Universidade de Évora - Instituto de Investigação e Formação Avançada

Programa de Doutoramento em Biologia

Tese de Doutoramento

Network analysis of connectivity thresholds in fragmented landscapes. A multi-species approach using birds in pine and oak forests

Pedro Alexandre Marques da Silva Salgueiro

Orientador(es)	António Mira
	João Eduardo Rabaça
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Thesis carried out by: Pedro Alexandre Marques da Silva Salgueiro
Host institution: CIBIO-UE – Research Center in Biodiversity and Genetic Resources – Pole of Évora – Research Group in Applied Ecology
Institution conferring the degree: University of Évora

<u>Supervision</u>:

João Eduardo Morais Gomes Rabaça

LabOr – Laboratory of Ornithology; [1]MED - Instituto Mediterrâneo para a Agricultura, Ambiente e Desenvolvimento, Universidade de Évora; Department of Biology, School of Sciences and Technology, University of Évora.

António Paulo Pereira de Mira

UBC – Conservation Biology Lab; [1]MED - Instituto Mediterrâneo para a Agricultura, Ambiente e Desenvolvimento, Universidade de Évora; Department of Biology, School of Sciences and Technology, University of Évora.

Sara Maria Lopes dos Santos

UBC – Conservation Biology Lab; [1]MED - Instituto Mediterrâneo para a Agricultura, Ambiente e Desenvolvimento, Universidade de Évora; Department of Biology, School of Sciences and Technology, University of Évora.

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[1] Since January 2020, MED - Instituto Mediterrâneo para a Agricultura, Ambiente e Desenvolvimento has replaced the former ICAAM – Institute of Mediterranean Agricultural and Environmental Sciences, and CIBIO-UE – Research Center in Biodiversity and Genetic Resources, Pole of Évora – Research Group in Applied Ecology.

This thesis was prepared as a compilation of scientific articles published or submitted for publication in journals registered in the Web of Science (WoS) that integrate some of the central chapters. These articles were carried out in collaboration with other authors. However, the candidate clarifies that he led all phases of the work of each article, including its conception, experimental design, data collection, analysis and writing.

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Para a Inês,

Que possas continuar a contemplar a natureza
Em todo o seu esplendor e magnificência,
Como os teus pais, tios e avós antes de ti.

“Do pinhão, que um pé-de-vento arrancou ao dormitório da pinha-mãe, e da bolota, que a ave deixou cair no solo, repetido o acto mil vezes, gerou-se a floresta. Acudiram os pássaros, os insectos, os roedores de toda a ordem a povoá-la. No seu solo abrigado e gordo nasceram as ervas, cuja semente bóia nos céus ou espera à tez dos pousios a vez de germinar. De permeio desabrocharam cardos, que são a flor da amargura, e a abrótea, a diabelha, o esfondílio, flores humildes, por isso mesmo troféus da vitória. Vieram os lobos, os javalis, os zagais com os gados, a infinita criação rusticana. Faltava o senhor, meio fidalgo, meio patriarca, à moda do tempo.
Ora, certa manhã de Outono…”

Aquilino Ribeiro, *in “*A casa grande de Romarigães”, 1957

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Uma tese de doutoramento é tida, na sua acepção conceptual clássica, como um percurso solitário; mas é, contraditoriamente, um percurso que não se faz sozinho. Ao longo desse percurso acompanham-nos colegas, amigos, família, conhecemos outros mais. Todos deixam algo connosco… muitos levam algo de nós. É, por isso, um percurso de crescimento – académico e profissional, claro está –, mas na sua disposição mais humana, de crescimento pessoal. As medalhas e cicatrizes apenas persistem para nos lembrarem que não há derrotas, apenas vitórias e lições… e por ambas estou grato.

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Ao meu irmão Nuno que "é bueda fixe e que sem ele a [minha] vida era miserável" nas palavras dele, que sou obrigado a concordar porque… é verdade. E não é por me ter revisto uma tese que julgo ser difícil para um arquitecto; mas sobretudo porque o admiro, pela sua forma de ver a vida, de lutar e persistir até encontrar o que quer, porque vale a pena não estarmos acomodados se não estamos bem – tens-me dado verdadeiras lições.

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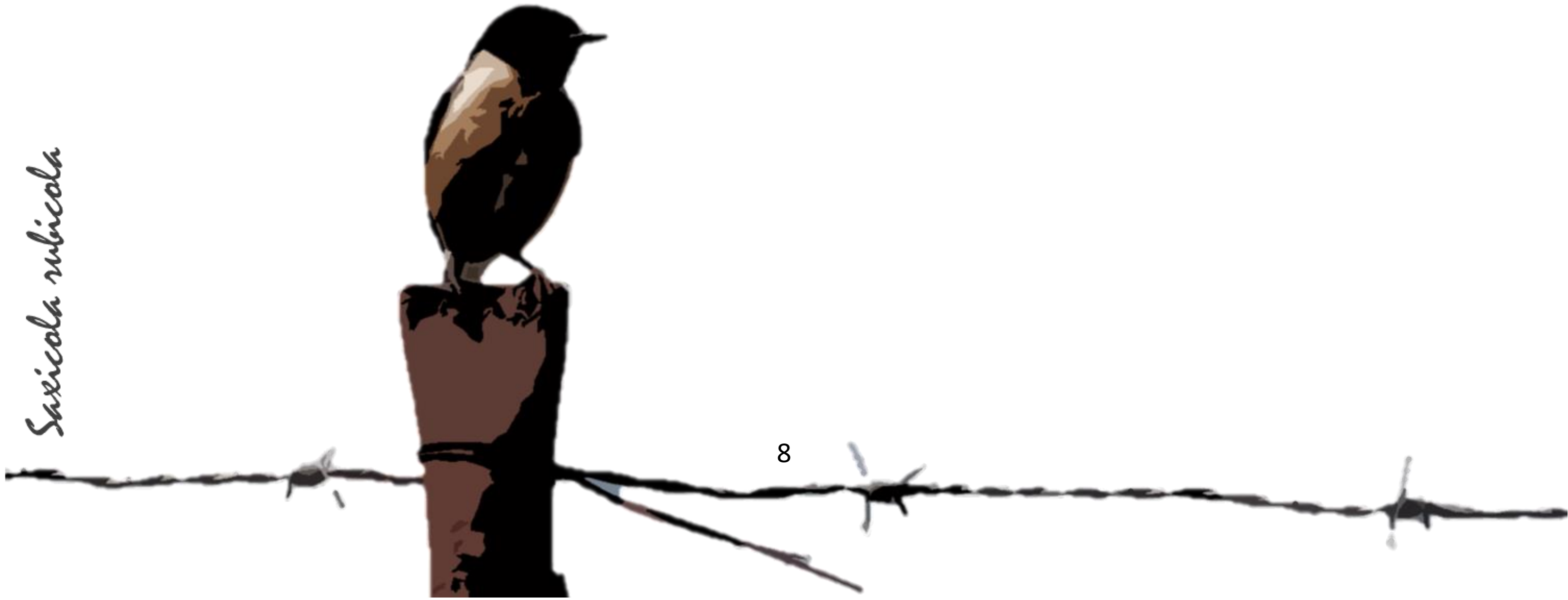

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Abstract

Over the last decades, the pervasiveness of human activities has leading landscapes worldwide to experience unprecedented changes often resulting on the loss, simplification or fragmentation of habitats. Concomitantly, species diversity and the self-regulated ecological processes mediated by landscape are severely threatened. This thesis extends the theoretical considerations of the fragmentation conundrum into real-world fragmented landscapes to determine the effects of structural and functional landscape connectivity in mediating the spatial distribution of bird communities. We describe conceptual approaches to capture landscapes' heterogeneity on different forest contexts to uncover the adequate surrogacy of the structural connectivity of the landscape. Critical ecological thresholds of forest cover are explored to preview community turnovers and establish the limits where populations are more sensitive. Finally, we demonstrate how functional connectivity mediates the spatial distribution of bird species and bird community composition. Our results point out that, though species reveal overall interdependent behaviour, they show highly specific responses to patch and landscape cues suggesting differences on how they perceive their quality and structure, respectively. Consequently, this denotes that the spatial distribution and composition of bird communities depend on the intrinsic ability of each species to move across the landscape (functional connectivity) and reach a patch, as well as on the capacity of patches to provide vital resources for different species. The implications of our findings leverage concrete and specific management strategies to prevent the downfall of avian diversity in the two most representative forest systems in Portugal: pine forest plantations and oak woodlands. We establish the limits beyond which major changes in community are expected and suggest practices that behold the maintenance of high bird diversity levels. Overall, we endorse sustainable approaches previewing exploitation alternatives that reconcile both human interests and the conservation of natural assets.

Keywords

Habitat fragmentation; Landscape connectivity; Landscape ecology; Community assembly; Bird community; Production forests; ‘Montado’ agro-forest-ecosystem; Forest landscapes management.

Análise de limiares de conectividade em paisagens fragmentadas. Uma abordagem multiespécies de aves em florestas de pinhal e quercíneas.

Resumo

O impacto das actividades humanas nas paisagens tem promovido alterações sem precedentes a uma escala global nas últimas décadas, resultando na perda, simplificação ou fragmentação dos habitats. Consequentemente, a diversidade de espécies e os processos ecológicos associados à dinâmica paisagística encontram-se profundamente ameaçados. Nesta tese são explorados os efeitos da conectividade estrutural e funcional da paisagem na distribuição espacial de comunidades de aves, transferindo para um contexto de paisagens reais as considerações teóricas formuladas no âmbito da investigação em fragmentação. Para o efeito, são descritas diferentes abordagens conceptuais na caracterização da heterogeneidade da paisagem, aferindo a adequabilidade de descritores de conectividade estrutural, em diferentes contextos florestais. São explorados os limiares de sensibilidade ecológica e alteração das comunidades ao longo de um gradiente reflectindo a disponibilidade de recursos. Por último, é investigado o papel da conectividade funcional na distribuição espacial e a composição das comunidades de aves. Os resultados demonstram que a percepção da qualidade de habitat e da estrutura da paisagem é dependente da espécie embora existam relações de interdependência entre estas. Isto implica que a distribuição espacial e os processos inerentes à composição das comunidades dependam da capacidade de cada espécie em alcançar parcelas de habitat adequado (conectividade funcional), e da disponibilidade de recursos providenciada pelas mesmas em satisfazer um conjunto diverso de espécies. As implicações dos resultados obtidos estendem-se à aplicabilidade de estratégias de gestão concretas e específicas que previnem a perda de diversidade avifaunística nos sistemas florestais mais representativos de Portugal – plantações de pinheiro e montado –, nomeadamente através da identificação dos limites além dos quais estão previstas alterações significativas na comunidade, e sugerindo práticas que contemplam a manutenção de níveis elevados de diversidade. Abordagens sustentáveis associadas a estratégias alternativas de exploração contribuirão para conciliar os interesses humanos e a conservação dos valores naturais.

Palavras-chave

Fragmentação de habitat; Conectividade da paisagem; Ecologia da paisagem; Agrupamento de espécies; Comunidade de aves; Florestas de produção; Montado; Gestão de paisagens florestais.

Chapter I

General introduction

In the past decades, human footprint on the environment assumed such unprecedented levels that lead to the classification of a new geological epoch – the Anthropocene (Ruddiman, 2003; Smith and Zeder, 2013). The intense pressure of human activities has inflicted profound geological and ecological changes (Zalasiewicz *et al.*, 2011; Waters *et al.*, 2016), modifying ecosystems and communities. Ultimately, these changes are threatening the conservation of natural assets and causing the extinction of several species to an extent only comparable to the great mass extinctions in the past (Dirzo *et al.*, 2014). Despite several global agreements attempting to halt biodiversity loss (*e.g.*, UN Aichi Targets), evidence reveals a continuing global decline (Butchart *et al.* 2010; Dornelas *et al.* 2014; Tittensor *et al.* 2014) with ongoing species loss and/or changes in communities (*e.g.*, homogenization).

Landscape modification driven by human activities is widely recognized as one of the most severe threats to global biodiversity (Fischer and Lindenmayer 2007; Hooper *et al.*, 2012), often resulting in species extinction, alteration of ecological processes and depletion of ecosystem services (Haddad *et al.*, 2015; Mitchell *et al.*, 2015). Over the last decades, landscapes worldwide have experienced major changes as land-use conversion and intensification further increase habitat loss, simplification or fragmentation (Newbold *et al.*, 2015). More than 75% of Earth's terrestrial ecosystems have experienced alterations due to human activities (Ellis and Ramankutty, 2008). In Europe, landscape changes have been mainly promoted by agricultural and forestry activities (Jongman 2002; Plieninger and Schaar, 2008), often resulting on the subdivision of larger natural patches into smaller ones, increasing patch vulnerability and constraining movements of animals (Kettunen *et al.*, 2007).

This thesis addresses the topic of habitat fragmentation as provided by landscape modification. Connectivity is further explored as a spatial property of landscapes that can be managed to prevent or soften the adverse impacts of fragmentation. In this chapter, we present the state-of-the-art on habitat fragmentation and landscape connectivity as applied to bird communities. We introduce the theoretical framework and the concepts upon which we develop this thesis and the research within, highlighting the current demands and challenges in this research field. Additionally, we frame these topics on the most representative Portuguese forest landscapes, exploring the conditions and threats laying upon them and the foreseeable changes they face in the future, as well as the resulting implications for the bird communities inhabiting them.

I.1. CONCEPTUALIZING HABITAT FRAGMENTATION

The response of organisms to landscape modification and habitat fragmentation is well documented for several taxa (Andrén, 1994; Didham *et al.*, 1996; Gibbons *et al.*, 2000). For instance, significant declines have been detected at both species (Inger *et al.*, 2015; Jeliazkov *et al.*, 2016) and community levels (Billeter *et al.*, 2008). These often result in net changes on ecological assemblages (Newbold *et al.*, 2015) and homogenization of communities (Gámez-Virués *et al.*, 2015) by reducing species diversity through replacement by widespread species (Clavero and Brotons, 2010; Gámez-Virués *et al.*, 2015).

I.1.1. Conceptualization of landscapes

The use of different approaches describing patterns of landscape modification and habitat fragmentation supported different conceptual paradigms (Haila, 2002) (Table I.1). The island biogeography theory by MacArthur and Wilson (1967) has dominated the human perspective on landscape topology over the years. This theory implicitly considers a binary categorization of the landscapes where landscape heterogeneity is translated into discrete and well-defined patches of suitable habitats (hypothetical islands) embedded in an unsuitable or hostile matrix. This theory conforms to pattern-oriented approaches (or discrete/patch models). Although it has contributed with valuable insights on the development of other theories (*e.g.*, metapopulation theory, Hanski, 1998), it is accounted as an overly simplistic way to characterize landscape heterogeneity. Possibly for that reason, many other discrete approaches that account for other levels of landscape heterogeneity followed, such as the patch-corridor-matrix (Forman, 1995) or the hierarchical patch-based model (Dunn and Majer, 2007).

Such developments, however, did not refrain further criticism on discrete approaches, pointing out other liabilities, such as: (1) landscape is often subjected to a human-centric perspective (Dunn and Majer, 2007) which may not be consistent with species perception (Fischer and Lindenmayer, 2006; Lindenmayer *et al.*, 2008; Franklin and Lindenmayer, 2009); (2) discrete conceptualizations of landscapes are often dubious because they neglect within patch heterogeneity (Price *et al.*, 2010); and as a consequence, (3) force interdependent responses of the organisms, *i.e.*, assume that multiple organisms respond similarly to landscape change (Betts *et al.*, 2014). Several authors thus argue that such approaches are potentially limited to landscapes with ideally contrasting patches while poorly contributing to understand ecological processes in other landscape types (Fischer and Lindenmayer, 2006; Lindenmayer *et al.*, 2008). For that reason, they are likely to produce unrealistic management practices in most landscapes (Fischer and Lindenmayer, 2006, 2007; Lindenmayer *et al.*, 2008).

Alternatively, species-oriented approaches (or gradient models) describe landscapes as spatial gradients reflecting gradual changes of resources, environmental conditions and ecological processes (Fischer and Lindenmayer, 2006). Although the continuum model (Fischer and Lindenmayer, 2006) is the most relevant approach developed on this matter, other landscape conceptualizations appeared as detachments from discrete models by considering spatial continua, such as the variegation model (McIntyre and Barrett, 1992), the Continua and Umwelt model (Manning *et al.*, 2004) and the habitat contours model (Fischer *et al.*, 2004a). Although appealing, the applicability of continuous models is still rare (but see Betts *et al.*, 2014), probably due to the unavailability of data in quantity and quality to properly characterize landscape complexity (Fischer *et al.*, 2004a).

Table I.1 – Summary table addressing the assumptions of each of the approaches conceptualizing landscape heterogeneity and habitat fragmentation, and the associated concepts or theories.

Attributes	pattern-oriented approaches (discrete/patch-based models)	species-oriented approaches (gradient models)
Landscape topology	Assumes clear contrast between patches and matrix	Defines landscapes as ecological gradients describing a continuum of change
Patch classification	Requires human defined patch-boundaries to correlate with species distribution	Classification is independent from human-centric perception
Spatial heterogeneity	Patches are assumed to be internally homogeneous	No assumptions on the internal homogeneity of patches
Species response	Species perceive landscape similarly and distribution is restricted to patches as assemblages (species responses are clustered)	Species distribute through space in complex (species-specific) and continuous way
Species turnover	Sharp transitions between discrete communities.	Changes in species composition occur gradually.
Ecological processes	Assumes that the correlation between landscape pattern and species distribution is a proxy for ecological processes	Attempts to study ecological processes directly
Supporting theories	• Island biogeography theory (MacArthur and Wilson, 1967) • Patch-corridor-matrix (Forman, 1995) • Hierarchical patch-based model (Dunn and Majer, 2007) • Community unit concept (Clements, 1936) • Metapopulation theory (Hanski, 1998) • Metacommunities theory (Leibold *et al.*, 2004)	• Continuum concept (Austin, 1985; Fischer and Lindenmayer, 2006) • Variegation model (McIntyre and Barrett, 1992) • Continua and Umwelt model (Manning *et al.*, 2004) • Habitat contours model (Fischer *et al.* 2004a) • Individualistic continuum concept (Gleason, 1917, 1926)

I.1.2. Conceptualization of species response

Beyond landscape attributes, the assumptions provided by gradient models also establish that species perceive and respond individualistically to landscape modification, and that the interdependence of species response is therefore highly underappreciated

(Didham *et al.*, 2012) (Table I.1, Figure I.1). This implies that the conceptualization of communities as coherent and functional assemblages (community-unit concept, Clements, 1936) does not prevail over a random and stochastic sum of species that coincidently occur in space and time (the individualistic continuum, Gleason, 1917, 1926) (Figure I.1). On the other hand, discrete models, while assuming an interdependent response (or dynamic synchrony effect) among organisms occurring at the same environmental conditions, support the existence of communities and metacommunities (Leibold *et al.*, 2004) as a corollary.

The paradigm of the individualistic continuum (or Gleasonian hypothesis) and community-unit concepts (or Clementsian hypothesis) remains unsolved. Lortie *et al.* (2004) proposed the “integrated community concept” which recognizes the synergistic effects of species-specific traits, interactions between organisms and stochastic processes structuring communities (see also Didham *et al.*, 2012). It advocates that communities can have a dualistic nature where the individualistic behaviour of species is somewhat embedded within ecological assemblages (Figure I.1). Yet, the processes underlying the composition of ecological communities have been subject of debate for a long time (Taper *et al.*, 1995; Austin, 1999; Baselga and Araújo, 2009; Leaper *et al.*, 2014) and the conceptualization of communities is still a non-consensual topic of discussion.

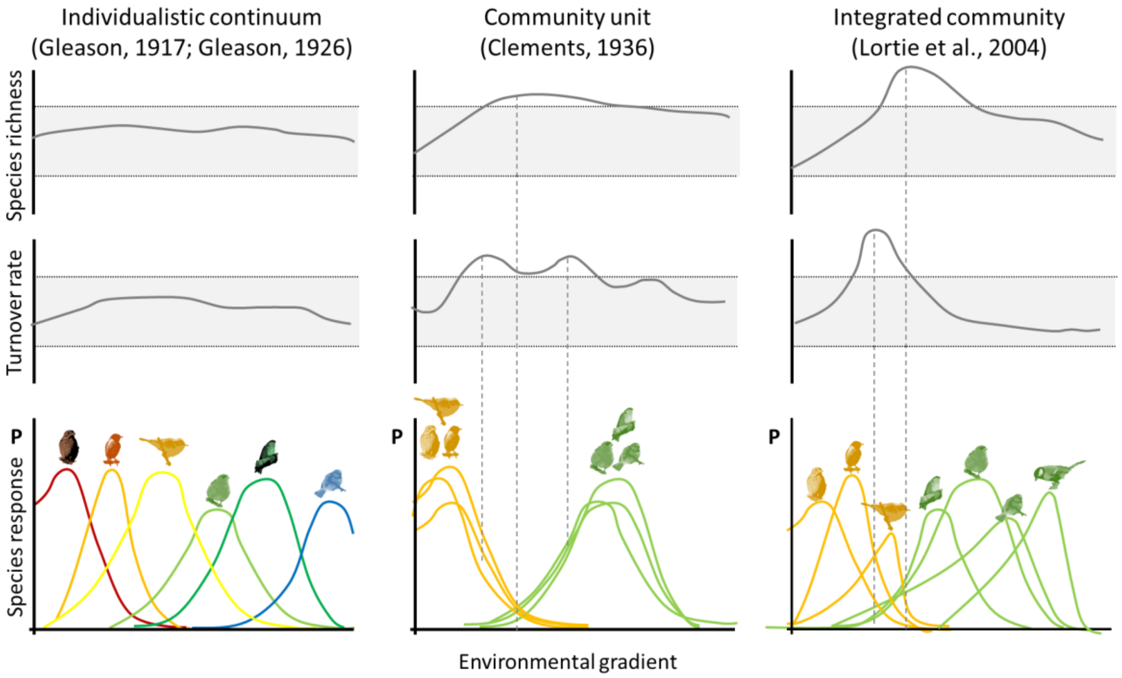

Figure I.1 – Conceptualization of species response and community parameters patterns along an environmental gradient, according to each of the three hypotheses. In the individualistic continuum hypothesis, species distribution do not overlap and no coherent assemblages are noticed, thus both richness and turnover rates assume a clear constant variation with no significant peaks as species substitute each other along the gradient. In the community unit hypothesis, species are sort into discrete assemblages, thus overlapping their distribution; richness and turnover show at least one distinct peak marking changes in community composition between both assemblages. The integrated community concept acknowledges the dualistic nature of community assembly, thus species distribute individualistically within assemblages balanced between the interspecific relations and species-specific tolerance; richness and turnover show at least one distinct peak marking changes in community.

I.1.3. Implications

The implications of these conflicts between opposing perspectives on how landscapes and species responses are conceptualized can have damaging consequences on the determination of the effects of habitat fragmentation on species and communities. Many studies addressing landscape modification rely on the estimation of the relative effects of habitat loss and fragmentation (Fahrig, 2003), thresholds of habitat amount (Andrén, 1994; Fahrig, 2002), or edge effects (*e.g.*, Harper *et al.*, 2005). These studies often establish limits beyond which major changes in species occupancy occur and communities are most vulnerable to species loss (the fragmentation threshold hypothesis, Fahrig, 2003). The way habitat amount, for instance, is captured from the landscape is important to provide reliable evidence on the susceptibility of a community and determine where extinction scenarios may be plausible (Betts *et al.*, 2007). However, choosing an inadequate conceptualization may conduct to misleading results, thus increasing the risk of developing ineffective management strategies (Fischer *et al.*, 2004a, 2004b; Lindenmayer *et al.*, 2008).

How to prevent further biodiversity loss from landscape modification and habitat fragmentation is a critical challenge to attend for in the near future (Balmford *et al.*, 2003), and researchers are challenged to provide concrete management alternatives that uphold or restore the conservation value of landscapes (Lindenmayer *et al.*, 2008; Driscoll *et al.*, 2013).

I.2. LANDSCAPE CONNECTIVITY

In human-modified landscapes, the dispersal of species can be severely disrupted, as patches of native habitats are lost or become increasingly fragmented and isolated (Diniz *et al.*, 2020). Landscape connectivity analysis has become a valuable tool with the potential to identify constraints and minimize or reverse such effects (Taylor *et al.*, 1993; Diniz *et al.*, 2020). Improving and restoring landscape connectivity (Taylor *et al.*, 1993) can enable species dispersal (Haddad *et al.*, 2003), colonization of newly available patches (Haddad *et al.*, 2015), and gene flow between populations (Whitlock *et al.*, 2000). Globally, it may prevent species and communities from local extinctions and uphold their persistence in the landscape (Gonzalez *et al.*, 1998; Bennett *et al.*, 2006; Staddon *et al.*, 2010).

Landscape connectivity can be defined as the degree to which the landscape facilitates or impedes movement of animals among resource patches (Taylor *et al.*, 1993) and can be characterized by two primary components: (1) structural, *i.e.*, the spatial arrangement of different types of habitat or other elements in the landscape (Calabrese and Fagan, 2004), and (2) functional, which refers to the behavioural response of individuals, species or ecological processes to the physical structure of the landscape, ignored in structural connectivity approaches (Taylor *et al.*, 1993, Tischendorf and Fahrig, 2000, Pe'er *et al.*, 2011).

The likelihood of a species to reach a patch depends, therefore, on both the permeability of the landscape where patches are embedded (the matrix) and the intrinsic species ability to engage in successful dispersal (Baguette *et al.*, 2013).

I.2.1. Species dispersal

Dispersal can be defined as the movement engaged by organisms, which can be expressed by potential gene flow across space (Ronce, 2007). It is a key process for species survival, enabling species to move on a landscape to reproduce, seek food, escape disturbance (predators or human pressure), or roam in search for suitable habitats (Morales *et al.*, 2010; Baguette *et al.*, 2013). For that reason, dispersal assumes an essential role in population and metapopulation dynamics, species spatial distribution and community assembly processes (Jønsson *et al.*, 2016).

Generally, dispersal is described as a three-stage process in which an organism departs from its breeding site (emigration), traverses the landscape (transfer), and settles in a new breeding site (immigration) (Ronce, 2007; Clobert *et al.*, 2012). Each of these stages challenges the organism in different aspects of its interaction with the environment. For instance, engaging in dispersal movements involves costs to individual fitness associated to exposure to predation risk, high energy demand for traversing non-suitable habitats, or competition while setting its territory in a new patch (Morris, 2003). Understanding the drivers of dispersal and the specific requirements and constraints that ensure this process is pivotal to report effective connectivity-based conservation strategies (Vasudev *et al.*, 2015).

However, the techniques currently available that allow the estimation of effective dispersal are scarce, expensive and occasionally unsuitable or logistically unfeasible for some *taxa* (Jønsson *et al.*, 2016). In addition, such techniques also struggle with some limitations. For instance, molecular or genetic approaches can only provide inference on successful dispersal events, linking dispersed individuals to source populations, which offer no evidence on the details of actual movement (*e.g.*, path selection, Jønsson *et al.*, 2016). Tagging and tracking techniques, on the other hand, allow to estimate effective dispersal while accounting for movement, but are often limited to larger animals (*e.g.*, radio tracking, Carvalho *et al.*, 2016) or apply capture-recapture methodologies which seldom provide robust dispersal data (*e.g.*, bird ringing) (Kays *et al.*, 2015).

Consequently, when these techniques are overwhelmingly impractical, many studies bypass these limitations by assessing landscape connectivity based on habitat use or spatial distribution. Although it can only be used as a proxy of dispersal ability, these approaches have performed well as a cost-effective method to build functional connectivity models when data on movement or dispersal ability is lacking (Keeley *et al.*, 2016; Ahmadi *et al.*, 2017; Khosravi *et al.*, 2018; Valerio *et al.*, 2019). Nevertheless, the implications and inferences of those studies must be carefully addressed, as such approaches may not suit every question (Diniz *et al.*, 2020).

I.2.2. Landscape permeability

Dispersal ability also depends on how a particular organism perceives the landscape (Tischendorf and Fahrig, 2000). Both landscape composition and configuration influence dispersal ability by altering movement patterns across the landscape through facilitation (*e.g.*, corridors and stepping-stones) or impediment (*e.g.*, barriers) (Rudnick *et al.*, 2012; Diniz *et al.*, 2020).

Structural and functional landscape connectivity can be easily assessed by means of a large set of indices and methods specifically designed for that purpose based on graph theory (*e.g.*, Saura *et al.*, 2011, Bodin and Saura, 2010) or circuit theory (McRae *et al.*, 2008). Graph theory has been applied as an analytical tool to assess habitat fragmentation effects on animal movement and species persistence, as well as to network optimization (Urban *et al.*, 2009, Luque *et al.*, 2012). In this representation, the landscape is presented as a set of nodes (*e.g.*, habitat patches) and links (potential ability of an organism to disperse between two nodes, Saura *et al.*, 2011). The network analysis will determine which patches (nodes) maintain more links with other patches (key connectors) and which are more isolated.

Circuit theory builds on an analogous graph approach where multiple random walks are simulated between nodes in the form of an electrical network (McRae *et al.*, 2008). Animal movement is represented by electrical current flowing between nodes connected by resistors, which determine the friction to which current (movement) is allowed to flow (McRae *et al.*, 2008).

In the last decade, both these methods offered important advances in ecological theory by inferring animal movements and ecological processes throughout the landscape. Nevertheless, these methods rely on the previous determination of a resistance surface that reflects the degree to which a landscape facilitates movements of the organisms. Explicitly, it consists on a spatial representation of the traversing costs of an organism, as imposed by the environmental constraints to which its movements are subjected (Zeller *et al.*, 2012). Diniz *et al.* (2020) addressed it as the "backbone of connectivity models", emphasizing that resistance surfaces must accurately capture the real costs to movement. Ideally, landscape resistance should rely on species empirical movement or dispersal data (Diniz *et al.*, 2020). However, as referred above, data on movement or dispersal ability is not often available. Alternatively, habitat suitability models can be used to infer landscape resistance by means of a negative linear or exponential transformation (Trainor *et al.*, 2013; Keeley *et al.*, 2016). Because dispersal generally occurs in non-habitat patches (Clobert *et al.*, 2012) such models may not conveniently capture dispersal habitat characteristics (Revilla and Wiegand, 2008; Vasudev *et al.*, 2015), thus possibly leading to an overestimation of resistance.

I.2.3. Landscape filtering

A growing number of studies linking landscape structure and functional connectivity to species occurrence (see Fletcher *et al.*, 2016) have been conducted, but much interest is growing nowadays on the application of these techniques in multispecies approaches (Mimet *et al.*, 2013, Brás *et al.*, 2013). Because landscapes have different permeability to different species, it is expectable that species connectivity will vary according to their dispersal ability (Liu *et al.*, 2018) and sensitivity to barriers (Breckheimer *et al.*, 2014).

Most species are expected to reach highly connected patches, but otherwise, landscape will filter out species for which the matrix restricts their movements, *i.e.*, the likelihood of most species reaching that patch is lower. Such process is generally acknowledged as landscape filtering, but other processes are expected to filter species from the regional pool of competitors. It is well established in literature and widely considered that local community composition and structure are driven by three filters linked to specific processes that operate hierarchically at different temporal and spatial scales (Zhang *et al.*, 2013; Cadotte and Tucker, 2017) (Figure I.2): (1) a landscape filter relates to the limitations imposed by resistance to dispersal, interfering with the ability of a species to reach a habitat patch; (2) a habitat filter defines the species able to settle and persist in a patch given the environmental conditions at site; and (3) the interaction (or biotic) filter which specifies the effects derived from the competitive interplay between species that can result in the facilitation, segregation or exclusion of a species (Figure I.2).

