from nutrients transported in the water current. Riparian ecosystems are regarded as nutrient sinks (Pinay *et al.* 1992), because the dissolved nutrients in superficial and underground current can be removed by the plant community and trough soil microbial processes (Komor & Magner, 1996). These nutrients make possible a structurally complex plant community with large biomass productivity and a wide variety of species, comparatively to the surrounding woodland matrix (Lavorel 1999, Naíman *et al.* 1993). Therefore, riparian areas have a complex plant community composed by trees and shrubs that produce fleshy fruit species, especially in the Mediterranean region (Ferreira & Aguiar, 2006). In summer, due to its vegetation complexity and abundance, the riparian gallery allows lower temperatures and high humidity absent in the surrounding woodlands matrices, and thus provide favourable environmental conditions for many animal communities (Fabião & Fabião 2007, Saab 1999).

Due to intensive alterations in the vegetation cover during centuries, the Mediterranean region landscapes have been undergoing changes, resulting in highly fragmented woodlands and a strong reduction in riparian galleries (Ferreira 2001, Pereira *et al.* 2015). In Mediterranean environments the riparian gallery plant community is more

complex and the floristic composition more diverse than those in the surrounding woodland matrix (Aguiar *et al.* 2000, Herrera & García 2008). Many of the ecological processes that take place in the surrounding matrix depend on the biodiversity and on the ecological processes of the riparian gallery (Herrera & García 2008, Saab 1999), for instance plant colonization, because riparian galleries are an important source of seeds (Herrera & García, 2008). As the surrounding matrix is often profoundly altered, the riparian gallery can be important for matrix functioning and ecological rehabilitation (Aguiar *et al.* 2000, Herrera & García 2008). Therefore, given their intrinsic characteristics riparian gallery attract many seed dispersers, particularly frugivorous birds that are the major seed dispersers in the Mediterranean basin (Machtans *et al.* 1996), because after feeding on fruits and by means of regurgitation and / or defecation they allow germination of seeds contained in feces (Debussche & Isenmann 1992, Martínez del Rio & Restrepo 1993). Riparian galleries present a large fleshy fruit production mostly in the end of the summer/winter that constitutes an important food supply allowing the presence of many animal species, including birds and mammals dispersing seeds, and contributing to explain the vegetation dynamics between the riparian gallery and the adjacent woodland vegetation (Espírito-Santo *et al.* 2000, Ferreira & Aguiar 2006, Fabião & Fabião 2007).

In a study in central Alentejo, southern Portugal, it was possible to identify three main groups of birds in the system riparian gallery-adjacent woodland matrix (Montado ecosystem): 8 species of birds typical of the riparian gallery (for example *Sylvia atricapila* or *Luscinia megarhynchos*), 6 species of birds typical of the woodland matrix (for example *Cyanistes caeruleus* or *Parus major*) and 5 species of birds of the interface riparian gallery-woodland matrix (for example *Sylvia melanocephala* or *Emberiza calandra*) (Pereira *et al.* 2014); it was also found that species richness is higher in the riparian gallery than in the surrounding woodland matrix (Pereira *et al.* 2014, Pereira *et al.* 2015). Although these bird species occur preferably in a certain area, they use all the area covered by the riparian gallery and the woodland matrix, especially woodland matrix birds that might have a role in seed dispersion, given their movements to the riparian gallery to feed on berries. Upon returning to the woodland matrix they will defecate and promote plant colonization in the matrix (Fleming & Kress 2013, Grünewald *et al.* 2010, Jordano *et al.* 2007, Cruz *et al.* 2013, Herrera 1984b). Seed dispersing bird communities in temperate areas disperse seeds almost continually throughout the year, with an accentuated peak in autumn which, in Europe, can be extended until winter (Debussche & Isenmann, 1992). Seed dispersion is an important

process that connects successive plant generations and influences vegetation dynamics (Heleno *et al.* 2011, Nathan & Muller-Landau 2000).

Although their biological value is high, the riparian ecosystems are rarely included in conservation systematic planning, despite the fact that they are increasingly threatened by human activities and invasive species, especially in the Mediterranean region (Nel *et al.* 2009). Namely its role in seed dispersal and consequent importance in explaining the surrounding vegetation dynamics is poorly studied (Nel *et al.* 2009). There are limitations in the study of seed dispersal mechanisms, for example, it can be difficult to track all seed dispersal destinations (Johansson *et al.* 1996). For this reason, Zamora & Matías (2014) considered the cumulative result of seed dispersal in vegetation, taking into account species abundance and distribution, in order to discuss the ecological basis of the different mechanisms of plant dispersion, in terms of the availability of dispersal agents, seed size and other ecological constraints (Jordano 1984, Wilson *et al.* 1990). Seed size is suggested as being an ecological factor of great importance for the evolution of dispersal mechanisms, for example in the genera *Vaccinium* spp. e *Sorbus* spp. studied by Wilson *et al.* (1990). Having into account that stream currents are considered important seed dispersal corridors within the landscape, it is noteworthy that there is a positive relationship between seed dispersal ability and the occurrence of species in the riparian gallery. Johansson *et al.* (1996) demonstrated that dispersion along the water lines influence riparian species and promote an explanation for the distribution patterns of species and their dispersion. Therefore, the water lines are considered very important to maintain regional biodiversity (Johansson *et al.* 1996), and it is also important to study seed dispersal processes into the adjacent matrix.

In our study, we used two methods to study seed dispersal patterns in the system riparian gallery – adjacent matrix: 1) search for seeds in seed traps and transects and 2) fluorescence detection (Levey *et al.* 2005) in seeds dispersed by birds. The aim of this study was to understand seed dispersal patterns by birds in the interface riparian gallery-woodland matrix, aiming to determine the influence of the riparian gallery in seed dispersal patterns in river systems and adjacent woodland areas, which are often profoundly altered and need ecological restoration, allowed by seed dispersal. To contribute to this goal we tried to answer three questions: 1) which riparian gallery plant species are more dispersed by birds; 2) the distance from seed parent plants and from the riparian gallery that most seeds are dispersed, and 3) what is the influence of seed sizes in the distance at which seeds are dispersed by birds. Such as demonstrated in other studies (Johansson *et al.* 1996,

Naiman & Décamps 1997, Levey *et al.* 2005, Cruz *et al.* 2013) the seed dispersal was expected to be greater closer to the parent plant. We expected also that seed dispersal is more intense nearby the riparian gallery, where the freshly fruit plants are more abundant and, as a consequence, we expect a decrease in seed dispersal in the woodland matrix as the distance to the riparian gallery increases.

# Methods

In central and south Iberia, human interference in dense and continuous Cork and Holm oak forests shaped what we, nowadays, know as Portuguese 'montado' (Pinto-Correia *et al.* 2011). The 'montado' is a woodland system where human intervention can promote biodiversity enrichment, with an adequate management (Pereira *et al.* 2015). Nowadays, this system includes a set of agricultural subsystems, forestry and pastors, with a low shrub layer and has the aim of promoting the cultivation of cereals, livestock and/or Cork production, creating a heterogeneous matrix with different tree densities (Pinto-Correia & Mascarenhas 1999, Ferreira 2001), forming a crossed mosaic of natural corridors such as riparian corridors (Pereira *et al.* 2014).

The study area was in Herdade da Mitra, an Évora University pole, 12 km from Évora (Mitra-Nature, 2014) and Degebe River affluent (Canaviais, Évora). Herdade da Mitra has a total area of 286ha limited at north and west by Valverde and Peramanca streams, at east by the Herdade de Alfabobeira and south by the Herdade do Barrocal (Mitra-Nature, 2014). In particular, the study area was in the riparian gallery of Valverde stream (approximately 4ha), extending to the surrounding woodland matrix (approximately 6 ha). In this study, the plant species studied were: common smilax *Smilax aspera*, mastic *Pistacia lentiscus*, wild olive *Olea europaea var. sylvestris*, common myrtle *Myrtus communis*, blackberry *Rubus ulmifolius*, common hawthorn *Crataegus monogyna* (only in Degebe) and strawberry tree *Arbutus unedo*, flowering in spring and fructifying in summer/autumn (except for *S. aspera* and *A. unedo* that flower in autumn). These species were selected based in a previous inventory that revealed these species as the more abundant freshly fruit plants in the region. Additionally, all these species are very important for bird's diet in autumn/winter (Herrera 1984b, Jordano 1986).

The periods of fruit availability, for the plant species in this study, are defined as periods varying from one to approximately five months and all species tend to ripen their fruits in late summer and autumn, independently of flowering time (Herrera 1984b, Verdú & García-Fayos 2000, Traveset *et al.* 2001a). In the case of *S. aspera* and *A. unedo*, fruits mature during the flowering period, meaning they are the product of last year's flowers (Herrera, 1984b). To quantify the number of seeds contained in the fruit of each species, we collected 30 ripe fruits on each species and counted the number of seeds of each fruit; we also measured the width of each fruit and of each seed for each plant species. We also

crossed our data with data from other studies, where the same species of plants were studied, in a similar study area (Table 10).

**Table 10** – Studied fleshy fruit species, average number of seeds per fruit, average size of the fruit (mm), average size of the seed (mm) and standard deviation (combined data from Fuentes, 1994; Herrera, 1981; Rodríguez-Pérez *et al.* 2005; Traveset *et al.* 2001a; Traveset, Riera, & Mas 2001b).

| Common name | Scientific name | Number of seeds/fruit | Fruit width (mm) | Seed width (mm) |
|---|---|---|---|---|
| Common smilax | *Smilax aspera* | 2 ± 1 | 7.3 ± 0.6 | 3.4 ± 0.4 |
| Mastic | *Pistacia lentiscus* | 1 ± 0 | 5.3 ± 0.7 | 3.7 ± 0,5 |
| Olive | *Olea europaea var. sylvestris* | 1 ± 0 | 8.8 ± 0.5 | 5.8 ± 0,5 |
| Common myrtle | *Myrtus communis* | 5 ± 3 | 8.5 ± 0.1 | 2.5 ± 0,1 |
| Elmleaf blackberry | *Rubus ulmifolius* | 37 ± 9 | 14.6 ± 1.1 | 1.8 ± 0,2 |
| Common hawthorn | *Crataegus monogyna* | 1 ± 0 | 8.1 ± 1.1 | 4.9 ± 0.7 |
| Strawberry tree | *Arbutus unedo* | 48 ± 7 | 17.7 ± 3.8 | 1.5 ± 0,2 |

## Mapping parent freshly fruit plants

Mapping parent plants enabled quantifying fleshy fruit plants in the study area and their abundance. Therefore, a total study area with approximately 10ha (calculated in Quantum GIS version Lisboa 1.8.0), including the riparian gallery (4ha) and the surrounding woodland matrix (6ha). This took place in the right margins of Valverde stream and Degebe River, a corridor of approximately 200m, measured perpendicularly from the stream into the woodland matrix. In Summer/autumn, when the stream has a low flow rate, it was possible to mark and study individuals of *Rubus ulmifolius* approximately 4m from the stream, the minimum study distance. The maximum distance perpendicularly to the stream was approximately 200m, where seeds of *Smilax aspera*, *Olea europaea var*. *sylvestris* and *R. ulmifolius* were collected. We mapped all parent plant locations, seed traps and transects in Quantum GIS (version Lisboa 1.8.0) and performed a monthly count to assess fruit abundance of each individual fleshy fruit plant marked. The first fructification study season was between August 2013 and April 2014 (Degebe), the second between September 2014 and February 2015 (in Mitra and Degebe) and the third, between August 2015 and November 2015 (Mitra only). The fruit abundance was assessed monthly in each parent plant due to variations in the number of fruits caused by their removal by birds (and other animals) and/or other factors that lead to the reduction in number of fruits. The assessment of fruit abundance was made with sub-sampling (due to the large number of fruits, in most

97

cases), and consisted in counting a portion of the fruits and extrapolating to the rest of the parent plant.

**Marking of fruits**

To understand the mechanism of seed dispersal in the interface riparian gallery-surrounding woodland matrix we marked fruits. In August 2014 we essayed a method using beads, with different colors and approximately 1mm, avoiding modifying or damaging the fruit so that birds could feed on them as naturally as possible (Herrera *et al.* 2016). The beads were sewed to the fruit´s pericarp (with sewing thread and needle) or inserted in the fruit interior, with the help of a dissection needle (Herrera *et al.* 2016). The differences between the two methods were related with fruit and seed sizes, for example, in the case of *Olea europaea var. sylvestris* fruits it was easier to sew the bead (the large seed occupies almost all the space inside the fruit), but in the case of *Arbutus unedo* or *Myrtus communis* fruits, we chosen to insert the bead into the fruit, because seeds are much smaller and occupy lesser space in the fruit. Therefore, in the same parent plant, we marked the most number of fruits possible, always using the same size and color bead, in the parent plant respectively. However, this method revealed to be impractical, since most of the fruits were damaged by marking, losing its vitality and was also possible to verify that marked fruits were not chosen by birds. This process is also a lengthy and no beads were recovered from bird droppings. Therefore, we used the method established by Levey *et al.* (2005) to mark the fruits: these were sprayed with a mixture of water and fluorescent powder, of different colours, and seed traps were set to collect bird droppings (Levey *et al.* 2005). We used fluorescent powder (fluorescent pigment *Holi Powder Color Run*, article code 90, manufacturer *WeGlow*), of 6 different colors (yellow, blue, orange, pink, green and red), diluted in water and sprayed directly in the fruits. The fruits of each plant were marked with a different colour, allowing to know exactly the identity of the parent plant of the seed found in the feces (Levey *et al.* 2005). In total, 29574 fruits were marked with fluorescence, corresponding to approximately 53355 seeds (Table 11). The colours were not repeated within the same species to be possible to determine, with maximum accuracy, the dispersal distance from each parent plant. This method revealed viable, as fruit's vitality was not affected by the mixture of water and fluorescent powder sprayed on them. Furthermore, it is a simple method, expeditious and inexpensive, with the added advantage of easy

detection in bird droppings and used previously in similar studies (Levey *et al.* 2005). In Degebe no fruits were marked with fluorescence.

**Table 11** – Number of fruits and seeds (within parentheses) of each species marked with fluorescence.

| Fluorescence | Species | | | | | |
|---|---|---|---|---|---|---|
| | *Smilax aspera* | *Pistacia lentiscus* | *Olea europaea var. sylvestris* | *Myrtus communis* | *Rubus ulmifolius* | *Arbutus unedo* |
| Yellow | 162 (324) | 3140 | 30 | 60 (300) | 10 (370) | 11 (528) |
| Blue | 260 (520) | 5600 | 0 | 25 (125) | 555 (2775) | 22 (1056) |
| Orange | 800 (1600) | 3000 | 46 | 48 (240) | 740 (3700) | 0 |
| Pink | 710 (1420) | 4500 | 160 | 0 | 170 (6290) | 45 (2160) |
| Green | 700 (1400) | 2500 | 0 | 0 | 0 | 22 (1056) |
| Red | 517 (1034) | 5600 | 6 | 35 (175) | 100 (3700) | 0 |

## Sampling of bird droppings

### Seed traps

Bird droppings were collected using seed traps, that consist of rectangular portions of white tissue, supported by branches of trees and bushes with wire in the four corners, assuring enough tension to enable the maximization of the seed trap area and allowing a depression to form, making possible for bird droppings to deposit and their subsequent collection.

