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Abstract

Biological invasions are amongst the biggest threats to biodiversity, as invasive species can displace or drive to extinction native species due to competition, predation or the spread of diseases. Nevertheless, the ecological effects of new invasions are unpredictable and sometimes found to be neutral. This might happen because natural communities are not always saturated and can accomodate exotic species without harming the native ones. Therefore, assessing the biotic interactions with native species is important in order to prioritize conservation efforts, and because those are valuable natural experiments for research in community ecology.

The aim of this work was to characterize and compare the ecological niche of an invasive passerine in Europe, the common waxbill *Estrilda astrild*, originary from Sub-Saharan Africa, with those of its co-occurring native bird species. I quantified passerine abundances with transect counts at several sites in mainland Portugal and characterized habitats at those sites, in order to test for relations between the abundance of common waxbills and other bird species and for habitat preferences of waxbills. I also characterized the ecological niche of common waxbills and native co-occuring passerines based on literature and field data and compared them on a multidimensional space.

Its abundance is higher in sites with plants associated to water, such as reeds, segdes, rushes and ricefields which provide suitable roosting, nesting and feeding places, although it can be inhabit other sites. Possibly because of its eclectic habitat choices, the common waxbill does not show strong spatial correlations with native passerines, except for a within-site correlation to Savi's warbler *Locustella luscinioides,* and for suggestive among-site scale correlations with the reed warbler *Acrocephalus scirpaceus* in the breeding season and with the house sparrow *Passer domesticus* in the post-breeding season.

The common waxbill occupies a very marginal position in the ecological space of the native avian community, with significantly higher distance from the native species than those have between themselves. The closest species to it is the reed bunting, *Emberiza schoeniclus* which is considerably closer to it than to the remaining native species. Also, more ecologically similar species do not tend to co-occur with the common waxbill. Overall, the waxbills seem to occupy a vacant niche in the unsaturated avian community. Therefore, the potential for interspecific competition seems rather limited, except perhaps in the case of the reed bunting, which is already facing conservation threats. The interactions with this species should be a subject of further study and a focus of conservation measurements.

I also provide detailed description of aspects of waxbill ecology that had not been described for its invasion range in Europe. The waxbill's breeding season extends at least from March to September and peaks around May. Its diet consists mainly of seeds, complemented with some arthropods, and shows little variation between April and September, except for a significant decrease in the proportion of arthropods from peak breeding to post-breeding season.

Resumo

As invasões biológicas estão entre as maiores ameaças à biodiversidade, já que as espécies invasoras podem deslocar ou conduzir à extinção espécies nativas devido à competição, predação ou propagação de doenças. No entanto, os efeitos ecológicos das novas invasões são imprevisíveis e, por vezes, neutros. Isso pode acontecer porque as comunidades naturais não estão sempre saturadas e conseguem acomodar espécies exóticas sem prejuízo para as nativas. Portanto, avaliar as interacções bióticas entre invasoras e nativas é importante no sentido de gerir esforços de conservação e também porque estas são valiosas experiências naturais para a investigação em ecologia de comunidades.

O objectivo deste trabalho foi caracterizar e comparar o nicho ecológico de um Passeriforme, o bico de lacre *Estrilda astrild*, originário da África sub-Saariana, com as espécies nativas co-ocorrentes.

As abundâncias de Passeriformes foram quantificadas com contagens em transectos realizadas em vários locais em Portugal continental, e os habitats nesses locais foram caracterizados, com o objectivo de avaliar as relações entre a abundância de bicos de lacre e de outras espécies de aves, e para avaliar as preferências de habitat dos bicos de lacre. Os nichos ecológicos dos bicos de lacre e dos Passeriformes nativos foram também caracterizados, com base na literatura e em dados de campo, e comparados num espaço multidimensional. A abundância de bicos de lacre é maior em locais com plantas associadas à agua, como caniços, juncos e arrozais, que oferecem locais de nidificação, descanso e alimentação adequados, embora possa ocorrer em outros locais. Possivelmente devido às suas escolhas eclécticas de habitat, não se verificam correlações espaciais fortes entre o bico de lacre e Passeriformes nativos, com excepção de uma sugestiva correlação a nível intra-local com a felosa unicolor *Locustella luscinioides*, e de correlações a nível entre-locais com o rouxinol pequeno dos caniços *Acrocephalus scirpaceus* na época de reprodução e com o pardal doméstico *Passer domesticus* após a época de reprodução.

O bico de lacre ocupa uma posição muito marginal no espaço ecológico da comunidade nativa, com uma distância significativamente maior às espécies nativas do que estas têm entre si. A espécie ecologicamente mais próxima é a escrevedeira dos caniços, *Emberiza schoeniclus*, consideravelmente mais próxima do bico de lacre do que das demais espécies. Além disso, espécies ecologicamente mais semelhantes ao bico de lacre não mostram tendência a co-ocorrer espacialmente com ele. Em geral, o bico de lacre parece ocupar um nicho ecológico previamente vazio, numa comunidade não saturada. Portanto, o potencial para competição interespecífica parece bastante limitado, excepto no caso da escrevedeira dos caniços, que já enfrenta ameaças de conservação. As interacções destas duas espécies merecem ser um objecto de estudo mais aprofundado e um foco de medidas de conservação.

Este trabalho fornece também uma descrição detalhada de aspectos da ecologia do bico de lacre que não haviam sido descritos para a sua área de invasão na Europa. A época de reprodução do bico de lacre estende-se, pelo menos, de Março a Setembro e tem um pico por volta de Maio. A dieta do bico de lacre consiste principalmente em sementes, complementada com alguns artrópodes, e mostra pouca variação entre Abril e Setembro, com excepção de uma diminuição significativa na proporção de artrópodes após o pico da época de reprodução.

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Chapter 1 Introduction

1.1 – Biological Invasions

An invasive species can be defined as an introduced species that, after becoming naturalized in its novel location, colonizes the ecosystem, spreading beyond its initial introduction site (Williamson, 1996; Richardson et al., 2000; Blackburn, 2009). On the other hand, conservationists usually refer to invasive species as organisms introduced by man into places out of their natural range of distribution, where they become established and disperse, generating a negative impact on the local ecosystem and species (IUCN, 1999). Here I adopt the broader first definition, without the assumption of a negative ecological effect. Rather than assuming a negative ecological effect *a priori*, the purpose of this work is to understand whether a very successful invasive species can potentially impact native communities negatively, or whether, on the contrary, its invading success may be helped by lack of competition with local species.

Biological invasions usually involve three stages: transport and introduction of organisms to a new location; establishment and population growth in the invaded location, and geographic expansion from initial successful populations (Blackburn et al., 2009; Shea & Chesson, 2002). For establishment and growth, a species must be able to increase in abundance at the invaded location. The factors, processes and interactions influencing this population growth are currently debated (Shea & Chesson, 2002; Blackburn, 2009; Hugo & van Rensburg, 2009). Resource availability, in terms of nutrients, light, water and space, is one of the factors that can account for invasion success (Stohlgren, 2006; Friedley et al., 2007). Other reported factors include dispersal capacity (Campbell & Reece, 2001; Duncan et al., 2006; Veltman et al., 1996); propagule pressure (i.e. number of individuals introduced, or number of introduction events; Blackburn et al., 2009; Cassey et al., 2004; Gamarra et al., 2005); environmental matching (i.e. whether environmental conditions match those of the native range; Blackburn & Duncan, 2001); or biotic interactions with the native community (Blackburn et al., 2009; Stohlgren, 2006; Campbell & Reece, 2001; Altieri et al., 2010; Friedley et al., 2007; Shea & Chesson, 2002). In particular, the role of interactions between community members in the success or failure of biological invasions is yet to be fully understood (Friedley, 2007; Blackburn et al., 2009; Koenig 2003; Hugo & van Rensburg, 2009; Levine, 2008). Features of the invaded site also matter: it has been demonstrated that some systems, including riparian corridors, agricultural areas and human disturbed habitats, are highly prone to invasion (Lonsdale, 1999; Blackburn et al., 2009; Shea & Chesson, 2002; Huston, 1994; Kawakami & Higuchi, 2003; MacGregor-Fors et al., 2010; Hugo & van Rensburg, 2009; Simberloff, 1995).

Invasive species can displace or drive to extinction native species, or alter ecological processes and habitats within local communities, which may result in a loss of biodiversity. Therefore, biological invasions are considered one of the biggest threats to biodiversity on a world-wide scale (Levine, 2008; Bauer & Woog, 2011). Through predation, competition for limited resources, the introduction of parasites or diseases, hybridization with native species, induced habitat alteration, or biotic homogenization, invaders can radically change both the species composition and functioning of native ecosystems (Levine, 2008; Blackburn et al., 2009). A flagrant example is the invasion of Lake Victoria by the Nile perch *Lates niloticus*: predation by this fish led to the extinction of two thirds of the lake's fish fauna (Witte et al., 1991). But biological invasions do not always induce such dramatic changes in the ecosystems. The traditional negative view of the exotic species might be the result of the alarm caused by those devastating invasions with negative consequences for local communities (Goodenough, 2010; Witte et al., 1991; Blackburn et al., 2009; Kawakami & Higuchi, 2003; Bruno et al., 2003), but may not be representative of the majority of invasion events. Global species extinctions attributed to invasive species have been linked to invasions by predators, parasites, or diseases and their effect on susceptible native prey, particularly in insular environments. Examples include introduced rats (*Rattus* spp.) and cats (*Felis catus*) on New Zealand , the brown tree snake (*Boiga irregularis*) in Guam, or several avian diseases in Hawaii (Levine, 2008; Friedley et al., 2007; Sax et al., 2007; Blackburn et al., 2009). Few if any examples have been linked to competitive exclusion alone, particularly between higher vertebrates. Interspecific competition by invasive species can have negative consequences for native populations, especially when resource availability declines (Freed & Cann, 2009). However, diminished resource availability and habitat destruction are often caused by human intervention, and it is possible that these processes would have negative consequences on the growth and survival rate of native species, even in the absence of the introduced species (Kawakami & Huguchi, 2003), or that a synergistic effect of habitat alteration and invader competition acts to cause the decline of native populations (Brazill-Boast et al., 2010).

1.2 – Relationships between invasive species and native communities

In theory, habitats with high levels of biodiversity are difficult to invade, since competition with native species would act as a barrier to biological invasions – the concept is referred to as the theory of biotic resistance (Elton, 1958; Shea & Chesson, 2002; Bulleri et al., 2008). But biological invasions can still occur in the presence of native competitors, particularly if the invaders have an ecological trait that allows them to outcompete the native species (Shea & Chesson, 2002). Intertidal communities, for example, can be invaded by organisms that compete with native species for physical space and resources (Shinnen & Navarrete, 2010). Exotic plants also establish in native communities where they are strong competitors for space and abiotic resources (Richardson et al., 2000).

Some experimental and observational studies indicate that diversity can sometimes reduce invasion success (Bruno et al., 2003; MacGregor-Fors et al., 2010), but large scale patterns mostly show the opposite, that systems with high biodiversity tend to have also higher numbers of exotic species (Lonsdale, 1999; Stohlgren, 1999; Shea & Chesson, 2002; Bonter, 2009; Friedley, 2007; Bruno et al., 2003; Bulleri et al., 2008; Hugo & van Rensburg, 2009). The *invasion paradox* (Stohlgren et al., 2006) refers to the discrepancy often observed between fine-scale and broad-scale native exotic species richness relationships: i.e., at a fine-scale negative correlations between numbers of exotic and native species are observed, while at larger scales the opposite is true. This is likely to happen because the strength of mechanisms that drive biological invasions differs at landscape and local community level (Altieri et al., 2010; Friedley et al., 2007; Blackburn et al., 2009; Hugo & van Rensburg, 2009; Shea & Chesson, 2002). For example, competition for resources could be more important in determining community assembly at a local scale, while at larger scales habitat heterogeneity allows for the co-existence of otherwise competing species (Bulleri et al., 2008; Davies et al., 2005; Hugo & van Rensburg, 2009). For example, spatial heterogeneity explains the scale dependence of the relationship between native and exotic diversity in grassland plant communities (Davies et al., 2005).

An alternative explanation for positive relationships between species diversity and invasion success is that high species diversity creates ecological niche opportunities for invaders. According to Shea and Chesson (see Shea & Chesson, 2002), if extrinsic factors that favor high numbers of native species also increase opportunities for invaders, for example, in terms of energy availability, the overall number of invasive species in communities that are richer in native species will be higher.