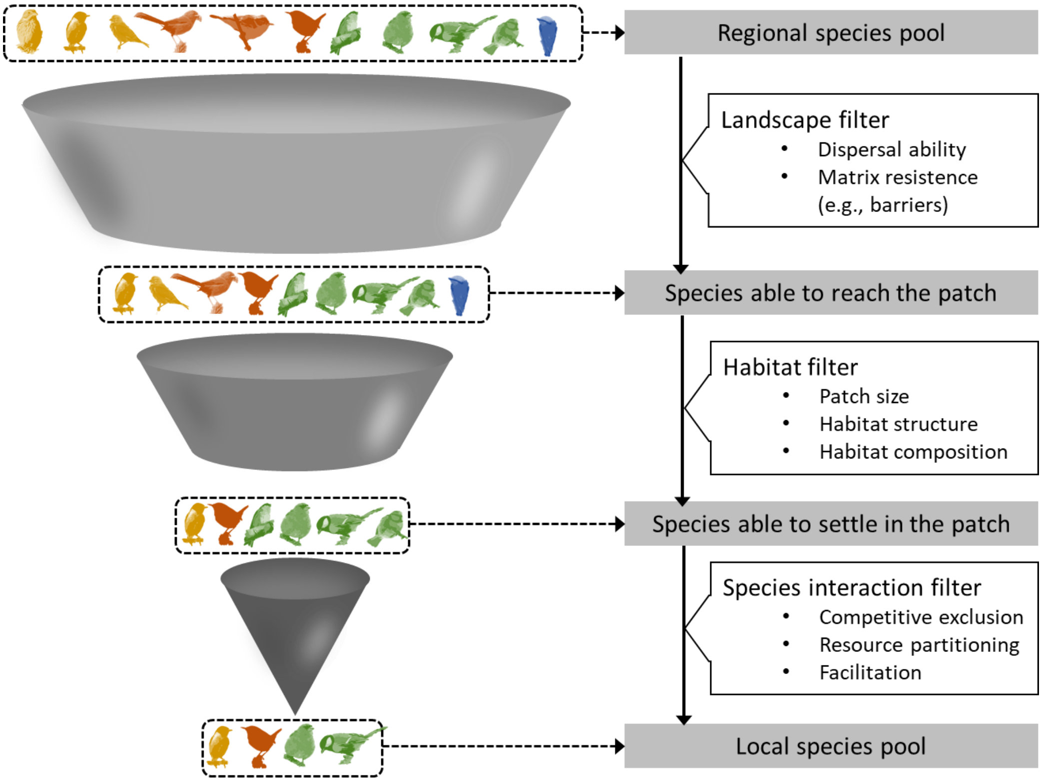

Figure I.2 – Classic diagram of the hierarchy of filtering effects (adapted from Cadotte and Tucker, 2017) and respective ecological processes to which a regional species pool is coerced into, thus resulting in the assembly of local communities. Bird colouring codes different assemblages, birds with the same colour exploit similar resources.

As the demand for designing conservation strategies based on multispecies approaches increases (Diniz *et al.*, 2020), ecologists must engage in assessments that behold species diversity instead of single or focal species. The most pressing issue here is to disentangle the effects of connectivity (landscape filtering) from the other filtering processes (Fletcher *et al.*, 2016) in determining the rules of assembly of local communities and inherently, the spatial patterns of diversity on the landscape.

Nonetheless, the real challenging point is to transfer this information into efficient conservation planning oriented towards the decision making process (García-Feced *et al.*, 2011, Saura *et al.*, 2011), going beyond a mere descriptive analysis.

I.3. EFFECTS OF HABITAT FRAGMENTATION AND LANDSCAPE CONNECTIVITY ON BIRD COMMUNITIES

Birds are often considered as suitable models for monitoring broad-scale environmental change (Koskimies, 1989; Canterbury *et al.*, 2000), since they are closely related to different environmental characteristics, namely concerning the structural complexity of the landscape (Willson, 1974; Mayer and Cameron, 2003; Padoa-Schioppa *et al.*, 2006, Skorka *et al.*, 2006; Larsen *et al.*, 2010). For that reason, birds are a noteworthy group to analyse the effects of fragmentation and connectivity.

In this section we summarize a survey of published works in fragmentation and connectivity using birds. We searched the Web of Science for published papers up to 2019 using the strings “bird and fragmentation” and “bird and connectivity” in the title. This did not aim to produce a complete review, instead a comprehensive search to outline the general trends of the existing research. Each paper on the list was validated, looking for effects of fragmentation and connectivity on bird communities (papers dealing with species richness, diversity, assemblages and other community parameters), species (papers dealing with spatial or temporal occurrence patterns, population size, or genetic structure), individual condition (nutritional condition, nesting success), and the processes associated to services provided by birds (seed dispersal, frugivory, pollination and other interactions). We excluded all papers dealing with migratory connectivity since this process occurs at larger scales than those used to examine landscape fragmentation. Titles and abstracts from the research focusing on connectivity were screened for the geographic area (country), habitat type, method to quantify connectivity, number of species analysed, ecological levels and the effects of connectivity on them.

We retrieved 408 papers dealing with habitat fragmentation or landscape connectivity on birds, of which only 42 (10.3%) explicitly addressed connectivity. To our knowledge, the first seminal papers debating the effects of fragmentation on bird communities date from 1984 (Figure I.3). Those works set the methodological bases to analyse the effects of habitat fragmentation, namely the need for evidence-based inference and scale-dependence issues (Haila and Hansky, 1984), or the complexity and specificity of fragmentation on individual bird species, weighing the joint effect of both patch size and habitat quality (Lynch and Wigham, 1984). From the early 90's onwards, research on habitat fragmentation and its effects on birds became more frequent, increasing steadily until 2008 and stabilizing thereafter (Figure I.3). Research explicitly addressing connectivity and birds, to our knowledge, only emerged in 1997 (four years after the seminal work of Taylor *et al.*, 1993, defining connectivity) when Phillipe Clergeau and Françoise Burel reported the presence of Short-toed Tree Creeper (*Certhia brachydactyla*) to be dependent on landscape spatial structure (Clergeau and Burel, 1997). Since then, research focusing on landscape connectivity for birds has also grown, though modestly compared to habitat fragmentation *sensu stricto*. In fact, in the last ten years, the number of published papers seems to have reached an asymptote, rarely overcoming five publications/year (Figure I.3). As a personal note, it is surprising the lag between connectivity explicit research and strict fragmentation given the potential of addressing connectivity to resolve fragmentation effects (Herrera *et al.*, 2018; Estrada-Carmona *et al.*, 2019). It matters, therefore, to understand what hampers further research on this subject.

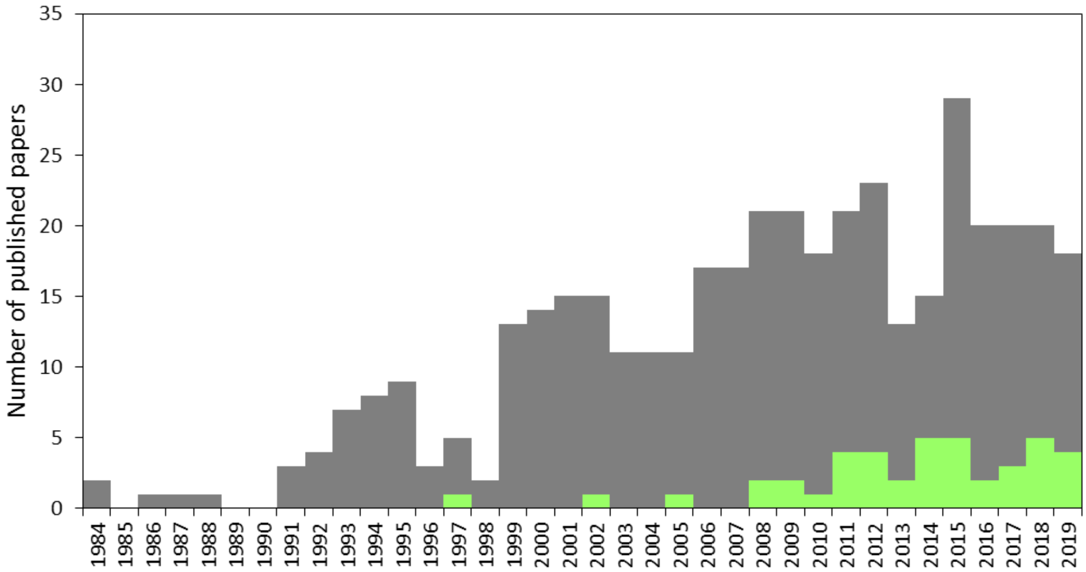

Figure I.3 – Number of published papers that explicitly address habitat fragmentation (in grey) or landscape connectivity (in green) effects on bird communities or species. Data was assembled from a comprehensive search of published papers up to 2019, reported by the Web of Science. The sample consists of 408 papers dealing with fragmentation or connectivity, of which 42 (10.3%) explicitly address connectivity.

The geographic distribution of the published papers on connectivity effects on birds, for instance, is highly biased (Figure I.4). Most of the research took place in America (both North and South), Europe and Australia. Together the countries from these continents hold 93% of the research, while in Asia and Africa information is scarce. Despite the lack of information on landscape connectivity for birds in those areas, connectivity for large mammals and carnivores groups has been profusely investigated in the last years in both Asia (*e.g.*, Ahmadi *et al.*, 2017; Khosravi *et al.*, 2018) and Africa (*e.g.*, Osipova *et al.*, 2018). Research on landscape connectivity for birds has been mostly addressed in countries like Australia and Brazil, where landscape changes have greatly modified sensitive and important ecosystems, like Box Gum Grassy Woodland (Lindenmayer *et al.*, 2020), native Eucalyptus forests (Mortelliti *et al.*, 2014), or the Atlantic Rain forest (Uezu *et al.*, 2005; Awade *et al.*, 2012; Martensen *et al.*, 2008, 2012).

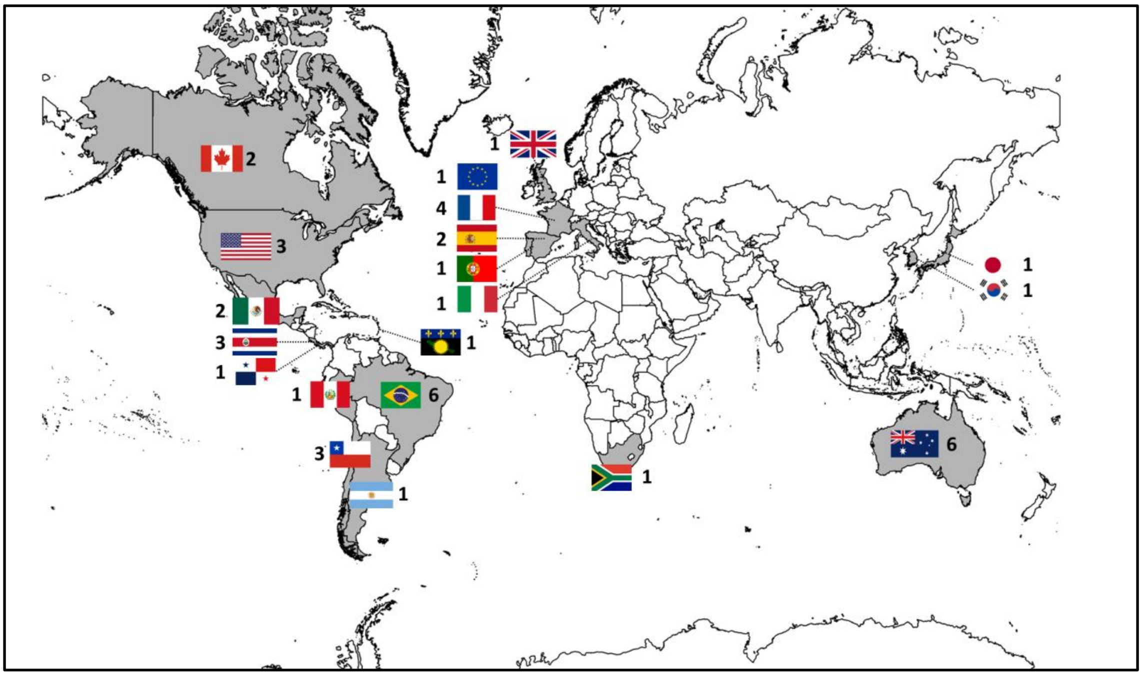

Figure I.4 – World map showing the geographical distribution of the research addressing the effects of landscape connectivity on birds.

However, other issues arise while exploring other technical and practical considerations of the assembled studies, which may follow important implications. For example, 74.4% of studies addressing connectivity focus on forest or woodland habitats, showing a highly biased tendency. Only a few other available from current literature investigate further relevant habitats, such as grassland (Duflot *et al.*, 2018), open-habitats (Zozaya *et al.*, 2012), understory (Martensen *et al.*, 2012), or urban areas (Grafius *et al.*, 2017). About 9.3% of the studies address several habitats instead of considering only one focal community. Comprehensively, the net loss of forest habitats would have long-lasting impacts on communities, as they usually require more time to achieve climax, through either regeneration or proper restoration practices.

Regarding the methods used to quantify connectivity, we found that most studies (58.1%) rely on either structural connectivity or model-based approaches (Figure I.5). Structural connectivity only considers landscape configuration to infer connectivity (Calabrese and Fagan, 2004), but has provided evidence for the use of corridors, gap crossing or permeability (*e.g.*, Vergara, 2011). Nonetheless, such approaches are subject to criticism, since their applications inherently assume that different species perceive landscape similarly, which may not hold true in some cases (Lindenmayer *et al.*, 2020).

Model-based approaches, on the other hand offer the possibility to consider species-specific associations to landscape characteristics. Moreover, current methodologies (*e.g.*, graph-based or circuit theory) allow to account for species dispersal ability, meaning that connectivity no longer depends solely of landscape characteristics, but also on species attributes, such as behaviour and movement ability (functional connectivity, Tischendorf and Fahrig, 2000). Both structural connectivity and model-based approaches have been more intensely used in multispecies approaches than in single-species, likely because such approaches require less information on species dispersal ability to calculate connectivity for a large set of species. Other less used methods (capture-recapture – 20.9%, genetic or molecular – 11.6%, and movement tracking – 7.0%) are applied more often (or at least more evenly) in single-species studies (Figure I.5).

Connectivity studies have also addressed different ecological levels of avian diversity. Species distribution, movement patterns and community parameters are amongst the most studied features on this subject (69.0%) (Figure I.5). Demographic, genetic and species interaction remain poorly explored, most likely because inference is difficult to attain, usually requiring tools and effort not commonly available, affordable or easily applied in this context (Jacobson and Peres-Neto, 2010). Nevertheless, most studies globally show that connectivity has positive effects at all ecological levels, meaning that increasing connectivity will tend to increase general diversity, from genes to communities. The extent to which connectivity affects these ecological levels, however, remains doubtful. Even though effects are positive, they wander between weak (connectivity has an effect, however weak compared to others, *e.g.*, landscape attributes; Mortelliti *et al.*, 2014; Kang *et al.*, 2015), uneven (connectivity has an effect, but only on some species; Uezu *et al.*, 2005), and clearly positive (Vergara, 2011; Mayhew *et al.*, 2019) (Figure I.5). Therefore, it is possible that responses to connectivity vary significantly and that inference may be driven by both species- (traits, *e.g.*, dispersal ability) and context-dependency effects (*e.g.*, landscape permeability).

As a corollary, even though this survey of published works is highly conservative (key-word search was constrained to title's information) it allowed a first insight on the effects of landscape connectivity on avian diversity. Quantifying landscape functional connectivity remains a challenge (Fletcher *et al.*, 2016; Jønsson *et al.*, 2016) and there is still limited inference and high uncertainty on how it mediates bird diversity in highly fragmented landscapes. Furthermore, data on species movement, dispersal or genetics still bores significant constraints when studying small animal species in spatially scattered populations (Jacobson and Peres-Neto, 2010), like birds. The amount of effort needed to gather robust and reliable movement data for several species is still an obstacle to attain evidence-based results over broader and finer scales.

Notwithstanding these limitations, the preliminary results show that evidence is mostly positive, though ranging from weak to strong effects. Remarkably, however, only a few studies (about 25%) explored and disentangled the effects of connectivity comparatively to other landscape attributes (*e.g.*, patch size, habitat quality; see also Fletcher *et al.*, 2016).

For these reasons, connectivity studies are still a small fraction of the research concerning overall landscape fragmentation and still hold many biases (*e.g.*, geographic, habitats, methods or ecological levels addressed). Robust and reliable data is, therefore, needed to produce evidence-based results that attest connectivity as an effective tool to tackle the already pressing impacts of habitat fragmentation and loss in human-altered landscapes.

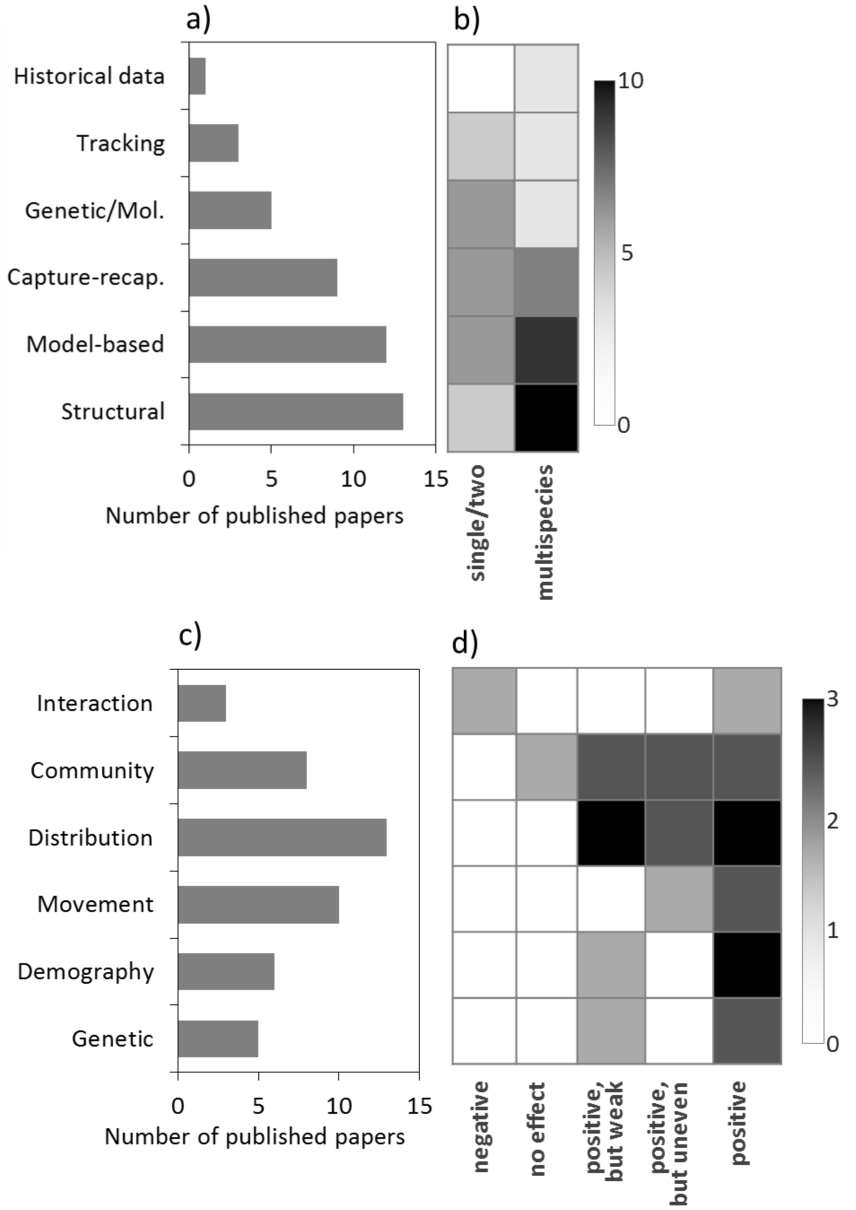

Figure I.5 – **a)** Number of published papers addressing the methods to quantify landscape connectivity, and **b)** regarding the number of species considered in those studies. Structural connectivity refers to approaches dealing only with landscape composition and configuration effects; model-based assume species-specific responses to landscape, generally accounting for dispersal ability; capture-recapture methods (Capture-recap) regard information from ringed birds, or from induced territorial response; genetic or molecular (Genetic/Mol.) studies examine genetic distances and gene flow; tracking involves studies on dispersal movements directly addressed from radio-tracking techniques; historical data compares data from long-term studies. **c)** Number of published papers addressing the different ecological levels, and **d)** magnitude of effects explained by landscape connectivity for each of the ecological levels. Genetic includes research on heterozygosity and allelic richness; demography attends to population level studies addressing colonization, immigration or breeding success; movement relates to studies using capture-recapture of radio tracking approaches; distribution studies investigate species spatial distribution and abundance; community studies analyse species richness, diversity or processes of assembly; and interactions investigate bird connectivity effects on ecological processes (*e.g.*, seed-dispersal).

I.4. MAIN OBJECTIVES

This thesis aims to determine the effects of landscape structural and functional connectivity in mediating the spatial distribution of bird communities inhabiting fragmented forest landscapes. Moreover, the studies here presented intend to uncover the ecological thresholds at which changes in community assembly occur. We aim at testing the following hypotheses derived from the general framework of the ecological niche theory (see Austin, 2007):

1. The adequacy of a model to describe species response to landscape structure depends on both landscape topography and species perception (the continuum concept by Austin, 1985; Fischer and Lindenmayer, 2006, vs. the island biogeography theory MacArthur and Wilson, 1967);
2. Species responses to habitat fragmentation are individualistic as species perceive landscape uniquely and differently (the individualistic continuum concept by Gleason 1917, 1926 vs. the community unit concept by Clements, 1936);
3. Environmental thresholds determine limits beyond which major changes in species abundance and community composition occur (the fragmentation threshold hypothesis by Fahrig, 2003);
4. Functional connectivity complements patch size and quality in effectively describing the spatial distribution of species (landscape filtering hypothesis);
5. Multispecies connectivity determines local community composition and diversity by incorporating the cumulative dispersal ability of each species to reach a patch (metacommunities theory by Leibold *et al.*, 2004; Galpern, 2011).

Those hypotheses were incorporated in the following specific goals:

1. Assess the conditions under which an adequate description of the landscape structure best suits species perception, taking into account landscape context and species trait dependency effects;
2. Characterize bird species responses to landscape change and how species assemble according to their habitat requirements;
3. Determine critical thresholds of habitat fragmentation beyond which a significant loss of species occurs;
4. Disentangle the effects of landscape connectivity from other key factors (*e.g.*, patch size and habitat quality) on bird species distribution;
5. Quantify the role of landscape functional connectivity in determining the spatial distribution of a bird community in fragmented landscapes;
6. Validate the effectiveness of multispecies connectivity over single-species connectivity approaches in determining bird community assembly.

In order to explore the specific objectives of the thesis, as well as to depict concrete implications of the studies, we extended the theoretical considerations of the fragmentation conundrum into real-world forest landscapes taking advantage of their patchiness to set non-manipulative experimental designs. Therefore, our research also intends to endorse sustainable landscape practices, allowing for forest management and exploitation to be compatible with the maintenance of high biodiversity levels.

I.5. STUDY AREAS

Many highly considered studies addressing habitat fragmentation and landscape connectivity are carried out in experimental landscapes where controlled conditions are provided (*e.g.*, Damschen *et al.*, 2006, 2012, 2019; Haddad *et al.*, 2015). Patch size, configuration and connectivity are manipulated to determine the effects of habitat fragmentation on biodiversity, animal behaviour, community dynamics and ecosystem functioning (Jenerette and Shen, 2012). Such studies allow for an unbiased estimation of effect sizes, causal inference and have provided valuable insights to ecological theory (Ims, 2005; Resasco *et al.,* 2017). Non-manipulated observational and modelling approaches seldom allow such accuracy (Jenerette and Shen, 2012). However, controlled situations rarely occur in nature and it is not clear to what extent the theoretical considerations find support in real-world landscapes (Fletcher *et al.*, 2016; Viljur and Teder, 2018). Beyond theory, gathering evidence from real-world landscapes can provide valuable information that can help landscape planners and managers to implement more sustainable management practices by integrating landscape connectivity and structure in exploitation plans.

Since our aim intends to provide both theoretical information on how bird communities are structured and translate such evidence into explicit management practices that can contribute to more sustainable landscapes, we approached our objectives on two real-world landscapes with different topology: (1) standard production pine forests, and (2) Mediterranean evergreen oak woodlands.

The thesis focuses purposely on those forest land uses because they are the most represented in Portugal. According to 2015's national forest inventory (ICNF, 2015), forests are the main land uses in the Portuguese mainland territory, occupying 36% of total area. Both evergreen oak woodlands and pine forest are, respectively, the first and second main forest cover in Portuguese mainland, each nearly occupying 1,000,000 ha (ICNF, 2015) (Figure I.6). Both occur along the Portuguese territory, but while evergreen oak woodlands are mainly restricted to the south or Mediterranean climate, pine forests distribute more profusely in the centre and north, subjected to a higher Atlantic influence (Figure I.6).

Both forest landscapes rely on a strong human presence and are currently exposed to major threats (see below) which may lead to changes in their structure and, consequently, on the biodiversity they hold. Therefore, advance on landscape-scale studies able to provide evidence-based implications on specific management practices are needed to reverse or alleviate such impacts.

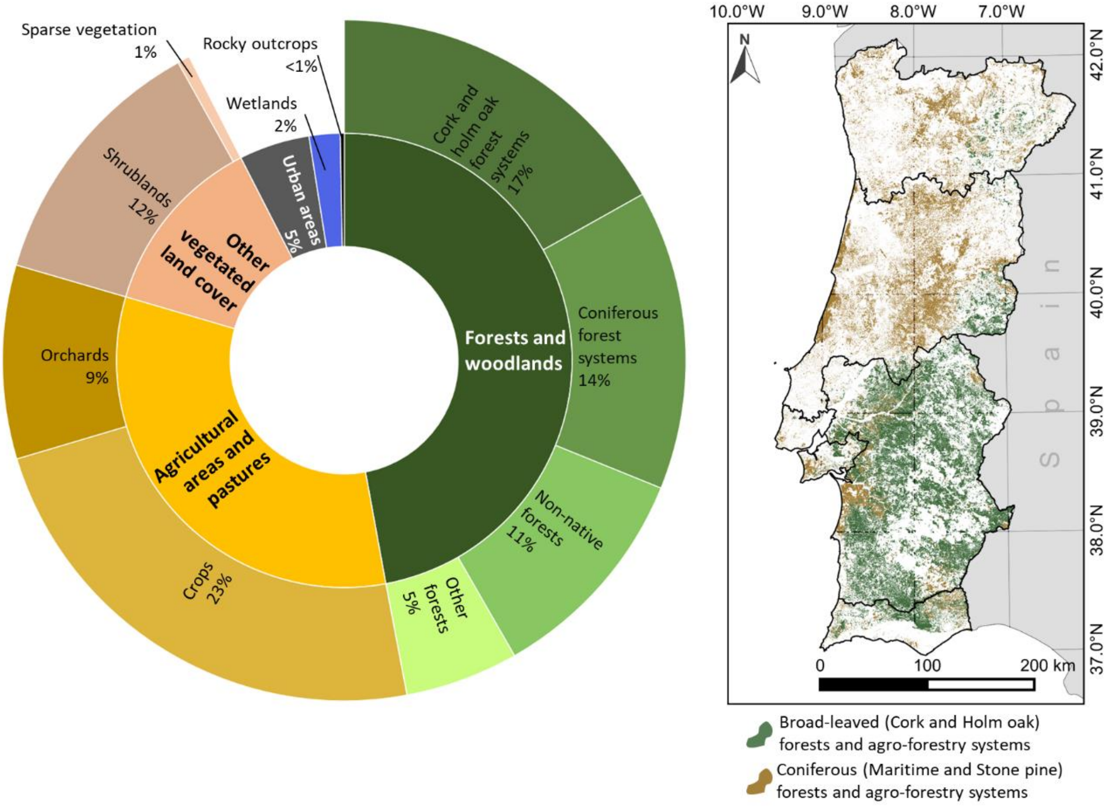

Figure I.6 – Proportion of the area occupied by the main land uses (left image), and spatial distribution of evergreen (only Cork and Holm oaks considered) and coniferous (Maritime and Stone pine) forests and agro-forestry systems across Portugal inland territory (right image). (Source: Land Use and Land Cover Map of Continental Portugal for 2018 – COS2018).

I.5.1. Standard production pine forests

Standard production forests mainly involve intensive forestry activities (*e.g.*, logging, plantation, thinning, understory management) of Maritime pine (*Pinus pinaster*), but also of other non-native plantations (*Eucalyptus* sp.). Each patch is under a rotational scheme passing from clear-cut patches where shrubs prevail (normally persisting for 5 years), newly planted forests subjected to regular thinning, and mature forests (with stands reaching 50 to 80 years for pines and 9-10 years for eucalypts). This results in a heterogeneous landscape mosaic of well-defined even-aged stands, which vary in composition, density, and age with neighbouring patches.

Pine forests are suffering a strong and continued decline since 1995 in Portuguese mainland territory (ICNF, 2015), though it has deaccelerated in the 5 years before 2015. Wildfires (Fernandes and Rigolot, 2007) and pests (namely the Pinewood nematode *Bursaphelenchus xylophilus,* Robinet *et al.*, 2020) have been the main hazards inflicting a reduction of the area covered by pine forests (ICNF, 2015). These have led to an abandonment or replacement of pine harvesting by other unmanaged land uses (*e.g.*, shrubland) or afforestation of new woody species, such as eucalypt. Conversion to eucalypt plantations, for instance, may be unfavourable to biodiversity in Mediterranean landscapes, as these plantations are the least diverse forested habitats, *e.g.*, for plant and bird communities (Proença *et al.,* 2010).

In general, pine forests are privately owned (though there are noticeable exceptions of national woods owned by the Portuguese State – ICNF, 2020), where small-estate management assumes greater significance in landscape planning. Each landowner manages its properties independently, contributing to the patchiness and characteristic mosaic of these landscapes.

Because standard production forests are highly dynamic, animal communities are continuously challenged by sudden habitat changes (Bennett *et al.*, 2006, Bergsten *et al.*, 2013). Hence, the occurrence of species is most likely susceptible to fragmentation and isolation effects. Therefore, the implementation of sustainable exploitation plans requires objective and quantitative approaches to identify those key elements that reinforce the spatial coherence of the whole landscape. In other words, we need to know how to keep landscape functional connectivity, while maintaining exploitation of the forest resource areas.

Some studies enclosed in this thesis were carried out in centre-west Portugal (centroid: 39°38’N 9°02’W, Figure I.7). The orography is mainly flat with a mean altitude of 70 m a.s.l., where calcareous sandy soils dominate. The area presents a Mediterranean oceanic bioclimate (Rivas-Martínez, 2011), since it is exposed to an Atlantic influence, resulting in dry and mild summers (T ~ 20 °C, P ~ 10 mm) and rainy winters (T ~ 8.5°C, P > 150 mm) (IPMA, 2020). Landscape is highly patchy, since small-state management dominates. Forestry is the main activity dominating the landscape (Figure I.8) and other land uses (*e.g.*, shrubland, non-native plantations) exhibit a scattered distribution embedded within the forest matrix (Figure I.7).

Pine forests do not excel for the high diversity of birds or the presence of species of conservation concern. However, bird communities inhabiting these land uses are strongly specialized in forest habitats, and some species are especially abundant in these forests (*e.g.*, Coal tit *Periparus ater,* Crested tit *Lophophanes cristatus,* Mistle thrush *Turdus viscivorus*, or the European nightjar *Caprimulgus europaeus*) (Catry *et al.*, 2010). Due to their high level of specialization and high patch contrast between different land uses, birds are confined to specific habitat patches and may perceive unsuitable habitats as barriers to dispersal (*e.g.*, due to visual obstruction, Prevedello *et al.*, 2010).

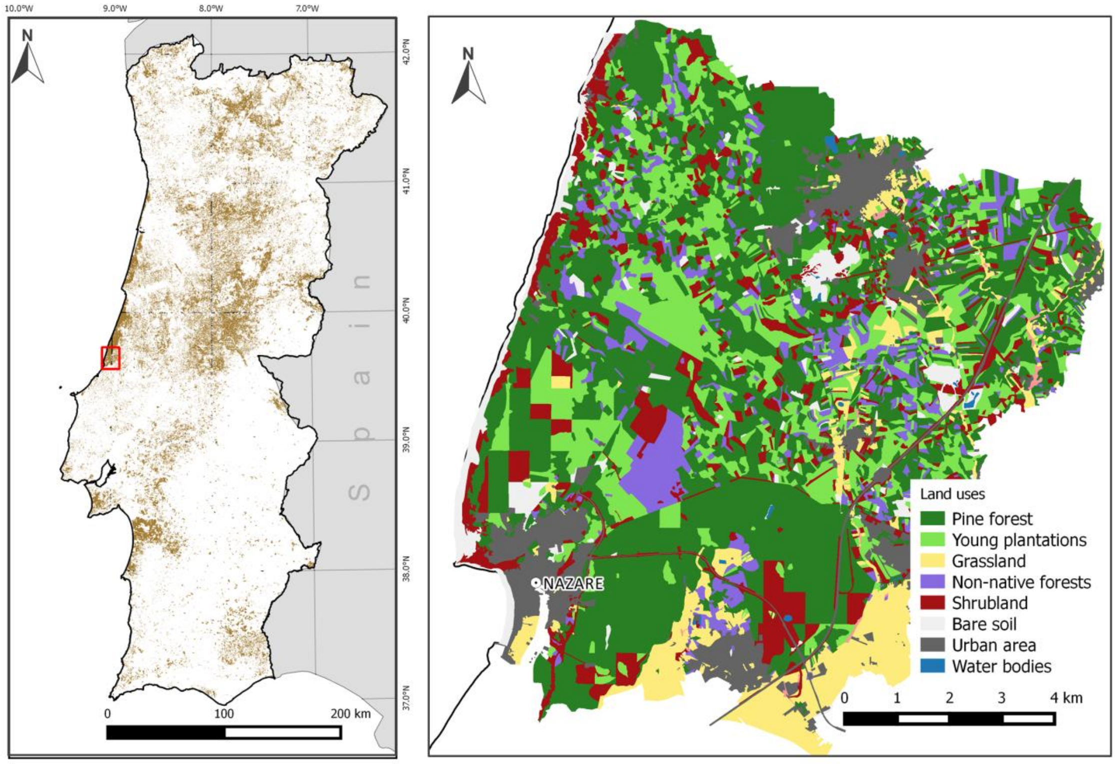

Figure I.7 – Location of the study area devoted to study fragmentation effects and connectivity on bird communities in standard production pine forests, plotted against the distribution of pine forests in the Portuguese mainland territory (left image) and main land uses in the study area (right image). Land use data source: own land cover map using Bing Maps aerial photography (year: 2011; resolution: 30cm).