In total 81 seed traps were installed, distributed between the riparian gallery (44 seed traps in Mitra and 42 in Degebe) and the surrounding woodland matrix (37 seed traps in Mitra and 27 in Degebe). The seed traps were installed on strategic branches of trees and bushes, where we observed higher bird activity and at several distances from the riparian gallery (the maximum average distance between seed traps was 45m, the minimum distance was 4m and the maximum distance to the stream was 134m). For data analysis we used 3 classes of distance to the stream: 0-40m (47 seed traps), 41-80m (18 seed traps) and distances greater than 80 m (16 seed traps). The bird droppings were collected from the seed traps once a week.

**Transects for sample seeds in bird droppings**

In order to increase the sample size of bird droppings, were performed 3 pedestrian transects in Mitra, covering the area between the riparian gallery and the surrounding woodland matrix, with special intensity in the areas surrounding seeds traps, as well as rocks, trees and shrubs. The transect 1 was established perpendicularly to the riparian gallery, with a width of approximately 2m and 150m of length, extending from the riparian gallery to the surrounding woodland matrix. The transects 2 and 3 were established parallel to the riparian gallery, since we verified that most fecal material was observed nearby the riparian gallery than in the woodland matrix, presumably due to a higher abundance of fleshy fruits along the riparian gallery. Transects 2 and 3 had approximately 100m length and 2m wide. Data from transect 1 were treated differently from data from transects 2 and 3. Transects were performed in zigzag in order to maximize sampling of bird droppings. Each transect was walked once a week. No transects were defined for Degebe; i.e. only seed traps were used.

**Bird droppings analysis**

The feces were dissolved in a drop of water and examined carefully to remove all the seeds, which were collected individually in *Eppendorf* tubes for later identification in the laboratory. The identification of seeds was performed using a reference collection constituted by seeds from the study area. The detection of fluorescence, both in fruits and seeds, was made using a black light flashlight (in a room with absence of white light).

**Data analysis**

The exploratory data analysis revealed very similar patterns for all seasons, therefore data was analyzed altogether, regardless of season and year. To evaluate seed dispersal in relation to the riparian gallery and the parent plants we used three types of distances using Quantum GIS (version Lisboa 1.8.0): the distance between parent plants and the stream, the distance between the seed traps and the stream, and the distance between the parent plants and the seed traps. In data analysis for transect 1, assessing distance that seeds are dispersed from the stream and the parent plant, all seeds collected were grouped in classes of distance with a 40m range (0-40, 41-80, 81-120 and so on). The distances between

transects 2 and 3 and the stream were not calculated because they were parallel to the stream, both with the same distance (approximately 20m). Because each plant species has a different number of seeds per fruit, data of fruit abundance was converted in abundance of seeds using means presented in Table 11, in order to use the same unit for both seed traps and transects, i.e. number of seeds.

We used Statsoft Statistica (version 7.0.61.0 EN) to perform two Chi square tests, one using data from the seed traps, without fluorescence detected, where we compared the number of seeds in the bird droppings with its abundance in a 40m radius for both study areas, Mitra and Degebe. We tested the null hypothesis that the seeds should be dispersed according to its abundance. Likewise we assessed whether seed dispersal of the species*, Smilax aspera, Pistacia lentiscus, Olea europaea var. sylvestris e Myrtus communis* found in the seed traps was proportional to its abundance, according to the distance to the stream. We used three classes of distance (0-40m, 41-80m and >80m). The species *Rubus ulmifolius* and *Arbutus unedo* were not used in this analysis because the first species was only dispersed in the class of distance near the stream (0-40m), and the second species was not dispersed by birds. In the second Chi square test, we used data collected in the two transects parallel to the stream in Mitra (transects 2 and 3), to compare the number of seeds dispersed in relation to the amount of seeds available for dispersal.

A binomial generalized linear model was used to assess the importance of the following variables in the presence (1) and absence (0) of seeds in the seed traps: species (*Smilax aspera*, *Pistacia lentiscus*, *Olea europaea var. sylvestris, Myrtus communis* e *Rubus ulmifolius*), distance to stream, seed abundance in a 40m radius and the interaction between these variables. These analyses were performed only for Mitra because sample size was too small for Degebe. Each weekly visit to the seed traps was accounted as a sampling unit for each species, as the abundance of fruits of each species in a 40m radius around the seed trap was estimated weekly. Since all species presented a similar distribution pattern, in other words, its abundance decreased from the stream, it was not considered any spatial correlation between the seed traps. For each species we considered only the period in which it was available in the environment (for example for *R. ulmifolius* we considered only the period August and September, as no fruits were present afterwards). Finally, a Kruskal-

Wallis test was used to assess if the median of seed dispersal from parent plants (detected with fluorescence) differed between plant species.

# Results

## Seed dispersal from the riparian gallery

### Seeds with no fluorescence collected in seed traps

For the studied species we observed that parent plants producing berries were more abundant closer to the stream, and as the distance to stream increased both the abundance and the dispersal of seeds decreased rapidly (Fig. 14). A Chi square test for each of the species revealed that seed dispersal was proportional to its abundance in each class of distance to the stream for the species *Smilax aspera* (Mitra: $X^2_2$= 2.39; P < 0.303), *Pistacia lentiscus* (Mitra: $X^2_2$= 4.01; P = 0.135), *Crataegus monogyna* (Degebe: $X^2_2$= 0.33; P < 0.100) e *Rubus ulmifolius* (Degebe: $X^2_2$= 0.16; P < 0.900). However, null hypothesis was rejected for the species *Myrtus communis* ($X^2_2$= 43.50; P < 0.001) and *Olea europaea var. sylvestris* (Mitra: $X^2_2$= 12.51; P = 0.002; Degebe: $X^2_2$= 56.68; P <0.001). For *M. communis* it was registered more dispersal than we expected in the class of distance closer to the stream (observed: expected = 94:60), whereas for *O. europaea var. sylvestris* the opposite occurred (observed: expected: 57:73 (Mitra); 89:192 (Degebe)).

Mitra                                    Degebe

a)  *Rubus ulmifolius* (Mitra - 14948/44; Degebe
    – 2257/55)
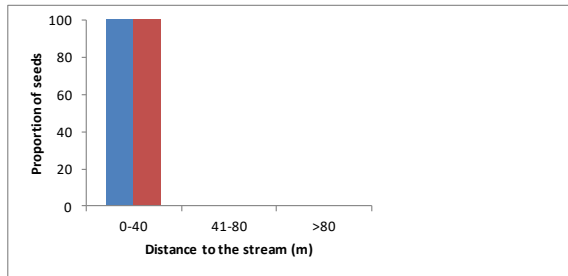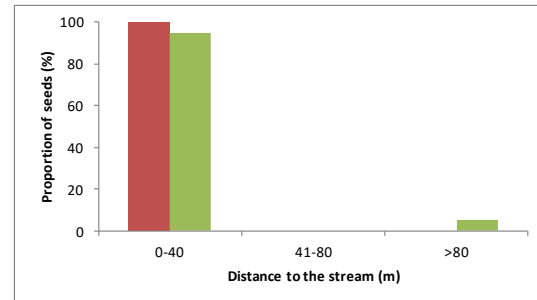


b)  *Olea europaea* var. *sylvestris* (Mitra -
    627/74; Degebe – 251/222))
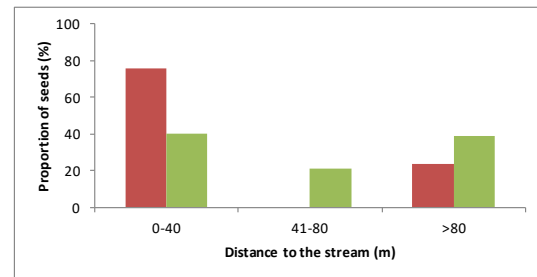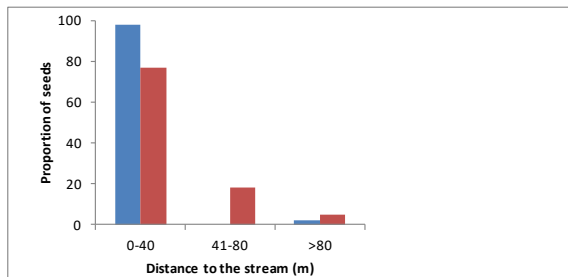


c)  *Smilax aspera* (Mitra - 7528/419)
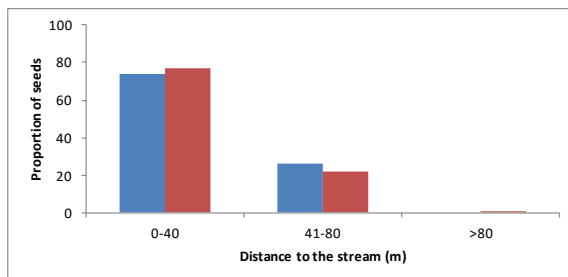


d)  *Pistacia lentiscus* (Mitra - 43858/169)
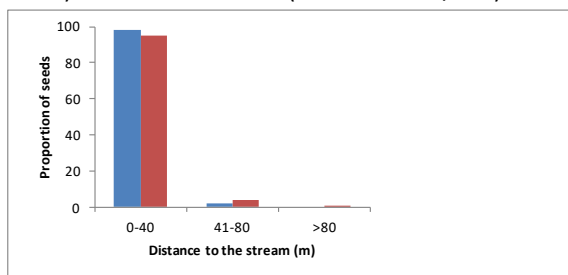


e)  *Myrtus communis* (Mitra - 3915/106)
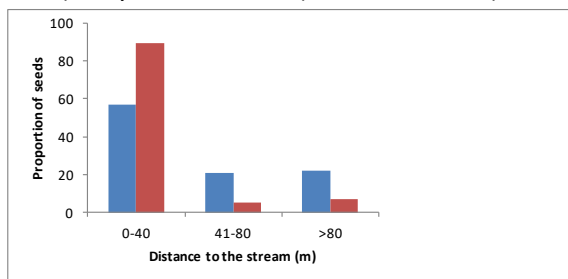
f)   *Crataegus monogyna* (Degebe – 377/3)
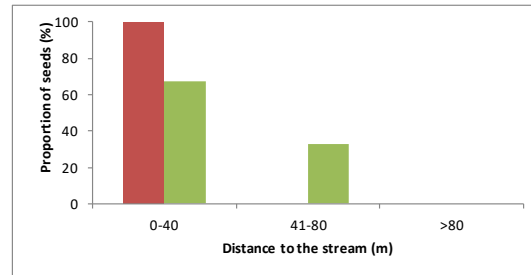


**Figure 14** – Comparison between the proportion of seeds available (the first column) and dispersed (the second column) for Mitra and Degebe (detected in bird droppings collected in seed traps), for each studied species, per classes of distance to the stream. The numbers presented within parentheses for seed abundance/dispersed seeds, refer to the total number of seeds.

The comparison between the abundance and dispersion of seeds allowed us to understand that *S. aspera* was the most dispersed species in Mitra (5.6%, Fig. 14a), followed by *P. lentiscus* (0.4%, Fig. 14b), which was also the most abundant species. Noteworthy, *A. unedo* was abundant, however we did not collected any seeds dispersed, which might be explained by the small size of the seeds in this specie (less than 1mm), and so more difficult to be detected. For Degebe the most dispersed species was *R. ulmifolius,* followed by *C. monogyna.*

The probability of occurrence of seeds in seed traps was influenced by the variables species, seed abundance and by the interaction of both variables (Table 12). Relatively to *R. ulmifolius*, the seeds of *O. europaea var. sylvestris* occurred significantly less in seed traps, and the other species did not differed from *R. ulmifolius*. The seed abundance was particularly important to explain the occurrence of seeds in seed traps (Tables 12 and 13), however the distance to stream did not influenced the probability of occurrence of seeds in the seed traps (Table 12).

**Table 12** – Generalized Linear Model to assess the influence of species, distance to stream (Dist_rib) and seed abundance (Abund) on a 40m radius in the presence or absence of seeds in the seed traps. Significant effects are shown in bold.

|  | Df | Chi-square | P |
|---|---|---|---|
| **Species** | 4 | 40.9 | **< 0.0001** |
| **Distance to stream (Dist_rib)** | 1 | 0.4 | 0.538 |
| **Seed abundance (Abund)** | 1 | 17.1 | **< 0.001** |
| **Species*Dist_rib** | 4 | 4.7 | 0,3142 |
| **Species*Abund** | 4 | 21.5 | **< 0.001** |
| **Dist_rib*Abund** | 1 | 3.9 | **0.0488** |
| **Species*Dist_rib*Abund** | 4 | 3.9 | 0.4208 |

**Table 13** – Generalized Linear Model results to assess the influence of species, distance to stream (Dist_rib) and seed abundance (Abund) on a 40m radius in the presence or absence of seeds in seed traps. For each variable and interaction we present the standard error, the Wald Chi square statistics and the P value. Significant effects are shown in bold.

| | Df | Coefficient | Standard error | Wald | P |
|---|---|---|---|---|---|
| **Intercept** | | -1.369 | 0.618 | 4.906 | 0.027 |
| | Ref: *Rubus ulmifolius* | | | | |
| **Specie** | *Smilax aspera* | 0.827 | 0.644 | 1.651 | 0.199 |
| **Specie** | *Pistacia lentiscus* | -0.810 | 0.663 | 1.492 | 0.222 |
| **Specie** | *Olea europaea var. sylvestris* | -1.518 | 0.667 | 5.187 | **0.023** |
| **Specie** | *Myrtus communis* | -0.489 | 0.665 | 0.541 | 0.462 |
| **Dist_rib** | | 0.011 | 0.018 | 0.380 | 0.538 |
| **Abund** | | 0.023 | 0.005 | 17.138 | **< 0.001** |
| | Ref: *Rubus ulmifolius* | | | | |
| **Specie \*Dist_rib** | *Smilax aspera* | -0.002 | 0.019 | 0.014 | 0.905 |
| **Specie \*Dist_rib** | *Pistacia lentiscus* | -0.007 | 0.020 | 0.125 | 0.723 |
| **Specie \*Dist_rib** | *Olea europaea var. sylvestris* | 0.014 | 0.019 | 0.527 | 0.468 |
| **Specie \*Dist_rib** | *Myrtus communis* | -0.007 | 0.019 | 0.129 | 0.719 |
| | Ref: *Rubus ulmifolius* | | | | |
| **Specie \*Abund** | *Smilax aspera* | -0.015 | 0.006 | 6.347 | **0.012** |
| **Specie \*Abund** | *Pistacia lentiscus* | -0.020 | 0.005 | 14.004 | **< 0.001** |
| **Specie \*Abund** | *Olea europaea var. sylvestris* | 0.085 | 0.020 | 18.518 | **< 0.001** |
| **Specie \*Abund** | *Myrtus communis* | -0.027 | 0.010 | 7.333 | **0.007** |
| **Dist_rib\*Abund** | | -0.001 | 0.001 | 3.881 | **0.049** |
| | Ref: *Rubus ulmifolius* | | | | |
| **Specie \*Dist_rib\*Abund** | *Smilax aspera* | 0.001 | 0.001 | 3.487 | 0.062 |
| **Specie \*Dist_rib\*Abund** | *Pistacia lentiscus* | 0.001 | 0.001 | 2.911 | 0.088 |
| **Specie \*Dist_rib\*Abund** | *Olea europaea var. sylvestris* | -0.001 | 0.001 | 3.339 | 0.068 |
| **Specie \*Dist_rib\*Abund** | *Myrtus communis* | 0.001 | 0.001 | 0.304 | 0.582 |

**Seeds with fluorescence collected in seed traps**

For the results of seeds with fluorescence collected in the seed traps, we calculated distance of dispersal between the seed traps (where the seeds were found) and the parent plants. In total, we marked 57 parent plants with fluorescence and collected 95 seeds with fluorescence from the seed traps only for Mitra. The distance of dispersal differed significantly between species (Kruskal-Wallis test: H (3, N= 95) = 45.68 p < 0.001). We observed, for *Smilax aspera*, that much of the seeds were dispersed in shorter distances (mean ± standard deviation: 33.6 ± 48.6m), while for *Pistacia lentiscus* seed dispersal covered greater distances (mean ± standard deviation: 84.3 ± 50.6m). For the species *Myrtus communis* and *Rubus ulmifolius* even greater dispersal distances (145.9 ± 206.4m e

373.8 ± 119.5m) were registered. We did not collect any seeds of *Olea europaea var. sylvestris* or *Arbutus unedo* with fluorescence (Table 14; Fig. 15).