The presence of a species can favour the establishment of another species throught facilitation. Facilitative interactions are encounters between organisms that benefit at least one of the participants and cause harm to neither (Bruno et al., 2003; Bulleri et al., 2008). They include direct interactions such as mutualisms or comensalisms, or indirect interactions such as habitat creation and ammelioration (Stachowicz, 2001; Bulleri et al., 2008). Examples include the creation of refuge habitat for marine fishes by coral reefs or plant seed dispersal by pollinators (Bruno et al., 2003; Stachowicz, 2001). Facilitation can have effects on individual fitness, population distribution and growth rates, species composition and diversity, and landscape-scale community dynamics (Bruno et al., 2003). It can also influence biological invasions, and have a positive effect on the establishment and growth of invader populations. For example, shading by the native shrub, *Atriplex vesicaria*, fosters the establishment of the exotic succulent, *Orbea variegata*, in South Australia, while native sessile invertebrates protect the introduced oyster, *Crassostrea gigas*, from predation on the rocky shores of Western Canada (Bulleri et al., 2008). These observations support the hypothesis that species-rich ecosystems are more prone to invasions due to the presence of more facilitators (Bruno et al., 2003), rather than being more resistant to invasions due to the presence of more competitors, and this may also explain the positive relations between numbers of exotic and native species at large spatial scales. Altieri and colleagues did find general agreement between their local-scale experiments and landscape observations of a positive relationship between native diversity and invasion success, through facilitation mechanisms acting at different trophic levels on an intertidal community (Altieri et al., 2010).

1.3 – Community saturation

If systems with higher species richness also often support more invaders, is the concept of community saturation relevant? Ecologists have been discussing this issue for some years. Local-scale experimental studies demonstrating a negative relation between numbers of exotic and native species (Bruno et al., 2003; MacGregor-Fors et al., 2010; Shean and Chesson, 2002) led to the generally accepted theory that local communities are saturated and limited by competitive interactions among species interactions – the unified neutral theory of biodiversity and biogeography (Hubbell, 2001). This theory assumes that natural communities are close to equilibrium, local richness is limited by the number of resources and physical factors, and species interactions are intense. However, resource limitation and other local factors often fail to set upper limits on local richness, and critical evidence for these limits is often lacking (Cornell, 1999). Environmental complexity, non-equilibrium population densities of local species, the effect of disturbance, immigration from the regional species pool and variation over ecological time all add dynamics to natural ecosystems (Cornell, 1999; Cornell and Lawton, 1992; Houlalan et al., 2007; Mouquet et al, 2003; Fangliang et al, 2005). Also, evidence for density compensation and invasion resistance does not appear in many assemblages (Cornell, 1999). In fact, ecological systems rarely show evidence of being saturated with species (Friedley et al., 2007; Sax et al., 2007; Shea & Chesson, 2002; Levine, 2008). This means that stable saturated communities that could be structured primarily by species interactions, such as competition, are not usually found in nature; instead, unsaturated assemblages are more likely to be common and even saturated assemblages may not show hard limits to richness over evolutionary time-scales (Cornell and Lawton, 1992). Houlalan et al. (2007) even suggest that variability in community abundance appears to be driven more by processes that cause positive co-variation between species (similar responses to the environment) than processes that cause negative co-variation between species (effects of competition for scarce resources).

This does not mean that competition does not occur or does not influence community structure, but calls into question whether communities are usually saturated and, thus, whether biological invasions always result in increased inter-specific competition. Alternatively, unsaturated communities with vacant niches might be more ubiquitous in nature, and prone to accommodate some invasive species without negative ecological consequences.

1.4 – Ecological niche and interspecific competition

The ecological niche of a species is determined by the relationships between the individuals and their physical and biological environmental (Shea and Chesson, 2002; Begon et al., 2006). The classical concept (Hutchinson, 1957) views the ecological niche as an n-dimensional hypervolume, where the dimensions are environmental conditions that define the range in which a species can persist – that meet the species' needs. The fundamental niche of a species is the range of environmental conditions within which this species can live indefinitely in the absence of negative interspecific interactions, and the realized niche is the restricted physical space actually occupied by a species, accounting for interactions with other species (Hutchinson, 1957; Begon et al., 2006). Both negative and positive interspecific interactions influence the realized niche, and recent theories that include facilitation interactions suggest that in some cases the spatial extent of the realized niche can be larger than the one predicted by the fundamental niche (Bruno et al., 2003).

When a species invades a habitat where interspecific competition is reduced, the resulting ecological release permits population niche expansion, and allows for population growth (Bolnick et al., 2007, Bolnick et al., 2010). According to some authors there is lack of empirical evidence to support this theory (Levine, 2008). In turn, invasive species can interfere with native species if their ecological niches overlap, in one or more dimensions, through competition for resources or space. There is an old debate in ecology about whether niche overlap is a sufficient condition for interspecific competition to occur. Some authors argue that natural populations are often maintained in low numbers by the pressure of predation, and although their niches overlap, their population numbers are never large enough to exploit resources to a degree in which competition occurs (Schroener, 1982). Another argument is that environments are variable over time, and therefore also the strengh of competition varies, being possibly intermittent. Schroener (1982) compiled a table of examples of temporal variability in overlap in use of resources among trophically similar species, and most of them have their period of least overlap during the lean season, i.e., either winter or dry season, when resources are scarcer or abiotic conditions are harsher. Thus, niche similarity between invasive and native species might not be a sufficient condition for interspecific competition to occur during favourable periods, but it may lead to it when environmental conditions exert selective pressure on populations. In this context, comparison of ecological niches between invasive and native species in the invaded range is useful, particularly to understand if a very successeful invader may be competing with native species for natural resources.

1.5 – Ecological effects of avian invasive species

Exotic birds are present nowadays in all continents, especially in urban, agricultural, and other human-dominated landscapes (Luniak, 2004; Hugo & van Rensburg, 2009; MacGregor-Fors et al., 2010). It is possible, for example, to hear the calls of european starlings *Sturnus vulgaris* in North America, South Africa or New Zealand (Ingold, 1998; Hugo & van Rensburg, 2009; Blackburn et al., 2009), or admire the bright colours of tropical yellow-crown bishops (*Euplectes afer*) and red munias (*Amandava amandava*) at various wetlands in Portugal (personal observations). Introduced birds, many of which are generalists, are often able to take advantage of habitats altered by human activities (Hugo & van Rensburg, 2009; MacGregor-Fors et al., 2010). However, despite the growing number of studies, there is little conclusive information on the effects that exotic bird species have on native avifauna.

One of the ways in which exotic birds can impact native bird species is through hybridization (Bauer & Woog, 2011; Blackburn et al., 2009). So far, only one case of hybridization is documented in continental Europe, where the spread of the non-native Ruddy Duck *Oxyura jamaicensis* severely threatens the indigenous White-headed Duck *Oxyura leucocephala* (Hughes *et al.* 1999, in Bauer & Woog, 2011). Outside Europe, similar examples for such hybridizations occur when crosses between the Mallard *Anas platyrhynchos* and other *Anas* taxa take place, for example, in Australasia (*Anas superciliosa*), North and Central America (*Anas rubripes, Anas fulvigula, Anas diazi*) and Africa (*Anas melleri, Anas undulata*) (Fox 2009, in Bauer & Woog, 2011).

Another way of impacting native species is when exotic birds act as transmission vectors for pathogens and parasites, introducing diseases into new locations (Blackburn et al., 2009). A classical example is the introduction of avian malaria *Plasmodium relictum*, a parasitic disease transmitted by mosquito vectors, in the Hawaiian Islands in the XIX century (Warner, 1968 in Blackburn et al., 2009). This introduction has been implicated in the decline and even possible extinction of many endemic Hawaiian birds that are more susceptible to the exotic parasite (van Riper III et al., 1986 in Blackburn et al., 2009).

Another source of concern for conservation ecologists is the effect that non-native birds may impact native species by to interspecific competition, e.g., for food or nesting sites. In theory, niche overlap can be a sufficient condition to allow for interspecific competition between bird species that inhabit the same area, at least under some circumstances (Schroener, 1982; Bonter et al., 2010; Poling & Hayslette, 2006; Freed & Cann, 2009; Kawakami & Higuchi, 2003; Ingold, 1998). A recent study on the invasion of Mexico by house sparrows *Passer domesticus* (see MacGregor-Fors et al., 2010) suggests that the presence of this species alters the bird community composition, causing communities to be highly dominated by house sparrows and a decrease in species richness. This happens due to the sparrows' competitive advantage, resulting from a combination of aggressiveness towards other species, a generalist diet, communal nesting habits and ability to exploit urban settlements (MacGregor-Fors et al., 2010). On the other hand, recent research on the colonization of North America by the Eurasian collared-dove *Streptopelia decaocto* showed that competition might not affect native dove species but that, on the contrary, a positive correlation between abundance of invasive and native dove species is present (Bonter et al., 2010). The same kind of correlation was found in a study of South African native and exotic bird species diversity (Hugo & van Rensburg, 2009). In the later case, alien and native birds tend to occupy different habitats and might use different resources at a local scale, e.g., birds that overlap in territory and in food preferences might adjust their foraging behaviour according to canopy structure (Kawakami & Higuchi, 2003) and patch composition (Jones et al., 2006). Thus, niche overlap, particularly in respect to diet preferences, between invasive and native bird species does not always mean that exclusive competition between these species will occur (Bonter et al., 2010; Poling & Hayslette, 2006; Freed & Cann, 2009; Kawakami & Higuchi, 2003). In other cases, invaders might act synergistically with human habitat alteration to change composition, structure, and diversity of native bird communities (Mac-Gregor et al., 2009; Brazill-Boast et al., 2010). It was even suggested that the extinction of native bird species on islands where colonization by invaders occurred might have happened previously to that colonization, caused by human impacts on the native avifauna, rather than occurring after invasion by alien bird species (Blackburn et al., 2009; Cole et al., 1995). Take together, current evidence suggests that competition for food may not generally have a major effect on native birds (Blackburn et al, 2009),

On the contrary, competition for nesting sites, particularly amongst cavity nesting birds, may have negative consequences for native species. Cavity breeders need a pre-existing cavity to build or use as their nest and often use a very specific type of place, both in terms of characteristics within the immediate vicinity of the nest and in terms of characteristics of the habitat surrounding the nest (Charter et al., 2010; Fisher and Wiebe, 2006; Purcell & Verner, 2008). Such specific cavities are in some areas limited, which may cause exclusive competition by agressive invasive species. Population declines of many species of native cavity nesting birds in North America are correlated with increasing european starling, *Sturnus vulgaris*, populations and nest-site competition appears to be implicated (Wiebe, 2003). For example, American northern flickers *Colaptes auratus* lose about 7% of nest cavities to invasive starlings, mostly early in the breeding season (Ingold, 1998; Fisher and Wiebe, 2006; Wiebe, 2003). The probability of renesting by flickers declined during the season, and clutch sizes also decrease, meaning that nest usurpation by stralings could affect the nesting success of flickers, forcing them to adapt to competition by starting reproduction earlier. Limiting factors also play a role in this competitive interaction: if there is an abundance of cavities, flickers and starlings can sometimes be found nesting in the same tree at the same time (Gutzwiller and Anderson,1986, in Ingold, 1998).

Introduced bird species have been found to have different effects on native bird communities at different locations. For example, Japanese white-eyes (*Zosterops japonicus*) introduced to Hawaii and the Bonin Islands, Japan, appear to have different effect on the native fauna. In Hawaii it was found a negative effect on one native bird species, due to exploitative competition for food (Freed & Cann, 2009, see also Mountainspring & Scott, 1985). But in the Bonin Islands there were no detectable negative impacts on the native species and, if anything, native species appear benefit from the presence of the invader due to mixed-flock formation during non-breeding season (Kawakami & Higuchi, 2003).

It has even been hypothesized that avian invaders can have benneficial effects on native bid communities, for example, by enhancing the dispersal of native plant species which these use as food, rather than depressing population numbers, or by acting as buffer species, being used as a food source by carnivores that prey on native avifauna (Cole et al., 1995). An introduced species can thus have negative, neutral or positive effects on the native avifauna at different locations, depending on their specific traits but also on features of the habitat and the local community.