Figure I.8 – A Maritime pine forest, even-aged stand.

I.5.2. Mediterranean oak woodlands – the 'montado' system

Mediterranean oak woodlands are a highly heterogeneous land use that resulted from centuries of traditional human activities (*e.g.*, agriculture, cattle grazing) which have gradually modified the once pristine forests (Blondel *et al.*, 2010) dominated by evergreen oaks, namely Cork oak (*Quercus suber*) and Holm oak (*Q. rotundifolia*). This long-last process resulted on a large scale fuzzy or variegated landscape (*sensu* McIntyre and Hobbs, 1999) where forest cover varies from densely wooded areas to agricultural plains of scarce tree cover or with islets of isolated trees (Pinto-Correia *et al.*, 2011). Along this gradient, the 'montado' is characterized as an agro-silvo-pastoral system with varying densities of oak trees (generally above 10%), in which the understory depends on human intervention expressed by a combination of agriculture, livestock grazing, and forestry activities (Pinto-Correia *et al.*, 2011; Godinho *et al.*, 2016; Pereira *et al.*, 2015). This system is one of the most biodiverse ecosystems in the Mediterranean, and for that reason, is classified as a High Nature Value (HNV) farmland (Andersen *et al.*, 2003) and is include in Annex I of European Habitats Directive (92/43/CEE), meaning, it is of conservation importance and concern.

Unlike standard production pine forests, Mediterranean oak woodlands show less abrupt spatial changes throughout the landscape and less dynamism over time. However, the characteristic savannah-type structure faces significant threats related to land abandonment, or management practices leading to areas of intensive agro-forestry production and livestock raising (Pinto-Correia and Mascarenhas, 1999; Plieninger and Schaar, 2008). Whether these changes will result in a new landscape structure is one of the main current concerns about 'montado' persistence (Pinto-Correia and Mascarenhas, 1999).

For the purpose of this thesis, we conducted the studies on the highly variegated Mediterranean landscape of southern Portugal, in the Évora district (centroid: 16271.45, -113395.21; EPSG: 3763-ETRS89 / Portugal TM06, Figure I9). The orography is mainly flat, though occasionally gently undulating, with altitude ranging between ~100 and ~450 m a.s.l.. The climate is typically Mediterranean with dry and hot summers (T > 24°C, P < 10 mm) and mild winters (T ~ 9°C, P ~ 90 mm) (IPMA, 2020). The area comprises the Mediterranean savannah-like woodland 'montado' (Pinto-Correia *et al.*, 2011) (Figure I.10), but other land uses are also present, such as: open farmlands for cattle grazing or cereal farming (grasslands), forest plantations (mainly *Pinus pinaster* and *Eucalyptus* sp.), orchards (olive groves and vineyards), and urban areas (Figure I.9).

Bird species diversity is generally high in Mediterranean oak woodlands (Catry *et al.*, 2010; Pereira *et al.*, 2015), taking advantage of the heterogeneity of the landscape (Tellería, 2001; Sanderson *et al.*, 2009; Bonthoux *et al.*, 2013) and structural characteristics of the habitats (Godinho and Rabaça, 2010; Catarino *et al.*, 2016). Pereira *et al.* (2015) described 92 species as usual breeders in 'montado' systems. Woodlark (*Lullula arborea*), Blue tit (*Cyanistes caeruleus*), Eurasian nuthatch (*Sitta europaea*) or Lesser spotted woodpecker (*Dryobates minor*) are among the most referenced or emblematic species of the system. Because the diversity of the ´montado' system relies on the spatial heterogeneity of the landscape (Blondel and Aronson, 1999; Tellería, 2001; Díaz *et al.*, 2003), its simplification can lead to significant losses in habitat suitability for species, or in the ability to provide structural and functional connectivity across a landscape (Fischer and Lindenmayer, 2002; Herrera *et al.*, 2018).

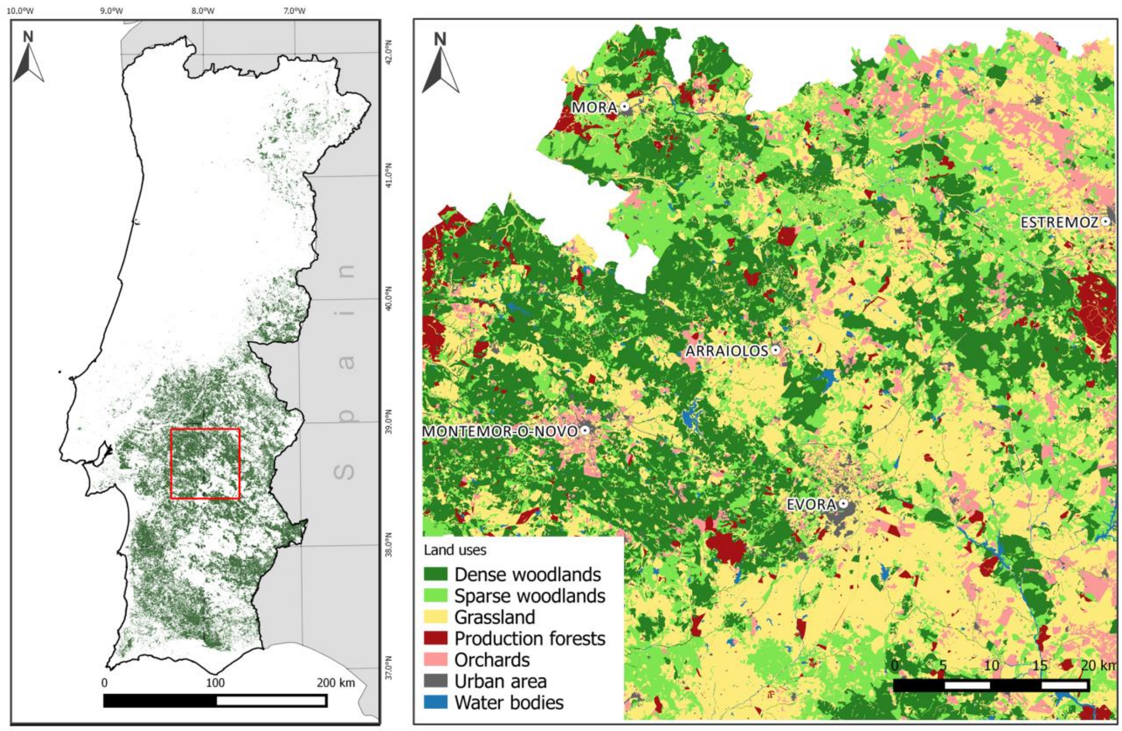

Figure I.9 – Location of the study area devoted to study fragmentation effects and connectivity on bird communities in Mediterranean oak woodlands, plotted against the distribution of evergreen oak forests in the Portuguese mainland territory (left image). Mapping of the main land uses in the study area (right image). Land use data source: CORINE Land Cover Level 5 classification (Guiomar *et al.*, 2009).

Figure I.10 – A Cork oak woodland representative of the 'montado' system.

I.6. THESIS STRUCTURE

This thesis is structured in five chapters: opens with the general introduction (Chapter I) where the theoretical framework and the concepts concerning the topics of research are introduced, and ends with general conclusions (Chapter V) where we unfold the main contributions and outline further research. In between, Chapters II to IV include the research developed and expressed in three scientific papers addressing the objectives of the thesis.

Chapter II consists on an exploratory paper, which determines the suitability of different conceptual approaches to capture landscapes' heterogeneity. Both patch- and gradient-based approaches are tested on different landscape contexts (variegated and mosaic), while accounting for species dependency effects. Overall, this chapter intends to provide evidence on the adequate approach to describe landscape structure considering both the nature of species perception and landscape type, thus providing support for application in subsequent research.

In Chapter III we explore individual bird species responses to landscape change by determining critical thresholds beyond which major changes in species abundance and community composition occur. While looking at the tree canopy gradient in 'montado' landscape we aim to ascertain the limits where populations are more sensitive, thus setting bases to prevent the critical downfall of biodiversity while improving the effectiveness of conservation, resource management and restoration practices.

Chapter IV demonstrates how functional connectivity mediates the spatial distribution of a bird community inhabiting a fragmented landscape subjected to long-standing forestry activity. Single- and multispecies connectivity are tested on species occurrence and community assemblage while accounting for habitat amount and quality to determine habitat and landscape filtering effects on local communities. In this chapter we aim to disentangle the effects of functional connectivity from other key factors on bird species occurrence, while assessing how it mediates the spatial distribution of local community composition and diversity.

In the last chapter (Chapter 5 – General conclusions), we summarize the main findings stemming from the studies and explore tangible implications, while framing them in the current agenda addressing further issues in fragmentation and connectivity. Based on the thesis results we then unfold the main contributions to the current knowledge and outline further research that advances on the study of habitat fragmentation and functional connectivity.

Appendix I.A: Published research on connectivity and birds

The following published studies were obtained from the Web of Science while searching for studies published up to 2019 using the strings "bird and connectivity" in the title. This is a comprehensive search to outline the general trends of the existing research and not a complete review.

Adams RV, Burg TM (2015) Gene Flow of a Forest-Dependent Bird across a Fragmented Landscape. PLOS ONE 10(11).

Amos JN, Harrisson KA, Radford JQ, White M, Newell G, Mac Nally R, Sunnucks P, Pavlova A (2014) Species- and sex-specific connectivity effects of habitat fragmentation in a suite of woodland birds. Ecology 95(6): 1556-1568.

Awade M, Boscolo D, Metzger JP (2012) Using binary and probabilistic habitat availability indices derived from graph theory to model bird occurrence in fragmented forests. Landscape Ecology 27(2): 185-198.

Awade M, Metzger JP (2008) Using gap-crossing capacity to evaluate functional connectivity of two Atlantic rainforest birds and their response to fragmentation. Austral Ecology 33(7): 863-871.

Buelow CA, Baker R, Reside AE, Sheaves M (2017) Spatial dynamics of coastal forest bird assemblages: the influence of landscape context, forest type, and structural connectivity. Landscape Ecology 32(3): 547-561.

Clauzel C, Jeliazkov A, Mimet A (2018) Coupling a landscape-based approach and graph theory to maximize multispecific connectivity in bird communities. Landscape and Urban Planning 179: 1-16.

Clergeau P, Burel F (1997) The role of spatio-temporal patch connectivity at the landscape level: an example in a bird distribution. Landscape and Urban Planning 38(43862): 37-43.

Doerr VAJ, Doerr ED, Davies MJ (2011) Dispersal behaviour of Brown Treecreepers predicts functional connectivity for several other woodland birds. Emu 111(1): 71-83.

Duflot R, Daniel H, Aviron S, Alignier A, Beaujouan V, Burel F, Cochard A, Ernoult A, Pain G, Pithon JA (2018) Adjacent woodlands rather than habitat connectivity influence grassland plant, carabid and bird assemblages in farmland landscapes. Biodiversity and Conservation 27(8): 1925-1942.

Estrada-Carmona N, Martinez-Salinas A, DeClerck FAJ, Vilchez-Mendoza S, Garbach K (2019) Managing the farmscape for connectivity increases conservation value for tropical bird species with different forest-dependencies. Journal of Environmental Management 250.

Fagan ME, DeFries RS, Sesnie SE, Arroyo-Mora JP, Chazdon RL (2016) Targeted reforestation could reverse declines in connectivity for understory birds in a tropical habitat corridor. Ecological Applications 26(5): 1456-1474.

Fleishman E, Thomson JR, Kalies EL, Dickson BG, Dobkin DS, Leu M (2014) Projecting current and future location, quality, and connectivity of habitat for breeding birds in the Great Basin. Ecosphere 5(7).

Geoffroy C, Fiola ML, Belisle M, Villard MA (2019) Functional connectivity in forest birds: evidence for species-specificity and anisotropy. Landscape Ecology 34(6): 1363-1377.

Gil-Tena A, Nabucet J, Mony C, Abadie J, Saura S, Butet A, Burel F, Ernoult A (2014) Woodland bird response to landscape connectivity in an agriculture-dominated landscape: a functional community approach. Community Ecology 15(2): 256-268.

Grafius DR, Corstanje R, Siriwardena GM, Plummer KE, Harris JA (2017) A bird's eye view: using circuit theory to study urban landscape connectivity for birds. Landscape Ecology 32(9): 1771-1787.

Herrera JM, Alagador D, Salgueiro P, Mira A (2018) A distribution-oriented approach to support landscape connectivity for ecologically distinct bird species. PLOS ONE 13(4).

Ibarra-Macias A, Robinson WD, Gaines MS (2011) Forest corridors facilitate movement of tropical forest birds after experimental translocations in a fragmented Neotropical landscape in Mexico. Journal of Tropical Ecology 27: 547-556.

Ibarra-Macias A, Robinson WD, Gaines MS (2011) Experimental evaluation of bird movements in a fragmented Neotropical landscape. Biological Conservation 144(2): 703-712.

Kang W, Minor ES, Park CR, Lee D (2015) Effects of habitat structure, human disturbance, and habitat connectivity on urban forest bird communities. Urban Ecosystems 18(3): 857-870.

Khimoun A, Peterman W, Eraud C, Faivre B, Navarro N, Garnier S (2017) Landscape genetic analyses reveal fine-scale effects of forest fragmentation in an insular tropical bird. Molecular Ecology 26(19): 4906-4919.

Kondo T, Nakagoshi N (2002) Effect of forest structure and connectivity on bird distribution in a riparian landscape. Phytocoenologia 32(4): 665-676.

Lopes EV, Mendonca LB, dos Santos MA, Lopez-Iborra GM, dos Anjos L (2016) Effects of connectivity on the forest bird communities of adjacent fragmented landscapes. Ardeola 63(2): 279-293.

Martensen AC, Pimentel RG, Metzger JP (2008) Relative effects of fragment size and connectivity on bird community in the Atlantic Rain Forest: Implications for conservation. Biological Conservation 141(9): 2184-2192.

Martensen AC, Ribeiro MC, Banks-Leite C, Prado PI, Metzger JP (2012) Associations of Forest Cover, Fragment Area, and Connectivity with Neotropical Understory Bird Species Richness and Abundance. Conservation Biology 26(6)1100-1111

Mayhew RJ, Tobias JA, Bunnefeld L, Dent DH (2019) Connectivity with primary forest determines the value of secondary tropical forests for bird conservation. Biotropica 51(2): 219-233.

Mazaris AD, Papanikolaou AD, Barbet-Massin M, Kallimanis AS, Jiguet F, Schmeller DS, Pantis JD (2013) Evaluating the Connectivity of a Protected Areas' Network under the Prism of Global Change: The Efficiency of the European Natura 2000 Network for Four Birds of Prey. PLOS ONE 8(3).

Mortelliti A, Fagiani S, Battisti C, Capizzi D, Boitani L (2010) Independent effects of habitat loss, habitat fragmentation and structural connectivity on forest-dependent birds. Diversity and Distributions 16(6): 941-951.

Mortelliti A, Westgate MJ, Lindenmayer DB (2014) Experimental evaluation shows limited influence of pine plantations on the connectivity of highly fragmented bird populations. Journal of Applied Ecology 51(5): 1179-1187.

Mueller T, Lenz J, Caprano T, Fiedler W, Bohning-Gaese K (2014) Large frugivorous birds facilitate functional connectivity of fragmented landscapes. Journal of Applied Ecology 51(3): 684-692.

Pavlacky DC, Goldizen AW, Prentis PJ, Nicholls JA, Lowe AJ (2009) A landscape genetics approach for quantifying the relative influence of historic and contemporary habitat heterogeneity on the genetic connectivity of a rainforest bird. Molecular Ecology 18(14): 2945-2960.

Perez-Hernandez CG, Vergara PM, Saura S, Hernandez J (2015) Do corridors promote connectivity for bird-dispersed trees? The case of Persea lingue in Chilean fragmented landscapes. Landscape Ecology 30(1): 77-90.

Robertson EP, Fletcher RJ, Austin JD (2019) The number of breeders explains genetic connectivity in an endangered bird. Molecular Ecology 28(11): 2746-2756.

Robertson EP, Fletcher RJ, Cattau CE, Udell BJ, Reichert BE, Austin JD, Valle D (2018) Isolating the roles of movement and reproduction on effective connectivity alters conservation priorities for an endangered bird. PNAS-USA 115(34): 8591-8596.

Robertson OJ, Radford JQ (2009) Gap-crossing decisions of forest birds in a fragmented landscape. Austral Ecology 34(4): 435-446.

Sekercioglu CH, Loarie SR, Oviedo-Brenes F, Mendenhall CD, Daily GC, Ehrlich PR (2015) Tropical countryside riparian corridors provide critical habitat and connectivity for seed-dispersing forest birds in a fragmented landscape. Journal of Ornithology 156: S343-S353.

Socolar JB, Diaz-Alvan J, Del Castillo PS, Pomara LY, O'Shea BJ, Poclin SC, Stotz D, Schmitt F, Graham D, Carnes BH, Inzunza ER (2018) Noteworthy bird records from northeastern Peru reveal connectivity and isolation in the western Amazonian avifauna. Wilson Journal of Ornithology 130(1): 94-111.

Uezu A, Metzger JP, Vielliard JME (2005) Effects of structural and functional connectivity and patch size on the abundance of seven Atlantic Forest bird species. Biological Conservation 123(4): 507-519.

Velez MCD, Silva WR, Pizo MA, Galetto L (2015) Movement Patterns of Frugivorous Birds Promote Functional Connectivity among Chaco Serrano Woodland Fragments in Argentina. Biotropica 47(4): 475-483.

Vergara PM (2011) Matrix-dependent corridor effectiveness and the abundance of forest birds in fragmented landscapes. Landscape Ecology 26(8): 1085-1096.

Vergara PM, Perez-Hernandez CG, Hahn IJ, Soto GE (2013) Deforestation in central Chile causes a rapid decline in landscape connectivity for a forest specialist bird species. Ecological Research 28(3): 481-492.

Zozaya EL, Brotons L, Saura S (2012) Recent fire history and connectivity patterns determine bird species distribution dynamics in landscapes dominated by land abandonment. Landscape Ecology 27(2): 171-184.

Zozaya EL, Brotons L, Saura S, Pons P, Herrando S (2012) Connectivity determines post-fire colonisation by open-habitat bird species: the case of the Ortolan Bunting Emberiza hortulana. Ardeola 59(1): 57-74.

Chapter II

Thinking outside the patch: a multi-species comparison of conceptual models from real-world landscapes

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Pedro A. Salgueiro[1,2,3,5], António Mira[1, 3,5], João E. Rabaça[2,4,5], Carmo Silva[1, 3,5], Sofia Eufrázio[1, 3,5], Denis Medinas[1, 3,5], Giovanni Manghi[6], Bruno Silva[1, 3,5], Sara M. Santos[1, 3,5]

[1]UBC – Conservation Biology Lab;

[2]LabOr – Laboratory of Ornithology;

[3]CIBIO-UE – Research Center in Biodiversity and Genetic Resources, Pole of Évora – Research Group in Applied Ecology;

[4]ICAAM – Institute of Mediterranean Agricultural and Environmental Sciences;

[5]Department of Biology, University of Évora. Mitra, 7002-554 – Évora, Portugal.

[6]NaturalGIS LDA, Open Source Geographic Information Systems, Estrada Municipal 527, Estrada da Igrejinha, Quinta do Aguilhão, 7005-874 Évora, Portugal

II.1. ABSTRACT

Context: When modelling a species' distribution, landscapes can alternatively be conceptualized following patch- or gradient-based approaches. However, choosing the most suitable conceptualization is difficult and methods for empirical validation are still lacking.

Objectives: To address the conditions under which a given conceptual model is more suitable, taking into account landscape context and species trait dependency effects. Patch- and gradient-based conceptualizations were built based on two structurally different landscapes: variegated and mosaic. We hypothesize that: (H1) gradient-based models better describe variegated landscapes while patch-based models perform better in mosaic landscapes; and (H2) gradient-based models will fit generalist species better while patch-based models will suit specialists better.

Methods: We modelled the distribution of eleven bird species in each landscape using each conceptualization. We determined the suitability of each conceptual model to fit statistical models by looking for cross-species responses and deviations from best models.

Results: We found no clear support for our hypotheses. Although patch-based models performed better in mosaic landscapes (H1), they also provided useful conceptualizations in variegated landscapes. However, when patches showed high heterogeneity, gradient-based approaches better fit specialist species (H2).

Conclusions: The suitability of a given conceptual model depends on the interaction between species habitat specialization and the intrinsic spatial heterogeneity of the landscape, and the ability of each conceptualization to capture it. Gradient-based models provide better information on resource allocation, while patch-based models offer a simplified perspective on landscape attributes. Future research should consider the nature of both species and landscapes in order to avoid bias from inadequate landscape conceptualizations.

II.2. KEYWORDS

Mosaic landscape; Variegated landscape; Continuum model; Discrete model; Habitat quality; Spatial heterogeneity.

II.3. INTRODUCTION

Advances in landscape ecology have provided new, yet sometimes conflicting, models to describe and interpret human-modified landscapes and habitat fragmentation (Dunn and Majer, 2007; Lindenmayer *et al.*, 2007; Didham *et al.*, 2012; Mimet *et al.*, 2014). Two main types of conceptual models can be broadly considered: discrete (patch-based) and continuum (gradient-based) approaches, each dealing differently with spatial continua (Fischer *et al.*, 2004a). Patch-based models implicitly categorize the landscape into suitable habitat patches embedded in an unsuitable or hostile matrix (*e.g.*, island biogeography theory by MacArthur and Wilson, 1967; Haila, 2002; and patch-corridor-matrix by Forman, 1995). Gradient-based models describe landscapes as a gradual change of resources, ecological processes and environmental conditions in space (*e.g.*, the continuum model by Fischer and Lindenmayer, 2006).

In spite of the valuable insights that patch-based models have provided (*e.g.*, metapopulation studies; Hanski, 1998), there is increasing criticism that their generalization is an overly simplistic way to understand ecological processes and the effect of management practices (Fischer and Lindenmayer, 2006, 2007). Landscape categorization is often subjected to a human perspective, which may not be consistent with a species perception (Fischer and Lindenmayer, 2006; Franklin and Lindenmayer, 2009). In particular, discrete conceptualizations of landscapes that are characterized by open woodlands of varying tree density (*e.g.*, savannahs, Woodward *et al.*, 2004) are often dubious because patch boundaries are difficult to define, neglect within-patch heterogeneity (Price *et al.*, 2010) and assume all organisms respond in the same way (Betts *et al.*, 2014). To overcome such limitations, Fischer and Lindenmayer (2006) proposed the continuum model, which considers spatial continua rather than discrete patches. Although conceptually appealing, the application of gradient-based models is still rare (see Ingham and Samways, 1996 or Betts *et al.*, 2014) probably due to a lack of habitat quality data with sufficient detail to properly characterize continua at the landscape level (Fischer *et al.*, 2004a). Most recently, some studies have attempted to explore different approaches using continuum data (McGarigal *et al.*, 2009; Frazier and Wang, 2013; Mimet *et al.*, 2014), although such applications are limited and model performance has not been thoroughly assessed in different types of real landscapes.

Choosing an inadequate landscape conceptualization to model species distributions may produce misleading results, increasing the risk of developing ineffective management strategies (Fischer *et al.*, 2004a, 2004b; Lindenmayer *et al.*, 2008). Researchers are increasingly studying under which conditions a given landscape conceptual model is more appropriate or constitutes a suitable alternative (Lindenmayer *et al.*, 2007). Fischer *et al.* (2004b) argued that the selection of an appropriate conceptual model depends on the species of interest and the landscape context. Recent research on considering a single landscape context by Price *et al.* (2009) and Bruton *et al.* (2015, 2016) pointed out the need to account for multispecies and life-history trait effects on the individualistic perception of landscapes given the lack of coherent responses of species. More recently, Brudvig *et al.* (2017) proposed a decision-making framework to guide conceptual model selection based on study objectives, landscape context and species traits. This framework provides a set of 'rules of thumb' meant to ease the process of environmental data acquisition according to an appropriate conceptualization of landscapes. For instance, environmental data collected on the scope of patch-based models would better apply to landscapes showing distinct patch boundaries (hard-edges) between few land-cover types; or to species exhibiting specific requirements, since suitable patches are more easily mapped as distinct from the inhospitable matrix. Conversely, the continuum model would better suit landscapes with low contrast (soft-edges) between patches (see also McIntyre and Barrett, 1992), or to generalist species using multiple habitats, since their plasticity would hamper clear species-habitat relations required by patch-based models (Brudvig *et al.*, 2017). However, empirical validation of the assumptions regarding the use and selection of appropriate conceptual models is still lacking, especially those using empirical data in real-world landscapes.

Our study uses the distribution of bird species to test the assumptions derived from the latest research on landscape conceptualization (Price *et al.*, 2009; Bruton *et al.*, 2015; Brudvig *et al.*, 2017). In order to avoid biases from single (Price *et al.*, 2009; Bruton *et al.*, 2015) or artificially built experimental landscapes (Brudvig *et al.*, 2017), we expanded our study to two structurally different real-world landscapes: a variegated savannah-like forest with a tree canopy cover gradient without abrupt changes, and a mosaic landscape with clearly defined forest patches. We set up four conceptual models to explain species occurrences: (1) a human-derived patch model considering supervised assistance for land use classification; (2) a contour-based patch model developed from the identification of community turnovers (thresholds marking strong changes in bird species composition) at each landscape; (3) a gradient-based continuum model considering gradients of change in environmental variables at the landscape scale; and (4) a gradient-based microhabitat model focusing on site-scale heterogeneity which is often not achievable from a landscape-scale characterization. Our aim was to identify the conditions under which a given landscape conceptual model was the better alternative (Lindenmayer *et al.*, 2007; Stoddard, 2010), as a function of both landscape context and species trait dependency effects. We evaluated conceptual models within each real-world landscape in order to test the following hypotheses: (H1) landscape context dependency effects – gradient-based models better describe the structural complexity of variegated landscapes while patch-based models provide better outcomes in classic mosaic landscapes; and (H2) species trait dependency effects – gradient-based models will better fit generalist species while patch-based models will better suit species with marked habitat requirements (specialists). However, it was not the aim of this study to provide a direct comparison between landscapes, as both differ structurally in their elements and the bird communities that occur within them. Instead, our aim was to assess how species respond to different conceptualizations within the two contrasting landscapes considering similar assumptions.

II.4. METHODS

II.4.1. Study area

The study was carried out in two different landscape types (Figure II.1): a Mediterranean oak woodland (southern Portugal, centroid: 38º39’N 7º59’W, EPSG code: 4326) and an Atlantic pine plantation (centre-west Portugal, centroid: 39º38’N 9º41’W, EPSG code: 4326).

The Mediterranean oak woodlands are a highly variegated savannah-like landscape (*sensu* McIntyre and Hobbs, 1999). The heterogeneous pattern of land use is a result of centuries of traditional human activities (agriculture, cattle grazing and forestry) that have gradually modified the once pristine evergreen cork oak (*Quercus suber*) and holm oak (*Q. rotundifolia*) forests (Blondel *et al.*, 2010; Pinto-Correia *et al.*, 2011). Sharp patch boundaries are difficult to identify because forest cover varies from densely wooded areas to agricultural plains with sparse tree cover or with islets of isolated trees (Pinto-Correia *et al.*, 2011).

The Atlantic pine plantations are standard production forests subjected to intensive forestry activities of maritime pine (*Pinus pinaster*) and non-native plantations (*Eucalyptus* sp.). Each patch is under a rotational scheme passing from clear-cut patches dominated by shrubs (normally 5 years) to newly planted forests subjected to regular thinning, and mature forests (reaching 50 to 80 years for pines and 9-10 years for eucalypts). This has resulted in a heterogeneous landscape mosaic of well-defined patches with stands varying in composition, density and age.

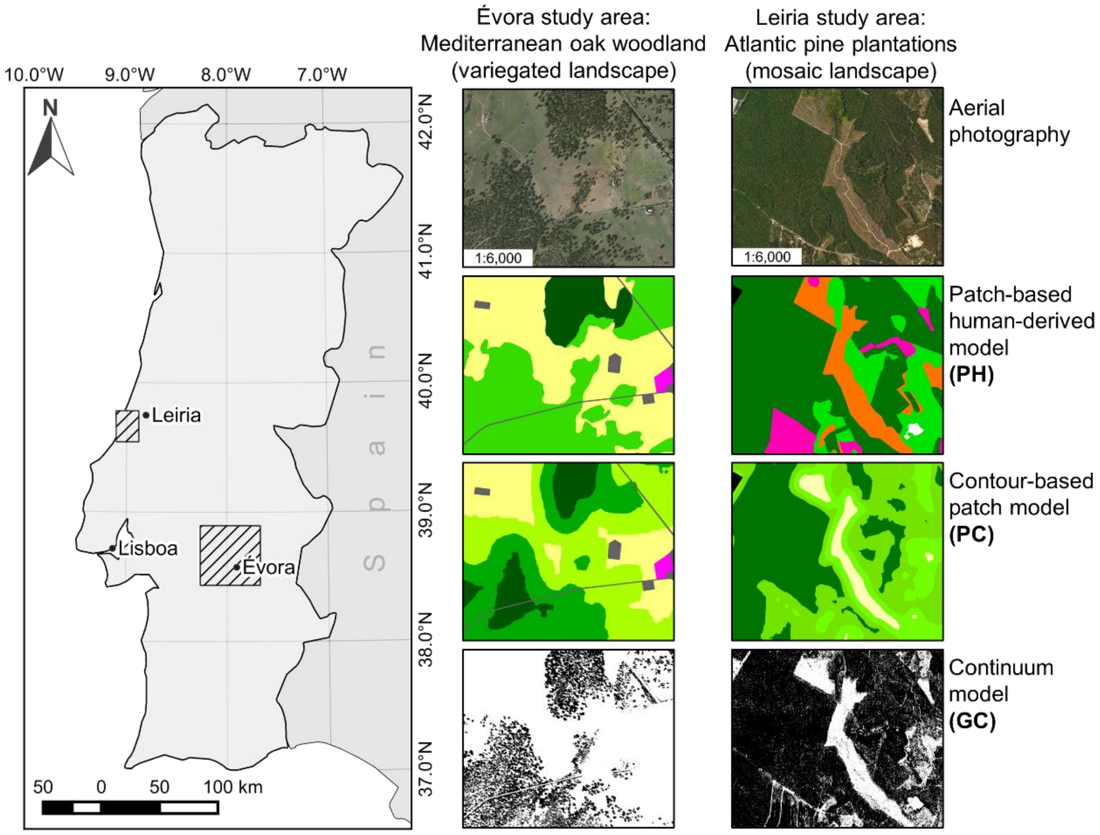

Figure II.1. – Location of the two study areas in Portugal (Mediterranean oak woodland at Évora study area and Atlantic pine plantations at Leiria study area) and representative detail of the three landscape-scale models for the same sample area.

II.4.2. Landscape conceptual models

Each landscape was described using four conceptual models (Figure II.1). Two of them used as patch-based conceptualizations of the landscape: (1) a human-derived patch classification – PH, and (2) a contour-based patch – PC. Other two were gradient-based conceptualizations: (3) a landscape-scale gradient–based continuum – GC, and (4) a site-scale gradient of microhabitat complexity – GM.

The human-derived patch model (PH) is considered a discrete mosaic landscape conceptual model (*sensu* Bennett *et al.*, 2006). Landscape characterization uses supervised assistance based on a land use classification. In Mediterranean oak woodlands, we used the CORINE Land Cover Level 5 classification (Guiomar *et al.*, 2009) coupled with fieldwork for validation. Atlantic pine plantation landscapes are very dynamic, so we produced our own land cover map using Bing Maps aerial photography (year: 2011; resolution: 30cm), and the delimitation and classification of each patch was validated in the field using a GPS device (Garmin eTrex20). We then reclassified the original classes to reduce their number (see Appendix II.A Table II.A1 and II.A2 for more detailed considerations on land use reclassification). Patch boundaries were sharp and well defined, and the landscape was composed of a mosaic of multiple patch classes (minimum size: $100m^2$), which avoids an unrealistic binary classification of habitat versus non-habitat (McIntyre and Hobbs, 1999; Fischer *et al.*, 2004b).