**Table 14** – Comparison of seed dispersal distances among plant species. The table presents data on distances between: seed traps and the parent plants marked with fluorescence, the parent plants and the stream, and the seed traps and the stream (m).

| Species | N | Distance between seed traps and parent plants (m) | Distance between parent plants and stream (m) | Distance between seed traps and stream (m) |
|---|---|---|---|---|
| *Myrtus communis* | 2 | 146.0 ± 206.4 | 22.2 ± 8.8 | 15.9 ± 0 |
| *Smilax aspera* | 67 | 33.6 ± 48.6 | 38.3 ± 5.5 | 49.8 ± 15.9 |
| *Pistacia lentiscus* | 4 | 84.3 ± 50.6 | 19.8 ± 0 | 23.2 ± 8.3 |
| *Rubus ulmifolius* | 22 | 373.8 ± 119.5 | 21.4 ± 16.5 | 37.3 ± 9.6 |

a) *Smilax aspera* (n=67)
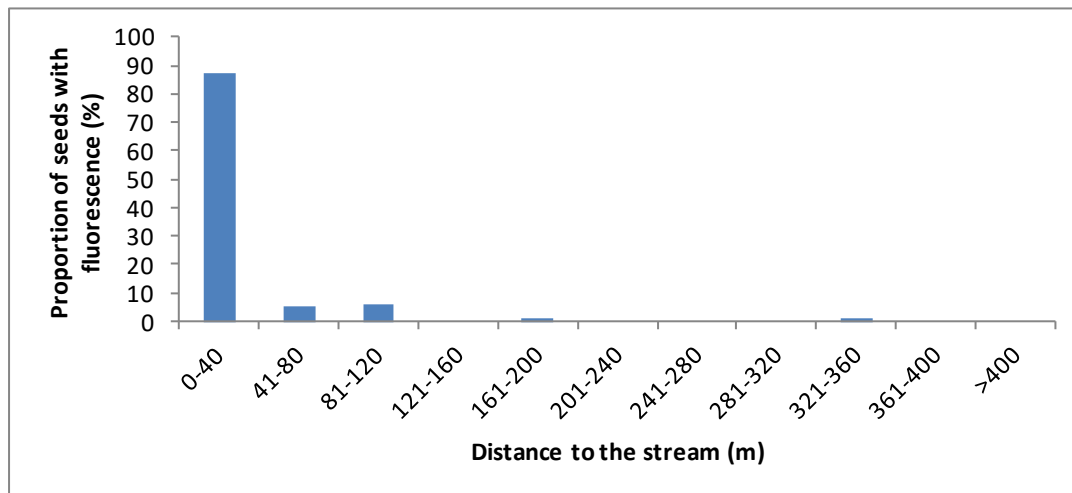
b) *Pistacia lentiscus* (n=4)
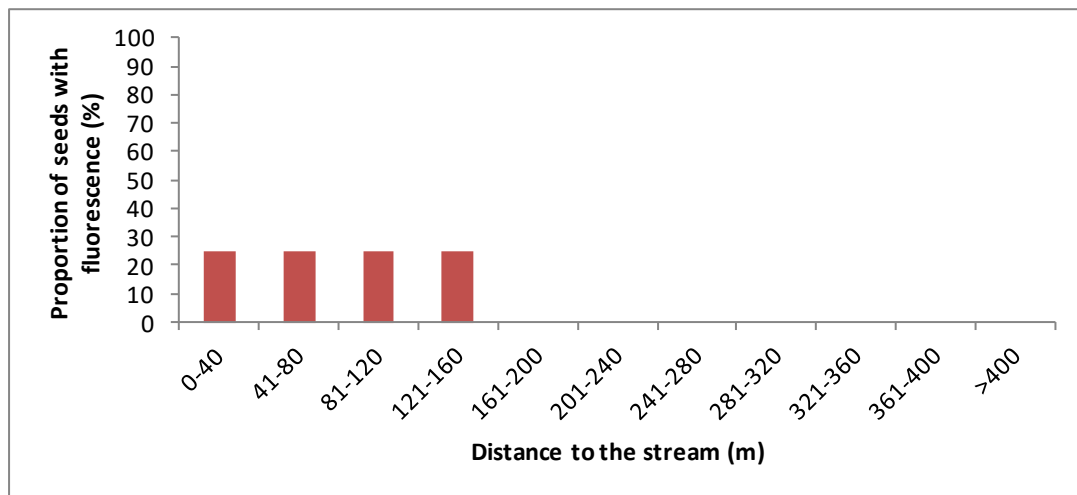


c) *Myrtus communis* (n=2)
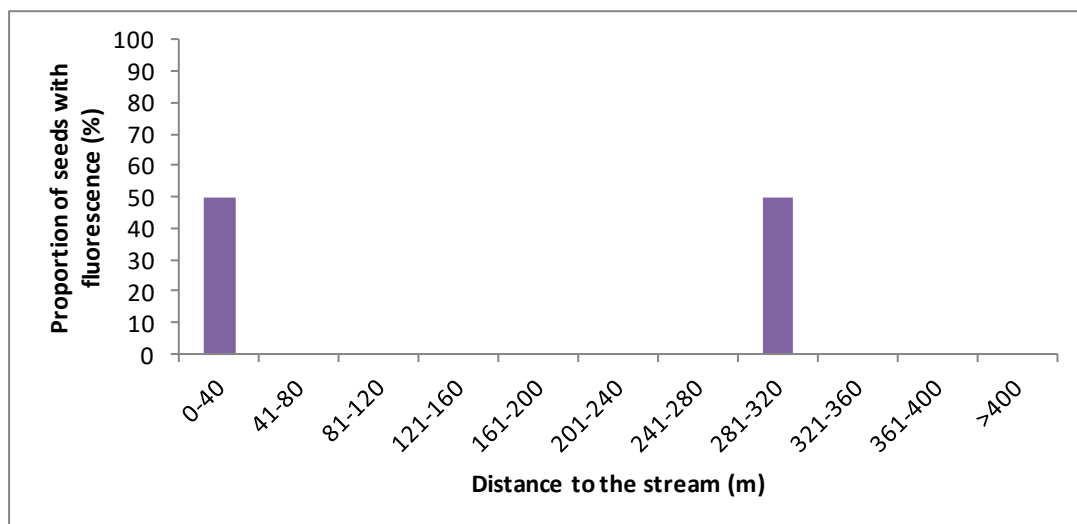
d) *Rubus ulmifolius* (n=22)
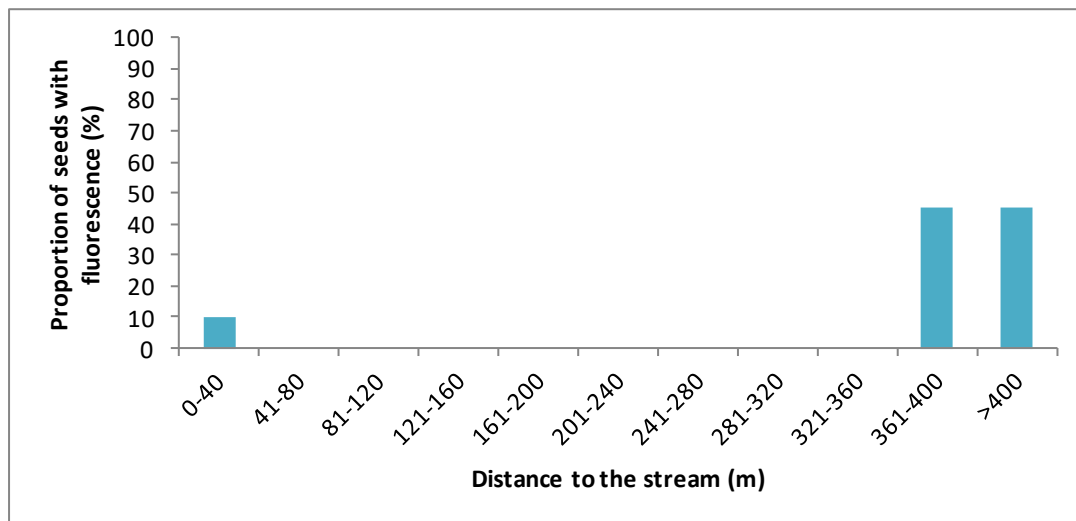


**Figure 15** – Proportion of seeds with fluorescence found in seed traps in relation to the distance from parent plants. The numbers within parentheses refer to the total number of seeds analysed for each species.

We compared distances of seed dispersal from the parent plants, in relation to the distance to the stream. Figure 17 shows that most of these distances were in the range of 11-40m from the stream, except for *R. ulmifolius,* with a higher percentage of seed dispersal closer to the stream (0-10m). In most species, seed dispersal distances to the stream decreased or remained similar as distance to parent plants increases, although it is visible that more plants were marked closer to the stream. This occurred due to a higher availability of fruits to mark closer to the riparian gallery.

a) *Smilax aspera* (67/22)
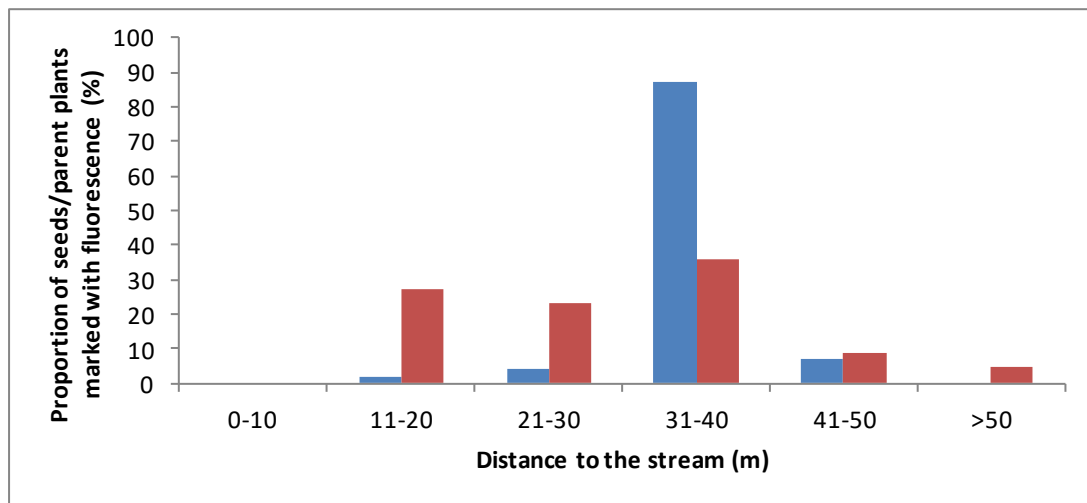


b) *Pistacia lentiscus* (4/15)
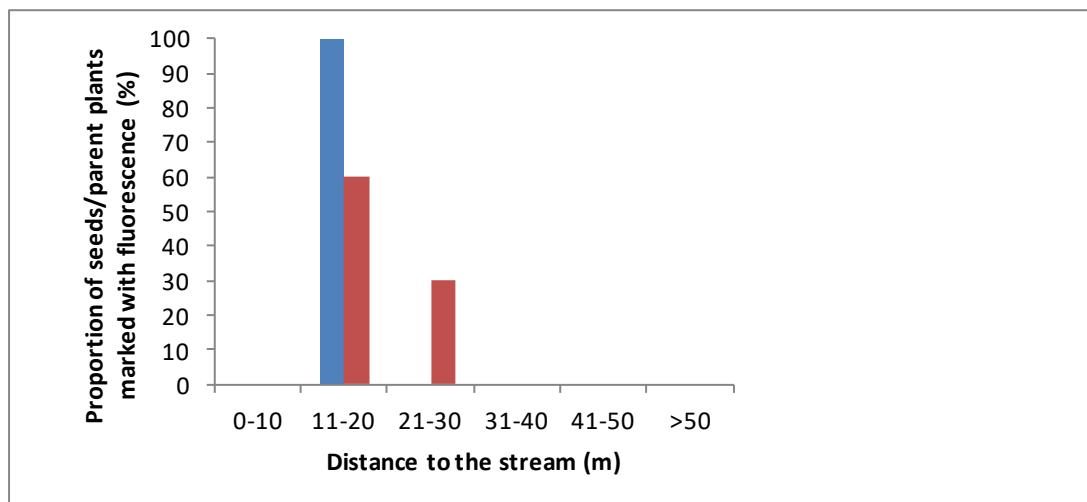
c) *Olea europaea var. sylvestris* (0/4)
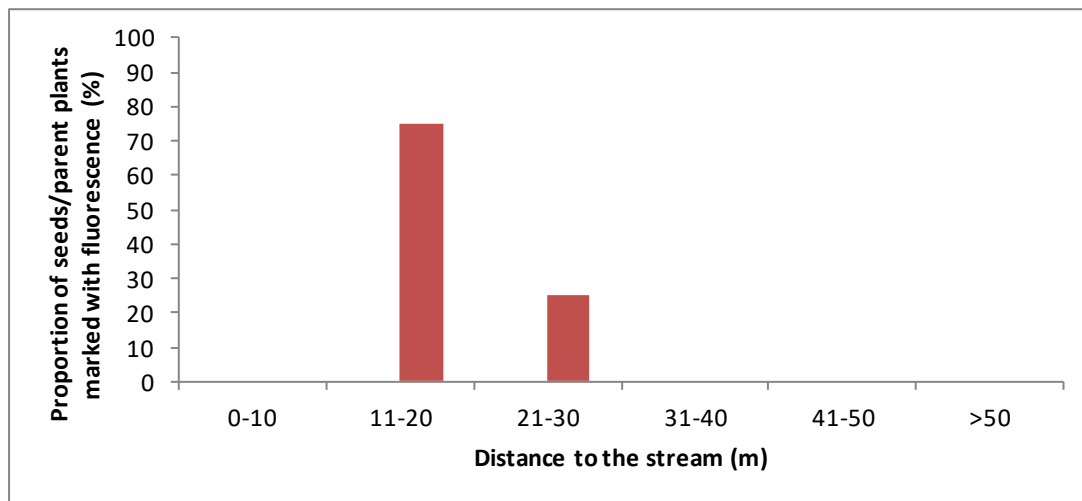