1.6 – Study species and objectives

Introduction of avian species in novel locations has increased in the last decades (Blackburn et al., 2009), and the effects of many of these introductions on native biota are still unkown. The invasion of the Iberian Peninsula by the common waxbill (*Estrilda astrild*) is an example of such a case. The common waxbill is a small granivorous passerine in the Estrildidae family. They are native to sub-Saharan Africa, but were widely transported by humans and have escaped from captivity or been deliberately released so that they are now established in several parts of the world, including Brazil, and several Atlantic and Indic islands (Guerrero et al*.*, 1989, Reino & Silva, 1998). Waxbills have escaped or been released in Portugal for the first time in the 1960s in the coastal wetland area of Óbidos lagoon, and expanded since then from this and other release points, now covering practically the entire territory with suitable habitat and expanding to Spain (Reino & Silva, 1998; Cramp & Perrins, 1994; Guerrero et al*.*, 1989; Vidal Rodriguez, 2004; Murgui, 2001). Recent observations suggest that, although initially dependent on wetlands for roosting and nesting, they are highly eclectic, and can be also found in irrigated farmland mosaic with hedges (Reino & Silva, 1998; Silva et al., 2002; Reino, 2005), where they exploit seed-rich patches like edges of crop fields (Cramp & Perrins, 1994). The invasion of Portugal has been well studied in terms of the rate of spread, factors influencing it, and possibilities of future expansion (Reino & Silva, 1998; Silva et al., 2002; Reino, 2005; Stiels et al., 2011), but possible interactions with native species have not been studied yet (Reino & Silva, 1998).

One likely factor for the success of the common waxbills' invasion in Portugal is their high reproductive rate, as they are capable of reproducing during most of the year (Reino & Silva, 1998; Cramp & Perrins, 1994). The rate of spread of the common waxbill seems to have been affected by spatial heterogeneity, as well as habitat availability and favorable climatic conditions (Reino & Silva, 1998; Silva, 2002; Reino, 2005), suggesting that habitat suitability also determined the success of this biological invasion. Their success in establishing among the native avian community might further be due to the species being a better competitor than the co-occurring native species with similar ecological niches or, alternatively, that they fill an empty ecological niche in the avian community and thus experience little competition. Distinguishing between these two scenarios is also important to assess whether this biological invasion is of concern in terms of conservation, as the native avifauna may or may not experience additional competition from waxbills.

In order to distinguish between these two alternatives, I conducted two main studies. The first aims to identify species that co-occur more closely with waxbills and, thus, may be more vulnerable to competition. The second assesses similarity in ecological niche between waxbills and native species, and compares it with niche similarities among natives, to evaluate the potential for competition between waxbills and members of the native community. If the common waxbill's ecological niche is similar to the niches of existing bird species, it might have established by being a strong competitor in a functionally saturated community, and may have the potential to harmfully impacting native communities through inter-specific competition. This would be supported by ecological distances between the waxbill niche and those of native species equal or inferior to the distances among the community of native species. If, on the contrary, the waxbill's ecological niche differs from those of native bird species more than the differences within the native community, this indicates that waxbills occupied a vacant niche, probably using previously unexploited resources or space, and likely posing no threat to native species. In addition to this, I collected various types of field data to characterize the waxbill's niche at a finer scale, because its ecological niche in the European invasive range was not studied to the same level of detail as for other passerine species.

Chapter 2 Methods

2.1 – Bird censuses

I conducted censuses in 23 sites approximately similarly spaced across the waxbill's invasion range in mainland Portugal (Figure 1), during two breeding seasons (June to September 2010 and April to July 2011). Sites were chosen based on presence of waxbills and distance from previously visited sites, and visit dates were approximately randomised to avoid correlations with latitude or longitude. Sampling sites covered many different types of habitat, such as coastal wetlands, riparian vegetation, mixed agricultural areas, and water courses in cereal field areas.

Figure 1 – map of the 23 censused sites. For numerical correspondence, see Table A in Appendix I.

Censuses were carried approximately 30 minutes (+/- 20 minutes) after sunrise. Transect counts were performed for 30 minutes, walking at a steady pace and noting all birds seen or heard within a 60 metres corridor (30 metres to each side of the observer). Sound recording (M-Audio Microtrack 24/96 solid-state recorder, with coupled omnidirectional microphone) was used for posterior identification of unknown bird sounds. The censuses were repeated for an average of 2.95 days, median 3 days (minimum 1, maximum 4) for each site, depending on technical or weather conditions, and following approximately the same route. The average transect length was 1.16 km ± 0.15 standard deviation (SD). Counts per 3-minutes intervals were used for comparisons within-sites. Total bird counts were converted to birds per km for comparisons among sites.

During the censuses, habitat features were recorded every 3 minutes, for rectangular patches of 30 meters to the left, 30 meters to the right and 30 meters to the front of the observer. The proportion of 10 different micro-habitats (Table I) were visually estimated to the nearest 5%. The average micro-habitat composition across the entire census was used for comparisons among sites.

Table I – Habitat categories recorded during censuses, and definitons.

Habitat type	Definition
Open agricultural areas	all open areas that are not cultivated, and consist of bare ground, grass fields or herbaceous plants.
Open non-agricultural areas	all open areas that are not cultivated, and consist of bare ground, grass fields or herbaceous plants.
Shrubs	areas with woody-stemmed plants, small and medium (up to 2,5 meters) branching from the base, and with several stems arising from or near ground level, including cactuses. Some young trees that were less than 2,5 meters and were in the middle of a shrubby area might have been included in this category due to imperfect detection.
Riparian trees	woody plants taller than 1,5 meters with a single woody stem and branching from at least 1 meter above ground typical of riparian galeries, always growing near water.

Non-riparian trees	woody plants taller than 1,5 meters with a single woody stem and branching from at least 1 meter above ground, including orchards (fruit and olive trees) except the ones typical from riparian galeries and growing near water.
Running water	water bodies with a stream or flow, both permanent and seasonal, including rivers, streams, irrigation channels, lakes, ponds, and salt or fresh water lagoons.
Reeds	tall, grass-like plants typical of wetlands or irrigated land, with a diferentiated stem; in Portugal these include *Arundo* spp. and *Phragmites* spp.
Sedges/rushes	short, grass-like plants typical of margins of water courses, without a differentiated stem; in Portugal these include *Juncus* spp. and *Typha* spp.
Ricefields	agricultural fields where rice was planted. These were separated from the remaining agricultural areas because rice plants are planted in submerged land, which makes ricefiels a unique habitat within the agricultural type.
Urban areas	areas with human-made structures such as railways, roads, buildings and other human constructions.

Analyses were restricted to native Passeriformes inhabiting wetland, farmland or mixed habitats with open areas, which are the broad habitats of waxbills (Cramp, 2000; Reino, 1998) and leaving aside birds of other guilds or that use other types of habitat (e.g. forest birds and aerial birds). Species larger than 30 g were excluded, as competition between waxbills (7-8 grams) and much larger birds is implausible. Only resident or regularly breeding birds were included, as bird censuses were carried out in the breeding season. Table II lists the 26 species that meet these criteria.

Table II – Native bird species used in analyses of intra-census and inter-site abundances.

Code	Species	Code	Species
Acr sci	*Acrocephalus scirpaceus*	Mot alb	*Motacilla alba*
Aeg cau	*Aegithalos caudatus*	Par cae	*Parus caeruleus*
Car can	*Carduelis cannabina*	Par maj	*Parus major*
Car car	*Carduelis carduelis*	Pas dom	*Passer domesticus*
Car chl	*Carduelis chloris*	Pas his	*Passer hispaniolensis*
Cet cet	*Cettia cetti*	Pas mon	*Passer montanus*
Cis jun	*Cisticola juncidis*	Phy col	*Phylloscopus collybita (ibericus)*
Eri rub	*Erithacus rubecula*	Pru mod	*Prunella modularis*
Est ast	*Estrilda astrild*	Sax tor	*Saxicola torquata*
Fri coe	*Fringilla coelebs*	Ser ser	*Serinus serinus*
Hip pol	*Hippolais polyglotta*	Syl atr	*Sylvia atricapilla*
Loc lus	*Locustella luscinioides*	Syl mel	*Sylvia melanocephala*
Lus meg	*Luscinia megarhynchos*	Tro tro	*Troglodytes troglodytes*

Spatial autocorrelation of waxbill counts was tested by calculating Moran's I (Valcu & Kempenaers, 2010) for every distance class, from consecutive 3-minutes time intervals, to time intervals separated by 8 intervals. Moran's I was only significant (Z value higher than 1.96, not controlling for multiple tests) in 5 out of 67 censuses (23 sites with an average of 2.95 censuses per site), and only for consecutive time intervals. This indicates that autocorrelation of waxbill counts is negligible for these data, and therefore the 3-minutes time intervals were used as independent data points in subsequent within-census analyses.

2.1.1 Relations between the abundance of common waxbills and other bird species

Pearson's correlations were used to test for intra-census correlations between the abundance of common waxbills and abundance of other bird species. For each native species, only site where it was detected were used. Since there are many species, rather than controlling for multiple comparisons, which is not feasible, I instead used these correlation coefficients only in a descriptive manner, to rank species by order of co-ocurrence with waxbills. I subsequently used that ranking to check whether species with more similar niches tend to co-occur more with waxbills, which would potentiate intra-specific competition.

Correlations were first calculated between the abundance of waxbills and that of each other species for each individual census, and averaged for each site. Then the correlation coeficcients for each species were averaged across sites. No common waxbills were detected in the censuses of two sites (Celorico da Beira and Évora), although they were present in these areas, as confirmed by mist-netting. Therefore, these two sites were not used for intra-census analyses.

I also correlated the abundances of waxbills at each site (average of the censuses conducted at each site, as individuals per km) with that of the other passerine species (also individuals per km) using Pearson's correlations. This was done separately for sites sampled during the breeding season (defined here as April to July; 13 sites) and post-breeding season (August and September; 10 sites). Most of the bird species sing more often while defending their breeding territories, and some of the species, particularly granivorous birds, tend to gather in flocks after breeding is completed. Thus, it may happen that some species are more detectable in June, when the males are singing and the juveniles start to fly, and go unnoticed in September. It may also happen, in the post-breeding season, that flocks of juveniles and post-breeding adults are observed and impact the censuses differently.

2.2 – Associations with habitat types

I also tested for associations of common waxbill abundances and habitat types across sites, with a multiple linear regression. In the regression model, waxbill abundance (as birds per km, average per site) is the dependent or response variable, and each type of micro-habitat (average per each site) is an independent or explanatory variable.

Waxbills abundance and most of the habitat variabes (Open agricultural, Open non-agricultural, Shrubs, Riparian trees, Non-riparian trees, Free water and Reeds) were approximately normally distributed across sites (Kolmogorov-Smirnov tests, all $Z < 1.26$, all $P > 0.08$, all $N = 23$). Two habitats (Sedges/rushes and Urban areas) were right-skewed (all $Z > 1.48$, all $P < 0.03$, all $N = 23$), and this was corrected with a log $(X+1)$ transformation (after transformation, all $Z < 1.11$, all $P > 0.17$, all $N = 23$). One of the variables, Ricefields, had many zero values (19 out of the 23 sites), and thus it was transformed into a binomial presence-absence variable.

Collinearity between variables, was assessed by examination of Pearson's correlations and by calculation of Variance Inflation Factors (VIF). The higher the VIF, the lower the tolerance (VIF = 1/tolerance), and, as a rule of thumb, it is desirable that the VIF is lower than 5 or 10 (or tolerance is higher than 0.20 or 0.10). Open agricultural and Open non-agricultural had a VIF slightly higher than 5 (VIF = 5.81 for Open agricultural) and were strongly correlated (r = 0.76), and therefore I merged them in a single variable, Open areas. This new variable and the remaining habitat categries all had low collinearity (Table III, and all pair-wise r < 0.54).

Table III – Variance inflation factors (VIF) for continuous response variables to be included in regression model. It was not possible to calculate the VIF for the variable Ricefields, as it was treated as a nominal variable.