The contour-based patch model (PC) is a simplification of the habitat contours model (Fischer *et al.*, 2004a). We defined habitat contours using bird community turnover data, where thresholds marking strong changes in bird species composition were transposed to landscape maps as contours delineating putative homogeneous patches. Bird community turnovers were computed, taking into account the whole bird community detected in each area (20 species in pine plantations; 33 in oak woodlands, see Appendix II.A Table II.A3 for complete listing). Species responses to the tree canopy gradient were modelled using Huisman-Olff-Fresco models (hereafter HOF models; Salgueiro *et al.*, 2018a). HOF models consist of a set of Gaussian response curves based on ecological niche theory, estimating the probability of occurrence and the turnover patterns for species and communities (Appendix II.A Figure II.A1; for details see Jansen and Oksanen, 2013). Contours are therefore community-based, instead of species-specific, as originally advocated by Fischer *et al.* (2004a). Most importantly, this approach provides an unsupervised land-use classification as an alternative to human-derived conceptualizations that may not be consistent with species perception.

The gradient continuum model (GC) follows the assumptions provided by continuum theory (Austin, 1985, 1999), in which landscapes are described by unrestricted and direct environmental gradients (Fischer and Lindenmayer, 2006). We used the tree cover density gradient (raster-based) as a proxy for distribution of habitat, foraging and nesting resources (Price *et al.*, 2009). In both landscapes, the tree cover density gradient was built from 2010 aerial photography data (resolution: 1m) by applying colour image segmentation and the k-means algorithm for unsupervised classification (Subbiah and Seldev, 2012). For these procedures, we used Orfeo Toolbox 3.20 (Orfeo Toolbox Development Team, 2013), in QGIS version 2.2 (Quantum GIS Development Team, 2013). This resulted in a reclassification where each individual pixel represented the presence of tree canopy, describing the structure of forest cover as a continuum of change (Fischer and Lindenmayer, 2006).

The microhabitat model (GM) produces a site-scale characterization describing local gradients of change in vegetation density and structure that captures highly detailed complexity at the patch scale in a way that is typically poorly represented in landscape conceptual models.

II.4.3. Explanatory variables

We extracted a set of variables for each conceptual model, aiming to describe landscape composition and configuration (Table II.1). For patch models (PH and PC), we extracted compositional parameters using the relative proportions of land uses from a vector map. Configuration patterns were determined by calculating the landscape Shannon's diversity index, number of patches and edge length. For the PC model, we calculated only total edge length. The PH conceptualization allows both hard and soft edges to be explored. We measured edge length between patches, where edges were defined as differences in vertical structure (for Atlantic pine plantations) or stem density (for Mediterranean oak woodlands). In the first case, hard edges were considered to exist between mature pine plantations and shrub/farmland/bare soil, while soft edges were found between mature plantations and young plantations or young plantations and shrub/farmland/bare soil. In Mediterranean oak woodlands, hard edges were considered the edge between grassland and dense oak forest cover, and soft edges were found between grassland and sparse oak forest cover or sparse and dense oak forest cover (see Table II.1 for land-cover class descriptions).

Continuum model (GC) variables were extracted using the tree canopy gradient raster map as a surrogate for tree density (Westfall and Morin, 2012; Godinho *et al.*, 2016). We defined composition as the percentage of canopy cover. The gradient was obtained by a ‘moving window’ procedure at different spatial extents (see below). To account for configuration, we followed the same procedure to compute measures of subdivision (the number of clusters of adjacent raster cells classified as canopy cover) and aggregation (clumpiness and aggregation index of raster cells classified as canopy cover) using FRAGSTATS (McGarigal *et al.*, 2012).

Finally, the GM variables described local habitat characteristics from field measurements such as density (cover) and structure (height, variation of height and cover) of vegetation strata (shrubs and trees) as a proxy of habitat quality (*sensu* Mortelliti *et al.*, 2010a). Field measurements were conducted in the same period as bird sampling at 20 random points within a 100m radius from the bird sampling sites. Shrub variables corresponded to total occurrence, and mean and covariance values of height of each sampling point data. In Mediterranean oak woodlands, we counted the number of mature and young trees (< 2m), and measured the tree diameter in Atlantic pine plantations at breast height as a proxy for forest plantation age.

Although different data sources were used to derive the habitat metrics for each landscape, we established a baseline of variables across conceptual models using Spearman correlation ranks for comparative purposes (see Appendix II.C). We found evidence for cross-model correlations, indicating that most conceptual models account for similar tendencies for both compositions (*e.g.*, densely forested areas are equally captured as such by different conceptual models) and configuration variables (*e.g.*, heterogeneous areas are equally captured as such by different conceptual models).

Finally, as documented in several studies (*e.g.*, Bennett *et al.*, 2006), species perceive landscape at different scales, sometimes due to a differential spatial use (Ingham and Samways, 1996). For landscape-scale models (GC, PH, PC), we considered three different spatial extents to detect scale-dependent responses (Grand and Cushman, 2003) at site (100m and 200m), meso- (500m) and macro- (1000m) scales (see Warren *et al.*, 2005).

Table II.1 – Summary of variables used to build generalized linear models for each conceptual model (PH –human-derived patch model, PC – contour-based patch model, GC – continuum model, GM – site-scale model) in the two landscape context study areas.

Model	Mediterranean oak woodlands	Atlantic Pine plantations
PH	% Grassland cover (<10% CORINE)	% Shrubland
	% Sparse forest cover (10-30%)	% Young plantations
	% Dense forest cover (>30%)	% Pine forest
		% Non-native plantations
	Shannon's diversity index	Shannon's diversity index
	Number of patches	Number of patches
	Total length of hard edges	Total length of hard edges
	Total length of soft edges	Total length of soft edges
PC	% Grassland cover (<1% canopy)	% Low forest cover (<15% canopy)
	% Sparse cover forest (1-20%)	% Medium forest cover (15-50%)
	% Medium cover forest (20-50%)	% High forest cover (50-70%)
	% Dense cover forest (>50%)	% Very high forest cover (>70%)
	Shannon's diversity index	Shannon's diversity index
	Number of patches	Number of patches
	Total edge length	Total edge length
GC	Percentage canopy cover	Percentage canopy cover
	Number of canopy clusters	Number of canopy clusters
	Clumpiness	Clumpiness
	Aggregation index	Aggregation index
GM	Number of trees	Number of trees
	Number of young trees	Mean diameter at breast height
	Mean shrub height	Mean shrub height
	Shrub height covariance	Shrub height covariance
	Shrub density	Shrub density

II.4.4. Bird surveys

Bird species data were obtained by means of 10 min point counts (Bibby *et al.*, 2000) with a distance limit of 100m. A total of 210 sampling sites, 105 per study area, were surveyed once during the breeding season (between April and May), when both resident and migratory species are more conspicuous. Surveys were made during the period of highest detectability (6:00 to 11:00 a.m., Palmeirim and Rabaça, 1994) and in favourable weather conditions (Bibby *et al.*, 2000). In order to enhance the statistical power and representativeness of the study area, we chose to sample a higher number of sites at the expense of a higher survey effort per site (Loos *et al.*, 2015). Atlantic pine plantations were sampled in 2011 and Mediterranean oak woodlands in 2013. All bird species that were seen or heard were recorded, but fly-over individuals, aerial-feeders or species with large home ranges were not included in the analysis. Species of the genus *Galerida* (*G. cristata* and *G. theklae*) were pooled and analysed together (hereafter *Galerida* spp.) due to the difficulty in accurately distinguishing these species (*e.g.*, Delgado and Moreira, 2000).

We calculated the Species Specialization Index (SSI) to evaluate habitat specialization for each species in each landscape separately (Julliard *et al.*, 2006). To avoid bias from original discrete classifications, we used the CLARA method (Maechler *et al.*, 2016) which defines the number of habitat classes in each landscape by computing a set of variables that cluster sampling sites sharing similar characteristics (Appendix II.B Table II.B1 and II.B2). The number of habitats was validated by analysing the silhouette coefficient to find the optimal number of clusters by considering the tightness within and separation between clusters (Rousseeuw, 1987). For each species, SSI was defined as the coefficient of variation of the averaged densities in each habitat class (Julliard *et al.*, 2006). Species were ranked accordingly (Appendix II.B Table II.B3 and II.B4). The SSI regards specialists as species that are more restricted to a single habitat class and generalists as species that use multiple habitats.

II.4.5. Data analysis

Our hypotheses take into account the decision-making framework proposed by Brudvig *et al.* (2017) and the studies of Price *et al.* (2009) and Bruton *et al.* (2015). We took into account the attributes of the landscapes (context dependency) and species habitat specialization (trait dependency) (Table II.2). We built an analytical procedure (see Figure II.2) based on two attributes: (1) 'coherence' in species responses and (2) the 'performance' of conceptual models. 'Coherence' regards which conceptual model consistently provides a good fit across the highest number of species in each landscape. A similar approach has been used in other studies (Price *et al.*, 2009; Bruton *et al.*, 2015), but this approach does not evaluate the suitability of alternative conceptual models. Therefore, we also evaluated our results by measuring the ability of an alternative conceptual model to also provide an acceptable fit, *i.e.*, the 'performance'.

The modelling procedure for each species followed the theoretical information approach of Burnham and Anderson (2002) using generalized linear models (GLM). Model selection was based on Akaike information criterion corrected for small sample sizes (AICc) and Akaike weights (ω_i). For each study area, we modelled count data of eleven species with a Poisson error distribution (log link function), which complied with statistical (species was present at least in 20% of the points, showing no significant spatial autocorrelation) and ecological criteria (acknowledged to have different requirements concerning habitat characteristics).

We started the procedure by screening explanatory variables for outlier presence, normality and collinearity (Spearman correlation ranks > 0.7, Tabachnick and Fidell, 1996). Whenever needed, variables were transformed (square root or logarithmic for continuous variables and arcsine of the square root for proportions, Zar, 1996), categorized to overcome the lack of normality or discarded to avoid model over-parameterization. We also tested for the quadratic terms of variables in order to detect non-linear relations, although further consideration was only given when the quadratic term overcame the linear term in at least 4 AICc units (Burnham *et al.*, 2011). For each variable, we selected the best response scale (100, 200, 500 and 1000m) by extracting the one with the lowest AICc from univariate GLM. We determined the four best explanatory variables of each conceptual model by calculating their relative importance (RVI – the sum of Akaike weights in statistical models where the variable was present) after running the function ‘dredge’ upon all variables (library ‘MuMIn’, Bartón, 2012). All possible statistical models (n=16) were computed separately for each of the four conceptual models. All resulting statistical models were grouped together (n=64), and ΔAICc and correspondent Akaike weights were calculated and ranked. The final ΔAICc dataset was obtained by setting a cut-off point at the 95% confidence interval on the cumulative sum of Akaike weights, below which models were discarded.

Table II.2 – Attributes of the landscapes and species used in this study. For landscape context dependency, we considered the number of land cover types, the contrast between patches and the edge structure. For species trait dependency, we calculated the Species Specialization Index ('SSI').

Attributes of landscape			Attributes of species	
Land cover types	Landscape contrast	Edge structure	Species	SSI
a) Mediterranean oak woodlands				
Grassland;	Weak	Soft edges	*Cyanistes caeruleus*	0.35
Sparse forest;			*Chloris chloris*	0.53
Dense forest			*Sylvia melanocephala*	0.53
			Carduelis carduelis	0.57
			Fringilla coelebs	0.57
			Turdus merula	0.59
			Certhia brachydactyla	0.67
			Luscinia megarhyncos	0.72
			Parus major	0.72
			Galerida spp.	0.79
			Sitta europaea	0.86
b) Atlantic pine plantations				
Pine forest;	Strong	Hard edges	*Parus major*	0.22
Shrubland;			*Serinus serinus*	0.28
Young plantations;			*Lophophanes cristatus*	0.30
Non-native plantations			*Chloris chloris*	0.32
			Erithacus rubecula	0.35
			Fringilla coelebs	0.36
			Certhia brachydactyla	0.45
			Turdus merula	0.48
			Lullula arborea	0.56
			Periparus ater	0.87
			Dendrocopos major	1.04

To check for the 'coherence' of each conceptual model, we summed the selection probability of the respective statistical models (conditional sum of Akaike weights). We tested whether a conceptual model was more important than expected by chance for each species by computing a multinomial randomization test comparing the observed probability of selection of each conceptual model (sum of Akaike weights) with the multinomial distribution generated by 10,000 iterations constrained by expected values of probability. We assumed equal probabilities of selection for each conceptual model (4 classes, 25% probability each). Observed selection values were considered significant whenever below or above 95% of the distribution of randomly generated expected values of probability. Selected conceptual models were compared with the expected results from both hypotheses, checking the number of cases (species) that were in agreement.

To evaluate the 'performance' of landscape conceptual models, we examined AICc changes (ΔAICc) of all species combined. We used a mixed model approach (Pinheiro *et al.*, 2014; Zuur *et al.*, 2009), where ΔAICc was treated as the response variable, the conceptual model (four levels) as the categorical fixed effect and the species as a random factor. We assumed that conceptual models with significantly lower ΔAICc had better performance. These two analyses enabled us to assess how each conceptual model performed in each landscape type separately. Following our second hypothesis, we also looked for the effect of species habitat specialization on the 'performance' of conceptual models. Another mixed model (Pinheiro *et al.*, 2014; Zuur *et al.*, 2009) was developed to account for random variation in species. ΔAICc was treated as the response variable and the interaction between species specialization (continuous variable) and conceptual model (four levels) as a categorical fixed effect.

The effects of minimum patch size and raster resolution on conceptual model selection were tested by means of a sensitivity analysis, considering different patch sizes in patch-based approaches (100 m^2, 1000 m^2 and 10000 m^2) and resolutions (1x1 m, 5x5 m and 10x10 m) in the continuum model. Our analysis supported the use of both lower patch size and higher raster resolution because no differences were found between the different categories, except for PC land-use data, where 100 m^2 was determined to be the best option (see Appendix II.D).

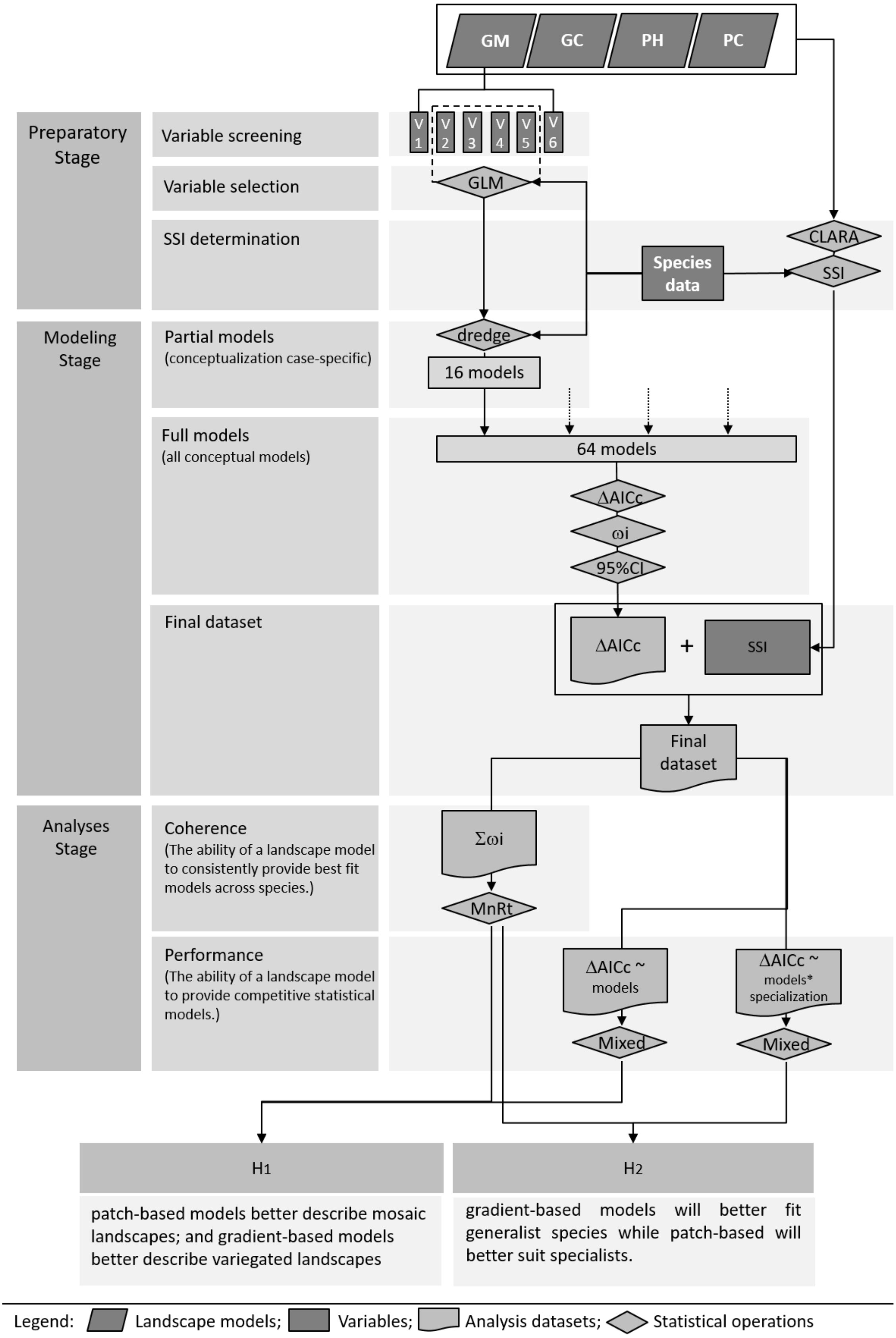

Figure II.2 – Scheme of the analytical approach employed. In the Preparatory Stage, after variable screening, we selected the best four variables of each conceptual model (PH –human-derived patch model, PC – contour-based patch model, GC – continuum model, GM – gradient microhabitat model) to explain each species abundance. At the modelling stage, partial GLMs →

for each conceptual model were computed through a 'dredge' procedure. Full models aggregate all GLMs from each conceptual model within the 95% confidence interval (95% CI) of the cumulative sum of Akaike weights ($\Sigma\omega_i$). For the final dataset, we joined the Species Specialization Index (SSI), *i.e.*, the coefficient of variation of each species abundance in a number the habitats defined through a CLARA ordination procedure (Appendix B Table B1-2). In analyses stage we checked 'coherence' performing a multinomial randomization test (MnRt) on the sum of Akaike weights ($\Sigma\omega_i$). For 'performance' of conceptual models a mixed model procedure was applied on ΔAICc to test the first hypothesis (H1) and considering specialization index to test the second hypothesis (H2).

All statistical analyses were performed in R environment, version 3.0.2 (R Development Core Team, 2013). During the GLM modelling procedure, we checked for possible over-dispersion of our response data (Anderson, 2008) using the package 'AER' (Kleiber and Zeileis, 2008). Additionally, we calculated the variance inflation factors (VIF) using package 'car' (Fox and Weisberg, 2011). As a 'rule of thumb', we discarded variables with VIF scores > 4 (Netter *et al.*, 1996). We plotted both model residuals and partial residuals to check for model fitting. Sampling sites that revealed a significant influence on model parameters were discarded (Cook's distance threshold = 4/n, where n is sample size). Residuals were tested for spatial autocorrelation using spline cross-correlograms (package 'ncf', Bjornstad, 2013). All of the analysed species showed spatial independence. A model was considered well fitted whenever residuals showed random dispersion and approximated a straight line close to zero, and all of the aforementioned assumptions were met.

II.5. RESULTS

II.5.1. Context-dependency in landscape conceptualization

In terms of the 'coherence' attribute, there were no consistent patterns of cross-species selection of a conceptual model in Mediterranean oak woodlands. Thus, there was no support for our first hypothesis, as only four species agreed with predictions from H1 (Table II.3). Nevertheless, the patch-based models (PH and PC together) provided greater coherence (higher number of species with higher probability of selection of these models; n = 7), while gradient-based models (GC and GM) were best suited to four species (Table II.3). Against our expectations, the continuum model (GC) fitted fewer species (n = 2). Our 'performance' results were in line with 'coherence' results because we did not find any significant differences in ΔAICc values between conceptual models

(Table II.4, Figure II.3). However, as a general tendency, the GC model (ΔAICc = 7.38 ± 4.06) was outperformed (higher ΔAICc) by all other conceptual models (mean ΔAICc: PH = 6.28 ± 4.96; PC = 6.34 ± 5.23; GM = 6.16 ± 2.54).

In Atlantic pine plantations, ‘coherence’ results were also inconclusive because no conceptual model was consistently selected and only five species responded as expected by the first hypothesis (Table II.3). Patch-based models fitted a higher number of species (n=5), but did not differ greatly from gradient conceptualizations (n=4). However, regarding model ‘performance’ (Table II.4, Figure II.3), the PH presented better fitted statistical models (mean ΔAICc = 5.64 ± 4.72, coefficient estimate = -0.930, $P < 0.01$) than GC, while the GM showed significantly lower fitted models (mean ΔAICc=7.28 ± 4.37, coefficient estimate = 1.177, $P < 0.01$). No differences were detected between PC and GC. ‘Performance’ results support the second part of the first hypothesis, *i.e.*, patch-based models provide better outcomes in classic mosaic landscapes.

Table II.3 – Summary of results of generalized linear models for each species in each study area ($\Sigma\omega_i$: sum of Akaike weights of all statistical models of each conceptual model; PH: human-derived patch model; PC: contour-based patch model; GC: continuum model; GM: site-scale model; Selected model: the best conceptual model for each species; Hypotheses: agreement with the stated hypotheses). Significant p-values (ns: > 0.05; *: <0.05; **: <0.01; ***: <0.001) are derived from the multinomial randomization procedure that identifies conceptual models with Akaike weight sums above the expectation. Species are sorted from most generalist to most specialist.

	$\Sigma\omega_i$								Selected model	Hypotheses
Species	PH		PC		GC		GM			
a) Mediterranean oak woodlands										
Cyanistes caeruleus (Blue tit)	**73.99**	***	12.87	**	5.13	***	3.31	***	PH	
Chloris chloris (Greenfinch)	**32.79**	*	23.23	ns	27.39	Ns	11.85	**	PH	
Sylvia melanocephala (Sardinian warbler)	0.00	***	0.00	***	0.00	***	**95.92**	***	GM	H_1; H_2
Carduelis carduelis (Goldfinch)	**58.40**	***	**32.19**	*	2.24	***	2.55	***	PH/PC	
Fringilla coelebs (Common chaffinch)	**62.68**	***	26.66	ns	5.33	***	1.33	***	PH	
Turdus merula (Common blackbird)	7.04	***	**81.26**	***	0.00	***	7.19	***	PC	
Certhia brachydactyla (Short-toed treecreeper)	13.82	**	1.37	***	9.17	***	**70.90**	***	GM	H_1
Luscinia megarhyncos (Common nightingale)	1.99	***	**77.92**	***	6.97	***	8.36	***	PC	H_2
Parus major (Great tit)	10.39	***	**66.14**	***	17.43	Ns	1.21	***	PC	H_2
Galerida spp. (Crested and Thekla larks)	6.06	***	0.00	***	**73.46**	***	15.63	*	GC	H_1
Sitta europaea (Eurasian nuthatch)	8.81	***	0.00	***	**33.50**	*	**52.99**	***	GM/GC	H_1

Table II.3 (cont.) – Summary of results of generalized linear models for each species in each study area ($\Sigma\omega_i$: sum of Akaike weights of all statistical models of each conceptual model; PH: human-derived patch model; PC: contour-based patch model; GC: continuum model; GM: site-scale model; Selected model: the best conceptual model for each species; Hypotheses: agreement with the stated hypotheses). Significant p-values (ns: > 0.05; *: <0.05; **: <0.01; ***: <0.001) are derived from the multinomial randomization procedure that identifies conceptual models with Akaike weight sums above the expectation. Species are sorted from most generalist to most specialist.

	$\Sigma\omega_i$									
Species	PH		PC		GC		GM		Selected model	Hypotheses
b) Atlantic pine plantations										
Parus major (Great tit)	**75.51**	***	8.18	***	6.58	***	4.99	***	PH	H_1
Serinus serinus (Serin)	22.41	ns	6.78	***	5.15	***	**60.70**	***	GM	H_2
Lophophanes cristatus (Crested tit)	27.44	ns	28.29	ns	**33.66**	*	5.85	***	GC	H_2
Chloris chloris (Greenfinch)	**61.06**	***	30.64	ns	1.30	***	2.02	***	PH	H_1
Erithacus rubecula (Robin)	18.36	ns	31.87	ns	25.18	Ns	19.71	ns	none	
Fringilla coelebs (Common chaffinch)	1.32	***	**89.12**	***	4.80	***	0.00	***	PC	H_1
Certhia brachydactyla (Short-toed treecreeper)	0.00	***	0.00	***	0.00	***	**96.97**	***	GM	
Turdus merula (Common blackbird)	22.73	ns	31.93	ns	22.68	Ns	18.17	ns	none	
Lullula arborea (Woodlark)	**79.54**	***	1.81	***	13.97	*	0.00	***	PH	H_1; H_2
Periparus ater (Coal tit)	22.89	ns	**59.57**	***	12.93	**	0.00	***	PC	H_1; H_2
Dendrocopos major (Great spotted woodpecker)	7.86	***	0.00	***	0.00	***	**87.38**	***	GM	

Table II.4 – Mixed-model results testing the effects of conceptual models on model performance (ΔAICc values). The conceptual model has four levels: GC – continuum model (reference level), PH – human-derived patch model, PC – contour-based patch model, GM – gradient microhabitat model. Significant p-values (ns: P > 0.05; *: P < 0.05; ***: P < 0.001).

a) Mediterranean oak woodlands

Terms	Coef.	SD	df	t-value	P
(Intercept)	6.805	0.906	401	7.515	***
PH	-0.712	0.390	401	-1.828	(.)
PC	-0.297	0.571	401	-0.520	ns
GM	-0.646	0.383	401	-1.684	(.)

b) Atlantic pine plantations

Terms	Coef.	SD	df	t-value	P
(Intercept)	6.929	1.024	484	6.770	***
PH	-0.930	0.323	484	-2.884	**
PC	0.006	0.296	484	0.019	ns
GM	1.177	0.449	484	2.622	**

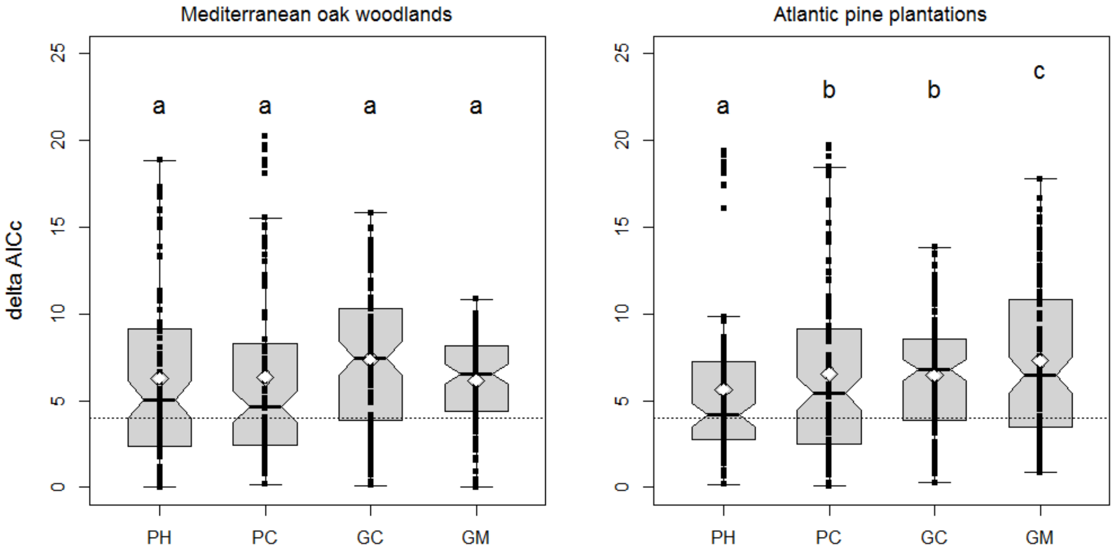

Figure II.3 – Boxplots showing the deviation and range of variation of each conceptual model (PH –human-derived patch model, PC – contour-based patch model, GC – continuum model, GM – gradient microhabitat model) (squares: ΔAICc values of all concurrent statistical models from species generalised linear models; dotted line: the 4 ΔAICc threshold). Models with low ΔAICc values have higher performance (higher fit to data) than models with high ΔAICc values. Conceptual models sharing a letter (‘a’ or ‘b’) are not significantly different at P=0.05.

II.5.2. Species traits dependency in landscape conceptualization

We were able to quantify all species along a gradient of habitat specialization. In Mediterranean oak woodlands, *Sitta europaea* and the *Galerida* complex were the most habitat specialized species. Conversely, *Cyanistes caeruleus* was the most generalist species. In Atlantic pine plantations, both *Parus major* and *Serinus serinus* were the most generalist species, while *Periparus ater* and *Dendrocopos major* showed higher habitat specialization. All habitat and species classifications are shown in detail in Appendix II.B Tables II.B1-4.

There was no clear support for our second hypothesis, regarding 'coherence' results in Mediterranean oak woodlands, as only three species supported it. Thus, *Sylvia melanocephala* distribution (generalist) was better explained by GM models while the PH approach provided better models for *Luscinia megarhyncos* and *Parus major* (specialist). However, contrary to what was expected, both species exhibiting the highest habitat specialization showed higher agreement with gradient models, while more generalist species showed a greater preference for patch-based models. Contrary to our second hypothesis, the 'performance' results followed a similar tendency (Table II.5, Figure II.4); we found that the GC and GM statistical models provided similar outcomes (coefficient estimate = 1.383, P = ns), showing higher 'performance' for specialist species in Mediterranean oak woodlands (GC slope = -8.03, $P < 0.01$; GM slope = -5.81, $P < 0.01$). On the other hand, PH and PC statistical models differ significantly from this relation (PH coefficient estimate = 13.406, $P < 0.001$; PC coefficient estimate = 22.152, $P < 0.001$), showing a higher performance towards generalist species (PH slope = 3.89, P = ns; PC slope = 13.08, $P < 0.001$).

In Atlantic pine plantations, only four species responded as expected by the second hypothesis. Gradient-based models only fitted two generalist species better (*Serinus serinus* and *Lophophanes cristatus*), while patch-based models only fitted two specialist species better (*Lullula arborea* and *Periparus ater*). 'Performance' results detected significant differences between the PC and GC in interactions with habitat specialization (coefficient estimate = 2.91, $P < 0.05$; Table II.5), meaning that PC tends to provide slightly better models towards generalist species (slope = 7.52, $P < 0.001$) (Figure II.4). All other models discriminated equally between the degree of habitat specialization (PH: slope = 3.52, $P < 0.05$; GC: slope = 3.53, $P < 0.01$; GM: slope = 1.44, P = ns).