d) *Myrtus communis* (2/5)
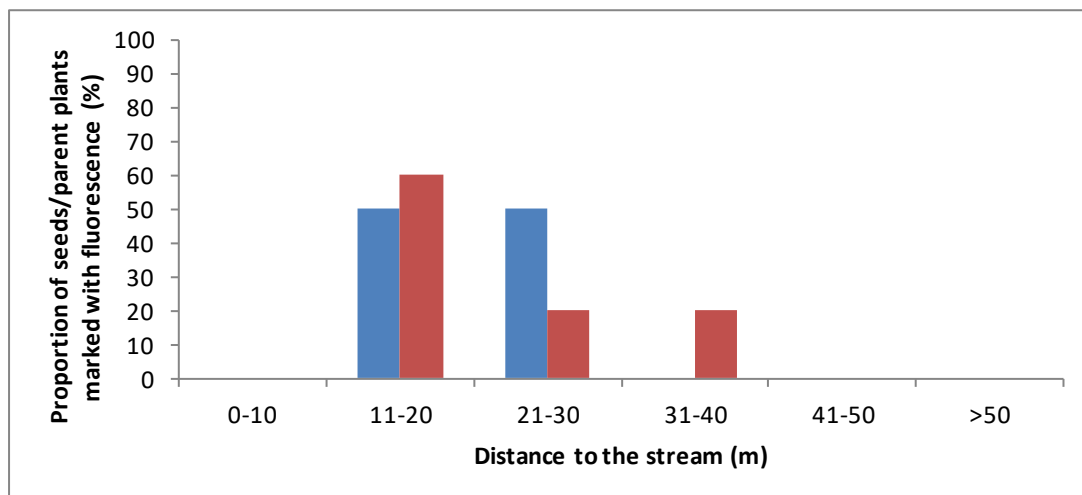
e) *Rubus ulmifolius* (22/7)
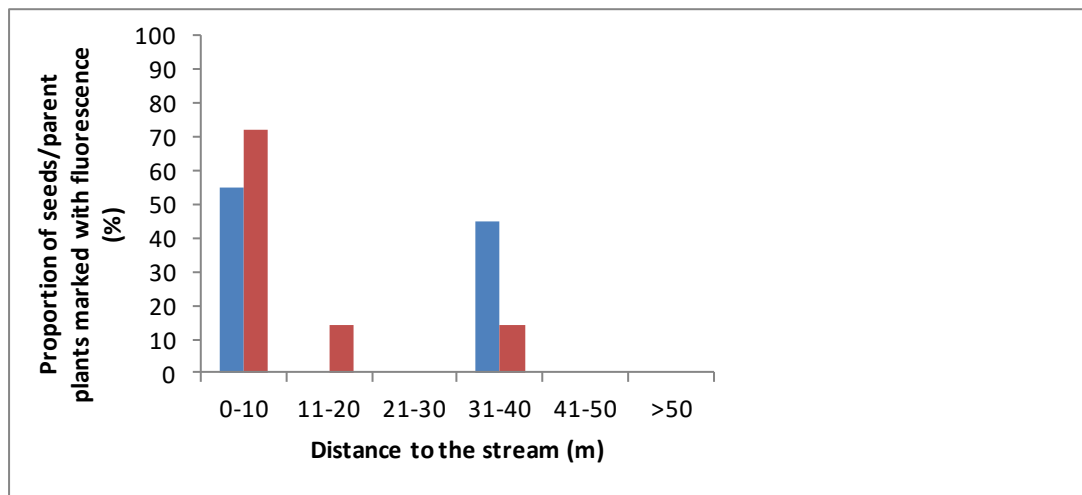


f) *Arbutus unedo* (0/4)
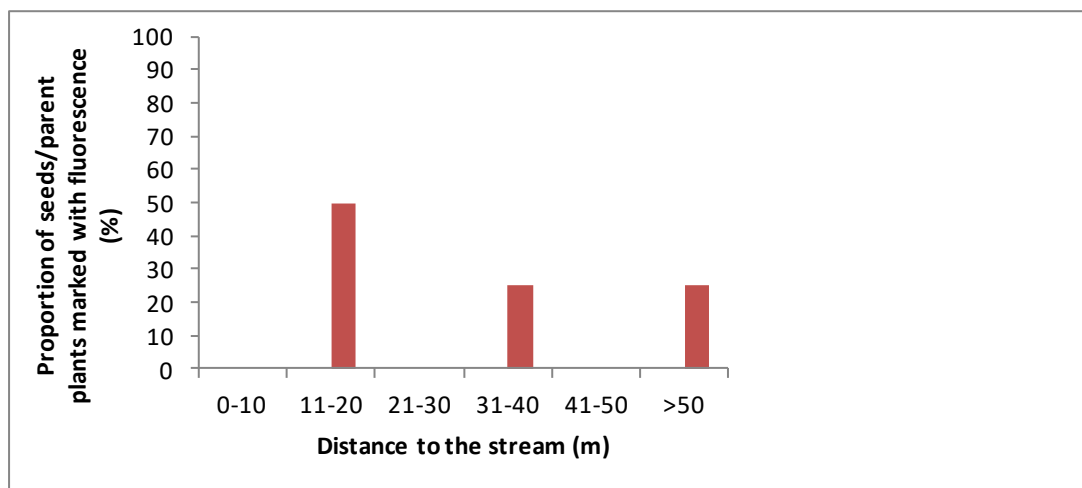


**Figure 16** – Comparison between the proportion of plants marked (in red) and seeds collected with fluorescence (in blue), in each class of distance from the stream. The numbers within parentheses seeds dispersed/plants marked, refer to the total number of seeds.

Using data of seeds collected with fluorescence in seeds traps, we compared the proportion of fruits marked with fluorescence that were consumed by birds. For this purpose, data was converted into seeds marked and seeds consumed by birds (Fig. 17). The most consumed species marked with fluorescence was *S. aspera*, followed by *R. ulmifolius*. However, the species with higher number of fruits marked was *P. lentiscus*. We did not collect any seeds of *O. europaea var. sylvestris,* or *A. unedo* with fluorescence.
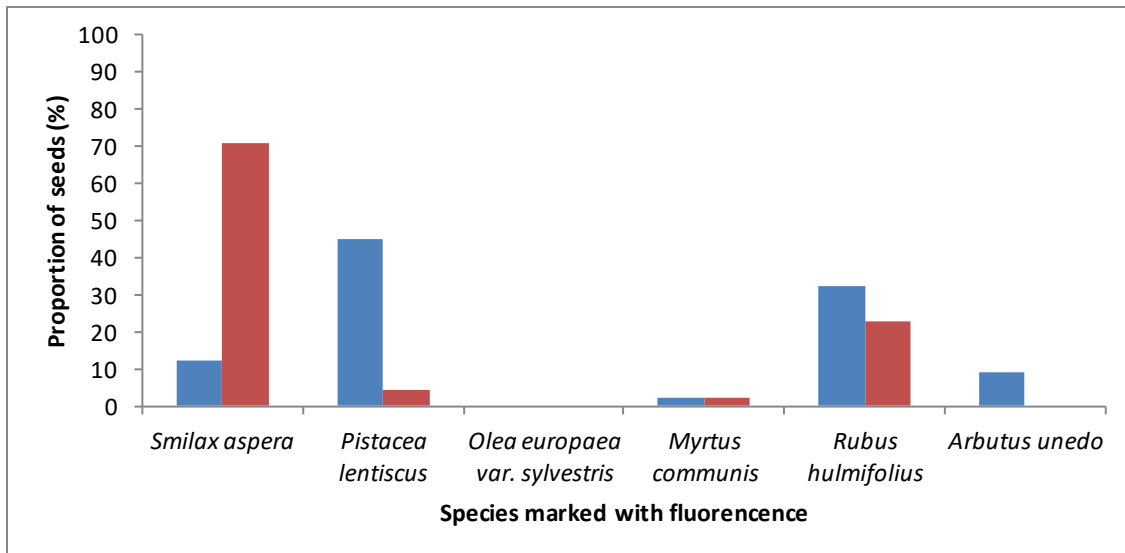
**Figure 17** – Comparison of the proportion of seeds marked with fluorescence (in blue; n=53355) and from those the ones consumed by birds (in red; n=95) (collected in seed traps). The numbers between parentheses refer to total number of seeds.

**Seeds collected in transect**

Data collected in transects (in which fluorescence was not detected) were examined using the same method used for the seed traps, comparing abundance and seed dispersal. For transect 1, we had under consideration distance to stream, and there was a higher abundance and seed dispersal in the riparian gallery close to the stream (Fig. 18). These results reinforce those obtained for the seed traps, where we obtained a higher abundance of fleshy fruit producing species closer to the stream, and this abundance decreased as the distance to the stream increased. However, unlike the seed traps, we detected seeds further away from the stream (at > 80 m), namely *Smilax aspera*, *Olea europaea var. sylvestris* and *Rubus ulmifolius*, although always in percentages below 25%.

a) *Smilax aspera* (7528/234)
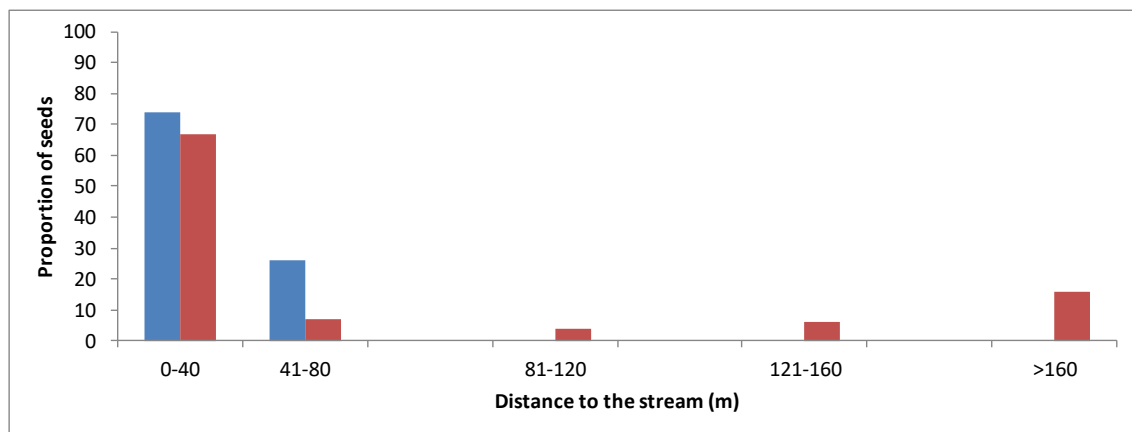


b) *Pistacia lentiscus* (43858/1)
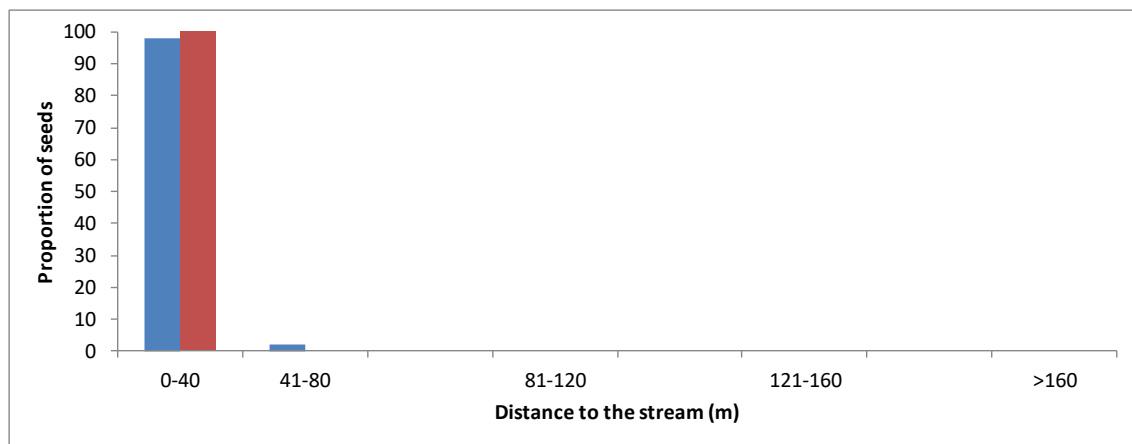


c) *Olea europaea var. sylvestris* (627/134)
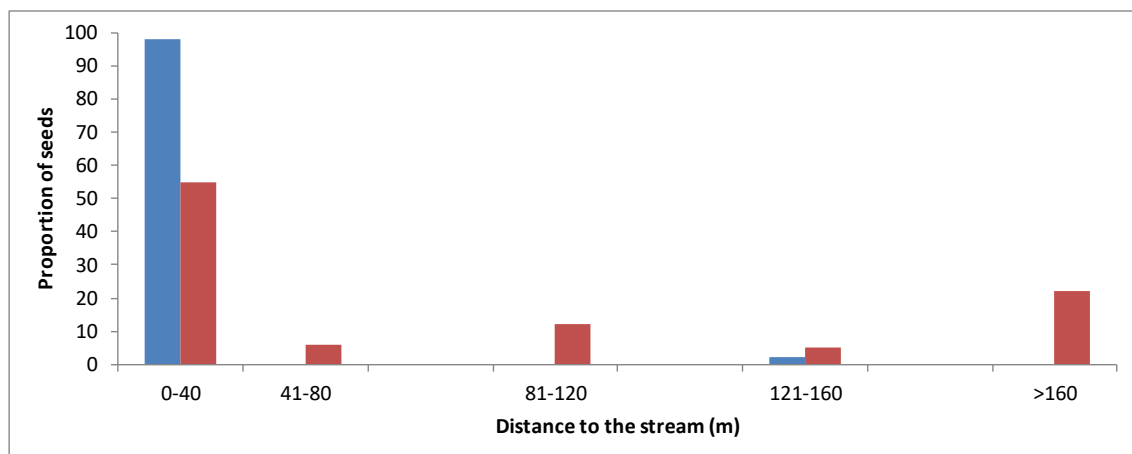
d) *Myrtus communis* (3915/9)
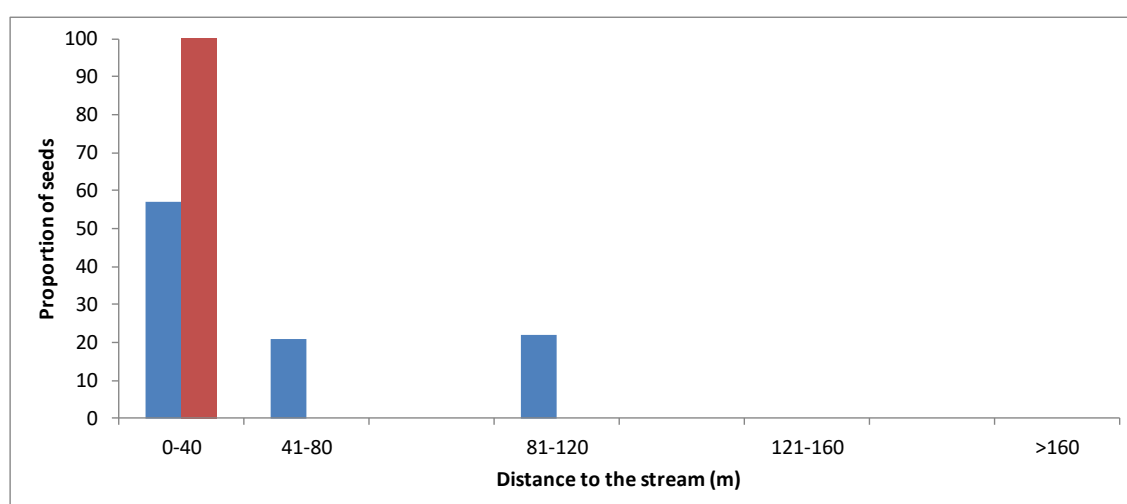