Shrubs	1.49
Riparian trees	1.34
Non-riparian trees	1.46
Water	2.22
Reeds	1.59
Sedges/rushes	2.83
Urban areas	2.56
Open	3.00

The model was first tested including all the variables, and stepwise forward and backward selection procedures based on Akaike Information Criterion (AIC) values were performed. The AIC is used for selecting a model which minimizes the Kullback-Leibler distance between the model and the data. It is defined as

$$AIC = -2 (\ln (\text{likelihood})) + 2 K$$

where likelihood is the probability of the data given a model and K is the number of free parameters in the model. Thus, the best model is the one having the smallest AIC (Burnham & Anderson, 2002). The stepwise selection procedure both removes and adds each variable to the model that returns the lowest model AIC value, one by one, until the deletion or inclusion of new variables does not further lower the AIC value. I did not enter all possible interactions between the habitat categories to the model because there is a large quantity of interactions, most not readily interpretable. Instead, after the initial selection procedure, I included interactions between the selected habitat categories and the remaining, one by one, selecting those that lowered AIC values and, after that, the new model with interactions went through a new round of stepwise forward and backward variable selection. The studentized residuals were verified to indentify cases for which the model would be poorly fitted. In a normal distribution, it is expected that 5% of the studentized residuals are above ±1.96, 1% above ±2.58 and 0.1% above ±3.29 (Field, 2000). Since the number of samples was 23, cases of studentized residuals above ±1.96 were inspected to understand if they should be removed to make the model more fit. Cook's distance was also examined to assess cases of unusual influential samples. This measure of influence is based on the difference between the regression parameter estimates and what they become if the ith data point is deleted (MacDonald, 2002). Values greater than 1 may have an unusual influence in the regression parameters (Cook & Weisberg, 1982; Field, 2000), and I inspected such cases to assess whether these observations should be eliminated from the model (Field, 2000).

Models were built using the software SPSS 19.0.

2.3 – Ecological niches

The species included in this analysis are the same selected for the census-based study of waxbill abundances. An addtional species not observed in the censuses, *Emberiza schoeniclus*, was included here, since it breeds regularly in Portugal and, although its distribution is very restricted, is known to occupy the same type of habitat as the common waxbill (Reino, 2005) and possibly have similar diet, at least in part of the year.

I collected information on various dimensions of the ecological niche of the common waxbills and native passerines from the literature and field-data. These include preferential habitat, breeding phenology, nesting preferences, diet, beak morphology, and foraging substrates (Table IV). Niche data was firstly collected from The Complete Birds of the Western Palearctic (Cramp, 1988, 1992; Cramp & Perrins 1993, 1994a, 1994b) and secondly complemented with data from Catry et al. (2010) when the detail of the information was insuficient or information relative to Portugal or the Iberian Peninsula was not available there. Data from Portugal or the Iberian Peninsula were preferentially used, since some data can differ between Western Palertic areas, particularly between areas at southern and northern latitudes (Cramp, 1988, 1992; Cramp & Perrins 1993, 1994a, 1994b). In addition to the literature-based data, data on the morphology of mist-netted birds was also used. In every field site mist-nests were set up 30 minutes before sunrise at places where waxbills were observed previously, and were usually closed between 11:30 and 13:30.

The niche dimensions are summarized in Table --, and each is described in detail next. Values for each species of all niche dimensions are given in Table.

Table IV – Ecological variables of bird species analyzed in this study. On the left column there broad dimensions, some of which were too complex to be summarized in one variable and were subdivided in finer variables (centre column). All variables are ordinal or dichotomic (categories on the right column) or, for morphological traits, continuous variables. For details see text below. Morfological variables were collected in the field and are marked with (f).

Niche dimension	Variables	Categories
Habitat	vegetation density water proximity antropogenization	open - medium - dense wetland - riparian vegetation - dryland natural - anthropogenized
Breeding phenology	Breeding phenology	Months
Nesting ecology	type of construction nesting water dependence nesting height support stucture	cavity – nest above water - dry soil ground – low height - high height vegetation - rock
Diet	seeds fruits and other plant material insects and invertebrates	never - ocasionally - seasonally - year round never - ocasionally - seasonally - year round never - ocasionally - seasonally - year round
Foraging substrate	foraging height presence of water	ground/grass - shrubs/reeds - tree height water - dryland
Bill index	Bill index (f)	bill lenght (mm) / bill depth (mm)
Weight	Weight (f)	mass (g)

Habitats were classified in relation to vegetation density, presence of water bodies and degree of anthropogenization. A *vegetation density* ordinal variable comprised three categories: open areas (defined as areas of open field, either rocky or with grasses or herbs and scattered shrubs), medium vegetation density (e.g., reedbeds, areas of scattered trees, shrubs or mixed vegetation with edges) and dense vegetation (e. g., forests). Reedbeds were included in the intermediate vegetation density category because vegetation is dense, but the habitat is open, lacking the canopy of typical closed habitat. A *water proximity* ordinal variable comprised: wetlands (wetland or bordering areas strongly associated with it), riparian vegetation (riparian corridors along water courses) or dryland (areas which are not dependent of the presence of water or associated with it, including farmland). An *anthropogenization* dichotomic variable comprised: natural (habitats with no human intervention) and anthropogenized habitat (habitat that has suffered human intervention, such as farmland, gardens and orchards).

Breeding phenology was characterized based on the months in which the birds are building the nest, laying eggs and caring for the nestlings. For simplicity of comparison purposes, each month was assigned the corresponding calendar number (i.e., March = 3) and the average of these values was calculated to create an index representative of the main breeding period that could be used to differentiate early breeders from late breeders.

Nesting ecology was classified according to the type of construction, dependence of water presence, height above the ground and support structure. A *type of construction* dichotomic variable comprised: cavity users if they occupy an existing cavity for nesting, or nest builders if they build the nest. A *nesting water dependence* dichotomic variable comprised: nest built above water, for example in reedbeds, or nest built above dry soil. A *nesting height* ordinal variable comprised: ground nesters, for species that nest on the soil, either bare ground or concealed in grassy vegetation; low height nesters, for species that build nests up to 1,5 m above the ground (e.g., reeds or shrubs); or high height nesters, for species that build their nest at more than 1,5 m above the ground (e.g., trees). A *support structure* dichotomic variable comprised: vegetation, for nests located on plants or on the soil concealed by vegetation; and rock, for nests on bare ground or rock crevices, and also on man-made structures such as buildings or electrical poles.

Diet was characterized by three ordinal variables: the preponderance of i) *seeds*, ii) *fruits and other plant material*, and iii) *insects and other invertebrates* in their diet. This allows for a separation of the diets according to the proportions of these elements, and discriminates among species that are granivorous, frugivorous, insectivorous or those having mixed diet. For each of these ordinal variables, species were classified as ingesting each item year-round, seasonally, occasionally or never.

Foraging substrate was classified according to height above the ground and the presence of water bodies. A *foraging height* ordinal variable comprised: ground/grass for species that forage on the ground or vegetation up to 1m above ground, even if they perch on higher substrates, shrubs/reeds for species that forage at the understorey level, mainly in shrubs and reeds, and tree height for species that forage at canopy height. A *presence of water* dichotomic variable comprised: presence of water, for species that forage above water or on water vegetation; and dryland, for species that forage on soil or on soil vegetation.

For the above literature-based variables, each species was scored based on the descriptions in the literature, and when it comprised more than one category an intermediate score was given. Information with qualifiers such as "sometimes" or "occasionally" was considered valid because they imply that a behaviour or habit occur in an expected but irregular fashion, depending on circumstances (e.g., lack of more suitable places to nest due to environmental disturbance or occasionally elevated demographic pressure). Information with qualifiers such as "rarely" was not considered because they imply that a behaviour or habits not expected or constant, depending on rare and extreme environmental circumstances.

Bill measurements in the literature differ in methodology, hence I measured bill length and depth from mist-netted birds in the study sites, following the indications described in Svensson (1992). Bill lenght was measured as the lenght of the bird's bill from the tip to feathering, and bill depth was measured at the plane of feathering at the forehead. Measurements were taken with an electronic caliper to the nearest 0,01 mm, and only adult birds were used. These measurements were used to calculate an index of *bill index* as bill lenght divided by bill depth. For 5 species that were not caught in mist nets (*Aegithalos caudatus*, *Motacilla alba*, *Emberiza schoeniclus*, *Erithacus rubecula* and *Fringilla coelebs*), or from which only juvenile birds were caught, measurements were collected on specimens from the Museu Zoológico da Universidade de Coimbra, with a caliper ruler, to the nearest 0,5 mm. It was not possible to collect data in either way for *Locustella luscinioides*, and those measures were provided by Dr. Júlio Neto, taken from birds captured at Salreu wetlands (Aveiro, Portugal).

The *weight* of each species was taken from adult birds captured in the field, using an electronic weight scale, and ocasionally a Pesola scale, to the nearest 0,1 g. For the remaining species, data were taken from the literature (Cramp, 1988; Cramp & Perrins 1994b), choosing data from the same subspecies that breeds in Portugal or Spain, or from birds captured in a close geographic area. The logarithm of mass for each species was used instead of the absolute mass, because it reflects proportional differences between species, which is more meaningful to characterize ecological similarity.

For both bill and body morphology, the measurements of both sexes were used, since it was impossible to separate the sexes of some species in the field (e.g. *Luscinia megarhynchos* and *Hippolais polyglotta*).

2.3.1 – Comparison of ecological niches

I used two methods to compare the multidimensional characterization of niches across species. I primarily used Non-metric Multidimensional Scaling (NMDS), which does not make assumptions on the distribution of data, to evaluate distances among niches in a non-dimensional space. As long as the rank-ordering of distances in the matrix is meaningful, NMDS can be applied to any kind of distances. I used the software Primer 5.0 to run NMDS, with a minimum of 30 restarts when analizing the distances in the similarity matrix, and distances among species was assessed by Euclidean distances in bidimensional space with standardized data. Additionally, I ran a Principal Components Analysis (PCA) to characterize axes of variation in terms of the original niche variables, and thus complement the interpretation of the NMDS result. I also used the software Primer 5.0 to run the PCA, standardizing the data. I used a T test to compare the average distance between the waxbill and native species (average of the euclidean distances from the similarity matrix), with the distances of native species among themselves.

I correlated the Pearson correlation coefficients, from either the intra-census and inter-site analyses of co-occurrence with waxbills, with the euclidean distance of the waxbill to each species, to test if species that co-occurred more closely with the common waxbill were more ecologically similar. This did not include *Emberiza schoeniclus*, which was not detected in the censuses.

The T test and the correlations mentioned above were carried out using the software Statistica 7.0.

2.4 – Other aspects of the niche of the common waxbill

For the common waxbills, as mentioned above, an additional effort was made to characterize their invasive ecological niche. Birds captured in mist-nets were checked for the presence of an incubation patch for determining the duration of the breeding season, and their feaces were collected to assess the percentage of ingested food items.

From a total of 639 common waxbills captured, I obtained and analysed faecal samples from 308, and checked for the brood patch of 249 females.

2.4.1 – Waxbill breeding phenology

To determine the duration of the breeding season, I checked for the presence of brood patch in birds captured in the field. The brood patch, or incubation patch, is developed a short time before the incubation starts: the down feathers of an area on the ventral surface are dropped, and the skin of this area appears thickened, frequently wrinkled, and the blood vessels increase in size and number. The skin returns to normal a short time after the young fledge, thus providing a good indication of breeding period. Females were sexed in the field primarily by the pattern of undertail feathers (i.e., males have black uniform undertail feathers, while females have black, brown or cream undertail feather with lighter irregular patches ranging from light brown to cream), and by the general vividness and size of ventral and mask red areas (i.e., generally larger and more vivid in males). Birds captured in 2010 were also sexed with molecular techniques (unpublished data), which showed that 97% of female identification based on plumage is correct. In addition to the 2010 females, only birds from 2011 that were unambiguously sexed by plumage as females were used in this analysis. Only data regarding adult birds were used, and I calculated the percentage of females with an incubation patch in relation to the total adult females captured, per month.

2.4.2– Seasonal variation in waxbill diet

To complement the literature-based diet data, and particularly to assess if the common waxbill ingests a larger amount of insects and arthropods in certain times of the breeding season, I collected and analysed feaces of the mist-netted birds. They were obtained by placing the captured waxbills in individual paper bags and collecting the feaces from each bird’s bag after the bird was released. Feaces were posteriorly placed in Petri dishes and examined under a stereoscopic magnifier, using between 10.5x and 45x magnification. Seeds, other plant parts, arthropods and mineral contents were identified and their proportions visually estimated to the nearest 5%. I calculated the percentage of food items in the feaces of captured birds, in total and per month. As aerial insects are more abundant during breeding season, reaching a peak in June, and start to decline around September (Bryant, 1975; Visser et al, 1998), I also tested for differences in the diet's items between the peak of the waxbill's breeding season, as evaluated by the brood patch data, and both the beginning and end of the sampling period with T tests. As the original data were percentages, they were arcsin transformed. These tests were performed using the software Statistica 7.0.

Chapter 3 Results

3.1 – Relations between the abundance of common waxbills and other bird species

At the intra-census level, correlations between the abundance of common waxbill and of other bird species were generally low (with one exception, all $|r| < 0.2$, Table V). The exception to this was a suggestively strong correlation with Savi's warbler (*Locustella luscinioides*, average $r = 0.8$), although this species was present at only two sites (Salreu and Santo André wetlands). Correlation coefficients with other species were quite low (average $|r| = 0.04$, ± 0.07 SD, $n = 24$ species).