Table II.5 – Mixed-model results testing the interaction effects of species specialization (SSI) and conceptual models on model performance (AICc values). The conceptual model has four levels: PH – human-derived patch model, PC – contour-based patch model, GC – continuum model, GM – gradient microhabitat model. Significant p-values (ns: $P > 0.05$; (.): $P < 0.1$; *: $P < 0.05$; **: $P < 0.01$***: $P < 0.001$).

a) Mediterranean oak woodlands

Terms	Coef.	SD	df	t-value	P
(Intercept)	12.859	4.461	398	2.883	**
PH	-8.848	1.682	398	-5.261	***
PC	-13.641	2.263	398	-6.028	***
GM	-1.339	1.718	398	-0.780	ns
SSI	-9.994	6.969	9	-1.434	ns
PH:SSI	13.406	2.695	398	4.974	***
PC:SSI	22.152	3.641	398	6.084	***
GM:SSI	1.283	2.838	398	0.452	ns

b) Atlantic pine plantations

Terms	Coef.	SD	df	t-value	P
(Intercept)	5.537	2.295	481	2.413	*
PH	-0.512	0.679	481	-0.754	ns
PC	-1.359	0.609	481	-2.229	*
GM	1.684	1.049	481	1.606	ns
SSI	2.948	4.298	9	0.686	ns
PH:SSI	-0.942	1.296	481	-0.727	ns
PC:SSI	2.907	1.161	481	2.504	*
GM:SSI	-1.219	2.202	481	-0.553	ns

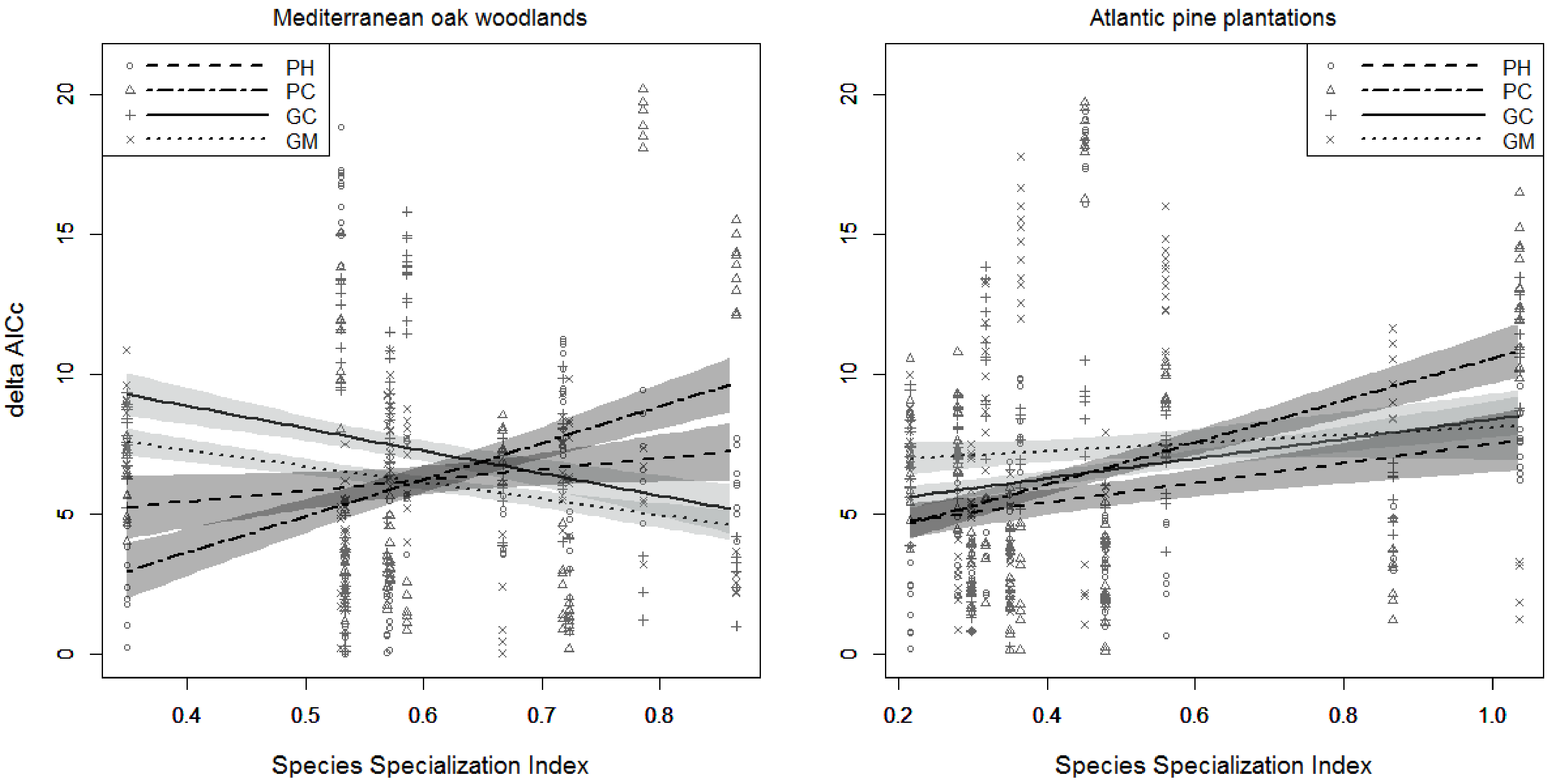

Figure II.4 – Linear regressions of ΔAICc values as a function of Species Specialization Index for each conceptual model (PH –human-derived patch model, PC – contour-based patch model, GC – continuum model, GM – gradient microhabitat model). Shaded areas show the Standard Error for each model. Lower ΔAICc values show higher performance (higher fit to data).

II.6. DISCUSSION

II.6.1. Context-dependency in landscape conceptualization

In variegated landscapes, our results did not meet our expectations, as continuum models did not show coherent cross-species results, nor did they perform significantly better than concurrent conceptual models. This is in disagreement with other authors who championed this hypothesis (McIntyre and Barrett 1992; Price *et al.*, 2010; Bruton *et al.*, 2015). In fact, we found that patch-based models can be as good as gradient-based alternatives, emphasizing the individualistic response of the species (Price *et al.*, 2009). For instance, *Cyanistes caeruleus* distribution models showed higher fit to a human-derived patch conceptualization. For this species, the percentage of grassland cover was reported as the most important variable showing a negative effect on species occurrence (Appendix II.E Table II.E1), meaning that a simple binary classification in grassland vs. forest habitats, typical of patch-based models, would be sufficient. Conversely, the tree canopy gradient present in the continuum model (Appendix II.E Table II.E1) provided better models for *Galerida* spp. Although these species mainly occur in grassland areas, there was some tolerance to increasing canopy cover, showing a gradual declining transition along the landscape gradient rather than a sharp change. On the other hand, the *Sylvia melanocephala* distribution model was highly determined by variables found only in the gradient-based microhabitat conceptualization (Appendix II.E Table II.E1), because it was able to capture highly detailed and ecologically meaningful data for this species (*e.g.*, species depends on shrub density for nesting purposes; Godinho *et al.*, 2010).

Regarding Atlantic pine plantations, our results suggest that human-derived patch models provided an adequate description of the landscape structure. Although PH may not reflect the response of many species (lacks coherence), the results show that it performed better than concurrent conceptualizations (higher performance). Human-derived patch conceptualizations capture more accurately the structure of mosaic landscapes because there is a strong contrast between patches, and patches themselves are internally homogeneous (Bennett *et al.*, 2006). Species also perceive spatial heterogeneity similarly as they are bound by this same structure of habitats (Didham *et al.*, 2012). Therefore, although reflecting a human perspective of the landscape, this conceptualization appears to be ecologically meaningful. The GM conceptualization showed an overall lower fit, as its performance was significantly lower than other approaches. However, for some forest-dependent species (*e.g.*, *Certhia brachydactyla* and *Dendrocopos major*), the GM performed better, with patch stand characteristics (*e.g.*, diameter at breast height, Appendix II.E Table II.E2) being particularly relevant. This means that patch-based models may occasionally fail to capture some important resources in mosaic landscapes and may not be sufficient to fully describe the ecological requirements of a species.

II.6.2. Species traits dependency in landscape conceptualization

In contrast to what was expected, patch-based models (PH and PC) showed higher performance for generalist species in Mediterranean oak woodlands, while gradient-based models (GM and GC) are better suited to specialist species. In their framework, Brudvig *et al.* (2017) argued that gradient-based models are more suitable for generalist species because their plasticity to several habitats would not be properly described by a patch-based conceptualization. However, our results show the opposite. Patch-based models seem to be good proxies of landscape complexity in variegated landscapes (*e.g.*, Herrera *et al.*, 2016), especially for generalist species, because they offer a simplified representation of the landscape (Fischer and Lindenmayer, 2006, 2007). Patch-based models are more prone to discriminating between habitat and matrix, while gradual changes in species occurrence probabilities are expected in gradient-based models. For instance, *Cyanistes caeruleus* occurs in forested areas independent of tree density (habitat) but not in grasslands (matrix). Thus, its probability of occurrence is mainly dependent on the presence of tree cover (Appendix II.E Table II.E2). Therefore, it is possible that gradient-based models capture too much detail of the spatial heterogeneity, hampering the discovery of clear species-gradient relationships.

Following Brudvig *et al.* (2017), it was also expected that patch-based models would provide better results for species exhibiting specific requirements, since suitable patches are more easily mapped apart from the inhospitable matrix. However, this hypothesis assumes that patches must be defined by considering species-specific habitat requirements, and human-derived land-use classifications may not provide the most suitable approaches if they are not species-oriented. We found that gradient-based models provided better outcomes for increasing habitat specialization, probably because they were able to capture higher landscape detail (including within-patch heterogeneity) compared to homogeneous patches. Thus, the way in which resources are distributed within the patch are also of concern and gradient-based models can characterize heterogeneity (*e.g.*, vertical complexity of vegetation, tree density) in a way that is not achievable by other conceptual models. Conversely, in Atlantic pine plantations, both gradient and patch based models behaved similarly while considering species habitat specialization, probably because patches in mosaic landscapes were highly homogeneous, likely due to the more uniform management practices (Bennett *et al.*, 2006). Consequently, resources were more homogeneously distributed within a patch and different conceptual models captured analogous attributes.

II.6.3. Conceptual model selection, caveats and future directions

Our results highlight the existence of a strong bias while using inappropriate conceptual models to describe species distributions, with observed deviations between best and alternative statistical models reaching ∆AICc values of 20. Therefore, the selection of a landscape conceptual model should be carefully considered. Our results provide two major conclusions regarding conceptual model selection: (1) the way in which landscapes are characterized by each conceptualization has strong implications for its suitability to model species distribution, often resulting in highly individualistic responses by species; and (2) intrinsic heterogeneity is a key attribute of the landscapes to account for when selecting the best conceptual model.

Some studies have also concluded that species responses are highly individualistic because conceptual models may lack consistency, depending on landscape context (Price *et al.*, 2009). However, checking for consistency in species response (as in other studies; *e.g.*, Price *et al.*, 2009; Bruton *et al.*, 2015) depends more on the circumstances of a conceptual model to match a species perception, rather than truly providing clear cross-species validation on the characterization of landscape structure. A species will be better represented by a conceptual model that approximates its own perception of the landscape, and the model that better discriminates species-specific resources will be ecologically more meaningful and better fitted. For instance, while using patch-based approaches (*e.g.*, human-derived), species are constrained to respond to land-use classes that may not reflect species habitats (Fischer and

Lindenmayer, 2006; Franklin and Lindenmayer, 2009). Unless land-use classifications are species-oriented, they will probably fail.

Our findings based on 'performance' show that the suitability of conceptual models in explaining species distributions depends on the interaction between landscape context and species habitat specialization. As our results build on deviations from the best statistical model, we were able to depict the relative suitability of alternative conceptual models. Overall, patch-based models provide useful conceptualizations in both mosaic (*e.g.*, Atlantic pine plantations) and variegated landscapes (*e.g.*, Mediterranean oak woodlands), but mostly for generalist species. Whenever patches were difficult to define, gradient-based approaches improved specialist species distribution models, likely due to their increased ability to capture spatial heterogeneity. Some authors (Price *et al.*, 2009; Stoddard, 2010) have suggested the importance of spatial heterogeneity in their studies, but we highlight this feature as a key attribute to account for in conceptual model selection, especially by considering how each conceptual model deals with spatial heterogeneity. Spatial heterogeneity reflects the spatial distribution of resources (*e.g.*, food, nest, shelter), which are by definition species-specific. Patch-based models offer a simplification of spatial heterogeneity into more general attributes (*e.g.*, non-forest vs. forest cover) by classifying internally heterogeneous patches into a unique land-use, which improves their performance for generalist species that are not tied to a specific habitat. Gradient-based models depict spatial heterogeneity more accurately. By avoiding landscape compartmentalization, they provide a better description of specific resources as environmental gradients. For instance, most conceptual models failed to capture some complexity of vegetation strata, and models including the description of microhabitat proved to be useful in both landscapes. The importance of habitat quality at the site-scale has been largely demonstrated (Bergman *et al.*, 2008; Price *et al.*, 2010; Bruton *et al.*, 2016), although the adequate specification of a conceptual model that addresses this scale efficiently is still lacking (Bennett *et al.*, 2006; Mortelliti *et al.*, 2010b). Site-scale habitat quality data are rarely used because of (1) the amount of information required to thoroughly describe the structural complexity and resource allocation at the landscape scale (Bruton *et al.*, 2015), (2) the limitations of the conceptual models (*e.g.*, difficulty incorporating patch heterogeneity in patch-based models; Price *et al.*, 2010) or (3) limited availability of remote sensing technology to capture highly detailed habitat structures (Bruton *et al.*, 2015), although recent developments in LiDAR and SAR technology show promising results (Nagendra *et al.*, 2013).

To prevent misleading predictions due to statistical artefacts, several authors (Lindenmayer *et al.*, 2007; Price *et al.*, 2009; Bruton *et al.*, 2015) proposed the adoption of pluralistic approaches to complement weaknesses of different conceptual models. Nevertheless, pluralistic approaches need to comply with a set of pre-defined assumptions that ease the process of conceptual model selection while guiding species-specific landscape characterization. Brudvig's *et al.* (2017) framework attempted to provide such guidance. We took two real-world contrasting landscapes as examples to validate the framework regarding landscape context and species habitat specialization. However, we found inconsistencies concerning conceptual model selection, as species showed contrasting responses according to their habitat specialization. Most studies are still based in experimental landscapes designed to test patch-matrix models (see Brudvig *et al.*, 2017). These approaches may overlook the importance of gradient-based approaches, degrading their applicability to real-world landscapes. Our study overcame such limitations by focusing on two real-world landscapes representing systems with distinct structures: the variegated (savannah-like) and the mosaic. Our results suggest that the framework assumptions outlined by Brudvig *et al.* (2017) still lack empirical validation. It is important to conduct further studies, especially concerning other species traits (*e.g.*, vagility, home range size) on real-world landscapes, as species responses appear to be highly individualistic.

II.7. ACKNOWLEDGMENTS

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Appendix II.A: Making of landscape models

Table II.A1 – Reclassification classes of land-use mapping for Mediterranean oak woodlands. CORINE land cover classes were the starting point for oak woodland landscape reclassification. Only the most representative land-uses are shown until a cumulative sum of 95% cover of the study area.

Reclassification	Original classification
Dense oak woodlands	(2.4.4) Agro-forestry systems (>50% tree cover)
	(3.1.1) Broad-leaved forest (>50% tree cover)
	(3.1.3) Mixed forest (>50% tree cover)
Grasslands	(2.1.1) Non-irrigated arable land
	(2.1.2) Permanently irrigated land
	(2.3.1) Pastures
	(2.4.1) Annual crops associated with permanent crops
	(2.4.2) Complex cultivation patterns
	(3.1.1) Broad-leaved forest (<10% tree cover)
	(3.2.1) Natural grasslands
	(3.2.2) Moors and heathland
Orchards	(2.2.1) Vineyards
	(2.2.3) Olive groves
Production forests	(3.1.1) Broad-leaved forest (*Eucalyptus* sp.)
	(3.1.2) Coniferous forest
	(3.1.3) Mixed forest dominated by non-native species
Sparse oak woodlands	(2.4.4) Agro-forestry systems (10-50% tree cover)
	(3.1.1) Broad-leaved forest (10-50% tree cover)
	(3.1.3) Mixed forest (10-50% tree cover)
Urban	(1.1.1) Continuous urban fabric
	(1.1.2) Discontinuous urban fabric
	(1.2.2) Road and rail networks and associated land
Waterbodies	(5.1.2) Water bodies

Table II.A2 – Reclassification classes of land-use mapping for Atlantic pine forests. We reclassified a detailed land-use map produced by us using aerial photo-interpretation and field validation. Only the most representative land-uses are shown until a cumulative sum of 95% cover of the study area.

Reclassification	Original classification
Bare Soil	Open areas without vegetation
	Rocky habitats
	Coastal dunes
	Quarries
Broad-leaved forests	Oak forests
	Riparian forest
	Poplar (*Populus* sp.) plantations
Farmland	Farmland
	Orchards
	Grasslands
Non-native plantations	*Acacia* sp. Plantations
	Eucalyptus sp. Plantations
Pine forests	Maritime pine (*Pinus pinaster*) forest
	Stone pine (*Pinus pinea*) forest
	Mixed pine forest
Shrubland	Shrubland
Urban	Urban area
	Green urban areas and parks
	Main roads
Young plantations	Young Maritime pine (*Pinus pinaster*) plantations
	Young Stone pine (*Pinus pinea*) plantations
	Young *Eucalyptus* sp. Plantations
Water bodies	Water bodies

Table II.A3 – List of bird species used to calculate turnover rates from HOF-models for Mediterranean oak woodlands and Atlantic pine forests.

Mediterranean oak woodlands	**Atlantic pine forests**
Scientific name (Common name)	**Scientific name (Common name)**
Alectoris rufa (Red-legged partridge)	*Certhia brachydactyla* (Short-toed treecreeper)
Carduelis cannabina (Common linnet)	*Chloris chloris* (European greenfinch)
Carduelis carduelis (European goldfinch)	*Dendrocopos major* (Great spotted woodpecker)
Certhia brachydactyla (Short-toed treecreeper)	*Erithacus rubecula* (Robin)
Chloris chloris (European greenfinch)	*Fringilla coelebs* (Common chaffinch)
Cisticola juncidis (Zitting cisticola)	*Garrulus glandarius* (Eurasian jay)
Columba palumbus (Common wood pigeon)	*Lophophanes cristatus* (European crested tit)
Coturnix coturnix (Common quail)	*Lullula arborea* (Woodlark)
Cuculus canorus (Common cuckoo)	*Parus ater* (Coal tit)
Cyanistes caeruleus (Blue tit)	*Parus major* (Great tit)
Dendrocopos major (Great spotted woodpecker)	*Picus viridis* (European green woodpecker)
Emberiza calandra (Corn bunting)	*Regulus ignicapilla* (Common firecrest)
Fringilla coelebs (Common chaffinch)	*Saxicola rubicola* (Stonechat)
Galerida spp. (Crested and Thekla Larks)	*Serinus serinus* (Serin)
Hippolais polyglota (Melodious warbler)	*Sylvia atricapilla* (Eurasian blackcap)
Lanius meridionalis (Southern grey shrike)	*Sylvia melanocephala* (Sardinian warbler)
Lanius senator (Woodchat shrike)	*Sylvia undata* (Dartford warbler)
Lophophanes cristatus (European crested tit)	*Troglodytes troglodytes* (Wren)
Lullula arborea (Woodlark)	*Turdus merula* (Common blackbird)
Luscinia megarhynchos (Common nightingale)	*Turdus viscivorus* (Mistle thrush)
Parus major (Great tit)	
Passer domesticus (House sparrow)	
Passer hispaniolensis (Spanish sparrow)	
Pica pica (Eurasian magpie)	
Saxicola rubicola (Stonechat)	
Serinus serinus (Serin)	
Sitta europaea (Eurasian nuthatch)	
Streptopelia decaocto (Eurasian collared dove)	
Sturnus unicolor (Spotless starling)	
Sylvia melanocephala (Sardinian warbler)	
Tetrax tetrax (Little bustard)	
Turdus merula (Common blackbird)	
Upupa epops (Hoopoe)	

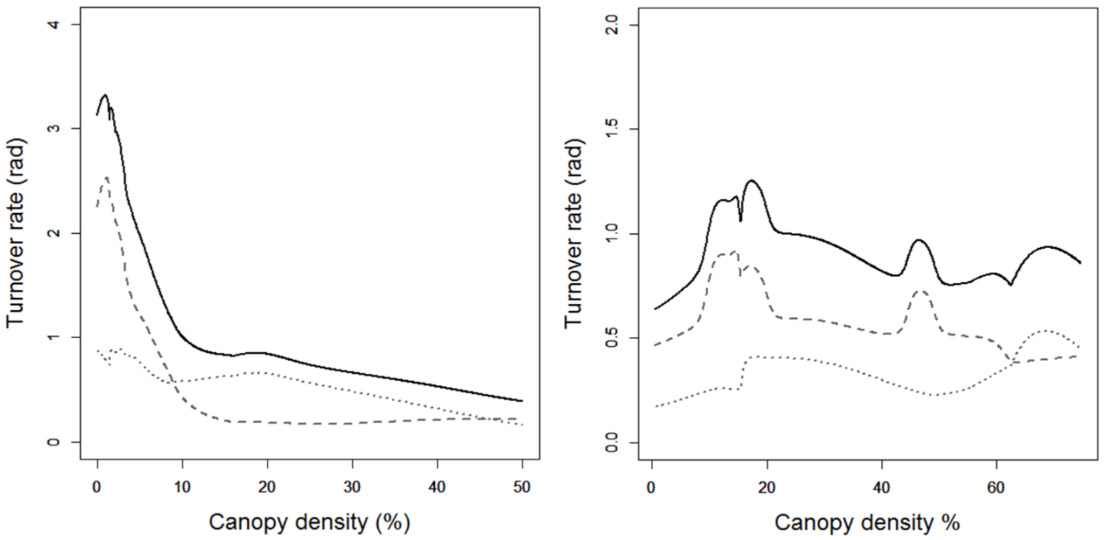

Figure II.A1 – Turnover rates (total turnover: solid line; positive turnover: dashed line, negative turnover: dotted line) calculated from HOF-models approach for bird communities inhabiting each different landscape-context study areas. Community turnovers are found at 1% and 20% tree canopy cover for oak woodlands variegated landscape where a 50% threshold was added following niche clustering assemblages in Salgueiro *et al.* (2008a). At pine forests mosaic landscape we considered community turnovers at 15%, 50% and 70% tree canopy cover.

Appendix II.B: Species Specialization Index

Table II.B1 – Mean and standard deviation values of the variables used in CLARA classification method for each resulting cluster for Mediterranean oak woodlands landscape.

	Cluster					
Variables	**1**	**2**	**3**	**4**	**5**	**6**
Number of trees	16.47±11.34	54.17±30.23	65.35±26.32	18.00±18.04	130.77±29.43	235.13±30.50
Number of young trees	7.94±10.32	2.28±4.69	15.50±16.45	5.71±7.85	7.95±7.90	24.93±39.13
Mean shrub height	133.1±37.53	3.29±10.04	90.25±27.85	263.93±33.89	49.12±22.67	59.52±21.44
Shrub height covariance	3.23±1.06	0.31±1.07	2.50±1.21	3.40±1.14	2.15±1.08	1.47±0.74
Percentage canopy cover	4.43±5.09	11.54±8.54	21.36±11.19	3.27±4.09	30.19±14.25	37.75±13.15
Dense forest cover	22.63±15.62	6.70±13.51	29.79±23.93	10.85±18.21	64.45±24.44	75.73±22.52
Grassland cover	54.26±20.28	35.24±19.36	18.97±11.25	68.44±17.98	12.72±10.5	5.81±5.37
Sparse forest cover	11.98±10.08	54.83±23.54	47.13±22.90	18.48±13.09	20.22±26.09	12.95±10.64
Shannon's diversity index	0.40±0.32	0.34±0.27	0.43±0.33	0.51±0.35	0.19±0.23	0.12±0.20

Table II.B2 – Mean and standard deviation values of the variables used in CLARA classification method for each resulting cluster for Atlantic pine forests landscape.

	Cluster		
Variables	**1**	**2**	**3**
Number of trees	4.85±10.61	116.23±50.41	46.77±33.01
Mean diameter at breast height	8.26±16.07	31.11±10.14	95.69±21.85
Mean shrub height	31.68±20.22	28.73±24.56	24.59±22.81
Shrub height covariance	0.53±0.18	0.61±0.25	0.71±0.28
Percentage canopy cover	57.45±19.48	72.02±18.16	78.97±14.9
Non-native plantations	5.35±10.51	5.98±9.75	3.52±7.63
Shrubland	35.2±25.33	6.17±8.07	7.64±10.58
Pine forest	35.92±19.49	25.99±20.65	72.22±22.97
Young plantations	20.14±16.48	54.75±23.62	9.71±13.78
Shannon's diversity index	1.01±0.3	0.92±0.39	0.69±0.47

Table II.B3 – Species mean abundances (and respective standard deviation) in each of the habitat clusters identified in Mediterranean oak woodlands landscape. Species are ranked by Species Specialization Index (SSI).

	Cluster						
Species	**1**	**2**	**3**	**4**	**5**	**6**	**SSI**
Cyanistes caeruleus (Blue tit)	1.18±0.88	2.06±1.43	1.73±1.04	0.71±0.76	2.09±1.06	2.07±1.10	0.35
Sylvia melanocephala (Sardinian warbler)	0.53±0.72	0.33±0.69	0.73±0.87	1.14±0.69	0.32±0.57	0.47±0.64	0.53
Chloris chloris (Greenfinch)	0.24±0.44	0.39±0.61	0.35±0.63	0.00±0.00	0.32±0.72	0.27±0.46	0.53
Fringilla coelebs (Common chaffinch)	1.41±1.62	2.33±1.81	2.15±1.35	0.14±0.38	3.23±0.87	3.33±1.29	0.57
Carduelis carduelis (Goldfinch)	0.76±0.97	0.17±0.51	0.19±0.49	0.86±1.46	0.77±1.11	0.47±0.83	0.57
Turdus merula (Common blackbird)	0.29±0.47	0.11±0.47	0.65±0.63	0.29±0.49	0.36±0.66	0.73±0.59	0.59
Certhia brachydactyla (Short-toed treecreeper)	0.35±0.61	1.28±1.07	1.54±0.99	0.14±0.38	2.14±1.04	1.93±0.88	0.67
Luscinia megarhyncos (Common nightingale)	0.12±0.49	0.00±0.00	0.38±0.57	0.57±0.53	0.36±0.58	0.27±0.46	0.72
Parus major (Great tit)	0.12±0.33	0.33±0.59	0.54±0.65	0.00±0.00	0.59±0.67	0.67±0.82	0.72
Galerida spp (Crested and Thekla larks)	1.41±1.28	1.56±1.58	0.54±0.65	1.43±1.13	0.18±0.50	0.07±0.26	0.79
Sitta europaea (Eurasian nuthatch)	0.24±0.44	0.50±0.71	0.46±0.81	0.00±0.00	1.14±0.94	1.40±1.18	0.86

Table II.B4 – Species mean abundances (and respective standard deviation) in each of the habitat clusters identified in Atlantic pine forests landscape. Species are ranked by Species Specialization Index (SSI).

	Cluster			
Species	**1**	**2**	**3**	**SSI**
Parus major (Great tit)	0.68±0.75	0.84±0.69	1.05±0.90	0.22
Serinus serinus (Serin)	0.60±0.91	0.37±0.50	0.39±0.69	0.28
Lophophanes cristatus (Crested tit)	0.52±0.65	0.47±0.70	0.80±0.77	0.30
Chloris chloris (Greenfinch)	0.72±1.17	0.68±0.95	0.38±0.55	0.32
Erithacus rubecula (Robin)	0.60±0.91	1.00±1.25	0.54±0.92	0.35
Fringilla coelebs (Common chaffinch)	1.04±1.06	1.58±1.22	2.21±1.36	0.36
Certhia brachydactyla (Short-toed treecreeper)	0.64±0.95	0.74±1.19	1.41±1.19	0.45
Turdus merula (Common blackbird)	0.68±0.95	0.26±0.45	0.39±0.67	0.48
Lullula arborea (Woodlark)	0.40±0.65	0.11±0.32	0.30±0.53	0.56
Periparus ater (Coal tit)	0.00±0.00	0.63±0.96	0.62±0.97	0.87
Dendrocopos major (Great spotted woodpecker)	0.08±0.28	0.05±0.23	0.36±0.61	1.04

Appendix II.C: Baseline comparison of variables across conceptual models using Spearman correlation ranks

Table II.C1 – Spearman correlations of composition variables between landscape conceptual models (grey areas) in Mediterranean oak woodlands (PH – human-derived patch model, PC – contour-based patch model, GC – continuum model, GM – site-scale model). Only correlations with |r|>0.3 are shown.

		GM	GC	PH			PC		
		Numb. trees	Canopy cover	Grassland cover	Sparse forest	Dense forest	Grassland cover	Sparse forest	Medium forest
GC	Canopy cover	0.803							
PH	Grassland cover	-0.651	-0.614						
	Sparse forest			-0.377					
	Dense forest	0.692	0.600	-0.416	-0.627				
PC	Grassland cover	-0.715	-0.767	0.802		-0.573			
	Sparse forest	-0.349	-0.517		0.408	-0.337			
	Medium forest	0.670	0.830	-0.486		0.579	-0.640	-0.504	
	Dense forest	0.435	0.646				-0.302	-0.545	0.303

Table II.C2 – Spearman correlations of configuration variables between landscape conceptual models (grey areas) in Mediterranean oak woodlands (PH – human-derived patch model, PC – contour-based patch model, GC – continuum model, GM – site-scale model). Only correlations with |r|>0.3 are shown.

		GC			PH				PC	
		Numb. canopy patches	Clumpiness	Aggregation index	Shannon's diversity	Numb. patches	High contr. edge	Low contr. edge	Shannon's diversity	Numb. patches
GC	Clumpiness									
	Aggregation index		0.701							
PH	Shannon's diversity		0.430							
	Numb. patches		0.451		0.793					
	High contr. edge		0.318		0.444	0.466				
	Low contr. edge				0.719	0.601				
PC	Shannon's diversity									
	Numb. patches				0.340	0.477	0.340		0.591	
	Total edge								0.818	0.699

Table II.C3 – Spearman correlations of composition variables between landscape conceptual models (grey areas) in Atlantic pine forest (PH –human-derived patch model, PC – contour-based patch model, GC – continuum model, GM – site-scale model). Only correlations with |r|>0.3 are shown.

		GM	GC	PH				PC		
		Numb. trees	Canopy cover	Pine forest	Young plantations	Shrubland	Non-native plantations	Low cover	Medium cover	High cover
GC	Canopy cover									
PH	Pine forest		0.656							
	Young plantations	0.325		-0.709						
	Shrubland	-0.410	-0.676	-0.439						
	Non-native plantations			-0.304						
PC	Low forest cover		-0.788	-0.429		0.634				
	Medium forest cover		-0.808	-0.597		0.472	0.337	0.324		
	High forest cover							-0.343		
	Very high forest cover		0.772	0.683		-0.429	0.358	-0.391	-0.722	-0.457

Table II.C4 – Spearman correlations of configuration variables between landscape conceptual models (grey areas) in Atlantic pine forest (PH –human-derived patch model, PC – contour-based patch model, GC – continuum model, GM – site-scale model). Only correlations with |r|>0.3 are shown.