e) *Rubus ulmifolius* (14948/19)
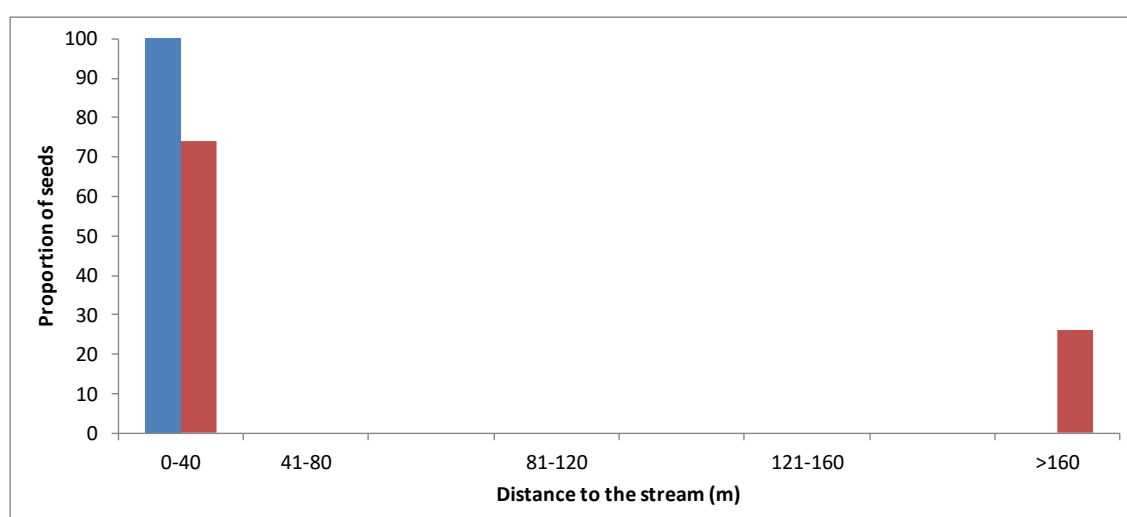


**Figure 18** – Comparison between the proportion of seeds available (in blue) and dispersed (in red) in transect 1 (detected in bird droppings), for each study species, in relation to the distance to the stream. The numbers within parentheses seed abundance/seeds dispersed, refer to the total number of seeds.

For transect 2 and 3, we only compared seed abundance and dispersal of each species, to assess which species was more dispersed by birds, since these two transects were parallel to the stream. The most abundant species was *P. lentiscus*, however the species with higher proportion of dispersed seeds was *S. aspera*, followed by *O. europaea var. sylvestris* (Figure 19). These two species were significantly more consumed than their abundance would predict, both for transect 2 ($X^2_5$ = 19661.4, P < 0.001) and transect 3 ($X^2_5$ = 5150.5, P < 0.001;

Figure 20). The fruits of *M. communis* and *R. ulmifolius* were consumed in accordance to their abundance. On both transects, we did not collected any seeds of *A. unedo*.

(a) (84076/1011)                                    (b) (84076/398)
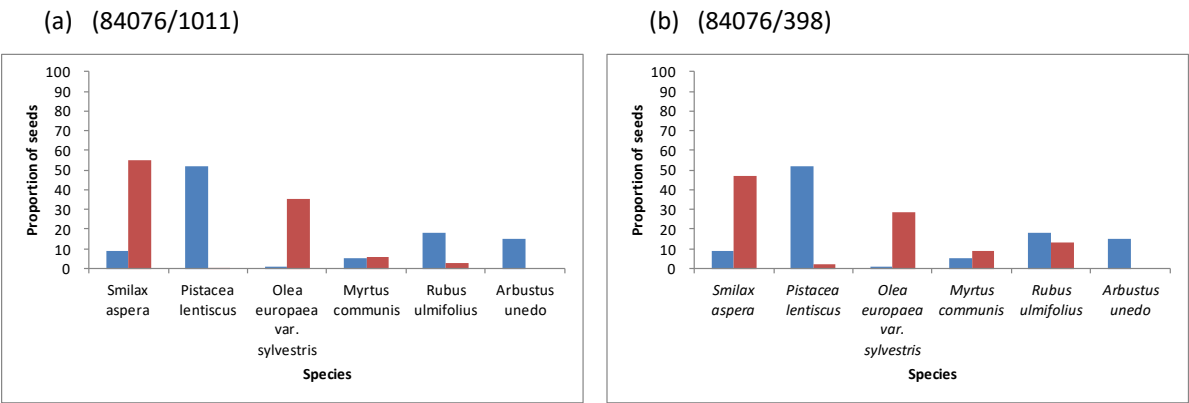


**Figure 19** – Comparison between seed abundance (in blue) and dispersal (in red), collected in transects 2 (a) and 3 (b). The numbers within parentheses seed abundance/seeds dispersed, refer to the total number of seeds.

In the previous results *S. aspera* and *O. europaea var. sylvestris* were the most present (Fig. 20) and we did not collect any seeds of *M. communis* and *A. unedo*. These results are concordant with the data referring to seeds with fluorescence collected on the three transects.

(a)
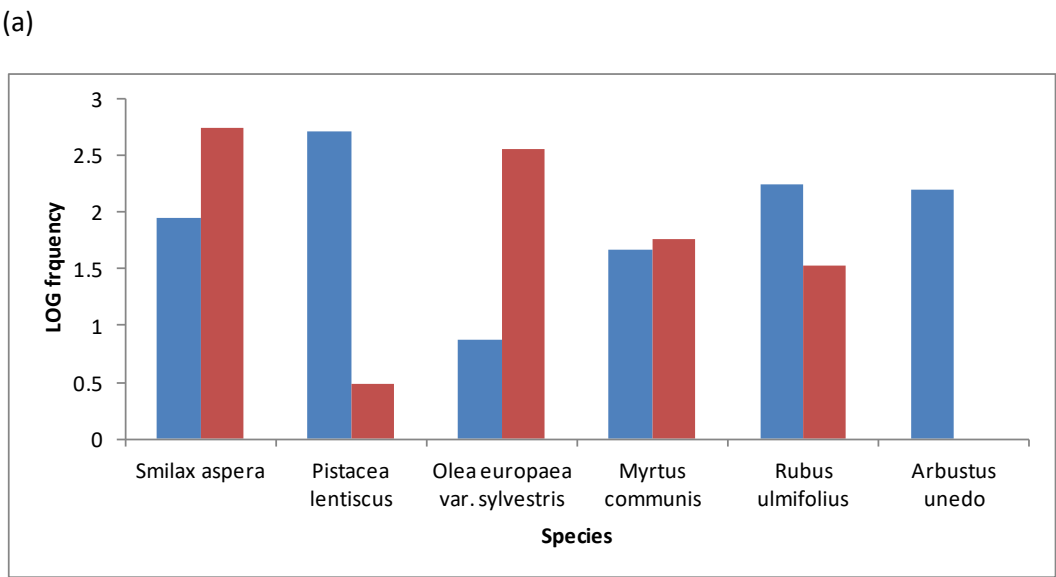
(b)
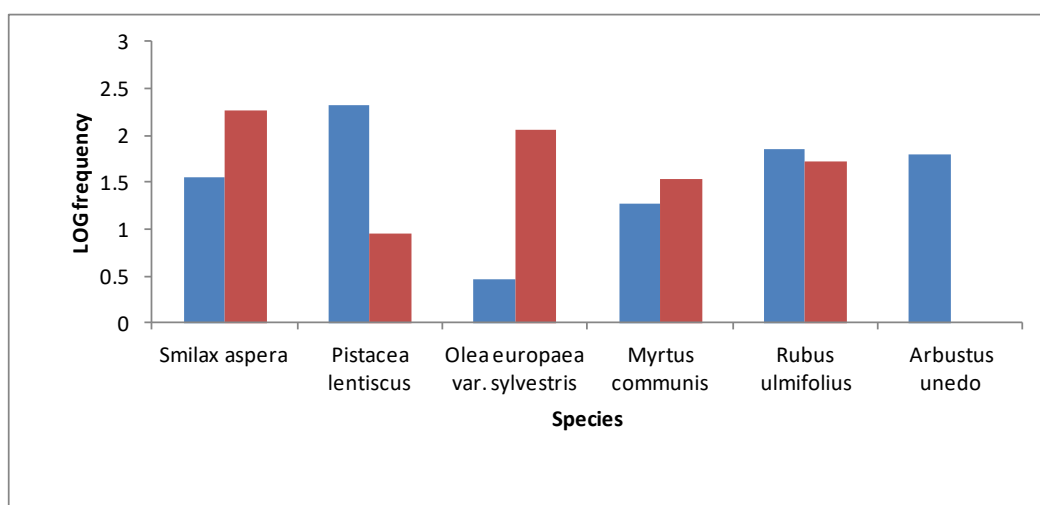


**Figure 20** – Comparison between the LOG observed (in red) and expected (in blue) values in a Chi-square test, comparing the abundance and consumption of seeds in transects 2 (a) and 3 (b), parallel to the stream.

Our results show that species with smaller seeds, as in the case of *R. ulmifolius*, were dispersed to larger distances from the parent plant (Fig. 21). This relation was notoriously inverse (rs= -0.8, P= 0.20), but it is not possible to take any firm conclusions because only for four species of plants were detected with fluorescence.
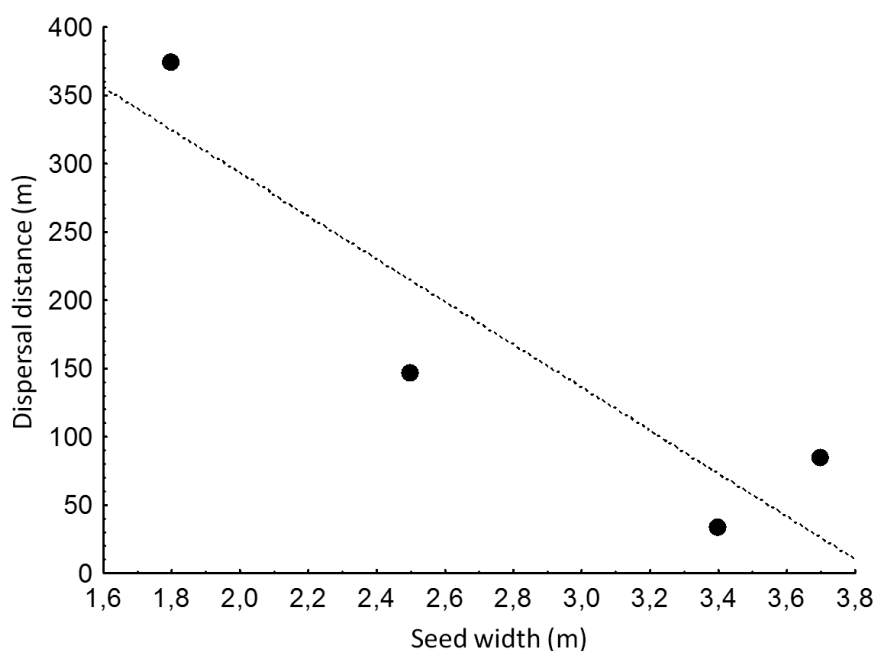


**Figure 21** – Relation between dispersal distance and seeds average width of for all studied species, except for Arbutus unedo with no collected seeds.

# Discussion

**Assessing seed dispersal in the riparian gallery and surrounding matrix using seed traps and transects**

Seed dispersal decreased sharply as the distance to riparian gallery increased, similar to findings of previous studies (Ferreira & Aguiar, 2006; Lavorel, 1999; Naiman et al. 1993), and this can be largely explained by the higher abundance of fleshy fruit plants closer to the stream. The results obtained for seed traps and transects show that *Smilax aspera* was the species with a higher number of seeds dispersed, always in distances between 0 and 40m from the stream, which in a first instance could be explained by the fact that this species had the highest number of parent plants marked with fluorescence. However, within the data set of seeds collected without fluorescence *S. aspera* was also the most abundant species. These results may be related with the fruit´s pericarp quantity and quality that has some kind of relation with the benefit obtained by birds when consuming the fruit (Herrera 1981a). Therefore, some species have specific dispersal agents to which the fruit is very nourishing, thus providing a high reward for the disperser (Howe & Estabrook, 1977). In other studies Herrera (1981b, 1984b) found that both resident and migratory birds concentrate their diet in *Pistacia lentiscus* comparatively to species like *S. aspera*, *Olea europaea var. sylvestris*, *Myrtus communis*, *Rubus ulmifolius* and *Arbutus unedo. R. ulmifolius* was the second most detected species with fluorescence, which might be explained by the fact that *R. ulmifolius* is the second species with higher number of seeds per fruit (37 seeds per fruit), which will increases the probability of collecting a larger number of seeds with fluorescence. As shown by Costa *et al.* (2014), most passerine species feed on *R. ulmifolius*, including granivorous and insectivorous species that are more common in the surrounding woodland matrix, which should increase the dispersal probability of *R. ulmifolius* (Costa *et al.* 2014). Insectivorous birds feed on fruits as a nutritional supplement (Fuentes 1994), while granivorous species can disperse small seeds which are not destroyed during ingestion and digestion (Heleno *et al.* 2011). Overall, birds are more prone to disperse seeds from berries than from fruits with less number of seeds, because berries produce many seeds, which increases probability of some seeds being defecated intact (Crawley 2000). The fact that insectivorous and granivorous birds also consume fruits of *R. ulmifolius* should contribute to explain why this species was dispersed

at larger distances from the stream. Our study shows that small sized seeds were dispersed further away from parent plants. This can be explained by the fact that seeds of smaller dimensions remain longer in bird's intestinal tract, as demonstrated by Traveset *et al.* (2001a). Studies by Stanley & Lill (2002), Stiles & White (1986) and Levey (1987) showed that seeds of larger dimensions remain in the intestinal tract of birds for a shorter period of time. Even if birds regurgitate seeds or smash fruits to discard seeds before swallowing them, they probably prefer fruits with larger seeds, because these are easier to regurgitate and digest (Levey 1987, Stanley & Lill 2002, Stiles & White 1986). In the results referring to transect 1 (perpendicular to the stream), it is noteworthy that there were a higher rate of dispersion in range distances farther from the stream, particularly for the species *S. aspera*, *O. europaea var. sylvestris e R. ulmifolius*. This can be explained by the fact that transect 1 initiated near the stream and extended to the surrounding woodland matrix, which allowed the collection of a larger amount of seeds, dispersed by several types of birds, either inhabiting in the riparian gallery, the woodland matrix or the interface between them. As we show in chapter 1, there is an increase of bird abundance in riparian galleries, due to great habitat heterogeneity, which promotes more interactions between seeds and their dispersers.