Table V – Average Pearson correlation coefficients for intra-census correlations between the abundance of common waxbills *Estrilda astrild* and native bird species (r), and standard deviation (SD). Column *sites* refer to the number of sites where each species was detected. *Estrilda astrild* was detected in 21 sites, but correlations were not run in censuses where the paired species was absent.

Species	r	SD	sites	Species	r	SD	sites
Acrocephalus scirpaceus	-0.01	0.24	12	*Parus caeruleus*	-0.15	0.08	10
Aegithalos caudatus	-0.16	0.09	4	*Parus major*	-0.06	0.24	14
Carduelis cannabina	-0.16	0.06	7	*Passer domesticus*	0.02	0.18	19
Carduelis carduelis	0.02	0.25	11	*Passer hispaniolensis*	-0.07	0.24	2
Carduelis chloris	-0.04	0.27	19	*Passer montanus*	-0.18	0.07	5
Cettia cetti	0.13	0.33	18	*Phylloscopus collybita*	-0.08	0.15	6
Cisticola juncidis	-0.03	0.24	17	*Prunella modularis*	-0.09	0.09	2
Erithacus rubecula	-0.01	0.22	14	*Saxicola torquata*	0.03	0.31	17
Fringilla coelebs	-0.11	0.11	7	*Serinus serinus*	0	0.32	14
Hippolais polyglotta	-0.03	0.18	4	*Sylvia atricapilla*	-0.01	0.22	15
Locustella luscinioides	0.83	0.17	2	*Sylvia melanocephala*	-0.02	0.23	17
Luscinia megarhynchos	-0.01	0.18	9	*Troglodytes troglodytes*	0.02	0.2	12
Motacilla alba	-0.04	0.18	6				

Correlations with other bird species across sites differed between the breeding and the post breeding season but, in general, they were not very strong. In the breeding season, *Acrocephalus scirpaceus* and *Cisticola juncidis* showed the strongest correlations with *Estrilda astrild* (both $r > 0.57$, Table VI). In the post-breeding season, *Passer domesticus* and *Carduelis carduelis* showed positive correlations with *Estrilda astrild* (both $r > 0.54$, Table VII). The correlation with *Acrocephalus scirpaceus* was positive in the breeding season and negative in the post-breeding season, and the opposite happened with *Carduelis carduelis*.

Table VI – Pearson correlation coefficients for inter-site correlations between the abundance of common waxbills *Estrilda astrild* and native bird species (r) for the breeding season. *Estrilda astrild* was detected in 12 sites. Column *sites* refer to the number of sites where each species was detected. N = 13 sites for all correlations.

Species	r	sites	Species	r	sites
Acrocephalus scirpaceus	0.63	7	*Parus caeruleus*	-0.39	6
Aegithalos caudatus	-0.32	2	*Parus major*	-0.23	8
Carduelis cannabina	-0.25	5	*Passer domesticus*	0.42	12
Carduelis carduelis	-0.20	7	*Passer hispaniolensis*	0.47	1
Carduelis chloris	-0.10	11	*Passer montanus*	-0.19	1
Cettia cetti	0.21	11	*Phylloscopus collybita*	-0.10	3
Cisticola juncidis	0.57	12	*Prunella modularis*	-0.21	2
Erithacus rubecula	-0.28	8	*Saxicola torquata*	-0.18	11
Fringilla coelebs	-0.27	3	*Serinus serinus*	-0.24	9
Hippolais polyglotta	-0.11	6	*Sylvia atricapilla*	-0.35	9
Locustella luscinioides	0.50	1	*Sylvia melanocephala*	-0.39	13
Luscinia megarhynchos	-0.16	7	*Troglodytes troglodytes*	-0.28	8
Motacilla alba	-0.20	4			

Table VII – Pearson correlation coefficients for inter-site correlations between the abundance of common waxbills *Estrilda astrild* and native bird species (r) for the post-breeding season. *Estrilda astrild* was detected in 9 sites. Column *sites* refer to the number of sites where each species was detected. N = 10 sites for all correlations.

Species	r	sites	Species	r	sites
Acrocephalus scirpaceus	-0.41	6	*Parus caeruleus*	-0.35	7
Aegithalos caudatus	-0.06	4	*Parus major*	0.12	8
Carduelis cannabina	0.33	1	*Passer domesticus*	0.76	9
Carduelis carduelis	0.54	7	*Passer hispaniolensis*	-0.45	2
Carduelis chloris	0.19	10	*Passer montanus*	0.41	3
Cettia cetti	0.02	9	*Phylloscopus collybita*	-0.16	4
Cisticola juncidis	0.32	7	*Prunella modularis*	--	0
Erithacus rubecula	-0.20	7	*Saxicola torquata*	-0.16	9
Fringilla coelebs	-0.46	6	*Serinus serinus*	-0.29	5
Hippolais polyglotta	--	0	*Sylvia atricapilla*	-0.40	8
Locustella luscinioides	0.05	1	*Sylvia melanocephala*	0.15	7
Luscinia megarhynchos	0.30	4	*Troglodytes troglodytes*	-0.22	5
Motacilla alba	-0.50	2			

3.2 – Associations with habitat types

Most habitat categories (except for Water) had a significant effect on the full linear model on waxbill abundances across sites (Table VIII). All variables had positive coefficients, suggesting that habitat heterogeneity is favoured by the common waxbill. After AIC-based forward and backward automatic selection procedures, the model retained only Reeds and Sedges/Rushes, which together returned the lowest AIC value, but with the effect of Sedges/Rushes only marginally significant (Table VIII). For the model including the variables Reeds and Sedges/Rushes, there were no studentized residuals with value above ± 1.96, and the highest Cook's distance value was <1 (*Di* = 0.22, for sample 18), which means that the model had no outliers or excessively influential cases.

Table VIII – Standardized coefficients of the variables in the linear regression model for habitat types, before and after AIC based stepwise selection (N = 23).

	Linear regression models			
	all variables		forward and backward selection	
Variables	standardized coefficients	p	standardized coefficients	p
Open	1.55	0.02		
Shrubs	0.71	0.04		
Riparian trees	0.79	0.03		
Non riparian trees	0.81	0.02		
Water	0.51	0.07		
Reeds	0.92	0.00	0.49	0.01
Sedges/rushes	0.95	0.01	0.35	0.06
Ricefields	1.55	0.01		
Urban	1.11	0.01		
	$R^2 = 0.671$		$R^2 = 0.395$	

After including the interactions involving these selected habitats and remaining ones and going through a new round of AIC-based variable selection, the model retained only the habitat Reeds and the interaction between Reeds and Ricefields, while Sedges/Rushes was no longer retained in this final model (Table IX). In sites with ricefields, the abundance of waxbills increases more with the percentage of reeds than in sites without ricefields (Figure). The model including the interaction between reeds and ricefields explains slightly more variation (R^2 = 41.11%) than the model that does not include the interaction (R^2 = 39.50%). There were no studentized residuals with value above ± 1.96, and the highest Cook's distance value was 1.267, again for sample 18 (Alcácer do Sal). However, the sample values did not result from data collection or data entry aerrors, thus it was retained.

Table IX - Standardized coefficients of the variables in the linear regression model for habitat types, after including interactions between variables and AIC based stepwise selection (N = 23).

	Model including interactions	
Variables	standardized coefficients	p
Reeds	0.23	0.30
Reeds*Ricefields	0.47	0.04
	R^2 = 0.411	

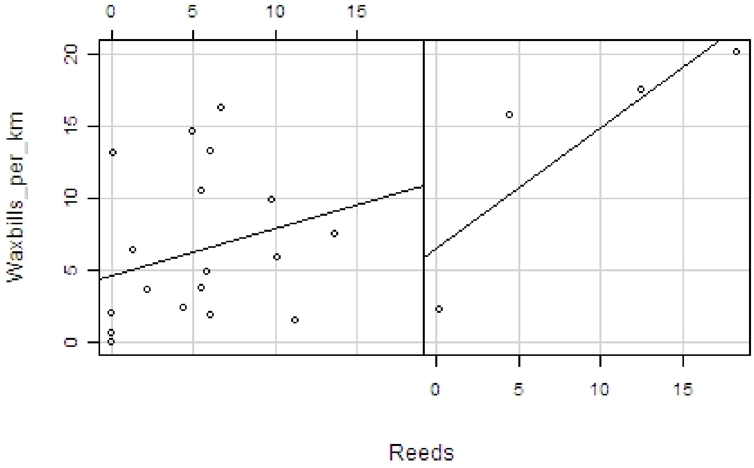

Figure 2 – Plots of the abundance of common waxbills (Waxbills per km) against the percentage of reeds (Reeds) for sites with ricefields (left panel) or no ricefields (right panel). Regression lines are included in each plot.

3.3 – Ecological niche characterization

Table A on Appendix I has the species values for all categorical niche variables (see also note on the following page for the description of the scales of the categorical variables). The NMDS analysis of niches had a stress inferior to 0.1 on two-dimensional space, which means that the representation the data on two axes is little distorted. Figure 3 shows the two-dimensional space of the NMDS analysis, where the common waxbill, *Estrilda astrild* (Est ast), occupies one of the most marginal positions in the ecological space. The average Euclidean distances among native species (10.88, N = 26) was significantly smaller than the average distance between waxbills and native species (13.78, N = 1; T-test, t = 3.30, df = 25, p = 0.003). The closest species to waxbills in this analysis was *Emberiza schoeniclus* (Emb sch), and the euclidean distance between the two species was 6.55 (Figure 3).

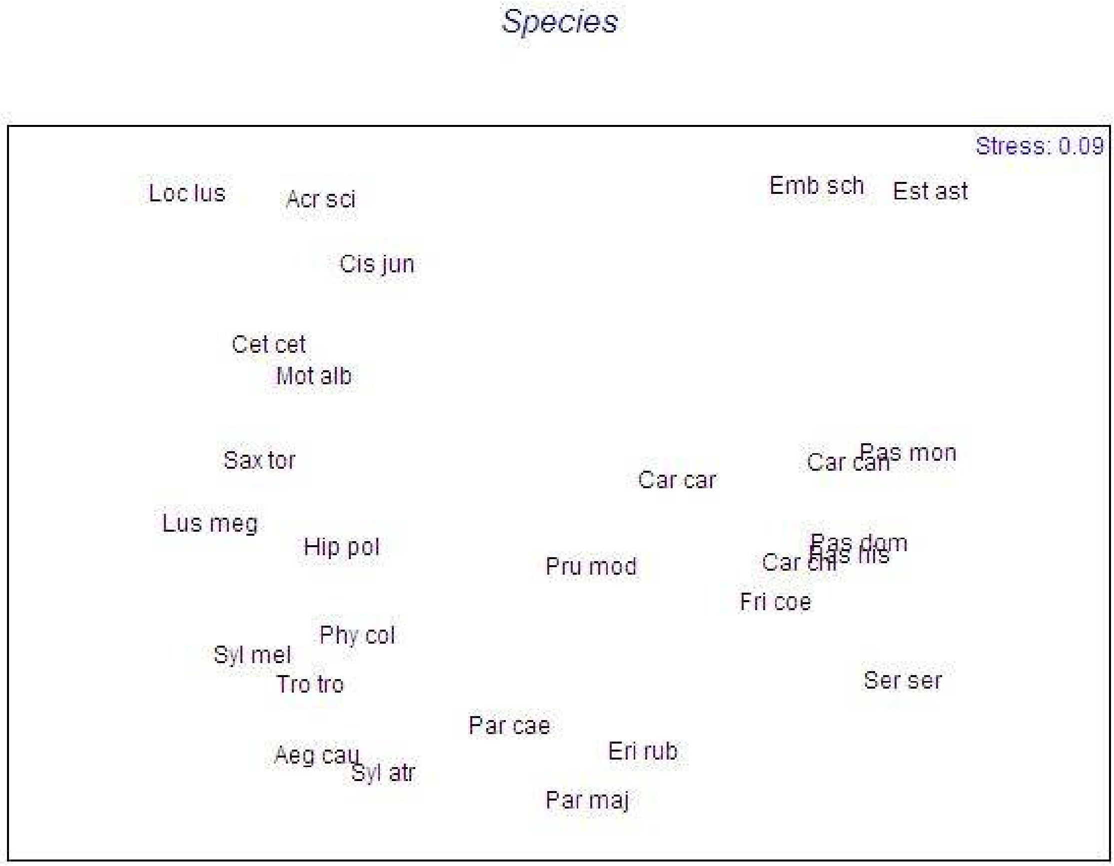

Figure 3 – plot of the NMDS of the comparison of the ecological niches of the common waxbill and native passerine species. For correspondence of species names, see Table II.