		GC			PH				PC	
		Numb. Canopy patches	Clumpiness	Aggregation index	Shannon's diversity	Numb. patches	High contr. edge	Low contr. edge	Shannon's diversity	Numb. patches
GC	Clumpiness									
	Aggregation index	-0.890								
PH	Shannon's divers	0.350	0.616	-0.427						
	Numb. patches		0.468		0.798					
	High contr. edge		0.605		0.605	0.573				
	Low contr. edge			-0.358	0.726	0.736				
PC	Shannon's divers.		0.821		0.674	0.407	0.576			
	Numb. patches		0.557		0.551	0.567	0.468	0.380	0.570	
	Total edge		0.767		0.667	0.476	0.603	0.337	0.908	0.702

Appendix II.D: Sensitivity analysis of grain size and minimum patch size

Table II.D1 – Sensitivity analysis regarding the grain size (1x1 pixel size – reference level –, 5x5 and 10x10 for Gradient continuum model) and minimum patch size (100m^2 minimum patch size – reference level –, 1000m^2 and 10000m^2 for human-derived and contour-based patch models) of landscape data for Mediterranean Oak Woodlands. Significant p-values (ns: P > 0.05; ***: P < 0.001).

a) Gradient Continuum model

Terms	Coef.	SD	df	t-value	P
(Intercept)	6.540	0.759	373	8.620	***
5x5 pixel	-0.086	0.230	373	-0.375	ns
10x10 pixel	0.294	0.231	373	1.270	ns

b) Human-derived patch model

Terms	Coef.	SD	df	t-value	P
(Intercept)	5.572	1.531	328	3.640	***
mps 1000m^2	0.254	0.204	328	1.240	ns
mps 10000m^2	0.372	0.203	328	1.834	ns

c) Contour-based patch model

Terms	Coef.	SD	df	t-value	P
(Intercept)	6.748	1.645	373	4.101	***
mps 1000m^2	0.865	0.216	373	3.994	***
mps 10000m^2	0.676	0.219	373	3.093	**

Table II.D2 – Sensitivity analysis regarding the grain size (1x1 pixel size – reference level –, 5x5 and 10x10 for Gradient continuum model) and minimum patch size (100m^2 minimum patch size – reference level –, 1000m^2 and 10000m^2 for human-derived and contour-based patch models) of landscape data for Atlantic Pine Forest. Significant p-values (ns: P > 0.05; **: P < 0.01; ***: P < 0.001).

a) Gradient continuum model

Terms	Coef.	SD	df	t-value	P
(Intercept)	6.409	0.754	375	8.501	***
5x5 pixel	0.275	0.220	375	1.248	ns
10x10 pixel	0.109	0.220	375	0.494	ns

b) Human-derived patch model

Terms	Coef.	SD	df	t-value	P
(Intercept)	5.344	1.432	330	3.731	***
mps 1000m^2	0.091	0.207	330	0.440	ns
mps 10000m^2	0.325	0.207	330	1.569	ns

c) Contour-based patch model

Terms	Coef.	SD	df	t-value	P
(Intercept)	6.875	1.664	377	4.130	***
mps 1000m^2	0.776	0.215	377	3.606	***
mps 10000m^2	0.693	0.218	377	3.178	**

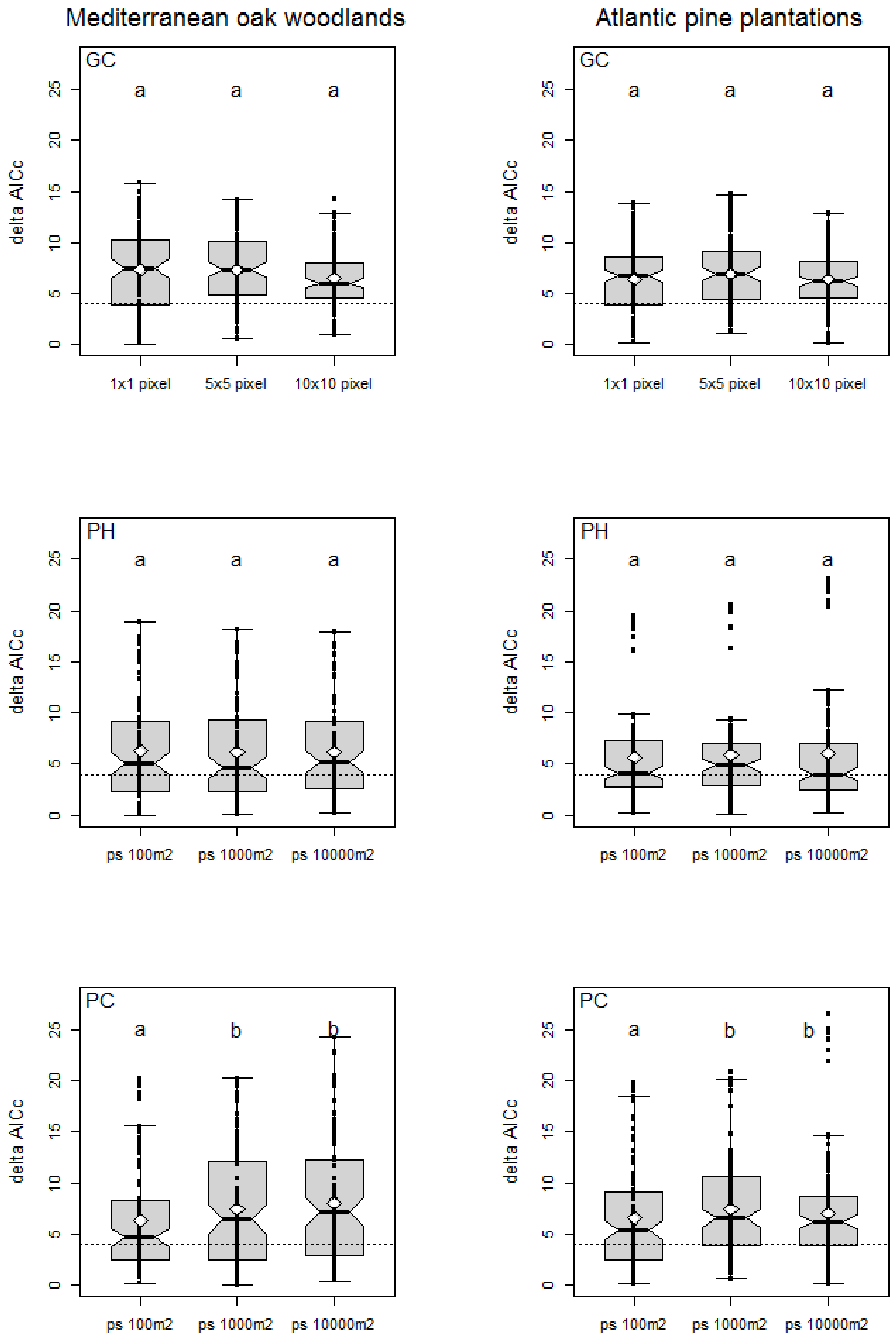

Figure II.1D – Boxplots showing the distribution of delta AICc values for each grain size (1x1 pixel size, 5x5 and 10x10 for Gradient continuum model – GC) and minimum patch size (100m^2 minimum patch size, 1000m^2 and 10000m^2 for human-derived – PH –, and contour-based patch models – PC) of landscape data for Mediterranean Oak Woodlands and Atlantic Pine Forest. Boxplots sharing the same letter (‘a’ or ‘b’) are not significantly different at P=0.05.

Appendix II.E: GLM results

Table II.E1 – Summary of variable selection of generalized linear models for each species at Mediterranean oak woodlands variegated landscape. For each variable is shown the coefficient estimate and corresponding 95% confidence interval, relative variable importance (RVI corresponding to the sum of Akaike weights of statistical models where the variable was present) in partial (95% confidence interval for statistical models within each landscape model) and full models (95% confidence interval with all landscape conceptual models: PH – human-derived patch model, PC – patch-based contour model, GC – continuum model, GM – gradient microhabitat model) and respective p-value (P; (.): P < 0.1; *: P < 0.05; **: P < 0.01; ***: P < 0.001).

	Model					**RVI**		
Species	**type**	**Variables**	**Scale**	**Estimate**	**CI95%**	**partial**	**full**	**P**
Carduelis	PH	(Intercept)		-0.251	[-2.12; 1.62]			
carduelis		Sparse cover forest	1000	-0.030	[-0.06; 0.00]	0.96	0.54	*
(Goldfinch)		Numb. patches	1000	-0.057	[-0.23; 0.03]	0.58	0.34	
		Grassland cover	500	0.007	[0.00; 0.03]	0.50	0.29	
		Shannon's diversity	1000	0.015	[-2.46; 2.57]	0.29	0.17	
	PC	(Intercept)		0.305	[-2.81; 3.42]			
		Numb. patches	500	-2.230	[-6.85; 0.33]	0.68	0.21	
		Total edge	200	0.000	[0.00; 0.00]	0.62	0.19	
		Grassland cover	1000	0.018	[0.00; 0.07]	0.58	0.19	
		Dense cover forest	1000	0.011	[-0.01; 0.06]	0.42	0.14	
	GC	(Intercept)		-3.659	[-23.25; 15.93]			
		Clumpiness	100	1.177	[-4.84; 12.10]	0.32	0.00	
		Aggregation index	100	0.544	[-19.52; 23.67]	0.26	0.00	
		Canopy cover	1000	0.005	[-0.03; 0.07]	0.28	0.00	
		Numb. canopy patches	200	0.000	[0.00; 0.01]	0.22	0.00	
	GM	(Intercept)		-1.843	[-3.06; -0.63]			**
		Shrub height cov.	-	0.057	[-0.19; 0.55]	0.32	0.01	
		Mean shrub height	-	0.025	[-0.08; 0.22]	0.35	0.01	
		Numb. young trees	-	-0.653	[-5.75; 1.94]	0.34	0.00	
		Numb. trees	-	0.000	[-0.01; 0.01]	0.23	0.00	
Chloris	PH	(Intercept)		-1.281	[-2.39; -0.17]			*
chloris		Grassland cover	500	-0.018	[-0.07; 0.01]	0.63	0.21	
(Greenfinch)		Hard edge	1000	-0.137	[-0.62; 0.09]	0.52	0.17	
		Shannon's diversity	500	0.512	[-0.85; 3.45]	0.39	0.14	
		Soft edge	100	-0.005	[-0.1; 0.06]	0.25	0.09	
	PC	(Intercept)		-1.099	[-3.85; 1.65]			
		Grassland cover	500	-0.017	[-0.09; 0.02]	0.52	0.12	
		Total edge	1000	0.000	[0.00; 0.00]	0.33	0.07	
		Medium cover forest	100	0.073	[-0.81; 1.39]	0.25	0.06	
		Numb. patches	1000	-0.133	[-4.98; 3.89]	0.24	0.06	
	GC	(Intercept)		1.122	[-7.01; 9.26]			

	Model					RVI		
Species	**type**	**Variables**	**Scale**	**Estimate**	**CI95%**	**partial**	**full**	**P**
C. chloris (cont.)		Canopy cover	200	0.017	[-0.01; 0.07]	0.56	0.15	
		Aggregation index	1000	-0.037	[-0.25; 0.07]	0.42	0.12	
		Clumpiness	100	-0.355	[-11.22; 9.2]	0.35	0.09	
		Numb. canopy patches	100	0.000	[-0.02; 0.01]	0.21	0.06	
	GM	(Intercept)		-1.527	[-2.42; -0.63]			***
		Shrub height cov.	-	-0.067	[-0.63; 0.23]	0.33	0.04	
		Mean shrub height	-	0.003	[-0.13; 0.16]	0.25	0.02	
		Shrub density	-	0.009	[-0.15; 0.23]	0.23	0.02	
		Numb. young trees	-	-0.046	[-1.16; 0.79]	0.25	0.02	
Certhia brachydactyla (Short-toed treecreeper)	PH	(Intercept)		0.683	[0.43; 0.94]			***
		Grassland cover	500	-0.019	[-0.03; -0.01]	1.00	0.14	**
		Sparse cover forest	200	-0.108	[-0.64; 0.14]	0.44	0.06	
		Hard edge	200	0.038	[-0.07; 0.30]	0.34	0.06	
		Soft edge	200	-0.001	[-0.02; 0.01]	0.19	0.04	
	PC	(Intercept)		0.618	[0.01; 1.23]			*
		Total edge	500	0.000	[0.00; 0.00]	0.79	0.01	
		Grassland cover	500	-0.012	[-0.03; 0.00]	0.77	0.01	
		Medium cover forest	200	0.302	[-0.04; 1.00]	0.63	0.01	
		Dense cover forest	1000	0.005	[0.00; 0.02]	0.43	0.01	
	GC	(Intercept)		1.930	[-1.01; 4.87]			
		Canopy cover	500	0.025	[0.01; 0.04]	1.00	0.09	**
		Aggregation index	200	-0.026	[-0.08; 0.00]	0.69	0.07	
		Numb. canopy patches	200	0.001	[0.00; 0.00]	0.54	0.05	
		Clumpiness	100	-0.294	[-5.09; 3.45]	0.36	0.03	
	GM	(Intercept)		0.157	[-0.32; 0.63]			
		Mean shrub height	-	-0.006	[-0.01; 0.00]	1.00	0.67	*
		Shrub density	-	0.105	[0.03; 0.20]	0.89	0.61	(.)
		Numb. trees	-	0.001	[0.00; 0.01]	0.53	0.39	
		Shrub height cov.	-	0.039	[-0.06; 0.25]	0.41	0.28	
Cyanistes caeruleus (Blue tit)	PH	(Intercept)		0.705	[0.48; 0.93]			***
		Grassland cover	200	-0.881	[-1.69; -0.12]	0.97	0.68	*
		Soft edge	200	-0.005	[-0.03; 0.00]	0.48	0.37	
		Shannon's diversity	100	-0.191	[-1.09; 0.26]	0.46	0.34	
		Sparse cover forest	100	0.014	[-0.30; 0.40]	0.26	0.20	
	PC	(Intercept)		0.619	[0.18; 1.05]			**
		Grassland cover	200	-0.010	[-0.03; 0.00]	0.78	0.10	
		Sparse cover forest	200	-0.108	[-0.65; 0.15]	0.43	0.05	
		Medium cover forest	100	0.097	[-0.16; 0.62]	0.43	0.05	
		Dense cover forest	500	-0.003	[-0.02; 0.01]	0.35	0.05	
	GC	(Intercept)		2.284	[-0.57; 5.14]			
		Aggregation index	500	-0.022	[-0.08; 0.01]	0.64	0.04	
		Canopy cover	500	0.006	[-0.01; 0.03]	0.46	0.02	

Species	Model type	Variables	Scale	Estimate	CI95%	RVI partial	RVI full	P
C caeruleus (cont.)		Clumpiness	100	-0.243	[-4.50; 3.34]	0.42	0.02	
		Numb. canopy patches	100	0.001	[0.00; 0.01]	0.32	0.01	
	GM	(Intercept)		0.573	[0.16; 0.98]			**
		Mean shrub height	-	-0.016	[-0.09; 0.02]	0.46	0.01	
		Numb. trees	-	0.001	[0.00; 0.00]	0.42	0.01	
		Shrub density	-	0.015	[-0.05; 0.13]	0.36	0.01	
		Shrub height cov.	-	-0.022	[-0.21; 0.07]	0.32	0.01	
Fringilla coelebs (Common chaffinch)	PH	(Intercept)		1.166	[0.88; 1.45]			***
		Grassland cover	1000	0.000	[0.00; 0.00]	1.00	0.63	***
		Soft edge	100	-0.008	[-0.04; 0.01]	0.47	0.31	
		Sparse cover forest	500	-0.002	[-0.01; 0.00]	0.46	0.30	
		Hard edge	1000	0.003	[-0.11; 0.13]	0.23	0.17	
	PC	(Intercept)		0.978	[0.59; 1.37]			***
		Grassland cover	1000	-0.001	[0.00; 0.00]	1.00	0.27	***
		Medium cover forest	200	0.125	[-0.12; 0.65]	0.48	0.13	
		Sparse cover forest	100	-0.041	[-0.45; 0.15]	0.28	0.09	
		Shannon's diversity	500	-0.055	[-0.87; 0.39]	0.23	0.08	
	GC	(Intercept)		0.531	[-1.79; 2.86]			
		Numb. canopy patches	200	0.002	[0.00; 0.00]	1.00	0.05	***
		Canopy cover	100	0.019	[0.01; 0.03]	1.00	0.05	***
		Aggregation index	1000	-0.007	[-0.06; 0.01]	0.34	0.02	
		Clumpiness	100	-0.095	[-2.5; 1.46]	0.18	0.00	
	GM	(Intercept)		0.639	[0.26; 1.01]			***
		Numb. trees	-	0.004	[0.00; 0.01]	1.00	0.01	***
		Mean shrub height	-	-0.003	[-0.01; 0.00]	0.91	0.01	(.)
		Numb. young trees	-	-0.043	[-0.42; 0.16]	0.33	0.00	
		Shrub density	-	0.002	[-0.07; 0.09]	0.23	0.00	
Galerida spp. (Crested and Thekla larks)	PH	(Intercept)		-2.487	[-5.13; 0.15]			(.)
		Shannon's diversity	200	1.281	[0.25; 2.60]	0.90	0.06	(.)
		Grassland cover	1000	0.029	[0.00; 0.06]	0.89	0.06	(.)
		Sparse cover forest	1000	0.016	[0.00; 0.04]	0.67	0.05	
		Dense cover forest	200	-0.743	[-3.08; 0.30]	0.54	0.03	
	PC	(Intercept)		-0.946	[-2.63; 0.74]			
		Medium cover forest	200	-1.098	[-1.87; -0.33]	1.00	0.00	**
		Sparse cover forest	500	0.013	[0.00; 0.03]	0.77	0.00	
		Dense cover forest	500	-0.037	[-0.17; 0.05]	0.62	0.00	
		Shannon's diversity	200	0.648	[-0.24; 2.52]	0.57	0.00	
	GC	(Intercept)		-6.755	[-11.46; -2.05]			**
		Canopy cover	100	-0.102	[-0.14; -0.06]	1.00	0.73	***
		Aggregation index	500	0.111	[0.01; 0.21]	1.00	0.69	*
		Clumpiness	100	-1.529	[-12.78; 4.07]	0.35	0.29	
		Numb. canopy patches	100	0.000	[-0.01; 0.01]	0.25	0.18	

Species	Model type	Variables	Scale	Estimate	CI95%	RVI partial	full	P
Galerida spp.	GM	(Intercept)		1.102	[0.38; 1.83]			**
(cont.)		Numb. trees	-	-0.018	[-0.03; -0.01]	1.00	0.16	***
		Shrub density	-	-0.140	[-0.39; 0.00]	0.73	0.11	
		Mean shrub height	-	-0.009	[-0.14; 0.08]	0.28	0.04	
		Numb. young trees	-	-0.020	[-0.93; 0.72]	0.20	0.03	
Luscinia	PH	(Intercept)		-1.545	[-2.72; -0.38]			**
megarhyncos		Hard edge	100	-6.168	[-2557; 2538]	0.65	0.01	
(Common		Grassland cover	500	-0.021	[-0.08; 0.01]	0.64	0.01	
nightingale)		Numb. patches	100	0.135	[-0.70; 1.65]	0.28	0.00	
		Shannon's diversity	500	-0.064	[-2.21; 1.71]	0.25	0.00	
	PC	(Intercept)		-18.754	[-4371; 4333]			
		Medium cover forest	200	17.485	[-4394; 4430]	0.97	0.72	
		Grassland cover	500	-0.016	[-0.17; 0.08]	0.35	0.29	
		Dense cover forest	500	0.005	[-0.01; 0.04]	0.35	0.28	
		Sparse cover forest	500	-0.003	[-0.03; 0.02]	0.32	0.25	
	GC	(Intercept)		-2.237	[-7.07; 2.60]			
		Canopy cover	500	0.044	[0.01; 0.09]	0.88	0.07	(.)
		Clumpiness	100	-1.126	[-12.24; 5.36]	0.33	0.02	
		Aggregation index	100	0.003	[-0.12; 0.14]	0.28	0.02	
		Numb. canopy patches	1000	0.000	[0.00; 0.00]	0.21	0.01	
	GM	(Intercept)		-3.083	[-4.58; -1.59]			***
		Shrub density	-	0.178	[0.00; 0.49]	0.73	0.06	
		Numb. young trees	-	0.461	[-0.33; 2.10]	0.52	0.04	
		Numb. trees	-	0.000	[-0.01; 0.01]	0.26	0.02	
		Mean shrub height	-	0.008	[-0.15; 0.22]	0.25	0.02	
Parus	PH	(Intercept)		-1.009	[-2.42; 0.40]			
major		Grassland cover	1000	-0.043	[-0.07; -0.01]	1.00	0.10	**
(Great tit)		Hard edge	1000	0.243	[-0.04; 0.68]	0.76	0.08	
		Sparse cover forest	200	0.373	[-0.14; 1.47]	0.56	0.06	
		Numb. patches	200	-0.010	[-0.43; 0.33]	0.19	0.02	
	PC	(Intercept)		-3.239	[-7.12; 0.64]			
		Medium cover forest	1000	0.019	[0.00; 0.04]	0.84	0.51	
		Grassland cover	1000	-0.028	[-0.10; 0.01]	0.63	0.44	
		Numb. patches	1000	1.255	[-0.66; 5.03]	0.57	0.35	
		Dense cover forest	1000	0.006	[-0.01; 0.04]	0.38	0.25	
	GC	(Intercept)		-2.336	[-5.22; 0.54]			
		Canopy cover	1000	0.054	[0.02; 0.08]	1.00	0.17	***
		Numb. canopy patches	100	0.002	[-0.01; 0.02]	0.36	0.06	
		Clumpiness	100	0.053	[-4.41; 4.93]	0.20	0.04	
		Aggregation index	100	0.000	[-0.06; 0.06]	0.20	0.04	
	GM	(Intercept)		-1.729	[-2.56; -0.9]			***
		Numb. trees	-	0.007	[0.00; 0.01]	1.00	0.01	**

Species	Model type	Variables	Scale	Estimate	CI95%	RVI		P
						partial	full	
P. major (cont.)		Numb. young trees	-	-0.062	[-0.94; 0.51]	0.29	0.00	
		Shrub density	-	0.014	[-0.13; 0.23]	0.28	0.00	
		Mean shrub height	-	-0.003	[-0.12; 0.10]	0.26	0.00	
Sitta europaea (Eurasian nuthatch)	PH	(Intercept)		0.193	[-0.20; 0.59]			
		Grassland cover	500	-0.020	[-0.04; 0.00]	0.92	0.09	(.)
		Sparse cover forest	200	-0.439	[-1.23; 0.02]	0.73	0.07	
		Shannon's diversity	200	-0.586	[-2.39; 0.29]	0.56	0.05	
		Soft edge	100	-0.011	[-0.09; 0.03]	0.39	0.04	
	PC	(Intercept)		-0.586	[-1.38; 0.21]			
		Grassland cover	200	-0.029	[-0.08; 0.01]	0.82	0.00	
		Dense cover forest	200	0.008	[0.00; 0.02]	0.71	0.00	
		Medium cover forest	100	0.303	[-0.15; 1.22]	0.57	0.00	
		Sparse cover forest	200	-0.018	[-0.81; 0.68]	0.29	0.00	
	GC	(Intercept)		0.870	[-3.77; 5.51]			
		Numb. canopy patches	100	0.012	[0.00; 0.02]	1.00	0.34	**
		Canopy cover	500	0.025	[0.00; 0.06]	0.79	0.26	
		Clumpiness	100	-3.448	[-10.02; 0.24]	0.70	0.24	
		Aggregation index	500	-0.003	[-0.13; 0.12]	0.45	0.15	
	GM	(Intercept)		-1.399	[-2.31; -0.49]			**
		Numb. trees	-	0.008	[0.00; 0.01]	1.00	0.53	***
		Shrub height cov.	-	0.171	[0.01; 0.47]	0.71	0.37	
		Mean shrub height	-	-0.004	[-0.01; 0.00]	0.67	0.34	
		Shrub density	-	-0.002	[-0.18; 0.16]	0.21	0.15	
Sylvia melanocephala (Sardinian warbler)	PH	(Intercept)		-1.272	[-1.96; -0.59]			***
		Soft edge	100	0.015	[-0.02; 0.09]	0.42	0.00	
		Shannon's diversity	200	0.250	[-0.87; 2.30]	0.35	0.00	
		Grassland cover	500	-0.002	[-0.03; 0.02]	0.29	0.00	
		Hard edge	1000	0.013	[-0.22; 0.33]	0.23	0.00	
	PC	(Intercept)		-1.428	[-2.58; -0.28]			*
		Dense cover forest	1000	0.033	[0.01; 0.06]	0.97	0.00	**
		Medium cover forest	1000	-0.002	[-0.03; 0.01]	0.27	0.00	
		Shannon's diversity	100	0.129	[-1.04; 2.01]	0.27	0.00	
		Numb. patches	100	0.114	[-4.07; 5.03]	0.24	0.00	
	GC	(Intercept)		-3.168	[-8.40; 2.07]			
		Canopy cover	1000	0.039	[0.00; 0.09]	0.86	0.00	
		Clumpiness	100	3.983	[-1.55; 14.6]	0.61	0.00	
		Numb. canopy patches	200	-0.002	[-0.01; 0.00]	0.60	0.00	
		Aggregation index	100	-0.017	[-0.18; 0.09]	0.40	0.00	
	GM	(Intercept)		-2.134	[-3.4; -0.87]			***
		Shrub density	-	0.310	[0.08; 0.57]	0.95	0.88	*
		Numb. trees	-	-0.008	[-0.02; 0.00]	0.94	0.87	*
		Numb. young trees	-	0.467	[-0.19; 1.82]	0.57	0.56	

Species	Model type	Variables	Scale	Estimate	CI95%	RVI partial	full	P
		Shrub height cov.	-	-0.036	[-0.56; 0.28]	0.26	0.28	
Turdus merula (Common blackbird)	PH	(Intercept)		-0.361	[-0.96; 0.23]			
		Grassland cover	1000	-0.047	[-0.08; -0.01]	1.00	0.07	**
		Soft edge	200	-0.002	[-0.04; 0.03]	0.27	0.01	
		Sparse cover forest	1000	0.000	[-0.01; 0.02]	0.20	0.01	
		Shannon's diversity	200	0.030	[-1.47; 1.76]	0.21	0.01	
	PC	(Intercept)		-0.124	[-1.35; 1.10]			
		Grassland cover	1000	-0.107	[-0.19; -0.03]	1.00	0.81	**
		Medium cover forest	1000	-0.014	[-0.04; 0.00]	0.71	0.54	
		Total edge	200	0.000	[0.00; 0.00]	0.39	0.34	
		Dense cover forest	100	0.003	[-0.01; 0.02]	0.35	0.31	
	GC	(Intercept)		-1.770	[-5.77; 2.23]			
		Numb. canopy patches	500	0.000	[0.00; 0.00]	0.57	0.00	
		Canopy cover	500	0.014	[0.00; 0.06]	0.52	0.00	
		Clumpiness	100	-1.121	[-9.06; 2.93]	0.37	0.00	
		Aggregation index	100	0.010	[-0.06; 0.13]	0.29	0.00	
	GM	(Intercept)		-3.201	[-5.12; -1.28]			**
		Mean shrub height	-	0.150	[0.02; 0.32]	0.87	0.07	
		Numb. trees	-	0.004	[0.00; 0.01]	0.68	0.05	
		Shrub density	-	0.088	[-0.07; 0.40]	0.53	0.03	
		Shrub height cov.	-	-0.006	[-0.54; 0.50]	0.27	0.01	

Table II.E2 – Summary of variable selection of generalized linear models for each species at Atlantic pine plantations mosaic landscape. For each variable is shown the coefficient estimate and corresponding 95% confidence interval, relative variable importance (RVI corresponding to the sum of Akaike weights of statistical models where the variable was present) in partial (95% confidence interval for statistical models within each landscape model) and full models (95% confidence interval with all landscape conceptual models: PH – human-derived patch model, PC – patch-based contour model, GC – continuum model, GM – gradient microhabitat model) and respective p-value (P; (.): P < 0.1; *: P < 0.05; **: P < 0.01; ***: P < 0.001).

	Model					**RVI**		
Species	**type**	**Variables**	**Scale**	**Estimate**	**CI95%**	**partial**	**full**	**P**
Certhia	PH	(Intercept)	-	-0.116	[-1.62; 1.38]			
brachydactyla		Non-native plantations	200	-0.540	[-1.79; 0.18]	0.67	0.00	
(Short-toed		Pine forest	200	0.006	[0.00; 0.02]	0.58	0.00	
treecreeper)		Young plantations	500	-0.010	[-0.04; 0.00]	0.58	0.00	
		Shrubland	200	-0.499	[-1.94; 0.20]	0.57	0.00	
	PC	(Intercept)	-	-0.890	[-2.27; 0.49]			
		Medium forest cover	100	-0.021	[-0.03; -0.01]	1.00	0.00	***
		Shannon's diversity	500	0.825	[-0.07; 2.43]	0.70	0.00	
		Numb. patches	200	0.030	[-0.07; 0.24]	0.36	0.00	
		Total edge	500	0.000	[0.00; 0.00]	0.27	0.00	
	GC	(Intercept)	-	-19.150	[-30.47; -7.83]			***
		Aggregation index	100	1.850	[0.68; 3.02]	1.00	0.00	**
		Clumpiness	500	1.953	[-0.36; 6.54]	0.63	0.00	
		Canopy cover	1000	-0.005	[-0.04; 0.01]	0.39	0.00	
		Numb. canopy patches	100	0.002	[-0.06; 0.07]	0.19	0.00	
	GM	(Intercept)	-	-1.041	[-1.94; -0.14]			*
		Diameter at breast height	-	0.016	[0.01; 0.02]	1.00	0.97	***
		Shrub density	-	-0.006	[-0.02; 0.00]	0.63	0.61	
		Numb. trees	-	0.000	[-0.01; 0.01]	0.21	0.25	
		Shrub height cov	-	0.004	[-0.82; 0.87]	0.20	0.24	
Chloris	PH	(Intercept)	-	-1.870	[-2.69; -1.05]			***
chloris		Non-native plantations	200	-2.272	[-4.38; -0.17]	1.00	0.59	*
(Greenfinch)		Shannon's diversity	100	1.499	[0.39; 3.00]	0.88	0.54	(.)
		Numb. patches	100	0.038	[-0.45; 0.67]	0.34	0.20	
		Soft edge	100	0.000	[0.00; 0.00]	0.26	0.16	
	PC	(Intercept)	-	-2.863	[-4.19; -1.54]			***
		Numb. patches	100	0.447	[0.18; 0.72]	1.00	0.31	**
		High forest cover	200	0.002	[-0.01; 0.03]	0.31	0.10	
		Low forest cover	1000	0.002	[-0.05; 0.07]	0.21	0.08	
		Total edge	200	0.000	[0.00; 0.00]	0.20	0.08	
	GC	(Intercept)	-	-4.829	[-17.58; 7.92]			
		Clumpiness	100	2.415	[0.40; 4.93]	0.91	0.01	(.)
		Aggregation index	1000	0.023	[-0.13; 0.29]	0.27	0.00	
		Numb. canopy patches	100	0.004	[-0.05; 0.08]	0.25	0.00	
		Canopy cover	100	-0.001	[-0.02; 0.02]	0.25	0.00	

Species	Model type	Variables	Scale	Estimate	CI95%	RVI partial	full	P
C. chloris (cont.)	GM	(Intercept)	-	-0.787	[-1.85; 0.27]			
		Numb. trees	-	-0.013	[-0.03; 0.00]	0.97	0.02	*
		Shrub density	-	0.004	[-0.01; 0.03]	0.36	0.01	
		Mean shrub height	-	-0.020	[-0.36; 0.22]	0.28	0.00	
		Diameter at breast height	-	0.000	[-0.01; 0.01]	0.25	0.00	
Dendrocopos major (Great spotted woodpecker)	PH	(Intercept)	-	-2.046	[-4.71; 0.62]			
		Shrubland	100	-12.888	[-5131; 5095]	0.73	0.06	
		Shannon's diversity	100	-1.361	[-6.12; 1.21]	0.55	0.04	
		Pine forest	200	0.007	[-0.01; 0.05]	0.41	0.03	
		Soft edge	500	0.000	[0.00; 0.00]	0.35	0.03	
	PC	(Intercept)	-	-1.949	[-3.84; -0.05]			*
		Medium forest cover	100	-0.028	[-0.09; 0.01]	0.71	0.00	
		Low forest cover	100	-8.639	[-4156; 4123]	0.52	0.00	
		Shannon's diversity	500	0.014	[-3.05; 3.17]	0.23	0.00	
		High forest cover	200	0.000	[-0.03; 0.03]	0.21	0.00	
	GC	(Intercept)	-	-4.844	[-25.68; 15.99]			
		Canopy cover	100	0.059	[-0.02; 0.18]	0.77	0.00	
		Clumpiness	100	1.277	[-1.77; 8.14]	0.40	0.00	
		Numb. canopy patches	100	-0.030	[-0.45; 0.29]	0.38	0.00	
		Aggregation index	500	-0.032	[-0.47; 0.22]	0.26	0.00	
	GM	(Intercept)	-	-8.769	[-14.45; -3.09]			**
		Diameter at breast height	-	0.045	[0.01; 0.08]	1.00	0.86	**
		Numb. trees	-	0.018	[0.00; 0.05]	0.78	0.63	
		Shrub height cov	-	1.337	[0.01; 4.07]	0.66	0.58	
		Shrub density	-	0.002	[-0.03; 0.05]	0.22	0.24	
Erithacus rubecula (Robin)	PH	(Intercept)	-	-0.771	[-1.57; 0.03]			(.)
		Young plantations	1000	-0.004	[-0.05; 0.02]	0.29	0.05	
		Non-native plantations	1000	-0.004	[-0.07; 0.04]	0.26	0.05	
		Pine forest	200	-0.001	[-0.01; 0.01]	0.25	0.04	
		Shrubland	200	-0.033	[-1.42; 1.13]	0.22	0.04	
	PC	(Intercept)	-	-1.450	[-2.87; -0.03]			*
		High forest cover	100	0.003	[0.00; 0.02]	0.39	0.14	
		Numb. patches	500	0.009	[-0.04; 0.09]	0.32	0.10	
		Total edge	500	0.000	[0.00; 0.00]	0.30	0.10	
		Medium forest cover	100	0.000	[-0.02; 0.01]	0.21	0.08	
	GC	(Intercept)	-	-2.289	[-8.1; 3.52]			
		Clumpiness	500	1.515	[-2.02; 9.13]	0.43	0.11	
		Canopy cover	1000	-0.001	[-0.04; 0.03]	0.26	0.07	
		Aggregation index	100	0.034	[-0.65; 0.94]	0.24	0.06	
		Numb. canopy patches	200	-0.001	[-0.04; 0.03]	0.21	0.06	
	GM	(Intercept)	-	-0.924	[-1.73; -0.12]			*
		Diameter at breast height	-	-0.001	[-0.01; 0.01]	0.29	0.05	