*S. aspera* and *O. europaea var. sylvestris* were more consumed by birds on transects 2 and 3 and, on seed traps bird's preference was *S. aspera* and *R. ulmifolius*, and no seeds of *O. europaea var. sylvestris* were collected. These results can imply, on one hand, that the area covered by the seed traps was larger than the area covered by transects 2 and 3 (covering together a 200m extension parallel to the riparian gallery, while seed traps were spread all over the study area). Therefore, the results of transects can demonstrate more precisely which plant species birds fed on most frequently. On the other hand, along transects 2 and 3 there was a higher abundance of *S. aspera* and *O. europaea var. sylvestris*, which might have influenced the amount of seeds collected. This suggests that *O. europaea var. sylvestris*, will also be dispersed very close to the parent plant, which reinforces the fact that smaller seeds like *R. ulmifolius* are dispersed over greater distances from the parent plant (Levey 1987, Stanley & Lill 2002, Stiles & White 1986). In studies by Rey & Gutierrez (1996) and Spennemann & Allen (1998), it was shown that birds' oral cavity size is the limiting factor for the dispersal of *Olea* spp. because, birds with a smaller oral cavity just peck the fruits' pericarp, expelling the seed under the tree, while birds with a larger oral cavity swallow the whole fruit, including the seed (Rey & Gutierrez 1996, Spennemann & Allen 1998).

In seed traps and all transects, we did not collected any seeds of *A. unedo*. Probably due to seed (with an average size of 1,5mm) and fruit dimensions, which should rarely be consumed entirety, often being only pecked, which reduces the probability of seed ingestion. Hammami *et al.* (2005) and Herrera (1995), verified that for *A. unedo* fructification it is necessary an adequate amount of precipitation, for the fruits to mature successfully. Consequently, water stress is an impediment for fruits to mature during late summer/early autumn summer, resulting on a late fructification, when the abundance of birds decreases (see chapter 1).

**Influence of distance to stream and distance to parent plant in seed dispersal**

This study suggests that seed dispersal is particularly influenced by local seed abundance, since we always marked more parent plants and collected more seeds in the areas closer to the stream than in areas farther away (more than 40m). Therefore, the resulting plant community depends on the abundance of parent plants by the riparian gallery, since the majority of birds generally consume the fruits and disperse the seeds of the species that are most abundant. Carlo & Morales (2008) found that the rate of fruit removal by birds increased in the areas with higher abundance of parent plants and that seed dispersal distance decreased away from parent plants. They also showed that more isolated parent plants, presented larger distances of seed dispersal than parent plants closer to each other (Carlo & Morales, 2008), thus occurring a positive feedback between seed dispersal in sites with higher fruit abundance (Aukema & Martínez del Río, 2002). A similar explanation can be invoked to explain our results for much higher seed dispersal closer to the stream.

Seed dispersal leads to a spatial pattern of plant colonization, determining structure and dynamics of plant communities (Tilman & Kareiva, 1997). These communities, present in riparian galleries, show a higher degree of environmental disturbances, influencing terrestrial and aquatic ecosystem ecology and promoting a higher structural and compositional diversity closer to the stream, rather than in the surrounding areas (Gregory *et al.* 1991). In fact, the results obtained from seed traps where fluorescence was detected, seeds of *Rubus ulmifolius* were dispersed to large distances, but parallel to the stream, so seed dispersal occurs along the riparian gallery, in the same type of habitat than the parent plant, as concluded in the paper by Carlo *et al.* (2013). Many studies stated that seed size is a key factor, influencing the dynamics of interactions between species and the mechanisms

of coexistence in plant communities (Rees & Westoby 1997, Rees *et al.* 2001, Coomes & Grubb 2003, Muller-Landau 2003). Therefore, seed size, might affect significantly seed dispersal and germination, seedlings development, plant survival and morphology (Coomes & Grubb, 2003; Rees *et al.* 2001), factors strongly related with plant abundance in many communities (Guo 2003, Muller-Landau 2003, Murray & Leishman 2003, Fenner & Thompson 2005). Seeds of larger dimensions have a higher probability of success in germination than smaller seeds, because larger seeds originate more robust seedlings, with the capacity of endure environmental risks, like water and sunlight stress (Wu *et al.* 2015). According to previous studies, although larger seeds have more competitive capacity (Azcárate *et al.* 2002; Turnbull *et al.* 1999), their development reduces the number of seeds produced in the fruit , while species with smaller dimensions such as *R. ulmifolius* possess a higher rate of seed dispersal and colonization capacity (Azcárate *et al.* 2002, Jakobsson & Eriksson 2000).

**Management considerations**

The seed dispersion enables ecological restoration by reestablishing the patterns and ecological processes that were destroyed by human activity (Crawley 2000, Howe & Miriti 2004, Parejo *et al.* 2014). The long-term intensive agriculture and grazing interferes not only in communities of plant species, but it also destroys the seed bank that allows the occurrence of local reforestation (Howe & Miriti, 2004). The effective ecological restoration creates habitat corridors surrounding the remaining vegetation, allowing their connectivity, and increasing the movements of pollinators and dispersers, from which plants depend on for their lifecycle (Tewksbury *et al.* 2002).

The mechanism of seed dispersal has extreme ecological importance, influencing plant germination rhythm and pattern, their adaptation to the habitat and coexistence of species of fauna and flora (Hurtt & Pacala 1995, Willson & Traveset 2000, Levine & Murrell 2003). Like in the study developed by Carlo *et al.* (2013), our study showed that patterns of seed dispersal by birds are much more orientated for distances closer to the riparian gallery, and they diminish as we enter the woodland matrix. We showed also that seeds could be dispersed to a distance of hundreds of meters from the parent plant, but the majority of the seeds were dispersed in the same type of habitat of the parent plant, which also was observed by Carlo *et al.* (2013). Therefore, our data, together with previous studies,

suggests that riparian gallery plays a limited role in surrounding matrix colonization, since most of the seeds are dispersed only close to the riparian gallery.

Seed dispersal in longer distances is the key to understand and predict the ability of plants to colonize fragmentized and degraded habitats and, for these to acquire the resilience to face the quick global climate changes, allowing better assessment and management of the ecological connectivity between landscapes (Carlo *et al.* 2013). This mechanism has also an important role in restoration and conservation of landscape fragments, because many birds depend on them for food and shelter (Moran & Catterall, 2014). The ability of plants to disperse their seeds to larger distances, in addition to justify its current geographic distribution, is an important factor that will affect the future distribution of many species in climate change scenarios (Hampe, 2011). This study suggests that *Rubus ulmifolius* is the species with higher capacity to colonize woodland matrix areas, from the riparian gallery. Equally, since seed abundance in riparian gallery is one of the key factors that determine the dispersal of the different species of seeds, it may be appropriate to manipulate species plant abundance in order to favor the dispersion of a given species of conservation concern.

# Chapter IV

Ecosystem services – Blackcap dispersing Blackberries and Wild olives in the riparian gallery and the woodland matrix replacement cost

# Abstract

Most economic valuation studies of species derive from stated preferences methods. Production function (PF) and replacement cost (RC) approaches to valuation of ecosystem services are used in situations where species perform key life support functions in ecosystems, such as seed dispersal, pollination, or pest regulation services. Fruit consumption among temperate birds has been repeatedly documented, particularly for blackcaps that rely heavily on fruits during autumn and winter in Mediterranean habitats. We conducted an RC analysis of the seed dispersal service performed by the Blackcap (*Sylvia atricapilla*) dispersing blackberries (*Rubus ulmifolius*) and wild olives (*Olea europaea* var. *sylvestris*) in the riparian gallery and in the immediate adjacent areas of southern Portugal. The primary objective was to estimate the number of seed-dispersed blackberries and wild olive that resulted from blackcaps and to determine the costs of replacing this service though human means. Depending on the replacement method, spreading seeds or planting saplings, the RC was calculated based on two different budgets and varied between 46.83€ and 2342.03€ for blackberry, and 10.55€ and 1982.46€ for wild olive. Planting saplings involved a much higher replacement cost that spreading seeds, a more expedite method, and the most similar to seed dispersal performed by birds. Assuming that seeds dispersed by blackcap will germinate, until the density of blackberry and wild olive trees in the study area is reached, the whole process may take several years depending on many environmental factors; however blackcaps perform this process freely. The complexity of factors that affect germination and sapling survival probably resulted in an underestimation of the environmental service provided by blackcap in this study. We addressed the limitations of our study, but we also highlight that replacement cost studies can became an important tool to achieve better management measures and biodiversity policies.

# Keywords

# Introduction

Fruit consumption among temperate birds has been repeatedly documented (e.g., McAtee, 1947, Turček 1961) and particularly blackcaps' tendency to frugivory has been known for some time (e.g. Turček 1961, Tutman, 1969). However according to Jordano & Herrera (1981) study *Olea europaea* is one of the species whose fruits are ingested with higher frequency by blackcap in the southern mediterranean region. Furthermore, the same authors demonstrated with their results that blackcaps wintering in Mediterranean habitats rely heavily on fruits, at least for a six-month period, including insects on their diet only as a minor element, as Berthold (1976) had already demonstrated that blackcaps, native to central Europe, prefer fruits to insects in autumn and winter.

Jordano & Herrera 1981 pointed out a striking constancy in birds condition must be related to the high nutritive value of Mediterranean fruits. Blackcaps are therefore feeding on highly nutritious fruits, that according to Tutman (1969) have high fat and protein values, like *Pistacia lentiscus* and *Olea europaea* var. *sylvestris*, in southern Spain and this may account for their extensive and sustained frugivory (Jordano & Herrera 1981). Plant seeds appeared regularly in Blackcap faeces – a total of 3360 were found in an apparently intact condition. This suggests a significant role for Blackcaps in the dispersal of Mediterranean fruit-producing plants (Jordano & Herrera 1981). According to Jordano (1982) between august 19th and November 4th about 32,4% of 2646 blackberry seeds were found in blackcaps fecal sample. In the study Jordano (1984), approximately 80% of blackberry seeds were removed by only four passerine species: blackcap, garden warbler *Sylvia borin,* European robin *Erithacus rubecula* and blackbird *Turdus merula,* but blackberry fruits are consumed by at least 16 other bird species. The results reported in this paper indicate that migrant birds remove a very high fraction of the seed crop produced by a rubus population, the fruit pulp representing the major food of these birds (Jordano 1982).

Evidence is accumulating which shows that frugivorous animals that are seed dispersers do not eat fruits at random with respect to fruit and seed detailed traits (Janzen 1981, Herrera 1981a, Howe & Smallwood 1982, Moermond & Denslow 1983) and therefore the potential exists for the different fruit and seed types and sizes produced by a given plant individual or population being dispersed by rather different species of disperser (Janzen 1982).

The production of very nutritive fruits during the birds wintering period represents the other side of a lightly coevolved seed dispersal system (McKey, 1975).

Biodiversity plays a key role in the structure and dynamics of ecosystems and so it is essential for maintaining basic ecosystem processes and supporting ecosystem functions (Cardinale *et al.* 2012, Naeem *et al.* 2012). Ecosystem services can be defined as ecosystem functions that are important for human activities and human well-being (Barbier *et al.* 1994) receiving direct and indirect benefits (MA, 2003), or as conditions and processes through which natural ecosystems, and the species that they contain, support human life (Daily, 1997). The benefits provided by natural ecosystems are both now widely recognized but still poorly understood (Pagiola *et al.* 2004). Economic valuation of ecosystem services can provide a useful tool to policymakers, in   raising awareness regarding the substantial benefits that ecosystems provide, targeting resources to provide most efficient protection of ecosystems and their services and contributing for the rational decision-making process (Glenk *et al.* 2013, Bateman *et al.* 2014, Laurans & Mermet 2014). Nevertheless, ecosystem services are often criticized for excluding the idea of biodiversity as an inherent value, beyond human needs (Schröter *et al.* 2014, Reyers *et al.* 2012, Deliège & Neuteleers 2014).

Focusing our attention in ecosystem services benefits often implies economic valuation. Economic valuation has a role to play, but it must be considered alongside other types of value, like socio-cultural, health and nature conservation values, reflecting also its intrinsic value of moral concretion and happiness (ICNF, 2015). Riparian ecosystems support important ecological functions within landscapes (Brinson *et al.* 1981), and are generally more productive than adjacent ecosystems because of their unique ecological conditions (Mitsch & Gosselink, 1993). Riparian galleries provide many ecosystem services: water and habitats for plants and animals that may be hunter and/or fished by humans, local and regional water flow regime stability (Friedman & Lee, 2002), maintenance of the atmospheric composition, climate amelioration, drinking water supply, waste assimilation, nutrient recycling, soil regeneration, crop pollination, food provisioning, maintenance of species and genetic diversity, the maintenance of the scenery of a landscape, recreational sites, and aesthetic and amenity values (Costanza & Folke, 1996). Nonetheless, placing a monetary value on the ecosystem services provided by riparian galleries is mainly a political and social process that largely depends upon the subjective value attributed to them by society. Many of these services only become apparent years or even decades later, which, at

first sight, appears to reduce the value of the presence of riverine vegetation (Brismar, 2002). Because the benefits derived from riparian systems are provided by nature without cost, it is difficult to compare the real economic value of ecological services provided by riparian systems with activities, such as agriculture and grazing with well-defined market values for the ecosystem goods that they provide. In addition, these more easily quantified activities receive subsidies that increase their value and encourage their development (Burns, 1984).

In temperate and Mediterranean European areas fleshy-fruited plants commonly produce mature fruit crops in late summer and autumn, and some species also in winter, when flocks of wintering migrant birds are abundant in those areas (Thompson & Willson 1979, Willson & Thompson 1982, Herrera 1984a, Herrera 1995, Skeate 1987, Snow & Snow 1988, Willson & Traveset 2000), and crops produced are large enough to satiate avian frugivore (Hampe *et al.* 2008). Riparian areas have relatively high biodiversity, maintain critical habitat for rare and threatened species, are refuge and source areas for prey and predators and provide corridors for migration (Naiman *et al.* 1988, Risser 1993). The composition of bird communities are determined not only by the regional pool of species, but also by landscape and patch features like the matrix type, patch width, size and shape, habitat configuration, floristic and physiognomic vegetation structure (e.g. Davis 2004; Gil-Tena *et al.* 2007). Hougner et al (2006) studied the roles of individual species in providing ecosystem services by addressing functions and processes in the ecosystems provided by those individuals and species. People value species' existence from an aesthetic and ethical perspective, but it is important that wild populations are also valued by their functional roles. With a deeper knowledge of those roles, there will be more opportunities to analyze the economic significance of populations and to value the ecosystem functions (strongly linked with ecosystems services) that they provide, such as the case of seed dispersal by frugivores (Hougner *et al.* 2006), pollination by insects or insect pest control by invertebrate and vertebrate predators (Östman *et al.* 2003). Seed dispersal is an ecosystem function that leads to several ecosystem services; for the sake of brevity in this chapter we refer to it as an ecosystem service.