If species ecologically more similar to waxbills co-occurred more often with them, this could augment the potential for inter-specific competition. But ecologically more similar species, as evaluated by the Euclidean distances above, did not tend to occur more closely with waxbills, as evaluated by the correlation coefficients of abundances within- or among-sites (within-sites: r = 0.21, n = 25, p = 0.31; among-sites: r = -0.32, n = 25, p = 0.13, and r = -0.37, n = 25, p = 0.07, for the breeding and post breeding season, respectively).

The two first Principal Components (PC) of a PCA analysis returned a cloud of species very similar to the NMDS (cf. Figure 3 and Fig. 4), and therefore these PCs can be used to interpret the ecological similarities and differences between waxbills and the native species. The eigenvalues and percentage of explained variance of the first three principal components are summarized in Table X.

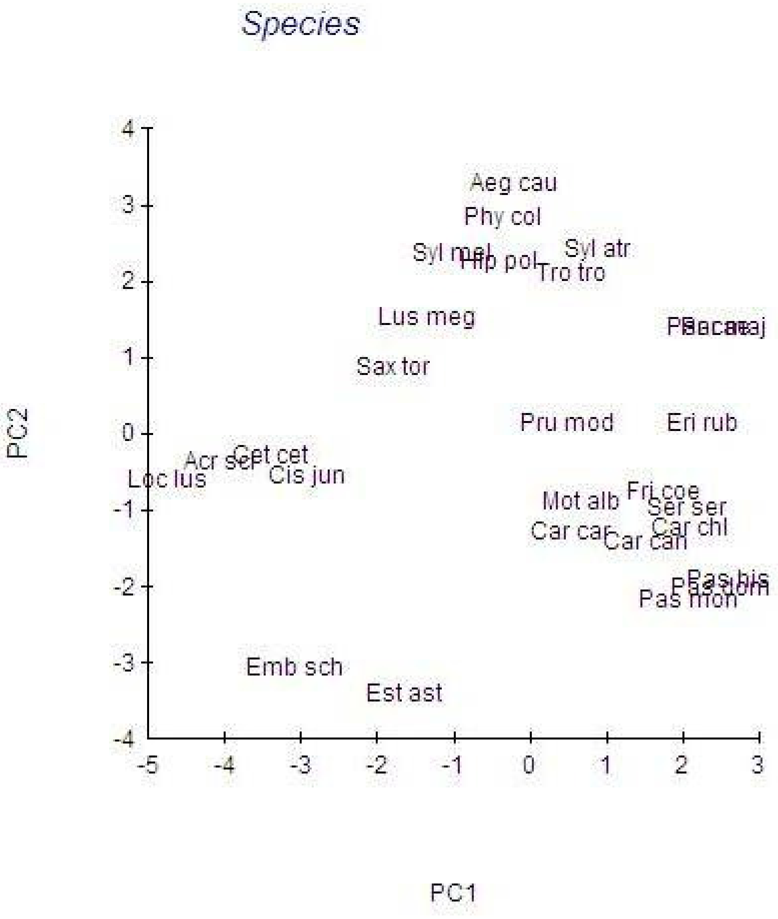

Figure 4 – First two axis of the principal component analysis of the ecological niches of bird species. For correspondence of species names, see Table II.

The variables with stronger loadings on that exerted more influence in PC1 (|r|>0.3) were nesting height, nesting water dependence, presence of water (on foraging grounds), and (habitat) anthropogenization (Table X). The loadings of all these variables are positive. These variables are related to the nesting ecology, foraging behaviour and habitat selection of the bird species. The variables with stronger loadings on PC2 (|r|>0.3) were related to diet, i.e., seeds (with a negative loading), insects and invertebrates, fruits and other plant material, and bill index (all three with positive loadings). PC3 was most strongly influenced by two variables, type of nest construction (with a positive loading) and the support structure of the nest (with a negative loading), and therefore it mostly provides additional information on nesting habits.

Table X – Eigenvalues, percentage variation and eigenvectors (i.e., coefficients in the linear combinations of variables) making up the first three PC's of the principal component analysis.

		PC1	**PC2**	**PC3**
	Eigenvalues	4.94	3.41	1.95
	% variation	32.9	22.7	13
	Cumulative % variation	32.9	55.6	68.7
Variable	vegetation density	0.256	0.223	0.209
	water proximity	0.28	0.192	0.342
	antropogenization	0.303	-0.255	-0.074
	Breeding phenology	-0.183	-0.3	-0.062
	type of construction	-0.25	0.024	0.499
	nesting water dependence	0.324	0.216	0.027
	nesting height	0.36	-0.071	-0.102
	support stucture	0.17	-0.092	-0.579
	seeds	0.214	-0.416	0.232
	fruits and other plant material	0.189	0.324	-0.217
	insects and invertebrates	-0.213	0.373	-0.204
	foraging height	0.179	0.267	0.127
	presence of water	0.365	0.219	0.011
	Bill index	-0.296	0.316	-0.209
	LOG weight	0.156	-0.247	-0.179

Looking at the principal component scores (Table XI), we can see that for the first axis of the PCA, *Estrilda astrild* has a score of –1.655, among birds such as *Saxicola torquata* and *Luscinia megarhynchos*. On the second axis, which is related to birds' diet and bill index, *Estrilda astrild* is the more marginal species, what a score of

–3.412, and the closest species is *Emberiza schoeniclus*. On the third axis, *Estrilda astrild* has a score of 1.138, among birds such as *Phylloscopus collybita* and *Prunella modularis*.

Table XI – principal component scores for all the species, for the first three principal components.

Species	**Score1**	**Score2**	**Score3**
Acr sci	-4.062	-0.358	-0.397
Aeg cau	-0.198	3.285	0.673
Car can	1.531	-1.418	1.710
Car car	0.539	-1.262	0.627
Car chl	2.087	-1.213	1.597
Cet cet	-3.410	-0.280	-0.492
Cis jun	-2.923	-0.535	0.046
Emb sch	-3.068	-3.051	0.338
Eri rub	2.269	0.140	-1.682
Est ast	-1.655	-3.412	1.138
Fri coe	1.755	-0.755	1.726
Hip pol	-0.395	2.276	0.683
Loc lus	-4.748	-0.599	-0.872
Lus meg	-1.347	1.536	-0.101
Mot alb	0.672	-0.877	-4.738
Par cae	2.357	1.399	-1.583
Par maj	2.547	1.404	-0.496
Pas dom	2.505	-2.017	-1.354
Pas his	2.604	-1.915	-0.804
Pas mon	2.095	-2.159	-0.096
Phy col	-0.357	2.840	1.170
Pru mod	0.499	0.141	0.979
Sax tor	-1.776	0.882	0.079
Ser ser	2.056	-0.948	2.018
Syl atr	0.887	2.420	0.794
Syl mel	-1.017	2.360	-0.005
Tro tro	0.552	2.119	-0.958

3.4 – Other aspects of the niche of the common waxbill

3.4.1 – Waxbill breeding phenology

Females with incubation patch were found throughout the sampling period (March to September) and the proportion of females with incubation patch peaked in May (61%; Figure 5). The birds start breeding at least in March, as some females already have a breeding patch, and breed at least until September, since there are still some females with a brood patch. The decrease in the percentage of females with a breeding patch after May may have been accentuated by the appearance of first year females already indistinguishable from adult plumage, but it nevertheless remained above 15% until the end of the sampling period (September; Figure 5).

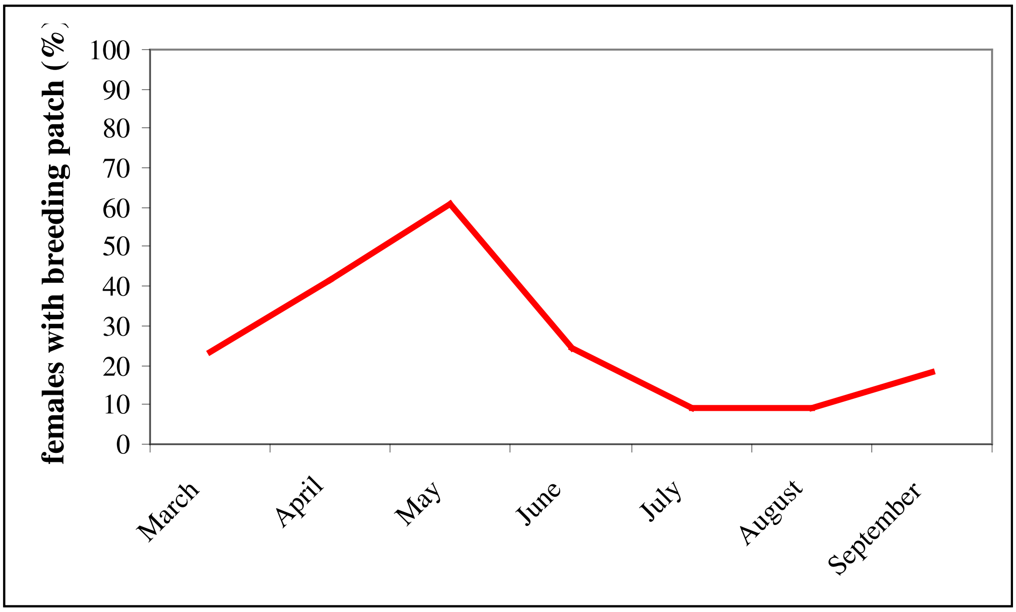

Figure 5 – variation in the percentage of female *Estrilda astrild* with an incubation patch, from March to September, averaged by month. N = 249 females; March, n = 17; April, n = 24; May, n = 28; June, n = 33; July, n = 32; August, n = 55; September, n = 60.

3.4.2– Seasonal variation in waxbill diet

Over 90% of the faecal samples of common waxbills was made up of seeds, while other plant material, arthropods, minerals and undetermined items accounted for less than 5% each. Seeds made up 92.97% ± 16.03 SD (N = 308 birds) of the faecal material, other plant material accounted for 3.02% ± 10.85 SD, arthropods for 1.19% ± 6.64 SD, grit minerals for 2.22% ± 5.88 SD and undetermined items made up 0.58% ± 6.37 SD of the material.

The percentage of different items in the faecal samples of common waxbills varied slightly along the course of the breeding season (Figure 6), with the proportion of seeds reaching a minimum of 86.35% ± 29.15 SD in June, and a corresponding maximum in the percentage of arthropods in the same month of 4.59% ± 16.56 SD.

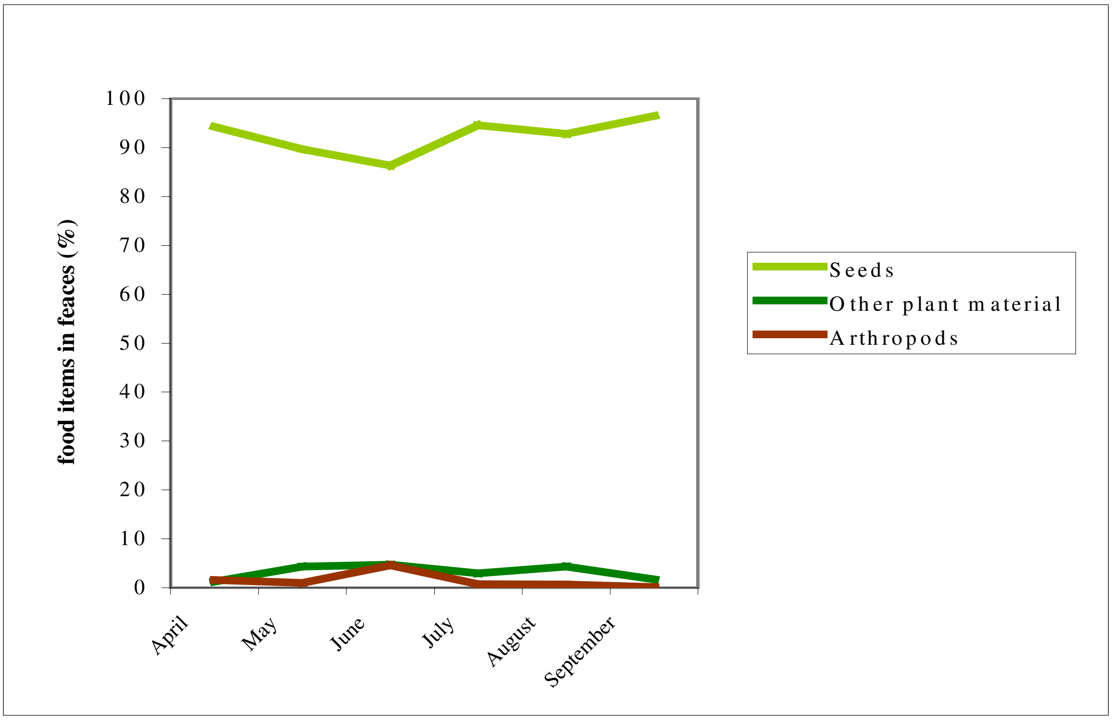

Figure 6 – Seasonal variation in the percentage of the items found in the feaces of the common waxbill, from April to September, averaged per month. N = 308; April, n =52; May, n = 42; June, n = 37; July, n = 34; August, n = 64; September, n = 79.