Species	**Model type**	**Variables**	**Scale**	**Estimate**	**CI95%**	**RVI partial**	**RVI full**	**P**
E. rubecula (cont.)		Mean shrub height	-	0.026	[-0.17; 0.35]	0.29	0.05	
		Shrub density	-	-0.002	[-0.03; 0.01]	0.28	0.05	
		Numb. trees	-	0.000	[-0.01; 0.01]	0.23	0.05	
Fringilla coelebs (Common chaffinch)	PH	(Intercept)	-	-0.050	[-0.86; 0.77]			
		Pine forest	500	0.012	[0.00; 0.02]	1.00	0.01	*
		Shrubland	200	-0.312	[-1.20; 0.12]	0.58	0.01	
		Young plantations	200	0.002	[0.00; 0.02]	0.40	0.00	
		Non-native plantations	500	-0.063	[-1.44; 0.97]	0.27	0.00	
	PC	(Intercept)	-	1.540	[0.66; 2.42]			***
		Low forest cover	1000	-0.041	[-0.08; -0.01]	0.95	0.80	*
		Total edge	500	0.000	[0.00; 0.00]	0.60	0.52	
		Numb. patches	500	-0.015	[-0.06; 0.01]	0.54	0.49	
		Very high forest cover	200	0.001	[0.00; 0.01]	0.35	0.32	
	GC	(Intercept)	-	-2.193	[-7.09; 2.7]			
		Canopy cover	200	0.012	[0.00; 0.03]	0.74	0.04	
		Aggregation index	100	0.218	[-0.21; 1.05]	0.52	0.02	
		Clumpiness	200	-0.432	[-2.26; 0.47]	0.48	0.02	
		Numb. canopy patches	200	0.004	[-0.02; 0.05]	0.30	0.01	
	GM	(Intercept)	-	-0.015	[-0.66; 0.63]			
		Diameter at breast height	-	0.005	[0.00; 0.01]	0.94	0.00	*
		Numb. trees	-	0.002	[0.00; 0.01]	0.65	0.00	
		Shrub density	-	0.003	[0.00; 0.01]	0.55	0.00	
		Shrub height cov	-	-0.021	[-0.72; 0.55]	0.24	0.00	
Lophophanes cristatus (Crested tit)	PH	(Intercept)	-	-0.902	[-2.24; 0.44]			
		Shrubland	200	-0.681	[-2.32; 0.19]	0.64	0.17	
		Pine forest	200	0.005	[0.00; 0.02]	0.59	0.16	
		Non-native plantations	1000	0.020	[-0.01; 0.08]	0.54	0.15	
		Soft edge	100	0.000	[0.00; 0.00]	0.27	0.07	
	PC	(Intercept)	-	0.205	[-0.73; 1.14]			
		Numb. patches	200	-0.111	[-0.33; 0.02]	0.71	0.19	
		Low forest cover	200	-0.411	[-1.53; 0.15]	0.60	0.17	
		Shannon's diversity	200	-0.145	[-1.51; 0.74]	0.38	0.11	
		High forest cover	200	0.002	[-0.01; 0.02]	0.27	0.09	
	GC	(Intercept)	-	-0.049	[-4.48; 4.38]			
		Clumpiness	200	-1.443	[-3.92; 0.06]	0.75	0.24	
		Aggregation index	100	0.014	[-0.01; 0.06]	0.55	0.18	
		Numb. canopy patches	1000	0.000	[0.00; 0.00]	0.48	0.16	
		Canopy cover	500	-0.007	[-0.05; 0.01]	0.38	0.14	
	GM	(Intercept)	-	-0.451	[-1.47; 0.56]			
		Mean shrub height	-	-0.070	[-0.28; 0.03]	0.56	0.04	
		Diameter at breast height	-	0.003	[0.00; 0.01]	0.51	0.03	
		Numb. trees	-	0.001	[0.00; 0.01]	0.26	0.01	

	Model					**RVI**		
Species	**type**	**Variables**	**Scale**	**Estimate**	**CI95%**	**partial**	**full**	**P**
		Shrub height cov	-	0.003	[-1.25; 1.27]	0.22	0.00	
Lullula	PH	(Intercept)	-	-4.937	[-7.65; -2.23]			***
arborea		Shrubland	200	2.973	[1.15; 4.79]	1.00	0.78	**
(Woodlark)		Soft edge	1000	0.000	[0.00; 0.00]	0.84	0.65	
		Shannon's diversity	100	0.485	[-0.46; 2.47]	0.48	0.38	
		Numb. patches	200	0.001	[-0.22; 0.23]	0.29	0.22	
	PC	(Intercept)	-	-3.931	[-6.94; -0.92]			*
		Medium forest cover	100	0.015	[0.00; 0.04]	0.76	0.01	
		Shannon's diversity	100	1.070	[-0.02; 2.86]	0.75	0.02	
		High forest cover	1000	0.023	[-0.02; 0.11]	0.51	0.01	
		Low forest cover	200	0.131	[-0.66; 1.49]	0.31	0.00	
	GC	(Intercept)	-	-2.484	[-14.41; 9.44]			
		Clumpiness	100	3.201	[0.20; 7.18]	0.87	0.12	
		Numb. canopy patches	100	0.053	[-0.01; 0.17]	0.65	0.09	
		Canopy cover	100	-0.007	[-0.05; 0.02]	0.42	0.06	
		Aggregation index	500	-0.016	[-0.29; 0.16]	0.25	0.04	
	GM	(Intercept)	-	-0.766	[-2.28; 0.75]			
		Numb. trees	-	-0.010	[-0.03; 0.00]	0.75	0.00	
		Mean shrub height	-	-0.182	[-0.74; 0.14]	0.61	0.00	
		Shrub density	-	0.007	[-0.02; 0.06]	0.37	0.00	
		Diameter at breast height	-	-0.002	[-0.02; 0.01]	0.32	0.00	
Parus	PH	(Intercept)	-	-0.546	[-1.49; 0.40]			
major		Pine forest	100	0.683	[0.02; 1.57]	0.86	0.61	
(Great tit)		Non-native plantations	100	0.526	[0.02; 1.47]	0.71	0.52	
		Shrubland	200	-0.429	[-1.69; 0.2]	0.58	0.42	
		Soft edge	1000	0.000	[0.00; 0.00]	0.42	0.33	
	PC	(Intercept)	-	0.170	[-0.82; 1.16]			
		Low forest cover	200	-0.402	[-1.19; 0.06]	0.71	0.06	
		High forest cover	1000	-0.004	[-0.04; 0.01]	0.33	0.03	
		Total edge	1000	0.000	[0.00; 0.00]	0.26	0.02	
		Shannon's diversity	100	0.008	[-0.56; 0.63]	0.21	0.02	
	GC	(Intercept)	-	-1.555	[-4.54; 1.43]			
		Aggregation index	100	0.014	[-0.01; 0.05]	0.62	0.04	
		Clumpiness	100	0.126	[-0.72; 1.55]	0.30	0.01	
		Numb. canopy patches	500	0.000	[0.00; 0.00]	0.27	0.01	
		Canopy cover	500	0.001	[-0.01; 0.02]	0.25	0.01	
	GM	(Intercept)	-	-0.431	[-1.07; 0.21]			
		Diameter at breast height	-	0.001	[0.00; 0.01]	0.40	0.02	
		Shrub height cov	-	0.200	[-0.36; 1.44]	0.37	0.02	
		Numb. trees	-	0.001	[0.00; 0.01]	0.35	0.02	
		Shrub density	-	0.000	[-0.01; 0.01]	0.23	0.00	

Species	Model type	Variables	Scale	Estimate	CI95%	RVI partial	RVI full	P
Periparus	PH	(Intercept)	-	-0.482	[-1.17; 0.21]			
ater		Shrubland	200	-3.365	[-6.02; -0.71]	1.00	0.23	*
(Coal tit)		Soft edge	200	-0.001	[0.00; 0.00]	0.66	0.14	
		Non-native plantations	100	-10.599	[-3885; 3851]	0.63	0.14	
		Numb. patches	100	0.074	[-0.34; 0.82]	0.31	0.08	
	PC	(Intercept)	-	-0.705	[-1.60; 0.19]			
		Medium forest cover	100	-0.050	[-0.09; -0.01]	1.00	0.59	*
		Low forest cover	100	-11.103	[-3821; 3788]	0.66	0.38	
		Total edge	200	0.000	[0.00; 0.00]	0.26	0.18	
		Numb. patches	500	0.003	[-0.05; 0.08]	0.25	0.16	
	GC	(Intercept)	-	-12.906	[-33.68; 7.87]			
		Aggregation index	100	0.124	[-0.01; 0.34]	0.76	0.10	
		Numb. canopy patches	200	-0.035	[-0.15; 0.02]	0.54	0.07	
		Canopy cover	500	0.003	[-0.03; 0.05]	0.24	0.03	
		Clumpiness	100	0.025	[-2.60; 2.83]	0.21	0.03	
	GM	(Intercept)	-	-3.332	[-5.29; -1.37]			***
		Diameter at breast height	-	0.017	[0.00; 0.03]	1.00	0.00	**
		Numb. trees	-	0.005	[0.00; 0.02]	0.61	0.00	
		Shrub height cov	-	0.600	[-0.58; 3.16]	0.47	0.00	
		Mean shrub height	-	-0.006	[-0.23; 0.18]	0.26	0.00	
Serinus	PH	(Intercept)	-	-0.610	[-2.15; 0.93]			
serinus		Shrubland	1000	-5.237	[-10.5; -1.02]	0.91	0.20	(.)
(Serin)		Shannon's diversity	100	0.698	[-0.04; 2.13]	0.67	0.15	
		Hard edge	1000	0.000	[0.00; 0.00]	0.36	0.08	
		Numb. patches	1000	0.002	[-0.01; 0.02]	0.33	0.07	
	PC	(Intercept)	-	-2.442	[-4.32; -0.56]			*
		Shannon's diversity	200	1.374	[-0.73; 4.68]	0.70	0.05	
		Total edge	200	0.000	[0.00; 0.00]	0.38	0.03	
		Numb. patches	1000	0.002	[-0.02; 0.03]	0.26	0.02	
		Medium forest cover	1000	0.002	[-0.05; 0.07]	0.21	0.01	
	GC	(Intercept)	-	6.751	[-18.23; 31.74]			
		Clumpiness	100	0.915	[-0.55; 4.10]	0.52	0.03	
		Aggregation index	500	-0.085	[-0.44; 0.09]	0.49	0.02	
		Numb. canopy patches	1000	0.000	[0.00; 0.00]	0.42	0.02	
		Canopy cover	100	-0.001	[-0.02; 0.01]	0.25	0.00	
	GM	(Intercept)	-	0.025	[-1.04; 1.09]			
		Mean shrub height	-	-0.246	[-0.56; -0.04]	0.83	0.48	
		Shrub density	-	-0.004	[-0.04; 0.02]	0.37	0.23	
		Numb. trees	-	-0.002	[-0.02; 0.01]	0.36	0.23	
		Shrub height cov	-	-0.084	[-1.76; 1.08]	0.25	0.17	

Species	Model type	Variables	Scale	Estimate	CI95%	RVI partial	full	P
Turdus merula (Common blackbird)	PH	(Intercept)	-	-1.334	[-2.16; -0.51]			**
		Shannon's diversity	100	0.175	[-0.46; 1.5]	0.34	0.08	
		Numb. patches	500	0.006	[-0.02; 0.06]	0.33	0.07	
		Soft edge	1000	0.000	[0.00; 0.00]	0.29	0.07	
		Hard edge	500	0.000	[0.00; 0.00]	0.23	0.05	
	PC	(Intercept)	-	-1.338	[-3.11; 0.44]			
		Low forest cover	200	-0.468	[-2.11; 0.37]	0.54	0.17	
		Medium forest cover	100	0.004	[-0.01; 0.03]	0.42	0.13	
		High forest cover	1000	0.001	[-0.04; 0.05]	0.21	0.08	
		Shannon's diversity	1000	0.024	[-2.50; 2.74]	0.20	0.08	
	GC	(Intercept)	-	2.039	[-11.39; 15.47]			
		Aggregation index	500	-0.041	[-0.28; 0.08]	0.41	0.09	
		Canopy cover	1000	0.007	[-0.03; 0.07]	0.36	0.08	
		Numb. canopy patches	1000	0.000	[0.00; 0.00]	0.22	0.06	
		Clumpiness	100	-0.030	[-2.16; 1.86]	0.20	0.05	
	GM	(Intercept)	-	-1.354	[-2.29; -0.42]			**
		Mean shrub height	-	0.017	[-0.16; 0.29]	0.26	0.05	
		Numb. trees	-	0.000	[-0.01; 0.01]	0.25	0.04	
		Shrub density	-	0.001	[-0.01; 0.02]	0.24	0.04	
		Shrub height cov	-	0.033	[-1.35; 1.64]	0.23	0.04	

Chapter III

Identifying critical thresholds to guide management practices in agro-ecosystems: insights from bird community response to an open grassland-to-forest gradient

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Pedro A. Salgueiro[1,2,3,5], António Mira[1, 3,5], João E. Rabaça[2,4,5], Sara M. Santos[1, 3,5]

[1]UBC – Conservation Biology Lab;

[2]LabOr – Laboratory of Ornithology;

[3]CIBIO-UE – Research Center in Biodiversity and Genetic Resources, Pole of Évora – Research Group in Applied Ecology;

[4]ICAAM – Institute of Mediterranean Agricultural and Environmental Sciences;

[5]Department of Biology, University of Évora. Mitra, 7002-554 – Évora, Portugal.

III.1. ABSTRACT

Landscapes are showing increased fragmentation and habitat loss due to land-use conversion and intensification, leading to species-poor and homogeneous communities. The identification of ecological thresholds above which major changes in community composition take place may prevent the critical downfall of biodiversity while improving the effectiveness of conservation, resource management and restoration practices. In this study, we provide a new insight on how species distribute along a highly variegated agro-ecosystem in the Mediterranean region. We aim to define the thresholds of occurrence of a bird community inhabiting a tree canopy gradient and determine the patterns of community change. We fit Huisman-Olff-Fresco models to bird occurrence data (assuming non-linear responses) to identify species-specific responses to the gradient, species richness and turnover patterns. The tree canopy gradient is responsible for major changes in bird community likely related to the variation of the tree stratum and canopy enclosure, which reflect different niche segregation opportunities. Maximum species richness was reached at 10% canopy cover while total turnover rate was higher than expected from a null model up to 10% canopy cover. Ecological thresholds can be used as indicators of specific resource limits responsible for changes in community composition and species occurrence, identifying where populations may be more sensitive. Choosing a single management scheme will invariably result in winners and losers, but optimal levels of management can be explored in order to maximize species diversity across Mediterranean agro-ecosystems.

III.2. KEYWORDS

Ecological thresholds; Bird community; Turnover patterns; Tree canopy cover gradient; Agroecosystems; Variegated landscape; Huisman-Olff-Fresco models.

III.3. INTRODUTION

Several studies (*e.g.*, Andrén, 1994; Monkkonen and Reunanen, 1999; Fahrig, 2001) specify the existence of ecological thresholds to gradients of habitat alteration (the fragmentation threshold), beyond which major changes in species occupancy occur. Ecological thresholds provide an alternative to usual post-disturbance reactive tools such as endangered species legislation (Johnson, 2013) and costly restoration practices (Holl and Howarth, 2000), by establishing preventive targets on biodiversity loss to guide policy and resource management (Huggett, 2005). Moreover, it may improve the effectiveness of conservation efforts in natural resource management (Huggett, 2005), by documenting the sensitivity of species to threatening processes such as habitat loss, simplification or fragmentation (*e.g.*, Betts *et al.*, 2007), loss of genetic diversity (Bruggeman *et al.*, 2010) or threat by invasive species (With, 2004). As landscapes worldwide have experienced strong changes over the last decades, caused by land-use conversion and intensification (Newbold *et al.*, 2015), such concrete environmental tools are needed to guide policy goals aiming to prevent biodiversity loss (Balmford *et al.*, 2003).

In agro-ecosystems these changes have been particularly noticed (Tscharntke *et al.*, 2005), as the European Common Agricultural Policy (CAP) is triggering a shift from traditional extensive agro-forestry management to intensive agriculture and forest production areas (Jones *et al.*, 2011). For instance, these changes have had a great impact upon the Portuguese 'montado', a characteristic large scale variegated landscape where tree cover varies gradually from presence of scattered trees to dense forest (*sensu* McIntyre and Hobbs 1999; Pinto-Correia *et al.*, 2011) classified as High Nature Value (HNV) farmland (Andersen *et al.*, 2003). The once structurally variegated landscape resulting from centuries of traditional human activities (*e.g.*, agriculture, cattle grazing and forestry; Blondel *et al.*, 2010) is changing as a result of either management intensification or land abandonment (Pinto-Correia, 2000; Plieninger and Schaar, 2008). Intensification is causing the 'montado' to disappear as a system, giving rise to a more heterogeneous landscape mosaic. Increasing crop cultivation or animal production areas with reduced tree cover are intermixed with denser and structurally complex forests resulting from land abandonment (Pinto-Correia and Mascarenhas, 1999). All these on-going changes can have strong impacts on biotic communities.

Significant declines of species are reported worldwide following landscape alteration (Billeter *et al.*, 2008; Inger *et al.*, 2015; Jeliazkov *et al.*, 2016), often resulting in net changes in ecological assemblages altering community composition (Newbold *et al.*, 2015), and in the homogenization of communities while reducing species diversity through replacement by widespread species (Clavero and Brotons, 2010; Gámez-Virués *et al.*, 2015). In agro-ecosystems, bird community is highly shaped by the open grassland-to-forest gradient (Berg, 2002; Catarino *et al.*, 2016; Herrera *et al.*, 2016) and changes along the gradient result in turnovers in bird composition (Sirami *et al.*, 2007). Some studies report that specialization (*i.e.*, the restricted ecological niche width of a species to a given set of resources; Devictor *et al.*, 2010) is most likely to occur at extreme ranges of landscape gradients (*e.g.*, Clavero and Brotons, 2010), but the open structure of forests can also favour the presence of transition species (Tellería, 2001; Sanderson *et al.*, 2009; Bonthoux *et al.* 2013). However, the limits of species occurrence, and where communities are most vulnerable to species loss, are still unknown. In addition, changes in habitat are also likely to affect the structure and dynamics of species assemblages by tampering with interspecific interactions (Bonthoux *et al.*, 2013). The adoption of inappropriate and unreliable community-based approaches, that do not account for contrasting responses of individual species (Monkkonen and Reunanen, 1999; Lindenmayer *et al.*, 2008), have limited the insight on how community and overall biodiversity are shaped along environmental gradients (Pardini *et al.*, 2010; Bonthoux *et al.*, 2013). Investigating both species and community responses to landscape gradients will help to integrate both intraspecific and interspecific processes in local biodiversity patterns changing along those gradients (Lepš *et al.* 2011).

Here, we aim to define thresholds of occurrence of a breeding bird community inhabiting an open grassland-to-forest gradient in a highly variegated agro-ecosystem in the Mediterranean region. We attempt to answer the questions: ‘what are the ranges of tree cover most vulnerable to species loss?’ and ‘what ranges of tree cover best fulfil the requirements for conservation purposes?’, thus providing a better understanding of how agro-ecosystems management can be optimized to meet biodiversity conservation targets. We identify patterns of community change based on ecological niche theory where species are assumed to respond non-linearly to gradients following unimodal (Gaussian-shaped) response curves (Austin, 2007), thus avoiding common constraints of linear approaches (Swift and Hannon, 2010; Johnson, 2013). Our approach applies Huisman-Olff-Fresco models (hereafter HOF models; Huisman *et al.*, 1993), which incorporate such species-specific response curves. We then use the cumulative changes in species distribution to define patterns of variation in community composition and identify bird assemblages by means of niche overlap. Thus, our approach integrates the (i) assessment of species-specific thresholds of occurrence based on niche width, (ii) turnover patterns where strong changes in community composition occur, and (iii) identification of species assemblages across a tree cover gradient.

III.4. METHODS

III.4.1. Study area

We conducted the study in a highly variegated Mediterranean landscape (McIntyre and Hobbs, 1999) of southern Portugal, in the Évora district (centroid: 16271.45, -113395.21; EPSG: 3763-ETRS89 / Portugal TM06). The area comprises 426,000 ha, dominated by the Mediterranean savannah-like 'montado' (Pinto-Correia *et al.*, 2011), an agro-ecosystem that includes semi-natural habitats with low intensity farming. The landscape consists of a spatially heterogeneous structure, ranging from densely wooded areas dominated by evergreen cork (*Quercus suber*) and holm oaks (*Q. rotundifolia*) to agricultural plains with scarce tree cover. The topography is generally flat, with altitude ranging between 100 and 450 m a.s.l.. The climate of the region is typically Mediterranean with warm and dry summers where temperatures reach up to 40° C, while winters are relatively mild and wet.

III.4.2. Tree canopy cover gradient

Tree cover is one of the most important features in determining bird diversity in Mediterranean agro-ecosystems (Godinho and Rabaça, 2010; Catarino *et al.*, 2016). Therefore, we used the gradient of tree canopy cover as a surrogate for habitat amount (Westfall and Morin, 2012; Godinho *et al.*, 2016). In fact, the spatial variation of open grassland to dense oak forest can represent a resource-related continuous gradient (Fischer and Lindenmayer, 2006) of basic food and shelter availability, nesting conditions, and movement ability for different bird species (Price *et al.*, 2009). The gradient was built from aerial photography data – based on colour image segmentation and using the *k*-

mean algorithm, an automated method of unsupervised classification (Subbiah and Seldev, 2012). Total tree canopy cover was determined within buffers centred on each bird survey plot. The canopy cover ranged from 0 to 65%, though in further analyses we considered a maximum of ~50% due to the lack of spatial replicates at high-density cover sites and outlier removal. The gradient was extracted using Orfeo Toolbox 3.20 (Orfeo Toolbox Development Team, 2013), in QGIS 2.2 (Quantum GIS Development Team, 2013).

III.4.3. Bird surveys

We surveyed bird species by means of 10 min point counts (Bibby *et al.*, 2000) with a distance limit of 100m. A total of 152 points were carried out, covering the tree canopy gradient with spatial replicates. In order to prevent double counts, a minimum distance of 500 m between points was considered. Sampling was conducted during the 2013 breeding season from 26th April to 24th May, when there is greater bird recruitment and spatial stability. A single visit was carried out at each point at the period of highest detectability (6:00 to 11:00 a.m.; Palmeirim and Rabaça, 1994). While reducing survey effort per site, we increased the number of sites, aiming to provide statistical power and the representativeness of the study area (Loos *et al.*, 2015). Fieldwork was conducted by one observer recording bird species that were seen or heard (Bibby *et al.*, 2000). Fly-over individuals or aerial-feeders (*e.g.*, barn swallow *Hirundo rustica*) were discarded from the analysis. Due to difficulty in distinguishing *Galerida cristata* and *G. theklae*, these species were pooled and analysed together (Delgado and Moreira, 2000). Overall, we analysed 33 species (see Appendix III.A for details) present in >10 sampled points (Peper *et al.*, 2011).

III.4.4. Species response to tree canopy cover gradient

HOF models (Huisman *et al.*, 1993) were used to identify species response to single gradients (Peppler-Lisbach and Kleyer, 2009; Peper *et al.*, 2011). These consist of seven (I-VII) hierarchical models of increasing response complexity (see Jansen and Oksanen, 2013 for details). Because bimodal responses could over fit data, we considered only five model types: I – no trend; II – monotone sigmoidal; III – monotone sigmoidal with an optima plateau; IV – symmetric unimodal; and V – skewed unimodal (Jansen and Oksanen, 2013).

Bird species presence/absence data were fitted using tree canopy cover as explanatory variables. A preliminary multi-scale screening with different buffer distances around point count was performed to define an optimal and coherent spatial scale across species responses (see Appendix III.B and data therein). The 200m spatial scale outperformed the others and was employed in further analyses.

To deal with false absences we fitted bird species occurrence data in a single visit occupancy model (Lele *et al.*, 2012). We estimated the probability of occupancy of a given species as a function of the tree canopy cover gradient while accounting for imperfect detection arising from time of day (minutes from sunrise) and time of year (days from spring equinox) effects. Occupancy models were performed using the package “detect” (Solymos *et al.*, 2016). We used the predicted probability of occupancy to correct putative false absences in bird data. A resampling procedure with replacement of false absences was applied in a loop routine (100 runs). At each loop, a HOF model was fitted to the corrected bird data. The final model was obtained by fitting the most frequent HOF model adjusted to the mean response curve of all runs. HOF models were run using maximum likelihood estimation and binomial distribution family (log-link function). We used Akaike’s information criteria adjusted to small samples (AICc) to select the best model for each species (Burnham and Anderson, 2004; Burnham *et al.*, 2011) after a bootstrap procedure.

Optimum location and niche width were extracted from the final HOF model for each species. The optimum (*sensu* Jansen and Oksanen, 2013) refers to a single point (type II, IV and V models) or a range of values (type III models) of the canopy gradient where the response curve reaches its maximum value. Niche width estimation followed the central border approach, where species’ tolerance to the gradient corresponds to $e^{-0.5}$ times the maximal probability of occurrence (Heegaard, 2002). This reflects a measure of the distance from the optimum (tolerance) (Heegaard, 2002), defining a range beyond which the species is subjected to non-optimal environmental conditions. We truncated estimates at minimum and maximum values of the canopy cover gradient (Jansen and Oksanen, 2013).

III.4.5. Changes in community composition

Changes in community were assessed by examining the patterns of variation of bird species richness and community turnover along the tree canopy gradient. Species richness was estimated following Peppler-Lisbach and Kleyer's (2009) approach: we summed the predicted probabilities of occurrence of all species, which reflect the variation in the number of species along the gradient. To validate species richness response we proceeded with two analyses. Firstly, we extracted fitted values from the response obtained from the HOF approach and applied Spearman rank correlations to check their correlation with the observed number of species. Secondly, the observed number of species was also modelled along the tree canopy cover gradient following a generalized additive model procedure (GAM, Poisson distribution with log link function). Fitted and 95% confidence interval values were extracted from the GAM model and plotted together with species richness response obtained from the HOF approach.

Afterwards, community turnover patterns were computed in order to detect the ranges at which composition changes. Total community turnover at each point of the canopy cover gradient was derived from the sum of slopes of each species response curve (Oksanen and Tonteri, 1995). Turnover rates were arc-tangent transformed to avoid the influence of species with steep slopes (Peppler-Lisbach and Kleyer, 2009). We divided total community turnover by the sum of predicted probabilities of occurrence at each given point to account for the effects of uneven number of species along the gradient (Peppler-Lisbach and Kleyer, 2009). Total community turnover was split into negative (species showing decreasing probability of occurrence at a given point) and positive turnovers (increasing probability of occurrence) (Peppler-Lisbach and Kleyer, 2009).

Turnover changes of species composition were tested against a null model through coenocline simulation (Gotelli and McGill, 2006). Species randomized occurrence data was simulated from coenoclines restricted to vary according to optimal responses, niche width and species density found in empirical data (Peppler-Lisbach and Kleyer, 2009). Randomized data was extracted from coenoclines as expected counts following a Poisson distribution at each point of the gradient (Simpson, 2014). The null model was obtained after the permutation of 1000 simulation runs of random species response curves. For each simulation, the resultant turnover rates (total, positive, and negative) were rescaled (*i.e.*, weighted by their respective mean; Peppler-Lisbach and Kleyer, 2009; Peper *et al.*, 2011). Confidence intervals (95%) for each turnover rate were then calculated based on 1000 randomizations.

III.4.6. Species niche clustering

Species niche clustering also involved a procedure of coenocline simulation. We used significant turnover values and species response curves to distinguish between assemblages. Assuming that each significant community turnover reflects a species composition change, most species optima would locate outside turnovers. We simulated species data for each assemblage following the same criteria defined in the community turnover analysis. At both ends of the gradient we simulated dummy species occurring at the first or the last 10 observations of the sampled gradient (Peper *et al.*, 2011). By running HOF models of dummy species we obtained lower and upper virtual optima for species groups located at the extremes of the sampled gradient. Since modelling coenoclines will be inherently biased as unimodal curves (Gauch and Whittaker, 1972), HOF model responses were constrained to behave according to the observed specific curve types. For each of the defined assemblages, we ran 1000 randomizations to limit the 95% confidence intervals for the species turnover. Species turnovers falling within the 95% confidence intervals were included as members of an assemblage.

All analyses were performed in R, version 3.0.2 (R Development Core Team, 2013). We used packages “eHOF” (Jansen and Oksanen, 2013) for HOF model fitting of empirical and simulated data, “mgcv” (Wood, 2006) for GAM, and “coenocliner” (Simpson, 2014) for coenocline simulation. All fitted values were calculated at each 0.05% interval of the tree canopy cover gradient.

III.5. RESULTS

III.5.1. Species responses to tree canopy cover gradient

Most species showed a clear response to the tree canopy cover gradient (Figure III.1; Appendix III.C Figure III.C1), though it varied greatly regarding both optima location and niche width. Ten species showed a marked preference for low tree canopy cover areas (<1%). Among these, two presented optima at low tree canopy cover (*Lanius meridionalis* and *Passer hispaniolensis*). All other species occurred mostly in open grassland and were constrained by increasing canopy cover (*e.g.*, *Tetrax tetrax*, *Cisticola juncidis*), showing a decreasing monotone sigmoidal curve (type II).

Unimodal patterns were detected in seven species (*e.g.*, *Sturnus unicolor, Lanius senator*), with optima peaking between 1 and 25%. Interestingly, optima location rarely overlapped, though these results should be carefully considered, as most of the species showed high tolerance to tree canopy cover when niche width occupied almost the whole range (*e.g.*, *Carduelis carduelis*, *Chloris chloris*).

The occurrence of fourteen species was limited by lower tree canopy cover. Yet many species showed high tolerance to the scarcity of tree canopy cover (*e.g.*, *Cyanistes caeruleus*, *Fringilla coelebs*), with their optima promptly peaking before 10% canopy cover and spreading along the forested range of the gradient. On the other hand, some species showed higher constraints, as optima only emerged at 30 (*Turdus merula*) or 40% tree canopy cover (*Dendrocopos major*).

Only two species did not exhibit clear responses to tree canopy cover, as their tolerance spreads all over the gradient (*Hippolais polyglota* and *Luscinia megarhyncos*), whilst showing an increasing monotone sigmoidal curve.

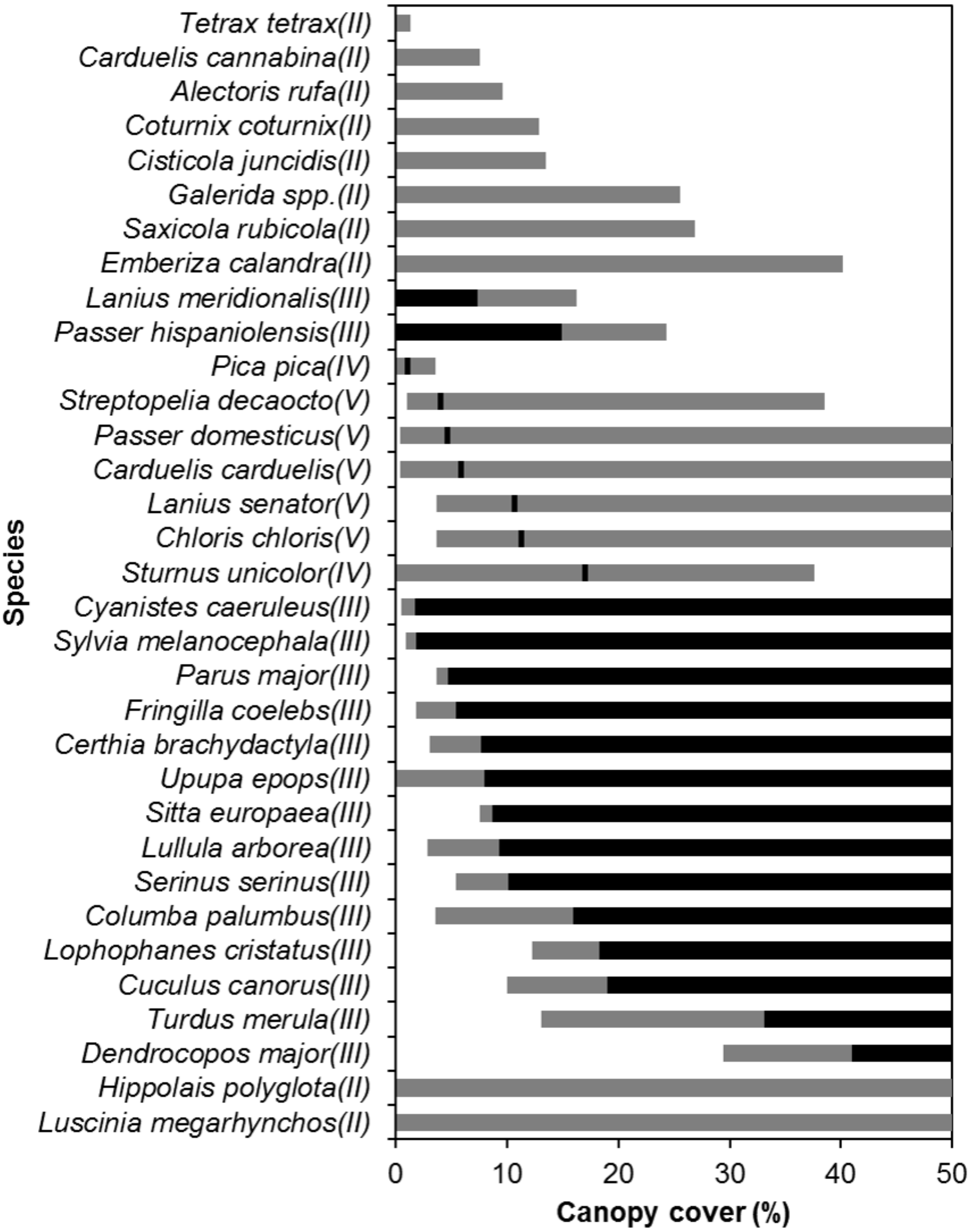

Figure III.1 – Optimum (black bars) and niche width (grey bars) of each species response model along the tree canopy cover gradient. The roman numbers in brackets refer to the HOF model type.