Another way to illustrate the economic significance of the services is to measure the cost of replacing them by man-made substitutes; for example, replacing pollination services performed by native bees by human artificial means (Hougner *et al.* 2006).

The valuation methods follow either of two strategies: (1) to reveal people's trade-offs with respect to ecosystem services from their behaviour on markets for related goods (revealed preferences (RP) methods), and (2) to ask people directly about what trade-offs they are willing to make through survey instruments such as face-to-face interviews and mail questionnaires (stated preferences (SP) methods, such as contingent valuation) (Freeman III, 2003). The RP methods includes the Production Function (PF) approach because economic values are measured from changes in producer and consumer surpluses at the market for the product for which the ecosystem service serves as an input, giving focus to the species functional roles in terms of species' provision of ecosystem services. SP methods, on the contrary, take functional roles into account only if people are aware of them. An alternative way to value species functional roles is to follow the replacement cost (RC) method. This method focuses on the costs of programs providing man-made substitutes for ecosystem services. Because society would not have to pay such costs if the ecosystem service is available, the idea is that such cost savings indicate the economic value of the service. However, three conditions have to be assured so that the method results in valid estimates of economic values (Shabman & Batie 1978, Bockstael *et al.* 2000, Freeman III 2003): 1) The man-made substitute provides functions that are equivalent in quality and magnitude to the ecosystem service; 2) The man-made substitute is the least cost alternative way of replacing the ecosystem service; 3) Individuals in aggregate would be willing to incur the replacement costs if the ecosystem service was no longer available.

A common way to put an economic value on species is to use the stated preferences (SP) approach that explores people's preferences for the existence of species (Nunes *et al.* 2003). Hougner *et al.* (2006) estimated the number of seed-dispersed oak trees that resulted from jays and determined the costs of replacing this service in an artificial way, using PF and RC approaches, which can be particularly invoked in cases of known functional ecological relationships. Applying production function and replacement cost approaches to estimate the economic value of ecosystem services provided by individual species requires a detailed ecological knowledge of the species (Hougner *et al.* 2006). Most economic valuation studies of species derive from stated preferences methods. These methods fail to take into account biodiversity values that the general public does not know about. Hence, production function (PF) and replacement cost (RC) approaches to valuation may be preferable in situations where species perform key life support services in ecosystems, such as seed dispersal, pollination, or pest regulation (Hougner *et al.* 2006). The RC method has

been used repeatedly for valuing ecosystem services, mostly those provided by biological communities, such as wetlands, rather than those provided by individual species species (Sundberg, 2004).

We used data of Blackcap's (*Sylvia atricapilla*) diet on blackberries (*Rubus ulmifolius*) and wild olives (*Olea europaea* var. *sylvestris*) and replacement costs by human means, in relation to the seed dispersal service provided by this bird species in the riparian gallery plus the immediate adjacent area to answer the following questions: 1) What is the economic value of blackberry seed dispersal that will recruit into saplings in the riparian gallery and in the surrounding matrix as an ecological service provided by Blackcap in autumn? 2) What is the economic value of wild olive seed dispersal that will recruit into saplings in the riparian gallery and in the surrounding matrix as an ecological service provided by Blackcap in autumn?

# Methods

**Study area**

We conducted an RC analysis of the seed dispersal service performed by the Blackcap in dispersing seeds of *Rubus ulmifolius* in the autumn in Herdade da Mitra and Degebe and *Olea europaea* var. *Sylvestris* in the winter in Degebe. The study area is in an Évora University pole, 12 km from Évora (Mitra-Nature, 2014) and Degebe River affluent (Canaviais, Évora). Herdade da Mitra has a total area of 286ha limited at north and west by Valverde and Peramanca streams, at east by the Herdade de Alfabobeira and south by the Herdade do Barrocal (Mitra-Nature, 2014). In particular, the study area was in the riparian gallery of Valverde stream (approximately 4ha), extending to the surrounding woodland matrix (approximately 6ha).

**Economic valuation of Blackcaps' seed dispersal Services**

The primary objective was to estimate the number of seed-dispersed *Rubus ulmifolius* and *Olea europaea* var. *sylvestris* by Blackcaps that will recruit into saplings of these two species, in the riparian gallery and the immediate adjacent area, and determine the costs of replacing this service through human means. In this study we followed the replacement cost (RC) method to value species' functional roles . Our ecological–economic analysis resulting in RC estimates consists of the following steps, presented in the next five subsections: a) Quantifying the number of seeds dispersed by Blackcaps; b) Quantifying the number of Blackcaps; c) Quantifying the area of dispersion of seeds dispersed by Blackcaps; d) Identifying human techniques for wild olive and blackberry regeneration; e) Estimating costs of spreading seeds for both species; f) Estimating costs of planting wild olive and blackberry saplings; g) Concluding about the replacement cost.

a)  Quantifying the number of seeds dispersed by Blackcap

We quantified the percentage of blackberry and wild olive seeds that were ingested by Blackcap among all passerine diet data of both study areas, Mitra and Degebe (chapter II). Furthermore, we used the number of blackberry and wild olive seeds dispersed, in each one of the study areas, recovered in the seed traps (see chapter III), and since no molecular biology tests were performed to identify the species responsible by each dispersion event, using the percentage of seeds ingested by Blackcap we estimated the percentage of seeds recovered in the seed traps possibly dispersed by Blackcap in the riparian gallery and the immediate adjacent woodland area.

b)  Quantifying the number of Blackcap

The Passerine migratory systems in Europe are associated to seasonal fluctuations outside of the breeding season (Keast & Morton 1980, Moreau 1972). In Lövei, *et al.* (1985) these fluctuations are notorius with higher capture rates in October and November and decreasing during winter and into the breeding period, with minimum values in June-August. The abundances of frugivorous bird populations wintering in the Mediterranean region vary from year to year in certain areas due to variations in resource availability (Finlayson 1981, Santos 1981, Herrera 1984a, Jordano 1984). The results of De Los Santos *et*

*al.* (1986) study suggested that blackcap local distribution and choice of wintering habitat is made according to local abundance of both wild fruits and of olives.

For our purpose we used Blackcap densities for all the study area (birds/10ha), in Mitra and Degebe, using our own data and data from the literature: 1) using three different estimations of the species density (minimum, medium and maximum) calculated from our census data collected for Chapter I; 2) densities of blackcap obtained by Jordano (1985) for a scrubland in Southern Spain in autumn and; 3) density of blackcap obtained by Tellería *et al.* (2013) for a oak forest in Southern Spain. Firstly, we used the maximum density of blackcaps obtained from our census data by the stream of the riparian galleries within 30 Km of Évora city, secondly we used the minimum density of blackcaps from our census data, which was obtained at 125m from the stream, and thirdly we averaged these two measures to obtain a medium density value. In relation to the data from the literature we used an average between Blackcap densities of September, October and November of 1981 (Jordano 1985). Although this study had blackcap density values for 1982 also, we chose to use 1981 for having a more approximated order of magnitude to our data and other data from studies for the same season (Lövei *et al.* 1985). Finally, we used also blackcap density data obtained in January 2008 by Tellería et al (2013).

### c) Quantifying the area of dispersion of seeds dispersed by Blackcap

We admitted that blackcap's dispersion area is circular and using the maximum distance of dispersion of blackberry and wild olive in our study areas, assessed with the seed trap method (see chapter III), measured from the stream to the seed trap. Because we did not assess dispersion in one half of the circular area we only calculated the semi-circle area (A= (Pi x r2)/2) (see Table 1 on the Appendix).

### d) Identifying human techniques for wild olive and blackberry regeneration

As we know, in many cases, man can substitute the role of vegetative dispersion agents. This vegetative propagation can be performed by seeding the seeds or by sapling plantation (Hougner *et al.* 2006). We chose to calculate replacement costs without the use of heavy machinery because manual seeding is likely to be the only feasible alternative in a wooded area such our study areas. Furthermore, the use of machinery would make the process of

seed distribution less natural and random, completely different than the one that birds perform, and according to McClurkin & Duffy (1973) and Xu *et al.* (1999) can cause soil compaction, decrease water infiltration and soil aeration and destroy soil structure.

e) <u>Estimating costs of spreading seeds and planting saplings of both species</u>

We contacted landscape architecture companies to request budgets to allow us to estimate the replacement costs of Blackcap's dispersion service. The budgets include seeds, saplings and labor costs. To cover all the 10ha study area, for Mitra and Degebe, the spread of the seeds would be made along 10 transects of 10m (5m to each side of the transect) x 500m. The spreading of the seeds would be made by only one person during one day for each study area and for each species of seed. For estimation of labor time we admitted that a person travels 5km/h by foot.

To estimate the costs of substituting the dispersal performed by blackcaps all the post-dispersal events, like seed predation (e.g. Janzen, 1971; Heithaus, 1981; Mittelbach & Gross, 1984; Levey & Byrne, 1993; Hulme, 1998) or germination rates, were not taken into account. To estimate the costs of planting the saplings we considered labor costs per area (m$^2$) (see Table 2 on the Appendix). The saplings have 10-30 cm height and their greater advantage is that they are already grown plants (Filipe Soares, Sigmentum, pers. Comm.) and already surpassed almost all the post-dispersal events constraining the effectiveness of plant regeneration (e.g. Rey & Alcántara, 2000).

It is easier to find in the market native species like blackberry or wild olive in the form of saplings than seeds, although in our case study, we can find them in both forms. Nevertheless it is easier to find the species of larger production trees such as olives at higher propagation rates than native varieties, with lower propagation and smaller production rates (Filipe Soares, Sigmentum, pers. Comm.). However, although seeding has relatively lower costs than planting the result of seeding is much more uncertain than that of planting (Filipe Soares, Sigmentum, pers. Comm.). This has to do with the fact that in temperate regions the vast majority of seeds will not germinate due to dormancy caused by different depths of dormancy in the seed bank for prolonged periods or the absence of light as most important requirement to terminate dormancy and induce germination (Thompson *et al.* 2003, Fenner & Thompson 2005).

In this point we assumed that the seeds dispersed by blackcap will germinate.

# Results

The number of blackberry seeds dispersed by blackcap varied between 21 and 857 for Mitra and 55 and 857 for Degebe. The minimum value refers to the minimum number of Blackcaps in the study area and the maximum value was calculated based on the literature. The number of wild olive seeds dispersed by blackcap varied between 5 and 237 for Degebe (the minimum value based on literature and the maximum in our study), and the number of seeds dispersed for Mitra was zero, so 5 seeds is the only number available for replacement cost calculations and based on a previous study (Tellería *et al.* 2013).

After calculating the replacement cost of the environmental service performed by Blackcap, using two replacement methods, spreading the seeds and planting the saplings, it is obvious, as expected, that planting involves a much higher replacement cost (Table 1). The replacement costs using the method of spreading seeds were 66.80€ for Blackberry and 68.92€ for wild olive. As for the replacement cost using sapling planting the first budget varied between 1857.18€ (Mitra) and 2342.03€ (Degebe and Mitra) for Blackberry and 1845€ (Mitra) and 1982.46€ (Degebe) for wild olive, and the second budget varied between 46.83€ (Mitra) and 1911€ (Degebe and Mitra) for Blackberry and 10.55€ and 528.51€ for wild olive in Degebe.

**Table 15** – Seeds, saplings, labor and Replacement costs (RC), of the estimation of blackcap dispersal of blackberry and wild olive seeds for 10ha in each study area (NSD – number of seeds dispersed), by spreading seeds and planting saplings in the study areas. Seed costs (S) presented per 10g for blackberry and per 100g for wild olive (Table 2 in the Appendix) and respective labor costs (L) for seed spreading (per day); Sapling costs (SP) presented are per sapling and respective labor costs for planting saplings (per m²). Two different budgets are presented for saplings costs, in the first one the value presented is per m2 and in the second one the value presented is per sapling planted. All the costs are presented in Euros (€) and include VAT (23% for labor and 6% for seeds and saplings). Source data in different scenarios used to estimate number of blackcaps: [1] estimated using data from Chapter II; [2] data collected from Jordano (1985) and Tellería, et al. (2013); [3,4,5] Chapter I – Minimum, medium and maximum number of blackcaps.

| Study area | Seed species | Seeds costs | | Sapling costs | | Diet[1] | | | Literature[2] | | | Min[3] | | | Med[4] | | | Max[5] | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | RC | | | RC | | | RC | | | RC | | | RC | |
| | | S | L | SP | L | NSD | Seeds | Saplings | NSD | Seeds | Saplings | NSD | Seeds | Saplings | NSD | Seeds | Saplings | NSD | Seeds | Saplings |
| Degebe | Rubus ulmifolius | 5.30 | 61.5 | 0.58 | 0.18 | 55 | 66.80 | 1876.90 | 857 | 66.80 | 2342.03 | 184 | 66.80 | 1951.72 | 451 | 66.80 | 2106.58 | 718 | 66.80 | 2261.44 |
| | | | | 1.01 | 1.22 | | | 122.65 | | | 1911.00 | | | 410.32 | | | 1005.73 | | | 1601.14 |
| | Olea europaea var. sylvestris | 7.42 | 61.5 | 0.58 | 0.18 | 237 | 68.92 | 1982.46 | 5 | 68.92 | 1847.74 | 21 | 68.92 | 1857.18 | 52 | 68.92 | 1875.16 | 83 | 68.92 | 1893.14 |
| | | | | 1.01 | 1.22 | | | 528.51 | | | 10.55 | | | 46.83 | | | 115.96 | | | 185.09 |
| Mitra | Rubus ulmifolius | 5.30 | 61.5 | 0.58 | 0.18 | 44 | 66.80 | 1870.52 | 857 | 66.80 | 2342.03 | 21 | 66.80 | 1857.18 | 52 | 66.80 | 1875.16 | 83 | 66.80 | 1893.14 |
| | | | | 1.01 | 1.22 | | | 98.12 | | | 1911.00 | | | 46.83 | | | 115.96 | | | 185.09 |
| | Olea europaea var. sylvestris | 7.42 | 61.5 | 0.58 | 0.18 | 0 | 0.00 | 1845.00 | 5 | 0.00 | 1847.74 | 0 | 0.00 | 1845.00 | 0 | 0.00 | 1845.00 | 0 | 0.00 | 1845.00 |
| | | | | 1.01 | 1.22 | | | 0.00 | | | 10.55 | | | 0.00 | | | 0.00 | | | 0.00 |

# Discussion

The fact that planting saplings involved a much higher replacement cost that spreading seeds can be explained by the fact that spreading seeds is a much more expedite method, therefore less expendable, and the most similar to seed dispersal performed by birds. One of the constraints of spreading the seeds is the predation that they can suffer by insects, mammals (rodents) and birds (e.g. Janzen 1971, Schupp 1988, Hulme 1994), which is also a constraint when the seeds are dispersed by birds. Hougner *et al.* (2006) and Löf & Madsen (1998) stated that the relatively low costs of seeding acorns do not take into account the fact that the result of seeding is less certain than that of planting. Furthermore, Löf & Madsen (1998) study results indicate that seeding should be avoided at places with many rodents or predatory insects or with many weeds.