The proportion of insects in waxbill diet peaked in June (Figure 6), which is one month after the highest proportion of females with brood patch (Figure 5). Comparing the proportion of insects in the diet between June (4.59% ± 16.56 SD) and both the beginning and end of the sampling period (April, 1.54% ± 4.56 SD and September, 1.71% ± 3.19 SD), arthropods were significantly more abundant in the June diets than in September (T-test, t = -2.29, df = 114, p = 0.02), but not than April (T-test, t = 1.30, df = 87, p = 0.20).

Chapter 4 Discussion

I found that the invasive common waxbill occupies one of the most marginal niches in the passerine communities across it geographic distribution in continental Portugal. Quantitative analyses of habitat suggest a quite eclectic habitat usage by waxbills, as long as plants associated with water are present, which may explain why they do not tend to co-occur with ecologically more similar species. Overall, this suggests that the common waxbill's successful invasion results from exploring a vacant niche in a non-saturated community and that negative effects on other passerines due to interspecific competition are generally unlikely. An already endangered passerine, *Emberiza schoeniclus*, is the ecologically most similar native to waxbills, and I suggest that conservation attention regarding possible effects of waxbills on the native fauna should focus on this threatened species.

4.1 – Relations between the common waxbill and the native avian community

Waxbills were generally more abundant in sites with more reeds and other plants associated with water, or with ricefields containing reeds on the edges. Reeds are used by the common waxbill for roosting and breeding, although it is also known to breed in other types of habitat, such as riparian vegetation and farmland areas with hedges (Reino & Silva, 1998). Common waxbills can also be found in ricefields when these are planted with rice and filled with water (pers. obs.), possibly due to the growth of seed grasses such as *Echinocloa crus-galli*, from which the waxbills feed (Höller & Teixeira, 1983; pers. obs.), and due to the presence of reeds on the edges. All other habitat types considered also tended to be positively related to waxbill abundances, suggesting that they favour heterogeneous habitats, as long as appropriate roosting sites such as reeds and shrubs (Reino & Silva, 1998; Guerrero et al., 1989) exist in the proximity. These models, however, explain less than 50% of the variation in the abundance of waxbill, which means that there are other factors, such as abiotic constraints (i.e., temperature and altitude), or food availability, influencing it.

Possibly because of this eclectic use of habitats, abundances of common waxbills were generally not related to those of native passerine species. At the within-site level, waxbill abundances was apparently strongly positively related to those of *Locustella luscinioides,* in the two sites where this species was recorded, i.e., close to large coastal reedbeds. The remaining low correlations with abundances of other species suggest that there are no strong associations between the common waxbills and the native bird species censused. At the among-sites level too, which covered the entire extent of its distribution range in Portugal, I observed only weak covariation between the abundances of waxbills and other species. Here, results were different for breeding and post-breeding season, the waxbill abundance being most strongly related to *Acrocephalus scirpaceus* in the breeding season, and to *Passer domesticus* in the post-breeding season. This may result from different selection of habitat by the common waxbills in the breeding and post breeding season. For example, in the breeding season the population is mostly made up of adults, which stay close to the nesting sites, and in the post-breeding season flocks composed of adults and juveniles may occupy good feeding habitat, which other granivorous species may also use. In fact, the censuses in the breeding season started in March, when the waxbills are still probably selecting nesting sites and building the nest, whereas the censuses of the post-breeding season were carried out from August to September, and the selected sites were those where flocks of waxbills had been previously reported. No suggestive negative relations between abundances of common waxbills and native passerines were found, either at the local or regional level.

In the analysis of niche similarities, the common waxbill occupies a marginal position, with a mean distance from native species significantly larger than the distances between native species. Some coexistent native bird species have even more similar ecological niches (e.g., *Passer domesticus* and *Passer hispaniolensis*) than the common waxbill has with any native species. This suggests that the common waxbill may occupy a vacant niche in the native avian community.

The niche dimensions that most separate the common waxbill from the native species are those related to its diet and bill morphology, as seen on the principal component scores. These dimensions are the same ones that separate the reed bunting, *Emberiza schoeniclus*, from the remaining native species. Overall, there are partial ecological similarities to different species, but not to the same species on several niche dimensions, and the niches are quite distinct when considered as a whole. For example, in relation nesting and foraging ecology and habitat preferences, the common waxbill is close to mixed habitat birds such as *Saxicola torquata* and *Luscinia megarhynchos*. In relation to other aspects of nesting ecology, the common waxbill is close to birds generally associated with trees such as *Phylloscopus collybita* and *Prunella modularis.*

The closest species to the waxbill, the reed bunting, has a considerably smaller distance from the common waxbill than from any of the other native species. These two species have somewhat similar diet, foraging behaviour, habitat selection and nesting ecology. Both the reed bunting and the common waxbill eat seeds, but there is considerable variation between them, since the waxbill eats mainly small grass seeds of Poaceae family (Goodwin, 1982; Oren & Smith, 1981; Rowlands et al., 1998; Höller & Teixeira, 1983), whereas the reed bunting's diet is based mainly on seeds and plant material from several different plant families, in winter, and on invertebrates, during breeding season (Hillcoat, 1994; Prys-Jones, 1977). The reed bunting selects breeding sites with dense low vegetation, associated with intense soil moisture, such as reedbeds (Nicholson 1994, Snow 1994), and also mixed habitats, but not extensive flooded reedbeds. Its association with water is indirect, vegetation type choice being predominant (Nicholson, 1994; Matessi, 1999), and more strict than that of the common waxbill, in relation to habitat. However, reed buntings have recently been spreading to agricultural lands, at least in some parts of its occupied range (Brickle & Peach, 2004). Regarding their nesting ecology, there are some similarities between the two birds, as the nest of the reed bunting is usually on ground or plants associated with water (Witherby et al. 1938; Haukioja 1970; Blumël 1982; Hermann 1983), and the common waxbill tends to nest close to water sources and will use shrubs, since it favours cavities in thick vegetation (Goodwin, 1982; Oren & Smith, 1981; Rowlands et al., 1998; Someren, 1956). Thus, their ecological niches appear similar to some extent. Adding to this, the subspecies of reed bunting that breeds in Portugal, *Emberiza schoeniclus lusitanica*, occupies a very limited area, in reedbeds where the waxbill can also be found (e.g., Salreu wetlands) and has reduced genetic variation and a small effective population size (Kvist et al., 2011). Therefore, due to the vulnerable status of reed buntings and some ecological similarity to waxbills, the potential for interspecific competition or interference between these two bird species merits further investigation.

If ecologically similar species would co-occur more with the common waxbill, the probability of interspecific competition to happen would increase, such as the consequent potential for harmful interactions. However, I found no evidence that ecologically more similar species to the common waxbill tend to co-occur with it, since correlations between niche similarity and co-occurrence with native birds were neither strong nor significant.

The marginal position of the common waxbill within the ecological space of the native community, its use of diverse habitat types, and the lack of association with other bird species suggest that the success of this invasion is probably due to the exploration of a vacant ecological niche, rather than due to efficient competition. Not all natural communities are saturated (Friedley et al., 2007; Sax et al., 2007; Shea & Chesson, 2002; Levine, 2008), and even saturated communities are not rigidly structured and may change over time, particularly after disturbance (Cornell and Lawton, 1992). In addition, Blackburn and Duncan showed that the outcome of bird introductions is not predicted by features generally related to biotic resistance but, instead, it depends on the combination of species traits and location (Blackburn & Duncan, 2001). The common waxbill profits from human-modified habitats, such as agricultural patches and ricefields, and from introduction of exotic plants which it uses for food or shelter, such as *Echinocloa* grasses or *Arundo* reed stands (Höller & Teixeira,1983). It is possible that a combination of unused natural resources, human modification of habitats and the introduction of essential support species was a key factor in allowing for the success of the invasion by the common waxbill in Portugal. Although niche similarity may not be a sufficient condition for interspecific competition to occur when resources are not limiting (Schroener, 1982), it may lead to competition when environmental conditions exert selective pressure on populations. The similarities between the ecological niche of the common waxbill and those of the native species are lower than among the native species themselves, and thus strong competition rather unlikely, except in the case of *Emberiza schoeniclus*.

4.2 - Other aspects of the niche of the common waxbill

I also provided detailed information on breeding phenology and diet of waxbills on their invasive range. Waxbills bred throughout the entire sample period (March to September), as females with brood patches were found throughout, which agrees with previous reports that waxbills in Portugal and Spain breed from February to November (Rufino, 1989; Tenreiro & Petronilho, 2002). The proportion of females with a brood patch peaked during May, suggesting that the reproductive peak of the common waxbills is between the months of April and June. This agrees with previous reports of peak breeding in waxbill in April–July for the Algarve and Trás-os-Montes regions (Bolton 1986; Vowles and Vowles 1987; Campinho et al. 1991). The decrease in the percentage of females with a breeding patch after May may have been accentuated by the appearance in the population of first year females already indistinguishable from adult plumage. The percentage of females that were born in previous years and exibit a breeding patch might thus be higher, and the peak of the breeding season for the common waxbill might be longer than the observed peak in May.

To my knowledge, the seasonal variation of the common waxbill's diet in Western Paleartic has not been studied; the existing diet studies are either in captivity or in locations where it was introduced to in other parts of the world (Goodwin, 1982; Oren & Smith, 1981; Silva & Oren, 1990; Moulton & Ferris, 1991; Rowlands et al., 1998). Regardless of the location, the importance of small grass seeds in the waxbill's diet appears constant. In fact, during fieldwork, waxbills were often observed clinging to grass stems and picking up very small seeds from the flowering heads (pers. obs.), and also seen feeding on *Echinochloa crus-galli*, in accordance with the the findings of Höller & Teixeira (1983). There was little variation in the proportion of seeds in waxbill diets from April to September. Seeds were the predominant item in faecal analysis throughout this period, complemented with some arthropods and grit. Although a minor component of the diet, arthropods were about three times more abundant after the peak of breeding season (June), compared to late breeding season (September). Hence, variation in the proportion of arthropods might be related to feeding offspring, but it could also be a consequence of decreasing insect abundances after the dry Summer weather (Bryant, 1975; Visser et al. 1998). It is not clear how waxbills feed their chicks, but some suggested that they might feed them insects, while others state that the parents regurgitate food items to their young (Someren, 1956; Goodwin, 1982).

4.3 – Conclusions

Several reasons might explain the success of the common waxbill's invasion of mainland Portugal. The capacity of breeding during a large part of the year, its consumption of rather common grass seeds, and their eclectic habitat preferences are probably important factors. Adding to this, I showed here that the common waxbill's ecological niche occupies a marginal position in relation to the native passerine community, and it does not tend co-occur with ecologically more similar species, suggesting that it explores a vacant niche in the avian community. To some extent, this vacant niche might have been created by human modification (outras refs, ler artigo europa), such as farming or introduction of exotic grasses that serve as food. It is possible that a combination of unused natural resources, human modification of habitats and the introduction of essential support species combined in allowing for the success of the invasion by the common waxbill in Portugal. Therefore, the common waxbill seems to have little in common with most native passerines, and competition with native passerines seems thus rather unlikely. However, *Emberiza schoeniclus* has an ecological niche quite proximal to that of the common waxbill, and the subspecies that breeds in Portugal is threatened. Therefore, conservation efforts should be focused on possible negative interactions between these two species.

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Appendix I

Table A – correspondence between censused site number, site name and geographical coordinates.

#	**Site**	**Geographical coordinates (º ')**	
1	Apúlia	41°29'N	8°46'W
2	Salreu	40°43'N	8°34'W
3	Elvas	38°52'N	7° 3'W
4	Almeirim	39°14'N	8°36'W
5	Arzila	40°11'N	8°33'W
6	Caminha	41°52'N	8°49'W
7	Tua	41°12'N	7°25'W
8	Santo André	38° 5'N	8°47'W
9	Celorico da Beira	40°39'N	7°22'W
10	Abicada	37° 9'N	8°35'W
11	Rio Seco	37°13'N	7°28'W
12	Alcochete	38°43'N	8°54'W
13	Paramos	40º58'N	8º38'W
14	Salinas da Junqueira	39º52'N	8º51'W
15	Paúl	40º11'N	7º38'W
16	Évora	38º37'N	7º50'W
17	Quarteira	37º03'N	8º03'W
18	Alcácer do Sal	38º22'N	8º31'W
19	Óbidos	39º23'N	9º12'W
20	Toulica	39º54'N	7º04'W
21	Colares	38º48'N	9º28'W
22	Lagoa dos Patos	38º09'N	8º05'W
23	Odemira	37º36'N	8º39'W

Table B – Scores of the bird species analysed for the ecological niche characterization and comparison. Sample sizes are indicated for bill index and weight based on field data; L = data from Cramp.

Species	**Habitat**			**Breeding phenology**	**Nesting ecology**				**Diet**			**Foraging substrate**		**Bill index**		**Weight**	
Species	vegetation density	water proximity	antropogenization	Breeding phenology	type of construction	nesting water dependence	nesting height	support stucture	seeds	fruits and other plant material	insects and invertebrates	foraging height	presence of water	Bill index (f)		Weight (f)	
name	open - medium - dense	wetland - riparian vegetation - dryland	natural - anthropogenized	months	cavity - nest	above water - dry soil	ground - low height - high height	vegetation - rock	never - ocasionally - seasonally - year round	never - ocasionally - seasonally - year round	never - ocasionally - seasonally - year round	ground/grass - shrubs/reeds - tree height	water - dryland	bill lenght (mm) / bill depth (mm)	sample size	mass (g)	sample size
Acr sci	2.00	1.50	1.00	6.50	2.00	1.50	1.50	1.00	2.00	1.00	4.00	1.50	1.50	4.28	3	11.85	21
Aeg cau	3.00	2.50	1.00	3.75	2.00	2.00	2.00	1.00	1.00	3.00	4.00	2.50	2.00	2.93	3	7.50	1
Car can	3.00	3.00	1.50	6.00	2.00	2.00	2.00	1.00	4.00	2.00	2.00	1.50	2.00	1.44	5	16.72	5
Car car	1.50	2.50	1.50	4.40	2.00	2.00	3.00	1.00	3.00	1.00	3.00	1.00	2.00	1.87	11	13.54	12
Car chl	3.00	3.00	1.50	5.00	2.00	2.00	3.00	1.00	4.00	1.00	3.00	2.00	2.00	1.33	15	23.18	15
Cet cet	2.00	1.50	1.00	5.00	2.00	1.50	2.00	1.00	1.00	1.00	4.00	1.00	1.50	3.30	9	13.90	10
Cis jun	1.50	2.00	1.50	5.57	2.00	2.00	1.00	1.00	2.00	1.00	4.00	1.00	1.50	3.25	16	8.51	15
Emb sch	2.00	1.00	1.00	6.00	2.00	1.00	1.50	1.00	4.00	1.00	3.00	1.50	1.50	1.52	3	18.60	L
Eri rub	3.00	2.50	1.50	3.75	1.00	2.00	2.50	1.50	3.00	3.00	3.00	1.00	2.00	2.28	1	15.23	4
Est ast	1.50	2.00	1.50	7.09	2.00	1.50	2.00	1.00	4.00	1.00	2.00	1.50	1.50	1.38	514	8.02	513
Fri coe	3.00	3.00	1.50	4.40	2.00	2.00	2.50	1.00	4.00	1.00	3.00	2.00	2.00	1.63	1	19.45	2
Hip pol	3.00	3.00	1.00	6.00	2.00	2.00	2.50	1.00	1.00	2.00	4.00	2.50	2.00	3.52	12	10.70	12
Loc lus	2.00	1.00	1.00	6.00	2.00	1.00	1.50	1.00	1.00	1.00	4.00	1.50	1.50	4.03	2	13.90	8
Lus meg	2.00	3.00	1.00	5.50	2.00	2.00	1.00	1.00	1.00	3.00	4.00	1.00	2.00	3.13	7	18.70	5
Mot alb	1.50	1.50	1.50	5.50	1.00	2.00	3.00	2.00	1.00	2.00	4.00	1.00	2.00	2.87	4	23.60	L
Par cae	3.00	2.50	1.50	5.00	1.00	2.00	3.00	1.50	2.00	3.00	4.00	3.00	2.00	1.89	4	9.68	5
Par maj	3.00	2.50	1.50	3.75	1.00	2.00	3.00	1.00	3.00	3.00	4.00	3.00	2.00	2.15	5	16.40	17
Pas dom	2.00	2.50	1.50	5.14	1.00	2.00	2.50	1.50	4.00	2.00	2.00	2.00	2.00	1.59	18	26.95	1
Pas his	3.00	2.00	1.50	5.50	1.50	2.00	3.00	1.50	4.00	2.00	2.00	2.00	2.00	1.59	1	25.60	2
Pas mon	2.00	3.00	1.50	6.00	1.00	2.00	3.00	1.00	4.00	2.00	2.00	1.00	2.00	1.61	2	19.05	5
Phy col	3.00	3.00	1.00	4.50	2.00	2.00	2.00	1.00	1.00	2.00	4.00	2.50	2.00	2.94	2	7.28	4
Pru mod	2.33	3.00	1.50	3.75	2.00	2.00	2.00	1.00	3.00	1.00	4.00	1.50	2.00	2.37	2	17.78	4
Sax tor	1.50	2.50	1.00	4.20	2.00	2.00	1.50	1.00	1.00	1.00	4.00	1.00	2.00	3.10	9	15.51	10
Ser ser	3.00	2.50	1.50	3.75	2.00	2.00	3.00	1.00	4.00	1.00	2.00	2.00	2.00	1.29	13	10.82	12
Syl atr	3.00	3.00	1.00	4.40	2.00	2.00	2.50	1.00	1.00	3.00	3.00	3.00	2.00	2.93	17	16.47	27
Syl mel	2.00	2.50	1.00	3.75	2.00	2.00	1.50	1.00	1.00	3.00	4.00	1.50	2.00	3.07	23	11.50	32
Tro tro	3.00	2.00	1.50	4.20	1.00	2.00	2.50	1.00	1.00	2.00	4.00	2.50	2.00	3.64	5	8.96	7

Numerical correspondence between scores of the bird species analysed for the ecological niche characterization and each category (Table) are as follows: for vegetation density, open =1, medium = 2, dense = 3; for water proximity, wetland = 1, riparian vegetation = 2, dryland = 3; for anthropogenization, natural = 1, anthropogenized = 2. For breeding phenology, each number corresponds to the average of the numbers of the calendar months in which the bird breeds. Nesting ecology scores are given as follows: for type of construction, cavity = 1, nest = 2; for nesting water dependence, above water = 1, dry soil = 2; for nesting height, ground = 1, low height = 2, high height = 3; for support structure, vegetation = 1, rock = 2. For diet, each item type was scored as never = 1, ocasionally = 2, seasonally = 3, year round = 4. Foraging substrate categories are given as follows: for foraging height, ground/grass = 1, shrubs/reeds = 2, tree height = 3; for presence of water, water = 1, dryland = 2. Bill index results from dividing bill lenght in milimeters for bill depth in milimeters. Weight is given in grams.

Table C – similarity matrix with euclidean distances between ecological niche scores of the bird species.

	Acr sci	*Aeg cau*	*Car can*	*Car car*	*Car chl*	*Cet cet*	*Cis jun*	*Emb sch*	*Eri rub*	*Est ast*	*Fri coe*	*Hip pol*	*Loc lus*	*Lus meg*
Acr sci														
Aeg cau	13.17													
Car can	14.06	13.93												
Car car	12.52	12.40	8.47											
Car chl	14.37	12.94	5.96	5.74										
Cet cet	5.49	10.43	14.44	10.96	13.53									
Cis jun	5.17	12.24	12.58	10.35	12.80	6.02								
Emb sch	11.46	16.88	9.05	10.95	9.94	13.36	11.33							
Eri rub	14.76	9.22	9.37	8.98	9.04	13.08	13.18	14.11						
Est ast	13.33	18.71	7.99	11.00	10.49	15.37	12.70	6.55	15.41					
Fri coe	14.30	12.24	6.49	6.18	2.18	13.51	12.52	10.56	8.45	11.62				
Hip pol	8.66	6.67	12.10	10.66	11.58	6.61	8.74	14.16	10.94	14.95	11.55			
Loc lus	3.76	13.30	16.45	14.55	16.46	5.12	7.45	13.69	16.32	15.88	16.47	9.02		
Lus meg	10.06	8.48	13.09	12.41	14.37	8.54	8.12	15.26	11.29	16.14	14.04	7.18	10.70	
Mot alb	10.05	11.09	14.25	10.42	13.60	7.28	9.51	14.47	11.23	15.35	14.01	8.58	10.08	9.59
Par cae	13.60	6.85	10.96	10.18	9.65	11.64	12.68	13.94	7.51	15.13	9.76	7.69	14.31	10.73
Par maj	15.22	7.57	11.44	10.08	9.13	13.45	14.09	14.62	6.34	16.49	8.58	10.22	16.36	12.68
Pas dom	14.60	13.75	5.41	7.67	6.19	14.85	13.32	10.05	8.24	9.38	6.65	12.53	16.94	14.06
Pas his	14.36	13.41	5.06	7.99	5.56	14.28	13.70	9.39	8.17	9.49	6.38	12.15	16.38	14.54
Pas mon	14.65	15.46	5.33	7.58	7.32	14.90	13.34	10.43	9.59	8.18	8.39	13.10	17.14	14.08
Phy col	11.12	3.97	12.63	10.93	11.39	8.47	10.13	15.44	10.00	16.79	10.86	3.79	11.49	7.72
Pru mod	12.23	9.69	10.09	6.12	6.95	10.39	9.56	12.45	8.29	14.29	5.70	9.62	14.06	11.06
Sax tor	8.82	9.28	14.30	10.06	13.10	5.66	6.38	15.21	12.29	16.58	12.60	7.07	9.49	7.04
Ser ser	16.88	13.99	7.64	7.76	4.09	16.00	15.54	12.39	9.45	12.80	3.93	13.79	18.91	16.77
Syl atr	13.46	4.29	12.39	11.82	11.89	11.35	13.02	16.52	9.37	17.23	11.51	5.97	13.85	9.29
Syl mel	12.09	4.40	14.24	11.95	13.92	9.35	10.36	16.75	9.51	18.42	13.20	7.43	12.42	5.60
Tro tro	11.06	5.57	14.44	11.93	12.85	8.54	11.07	16.34	9.90	18.07	12.35	5.82	11.07	9.97

C – similarity matrix with euclidean distances between ecological niche scores of the bird species (cont.).

	Mot alb	*Par cae*	*Par maj*	*Pas dom*	*Pas his*	*Pas mon*	*Phy col*	*Pru mod*	*Sax tor*	*Ser ser*	*Syl atr*	*Syl mel*	*Tro tro*
Acr sci													
Aeg cau													
Car can													
Car car													
Car chl													
Cet cet													
Cis jun													
Emb sch													
Eri rub													
Est ast													
Fri coe													
Hip pol													
Loc lus													
Lus meg													
Mot alb													
Par cae	9.49												
Par maj	12.12	4.70											
Pas dom	12.84	9.50	9.40										
Pas his	12.84	9.27	9.44	3.70									
Pas mon	12.99	11.45	11.95	4.70	5.84								
Phy col	10.22	6.98	8.60	12.94	12.68	14.21							
Pru mod	11.79	9.52	8.36	9.90	10.33	11.21	8.24						
Sax tor	8.78	11.61	12.74	14.49	14.87	14.85	7.15	8.12					
Ser ser	15.81	11.20	9.68	7.21	6.07	9.11	13.13	8.82	15.43				
Syl atr	11.33	6.44	7.83	12.11	11.80	13.78	4.74	10.44	10.48	12.77			
Syl mel	9.92	8.95	9.64	14.12	14.40	15.25	5.82	9.55	7.14	15.42	6.90		
Tro tro	8.94	7.13	8.22	13.47	13.06	14.98	5.22	9.81	8.75	14.10	6.60	7.37	