The overall predation rate for wild olive by rodents was studied by Alcántara *et al.* (2000) and two values were reported: 35% using an observational approach and 51% using an experimental approach, and varied in relation to microhabitats and seed size, being higher in dense scrub patches than in sparse patches, and lower for large seeds than for medium and small seeds. In the Rey & Alcántara (2000) study, 63.4% of the dispersed olive seeds escaped subsequent predation. Blackberry seeds predation rate has not been studied yet but is is know that it exists and it may be considerable (Traveset *et al.* 2001b).

The obvious differences between the replacement costs of both methods are due to our choice in terms of labor costs, daily labor costs in the case of spreading seeds and by square meter for planting saplings. So that the replacement costs are comparable maybe we should have used the same unit in labor costs, but it is not logic to expend 1500€ to spread 5 seeds (the smaller number of olive seeds dispersed based on literature, see Table 1) in 10ha.

We decided to present the costs of planting saplings, because the effectiveness of spreading the seeds in terms of generating new plants is inferior, and the assumption that all seeds dispersed would germinated is obviously not true. In fact, literature on the subject refers a very small proportion of seeds dispersed that reach the sapling stage, and were classed as plants that have acquired vegetative adult characters, generally about 1 year after germination by Rey & Alcántara (2000). According to these authors the proportion for olive is 0.89%, and Debussche & Isenmann (1994) observed a 0.31% seedling survival for blackberry. These highly small proportions are due to inumerous constraints that these

species face in nature, for example conspecific competion and sunlight and water availabibity.

The almost year-round high degree of frugivory of Blackcap has been described several times (Berthold 1976, Jordano & Herrera 1981, Herrera 1984, Jordano 1995).

Having into account studies like Janzen (1981), Herrera (1981a), Howe & Smallwood (1982), Moermond & Denslow (1983), we can say that seed dispersers do not eat fruits at random. The seed dispersal dynamics is complex and depends on the different species of disperser that disperse different fruits, seed types and sizes produced by a given plant individual or population (Janzen 1982). For example, differences between the main dispersers of Blackberry in flight patterns and first-stop sites after leaving a clone have been described for Southern Spain by Jordano (1982). Hampe (2001) refers that Blackcap preferably moves within the gallery forest and their families have a small home-range, concentrating at fruit-rich sites when ripe fruits become available, which leads to the deposition of many seeds beneath the parent plant. Moore (2001) and Traveset *et al.* (2001b), have shown that the passage of seeds through the digestive tracts of birds is important in determining their future germination behavior and, although it did not affect dormancy length, the speed at which seeds germinated is modified to a large or small extent. For example, Blackberry seeds germination speed is influenced by the species of bird that eats the fruit. This happens because the seed coat suffers mechanical and/or chemical scarification passing through the digestive tract of frugivores. Plants evolved physical and chemical adaptations in fruits and seeds to direct dispersal and to maximize the proportion of seeds that are successfully dispersed and established (Traveset, *et al.* 2007). Seed-mixing and the number of seeds defecated in a dropping can be very relevant to the future establishment success of a plant. Therefore, seed dispersal is a highly complex ecosystem service that is very difficult to reproduce and, consequently calculating replacement costs, having this complexity into account.

Given the fact that many factors will influence the survival of saplings the values presented here are certainly minimum values, because the survival rate of seedlings in the wild is very small (Debussche & Isenmann 1994, Rey & Alcántara 2000). If one would consider labor costs involved in replacing or watering seedlings in the wild to ensure their survival, the labor costs presented here would be much higher. This exercise clearly shows that Blackcaps will do such service for free, although it may take several years, until the density of blackberry and wild olive trees in the study area is reached.  This is a pilot study of the kind,

and many more studies are needed to fully address replacement costs in relation to seed dispersal. However, given the current degradation of ecosystems it will be increasingly difficult for blackcaps or other bird species to deliver important ecosystems services such as seed dispersal, as described in this study.

# General Discussion

## The ecological importance of the riparian galleries

Riparian galleries are ecosystems with high diversity of plants, animals and environmental processes (Nilsson & Svedmark 2002, Salinas & Casas 2007) and serve multiple roles, including water provision, nutrient retention (Jacobs *et al.* 2007), refuge for unique species (Sabo *et al.* 2005) and as movement and dispersal corridors (Machtans *et al.* 1996, Beier & Noss 1998, Burbrink *et al.* 1998). In fact, riparian galleries are constituted by very heterogeneous habitats with great availability of food and shelter resources, for the fauna, provided by the vegetation present in the margins of the water course (Rodewald & Bakermans 2006, Tabacchi *et al.* 1998). Riparian galleries function as key landscapes in the maintenance of biological connections through environmental gradients (Klapproth & Johnson 2009, Merritt *et al.* 2010, Naiman & Décamps, 1997) and regulation systems between aquatic and terrestrial biotopes (Sabo *et al.*, 2005). The riparian ecosystems are rarely included in conservation systematic planning, although their biological value is high and they possess and frequently high and unique biodiversity (Sabo *et al.* 2005), despite the fact that they are increasingly threatened by human activities and invasive species, especially in the Mediterranean region (Nel *et al.*, 2009). Namely its role in seed dispersal and consequent importance in explaining the surrounding vegetation dynamics is poorly studied (Nel *et al*, 2009). This thesis assessed the general importance of riparian galleries for bird communities. Firstly I evaluated in particular the role of food resources and shelter for species that are characteristic of the riparian gallery, and for species of the surrounding matrix. Secondly, I examined the diet of the avian community, assessing the seasonal variation in food resources. Thirdly, I examined the role of birds as seed dispersers in the interface riparian gallery-surround matrix, and evaluated the economical value of a main disperser, the blackcap (*Sylvia atricapilla*).

# The importance of the riparian gallery for bird communities

The importance of the riparian gallery for birds is well known, and our study provided a first step to understand seasonal variations in the patterns of bird species richness and abundance of riparian vs. adjacent matrix passerines. Our data also showed that riparian galleries attract insectivorous and frugivorous birds throughout the year. Our study shows that species richness and bird abundance (total number of individuals) in Mediterranean riparian galleries of southern Portugal were strongly influenced by distance to stream and season. Both, species richness and bird abundance, were significantly higher in the riparian gallery than in the adjacent matrix. Species richness was significantly higher during the summer-autumn migration period, and bird abundance significantly lower during the breeding season. This may be explained by several factors including better shelter conditions (this study) and higher abundance of food resources (Brinson *et al.* 1981, Naiman *et al.* 1988, Risser 1993) in the riparian gallery, particularly in Mediterranean areas where the surrounding matrix is fairly open. The abundance of fruits in autumn and winter, throughout the Mediterranean, is also higher in riparian areas, which is mainly a result of a higher vegetation complexity when compared to a surrounding open forest such as the cork oak- holm oak "montado" of southern Portugal. In summary, our results strengthen the importance of riparian galleries in Mediterranean areas for bird species richness and abundance in the summer-autumn migration and winter periods. Furthermore, we also observed a higher percentage of bird movements in summer from the surrounding matrix towards the riparian gallery, probably as a result of higher fruit abundance in summer-autumn or for thermal shelter reasons. These movements into the riparian gallery were described by previous studies (Woinarsky *et al.* (2000, Gillies *et al.* 2011, Levey *et al.* 2005), but these authors have linked them to shifts in resource availability and shelter from predators. Our afternoon census and temperature data were inconclusive in showing the importance of shelter offered to birds by riparian galleries in summer, but other studies report that riparian microclimates are generally cooler, and with higher relative humidity than the microclimates of adjacent areas (Brosofske *et al.* 1997, Danehy & Kirpes 2000).

## Bird Diet and Seed Dispersal

Our results show clearly that food resources for passerines (arthropods and fruits) are more abundant in riparian galleries than in the adjacent matrix, particularly during the summer-autumn migration period. Our study shows also consistent difference in the diet and feeding ecology between passerines that inhabit the riparian gallery and the adjacent matrix. Such differences appear to arise from seasonal differences in the abundance of arthropods and fruits in these two habitats, which should be important to explain the higher density of birds in the riparian gallery. The stable isotope data shows also that riparian species fed on a consistently higher trophic level in spring, summer and autumn but in winter they fed on lower trophic level food items, i.e. mostly fruits.

Woodland passerines seemed to feed more on *Araneae* than riparian passerines. This higher consumption of *Araneae* was already reported by Ceia *et al.* (2016) for three typical bird species from the montado and Pinkowski (Feeding of nestling and fledgling Eastern Bluebirds, 1978) for Eastern bluebird (*Sialia sialis*) in Michigan (USA) during the breeding season, when spiders are particularly important early in the season and for newly-hatched young. Seed dispersal was particularly influenced by local seed abundance and decreased sharply as the distance to the riparian gallery increased, similar to findings of previous studies (Ferreira & Aguiar 2006, Lavorel 1999, Naiman *et al.* 1993), and this can be largely explained by the higher abundance of fleshy fruit plants closer to the stream. The results obtained for seed traps and transects show that *Smilax aspera* and *R. ulmifolius* (dispersed further from the stream) were the species with a higher number of seeds dispersed and detected with fluorescence. These results may be related with the fruit´s pericarp quantity and quality and consequently the benefit obtained by birds (Herrera, 1981a) and in the case of *R. ulmifolius,* as shown by Costa *et al.* (2014), by its higher consumption. We present evidence showing that small sized seeds were dispersed further away from parent plants. A previous study (Traveset *et al.* 2001a) shows that smaller seeds remain longer in the birds' intestinal tract, which may be important to explain the fact that such seeds are dispersed longer distances. Because seed abundance in the riparian gallery emerged as a key factor determining the dispersal of the different species of seeds, it may be appropriate to manipulate species plant abundance in order to favor the dispersion of a given species of conservation concern.

## Seed dispersal as an Ecosystem Service

The seed dispersion enables ecological restoration by reestablishing the patterns and ecological processes that were destroyed by human activity (Crawley 2000, Howe & Miriti 2004, Parejo *et al.* 2014). Seed dispersal is a highly complex ecosystem service that is very difficult to reproduce and, consequently we calculated replacement costs, because it depends on the different species of disperser that disperse different fruits, seed types and sizes produced by a given plant individual or population (Janzen 1982). Our study shows that planting saplings involved a much higher replacement cost than spreading seeds, which can be explained by the fact that spreading seeds is a much more expedite method, therefore less expendable, and the most similar to seed dispersal performed by birds. One of the constraints of spreading the seeds is the predation that they can suffer by insects, mammals (rodents) (Löf & Madsen, 1998) and birds (e.g. Janzen 1971, Schupp 1988, Hulme 1994), which is also a constraint when the seeds are dispersed by birds. Alcántara *et al.* (2000) studied wild olive seed predation and Traveset *et al.* (2001b) stated that blackberry seed predation may also be considerable.

We decided to present the costs of planting saplings, because the effectiveness of spreading the seeds in terms of generating new plants is inferior, and the assumption that all seeds dispersed would germinated is obviously not true. In fact, literature on the subject refers to a very small proportion of seeds dispersed that reach the sapling stage (Rey & Alcántara 2000, Debussche & Isenmann 1994), due to inumerous constraints that these species face in nature, for example conspecific competion, sunlight and water availabibity. This is a pilot study of the kind, and many more studies are needed to fully address replacement costs in relation to seed dispersal. Present riparian forest habitats have been altered at an alarming rate, therefore it will be increasingly difficult for blackcaps or other bird species to deliver important ecosystems services such as seed dispersal, as described in this study.

## Future research

Taking into consideration the movements registered between the riparian gallery and the surrounding woodland matrix, in order to evaluate the role of shelter for birds in summer, we should choose several riparian galleries and surrounding matrices with different vegetation complexity and register all the bird movements between the riparian gallery and the surrounding matrix in the hottest hours of the day.

There are limitations in the study of seed dispersal mechanisms, for example, it can be difficult to track all seed dispersal destinations (Johansson *et al.*, 1996). For this reason, Zamora & Matías (2014) considered the cumulative result of seed dispersal in vegetation, taking into account species abundance and distribution, in order to discuss the ecological basis of the different mechanisms of plant dispersion, in terms of the availability of dispersal agents, seed size and other ecological constraints (Jordano 1984, Wilson *et al.* 1990). The fluorescent marking that we performed turned out to be efficient in terms of assessing the accurate dispersal distances of each parent plant. Although, this method efficiency depends on the marking effort, so would recommend repeating the method but increasing the number of parent plants marked with fluorescence and the number and area of the study areas. The marked plants would be analyzed in terms of numbers of seeds per fruit and seed dimensions, since seed size is suggested as being an ecological factor of great importance for the evolution of dispersal mechanisms, and to understand the dynamics of seed dispersal processes into the adjacent matrix. Furthermore, it would be useful to understand which species of birds disperse which species of berries in terms of the distance travelled, which is obviously dependent on the extension of the vital area of each bird species. In future studies fecal samples could be identified using molecular methods.

Finally, it would be important to perform more attempts of valuating the ecosystem service of seed dispersal by birds. A more realistic analysis would entail to mark and follow seeds and saplings and follow their survival in the long-term.

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# Appendix

**Table A1 –** Maximum dispersal distances from the seed trap to the stream (Chapter III) and dispersal area for blackberry and wild olive for each study area. [1] In Degebe, no blackberry seeds were collected in the matrix seed traps so, we used an individual located at 239.5m from the stream.

| Study area | Seed species | Max. dispersal distances (m) | Dispersal area (m$^2$) |
|---|---|---|---|
| Degebe | *Rubus ulmifolius* | 0 | 90101.19[1] |
|  | *Olea europaea var. sylvestris* | 244.0 | 93518.85 |
| Mitra | *Rubus ulmifolius* | 40.3 | 2551.11 |
|  | *Olea europaea var. sylvestris* | 116.5 | 21319.22 |

**Table A2 –** Costs of blackberry and wild olive seeds (Sigmentum, 2016). [1] With a 6% VAT included (the legal rate for Portugal); [2] Average weight from Alcántara *et al.* (2000).

| Species | Quantity (g) | Price (€)[1] | seeds/g | Seed weight (g) | Total number of seeds |
|---|---|---|---|---|---|
| *Rubus ulmifolius* | 1000 | 79.50 | ND | 0.170[2] | 500000 |
|  | 10 | 5.30 | ND | 0.170[2] | 5000 |
| *Olea europaea var. sylvestris* | 1000 | 26.50 | 500 | 0.002 | 5882 |
|  | 100 | 7.42 | 500 | 0.002 | 588 |