III.5.2. Changes in community composition

The species richness curve suggests a unimodal right skewed response along the tree canopy cover gradient with a maximum at 10% canopy cover (Figure III.2). An abrupt trend was observed at lower canopy gradients, where the number of species decreases with declining canopy. Predicted richness data correlated with empirical data (Spearman rank correlation: r_S=0.43; $P < 0.001$). Compared with GAM procedure ($P < 0.001$; adjusted R-square = 0.454; explained deviance = 46.8%), the HOF method slightly underestimated species richness. However, the general pattern was similar in both methods and HOF predictions were within the 95% confidence interval of GAM estimates (Figure III.2).

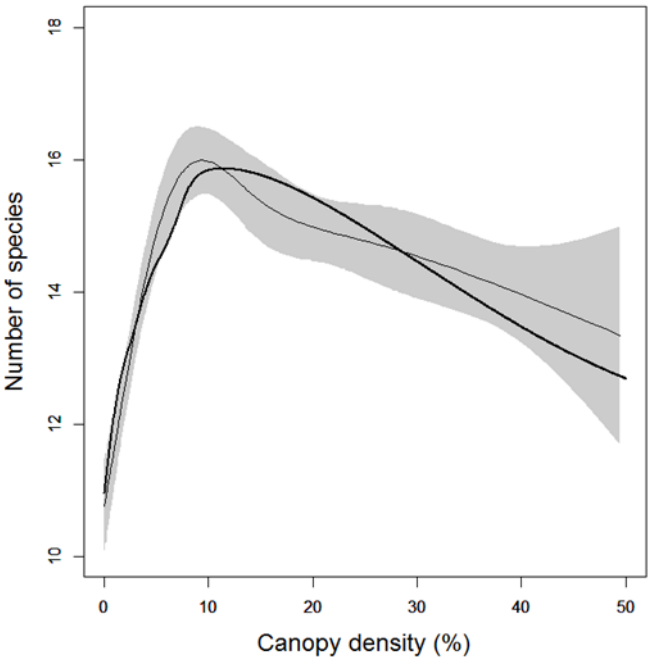

Figure III.2 – Predicted number of species (sum of species occurrence probabilities) along the tree canopy cover gradient using HOF approach (thick line) and predicted number of species using GAM approach (mean value – thin line; 95% confidence intervals – grey shaded area).

Total community turnover rate reached a maximum value at ≈1% canopy cover, mostly due to a positive turnover (Figure III.3A, solid black line). The bird community underwent a major change due to the emergence of species associated with forested areas. A smoother curve in negative turnover was observed at ≈25% (Figure III.3B, solid black line) which can be related to the decrease of the occurrence probability of most species with unimodal responses that had their optima below this percentage of canopy cover (Figure III.1). Total community turnover was significantly higher than expected from the null model until ≈10% canopy cover (Figure III.3A). However, beyond this value it did not differ significantly from expected values. Also, only a few species increased their likelihood of occurrence, resulting in lower values of positive turnover (Figure III.3B). Negative turnover showed moderately high rates below 10% canopy cover, meaning that some species had a decreasing probability of occurrence along the tree canopy cover gradient (Figure III.3C).

III.5.3. Species niche clustering

According to the above mentioned results, we defined the following criteria to classify the species assemblages: (i) farmland species – species with virtual optima < 1% and decreasing monotone sigmoidal response curves with or without optima plateau (type II and III), (ii) transition species – species reaching optima between 1% and 25%, with unimodal responses (type IV and V), and (iii) forest species – species reaching optima >1%, with sigmoidal response curves with or without optima plateau (type II and III).

Following these criteria, 30 out of 33 species were assigned to one of the assemblages (Table III.1). Farmland bird species (n = 8, *e.g.*, *Tetrax tetrax*, *Lanius meridionalis*) could be discretely separated from other forest species, assuming a strong negative rate of occurrence with increasing canopy cover (Figure III.4A). Transition species (n = 6, *e.g.*, *Lanius senator*, *Sturnus unicolor*) showed an increasing occurrence probability, peaking below 25% canopy cover and decreasing afterwards (Figure III.4B). Forest species (n = 16, *e.g.*, *Cyanistes caeruleus*, *Dendrocopos major*) were separated from other species, exhibiting a consistent increase in occurrence probability along the gradient, reaching optimum values (null rate of change) as the percentage of canopy increased (Figure III.4C). Only three species were not assigned to an assemblage (*Emberiza calandra*, *Galerida* spp. and *Pica pica*, see Table III.1) as the larger or narrower tolerance of the species did not comply with the expected response defined by the criteria.

Table III.1 – Species classification within the identified assemblages, and correspondent model types with curve response behavior.

Assemblage	Species	Model type
Farmland species	*Alectoris rufa*	Decreasing monotone sigmoidal curve (type II)
	Carduelis cannabina	Decreasing monotone sigmoidal curve (type II)
	Cisticola juncidis	Decreasing monotone sigmoidal curve (type II)
	Coturnix coturnix	Decreasing monotone sigmoidal curve (type II)
	Lanius meridionalis	Sigmoidal with left optima plateau (type III)
	Passer hispaniolensis	Sigmoidal with left optima plateau (type III)
	Saxicola rubicola	Decreasing monotone sigmoidal curve (type II)
	Tetrax tetrax	Decreasing monotone sigmoidal curve (type II)
Transition species	*Carduelis carduelis*	Right skewed unimodal (type V)
	Chloris chloris	Right skewed unimodal (type V)
	Lanius senator	Right skewed unimodal (type V)
	Passer domesticus	Right skewed unimodal (type V)
	Streptopelia decaocto	Right skewed unimodal (type V)
	Sturnus unicolor	Symmetric unimodal (type IV)
Forest species	*Certhia brachydactyla*	Sigmoidal with right optima plateau (type III)
	Columba palumbus	Sigmoidal with right optima plateau (type III)
	Cuculus canorus	Sigmoidal with right optima plateau (type III)
	Cyanistes caeruleus	Sigmoidal with right optima plateau (type III)
	Dendrocopos major	Sigmoidal with right optima plateau (type III)
	Fringilla coelebs	Sigmoidal with right optima plateau (type III)
	Hippolais polyglota	Increasing monotone sigmoidal curve (type II)
	Lophophanes cristatus	Sigmoidal with right optima plateau (type III)
	Lullula arborea	Sigmoidal with right optima plateau (type III)
	Luscinia megarhynchos	Increasing monotone sigmoidal curve (type II)
	Parus major	Sigmoidal with right optima plateau (type III)
	Serinus serinus	Sigmoidal with right optima plateau (type III)
	Sitta europaea	Sigmoidal with right optima plateau (type III)
	Sylvia melanocephala	Sigmoidal with right optima plateau (type III)
	Turdus merula	Sigmoidal with right optima plateau (type III)
	Upupa epops	Sigmoidal with right optima plateau (type III)
Not classified	*Emberiza calandra*	Decreasing monotone sigmoidal curve (type II)
	Galerida spp.	Decreasing monotone sigmoidal curve (type II)
	Pica pica	Symmetric unimodal (type IV)

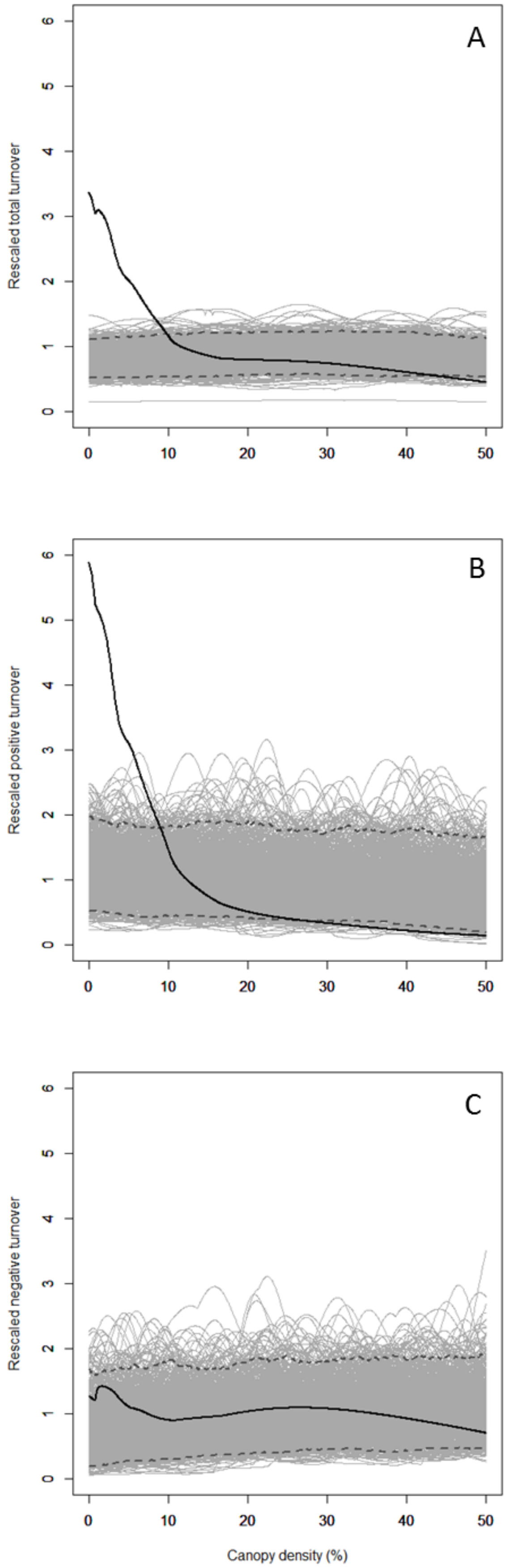

Figure III.3 – Rescaled adjusted community turnover rates (black lines; A – total, B – positive and C – negative turnovers) comparatively with 95% confidence interval of the null model (dashed lines) set by the 1000 randomize runs of coenoclines (grey shade).

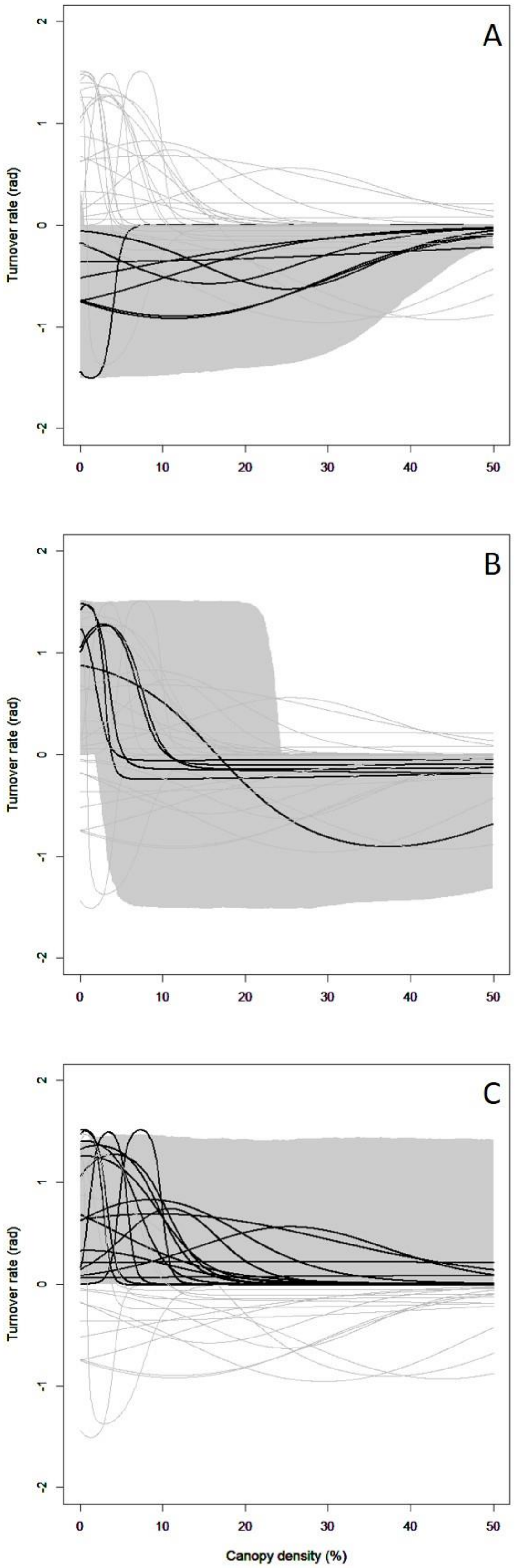

Figure III.4 – Species group assemblages based on rates-of-change along the tree canopy cover gradient (A – farmland, B – transition, C – forest species). Shaded grey areas show the 95% confidence interval set by the 1000 randomized simulations marking the range where species turnovers are expected to vary considering each assemblage. Black lines show species' turnovers that fall inside the range, and therefore, belonging to that given assemblage, and grey lines show species' turnovers that fall outside the same range, thus not belonging to the assemblage. Species grouping within the identified assemblages are shown in Table III.1.

III.6. DISCUSSION

III.6.1. Critical thresholds of the bird community

In this study, we developed a framework that allowed us to determine species-specific thresholds of occurrence along a resource gradient. Moreover, we were able to define community-level thresholds determining species richness, composition turnover and assemblage patterns along the gradient.

Our results show the existence of environmental thresholds indicating major changes in community composition. We identified a rather sharp change occurring early in the gradient (between 1% and 10% tree canopy cover) with a strong shift of the bird community, mainly due to an increase of forest related species (*e.g.*, *Cyanistes caeruleus*, *Sitta europaea*) replacing the declining farmland species (*e.g.*, *Coturnix coturnix*, *Cisticola juncidis*). The persistence of many species within a short range interval of tree canopy cover (1 to 25%) increased species richness to peak at 10%. This is in line with former studies on similar systems: open woodlands of sparse tree cover increase habitat heterogeneity that favours the presence of open, transition and forest species (Tellería, 2001; Sanderson *et al.*, 2009; Bonthoux *et al.*, 2013). The right skewed unimodal pattern of species richness along the gradient reflects a lower number of species at open grassland areas, likely related to a reduction of niche segregation opportunities due to the loss of the tree stratum (MacArthur and MacArthur, 1961). Beyond 10% canopy cover, the smoother decrease in species richness with increasing canopy enclosure suggests that only forest species will prevail at higher cover levels.

According to optima location and response curve type, we found support for the existence of three assemblages: (i) farmland species with optima below 1% canopy cover, (ii) transition species with unimodal responses showing optima between 1 and 25%, (iii) and forest species with optima plateau. The first two assemblages were markedly constrained to distinct ranges of the gradient, related to specific requirements of species (narrower niche width); while the later showed a broader distribution within the forest range, reflecting the strong plasticity of the species to tree canopy cover variation (larger niche width). Our results are in line with those obtained by Clavero and Brotons (2010) who found that most of the specialized birds showed preference for extreme range of agricultural-forest gradient in Mediterranean landscapes. In our study, farmland species show a narrower niche width. In contrast, forest species showed high tolerance to low canopy cover by also occupying islets of isolated trees and areas of scarce tree cover, as was found in other studies (*e.g.*, Bonthoux *et al.*, 2013). Assemblage segregation within forest communities is not always detected, leading to confounding effects in threshold determination (*e.g.*, Radford *et al.*, 2005). However, we were able to detect a transition assemblage peaking within a restricted range of canopy cover (between 1% and 25%), supporting the suggestion that specialization can occur at intermediate levels of tree canopy cover (Tellería, 2001; Bonthoux *et al.*, 2013) or edge habitats (Suarez-Rubio *et al.*, 2013).

Our results suggest that the bird community is structured in well-defined assemblages, as a marked change in community composition occurs segregating open grassland from forest assemblages (the community-unit concept, Clements, 1936). However, it should be noted that the absence of significant turnovers at intermediate levels of tree canopy cover might suggest that many species distribute continuously along the forested range (the individualistic continuum concept, Gleason, 1917; Gleason, 1926). Therefore, even though co-occurrence patterns of species show that they respond in a similar way to landscape change, some still may show an individualistic behaviour, adjusting their optima or tolerance ranges to avoid niche overlap (Austin, 1999). This result suggests a dualistic nature of community assembly reflecting a balance between the individualistic behaviour of species and interspecific relations within ecological assemblages (see the ‘integrated community’ concept by Lortie *et al.*, 2004).

III.6.2. Management implications

It is increasingly common for managers and policy-makers to address ecologists and conservation researchers on preventive goals that guarantee sustainable exploitation levels (Villard and Jonsson, 2009). Our approach attempted to answer the questions: ‘what are the ranges of tree canopy cover most vulnerable to species loss?’ and ‘what ranges best fulfil the requirements for conservation purposes?’. Our study strongly suggests the existence of thresholds identifying changes in community composition and marking the limits of species occurrence where populations may be more sensitive to forest cover management. Ecological thresholds can, therefore, be used as indicators of specific resource limits responsible for those changes.

Our results also suggest that bird specialization occurs at different ranges of the gradient, highlighting the potential of variegated agro-ecosystems to hold high bird diversity. In such landscapes, defining a fixed tree cover management scheme across landscape will invariably result in winners and losers. Managing for a heterogeneous tree cover management scheme (with areas of very low tree cover intermixed with areas with higher tree cover) will result in higher species richness. Also, local management practices can focus on optimizing the potential of an area by adjusting to more effective conservation targets. For instance, species richness can be enhanced by maintaining a diverse variegated system averaging low forest cover density (≈10% tree canopy cover). Nonetheless, this may result in inadequate protection for the extreme range specialist species (Radford *et al.*, 2005). Therefore, to best preserve open grassland threatened species very sensitive to tree canopy cover (*e.g.*, *Tetrax tetrax*; BirdLife International, 2004) managers should aim at keeping a scarce tree cover (<1% cover). Low forest cover areas can promote a rich community of birds, but maintaining a tree canopy density between 1% and 25% will also help to safeguard the occurrence of species showing current population trends in moderate decline (*e.g.*, *Lanius senator*; EBCC, 2011).

As current management practices are driving Mediterranean agro-ecosystems to either management intensification or land abandonment (Pinto-Correia and Mascarenhas, 1999; Plieninger and Schaar, 2008), the characteristic savannah-type structure often associated with a tree cover gradient may be at risk as the extreme ranges of the open grassland-to-forest gradient are presently being favoured. This may result in deleterious effects on bird community, as many species find their optima between low to medium tree cover, which provide habitat conditions for nesting and/or foraging. Also, since both farmland and forest bird species show some tolerance to low tree canopy cover, functional connectivity of the landscape may be facilitated by its variegated structure or by the existence of small suitable areas that can be used as 'stepping stones' (Fischer and Lindenmayer, 2002; Saura *et al.*, 2014).

III.6.3. Caveats

In order to acknowledge the potential role of ecological thresholds as a conservation tool, managers must be informed on the limitations and potential pitfalls regarding their use. Ecological systems are complex, nonlinear, and strongly influenced by stochasticity, and almost any prediction or measurement will contain a given amount of uncertainty (Mangel *et al.*, 1996). Therefore, managing near thresholds will further increase the susceptibility of a community to breakdown and where extinction scenarios may be plausible (Betts *et al.*, 2007). Even small changes in resource-gradients can have a pronounced effect on local populations. Furthermore, time lag responses of species to local extinction are likely to occur, and presence alone does not infer a population's viability. Some information on productivity and/or long-term monitoring to assess population stability is needed.

In addition, the application of different data sources or procedures to extract tree cover gradients (*e.g.*, Godinho *et al.*, 2016) may result in small deviations from the ones obtained in this study. Moreover, it is expected that response curve behaviour and ecological thresholds should vary with the existence of additional interacting factors (Huggett, 2005). Multivariate environmental gradients could better capture landscape variability, accounting for both composition and configuration patterns (Betts *et al.*, 2006; Swift and Hannon, 2010; Herrera *et al.*, 2016). Yet, reading multivariate gradients may be highly subjective (see Guénette and Villard, 2005) and hamper the extraction of on-the-ground manageable practices.

Even though the outcomes provided by our study should be prudently considered in agro-ecosystem management and landscape planning, these limitations do not hinder the validity of our results. Our approach deals with uncertainty by acknowledging it in species responses along the gradient while accounting for imperfect detection. Model selection followed a simulation procedure that allowed for the estimation of the best-fitted model while considering ranges of variation in species response. This information can be applied to set preventive targets on exploitation practices to hold viable populations of species, richer communities and the provision of natural services.

III.7. ACKNOWLEDGMENTS

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Appendix III.A: Summary of point count data

Table III. A1 – Summary table of point count data. For each species are shown the values of total abundance across all point counts, range of species abundances and the number of locations where each species was recorded.

Scientific name	Common name	Total abundance	Range	Number of locations
Alectoris rufa	Red-legged partridge	17	[1; 3]	12
Carduelis cannabina	Common linnet	22	[1; 3]	14
Carduelis carduelis	European goldfinch	117	[1; 4]	67
Certhia brachydactyla	Short-toed treecreeper	160	[1; 4]	92
Chloris chloris	European greenfinch	41	[1; 3]	32
Cisticola juncidis	Zitting cisticola	63	[1; 3]	45
Columba palumbus	Common wood pigeon	14	[1; 2]	13
Coturnix coturnix	Common quail	56	[1; 3]	43
Cuculus canorus	Common cuckoo	38	[1; 3]	34
Cyanistes caeruleus	Blue tit	230	[1; 5]	122
Dendrocopos major	Great spotted woodpecker	12	[1; 2]	11
Emberiza calandra	Corn bunting	378	[1; 9]	122
Fringilla coelebs	Common chaffinch	312	[1; 7]	114
Galerida spp.	Crested and Thekla Larks	156	[1; 6]	82
Hippolais polyglota	Melodious warbler	16	[1; 2]	13
Lanius meridionalis	Southern grey shrike	22	[1; 2]	20
Lanius senator	Woodchat shrike	38	[1; 4]	31
Lophophanes cristatus	European crested tit	15	[1; 2]	14
Lullula arborea	Woodlark	110	[1; 3]	73
Luscinia megarhynchos	Common nightingale	58	[1; 3]	46
Parus major	Great tit	53	[1; 2]	46
Passer domesticus	House sparrow	49	[1; 13]	19
Passer hispaniolensis	Spanish sparrow	258	[1; 50]	27
Pica pica	Eurasian magpie	17	[1; 4]	11
Saxicola rubicola	Stonechat	49	[1; 3]	38
Serinus serinus	Serin	73	[1; 3]	50
Sitta europaea	Eurasian nuthatch	84	[1; 4]	55
Streptopelia decaocto	Eurasian collared dove	38	[1; 3]	35
Sturnus unicolor	Spotless starling	142	[1; 10]	66
Sylvia melanocephala	Sardinian warbler	77	[1; 3]	55
Tetrax tetrax	Little bustard	18	[1; 3]	11
Turdus merula	Blackbird	58	[1; 2]	50
Upupa epops	Hoopoe	61	[1; 2]	56

Appendix III.B: Multi-scale analysis

Multi-scale analysis

Initially we tested each species response taking into account different spatial scales of the explanatory variable (100m, 150m, 200m, 250m, 300m, 400m and 500m). This preliminary analysis arose from the need to select a cross-scale coherent response type for each species and define an optimal spatial scale. The species-specific model type was selected as the one exhibiting the lowest variation (ΔAICc) comparatively to best-fitted response with lowest AICc score across all spatial scales (Figure III.B1). Then, we selected the spatial scale that consistently showed the lowest AICc scores of the set of selected models (Figure III.B2, Table III.B1). The 200m spatial scale outperformed all the others (Figure III.B2), which seems to be in line with other studies that postulate a buffer interval between 125-250m as optimal scale for bird diversity indicators (Morelli *et al.*, 2013).

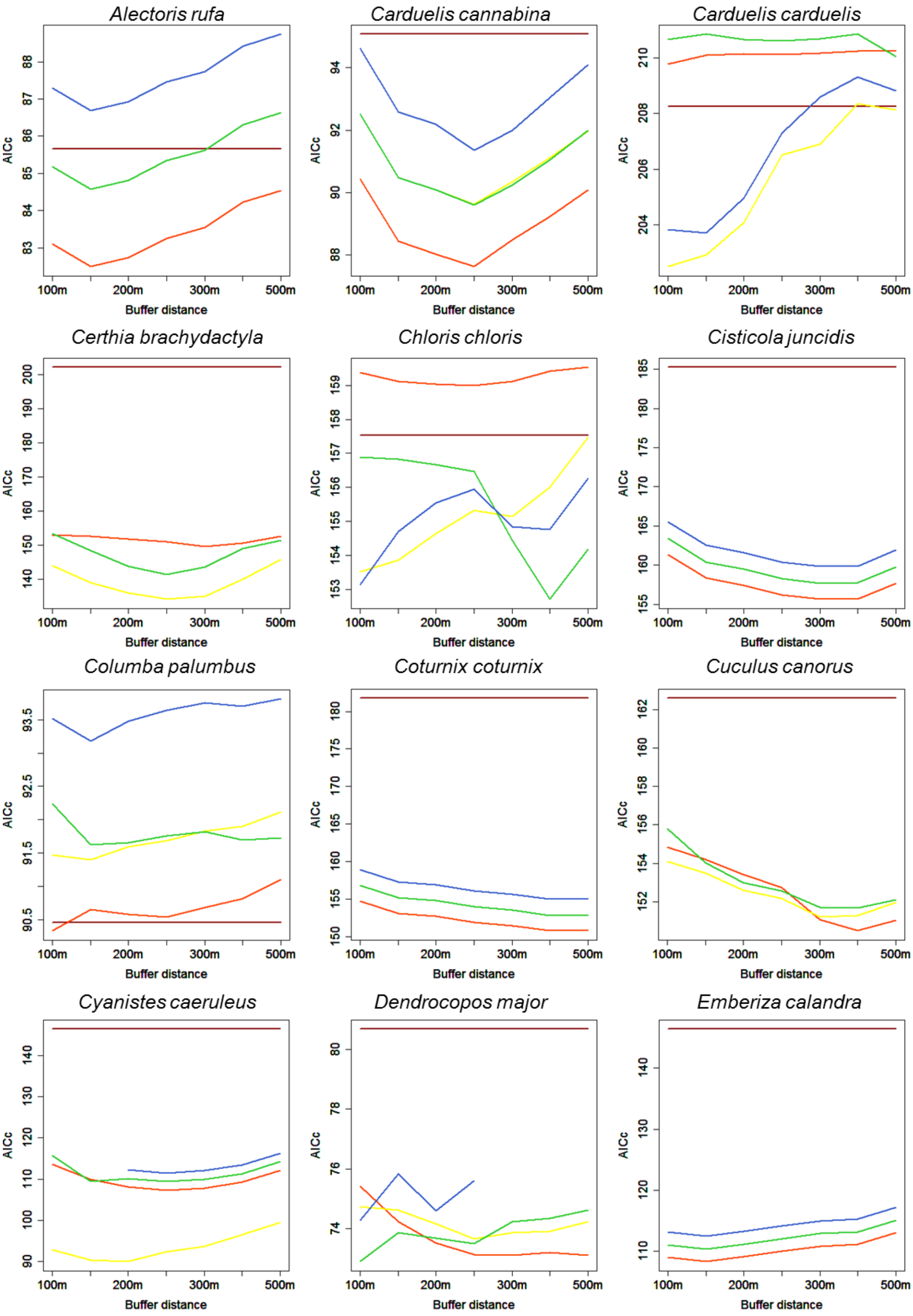

Figure III.B1 – AICc scores for each HOF model type (I – dark red; II – orange; III – yellow; IV – green; V – blue) considering the seven buffer distances used to test scale effects (100m; 150m; 200m; 250m; 300m; 400m; 500m).

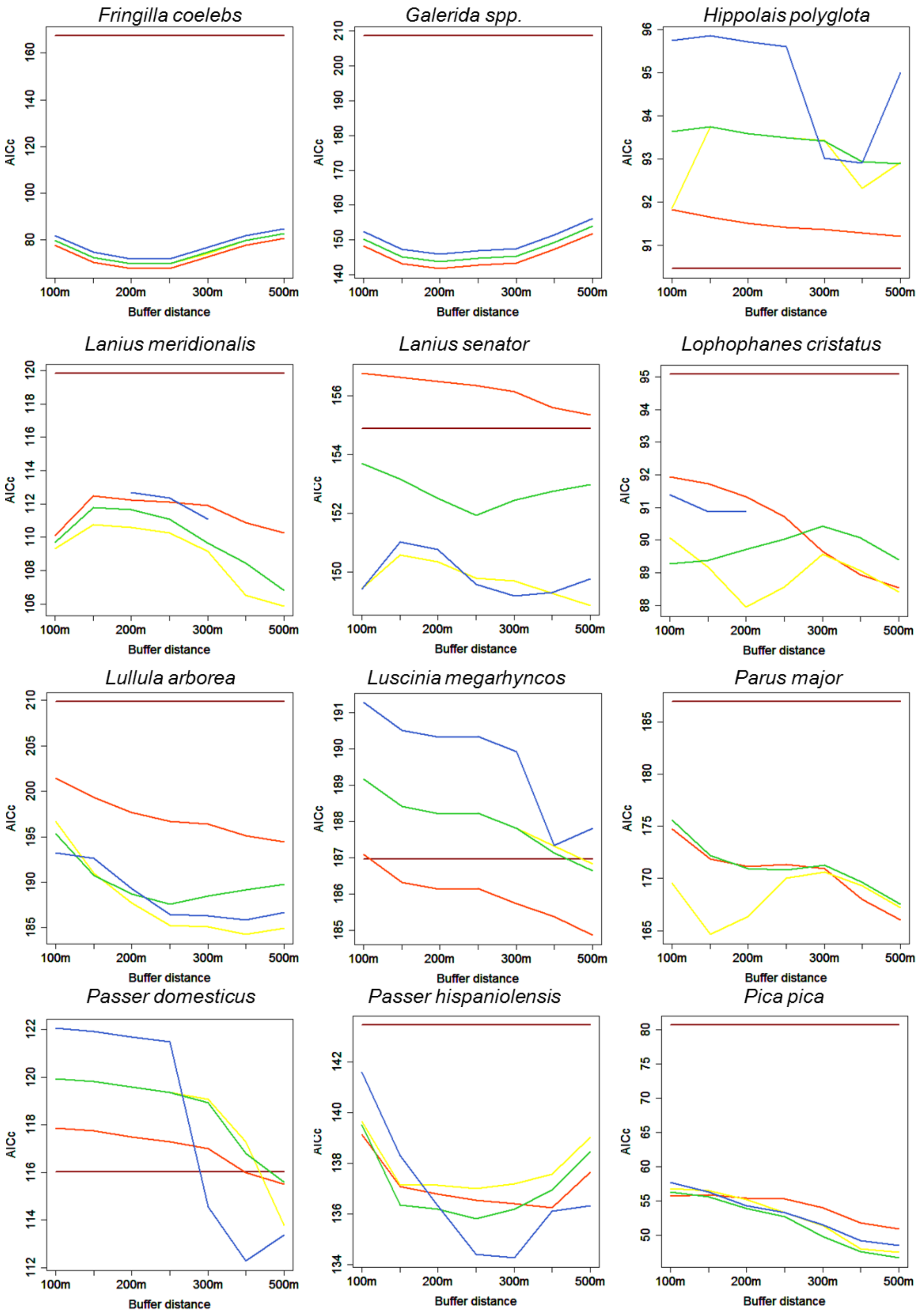

Figure III.B1 (cont.) – AICc scores for each HOF model type (I – dark red; II – orange; III – yellow; IV – green; V – blue) considering the seven buffer distances used to test scale effects (100m; 150m; 200m; 250m; 300m; 400m; 500m).

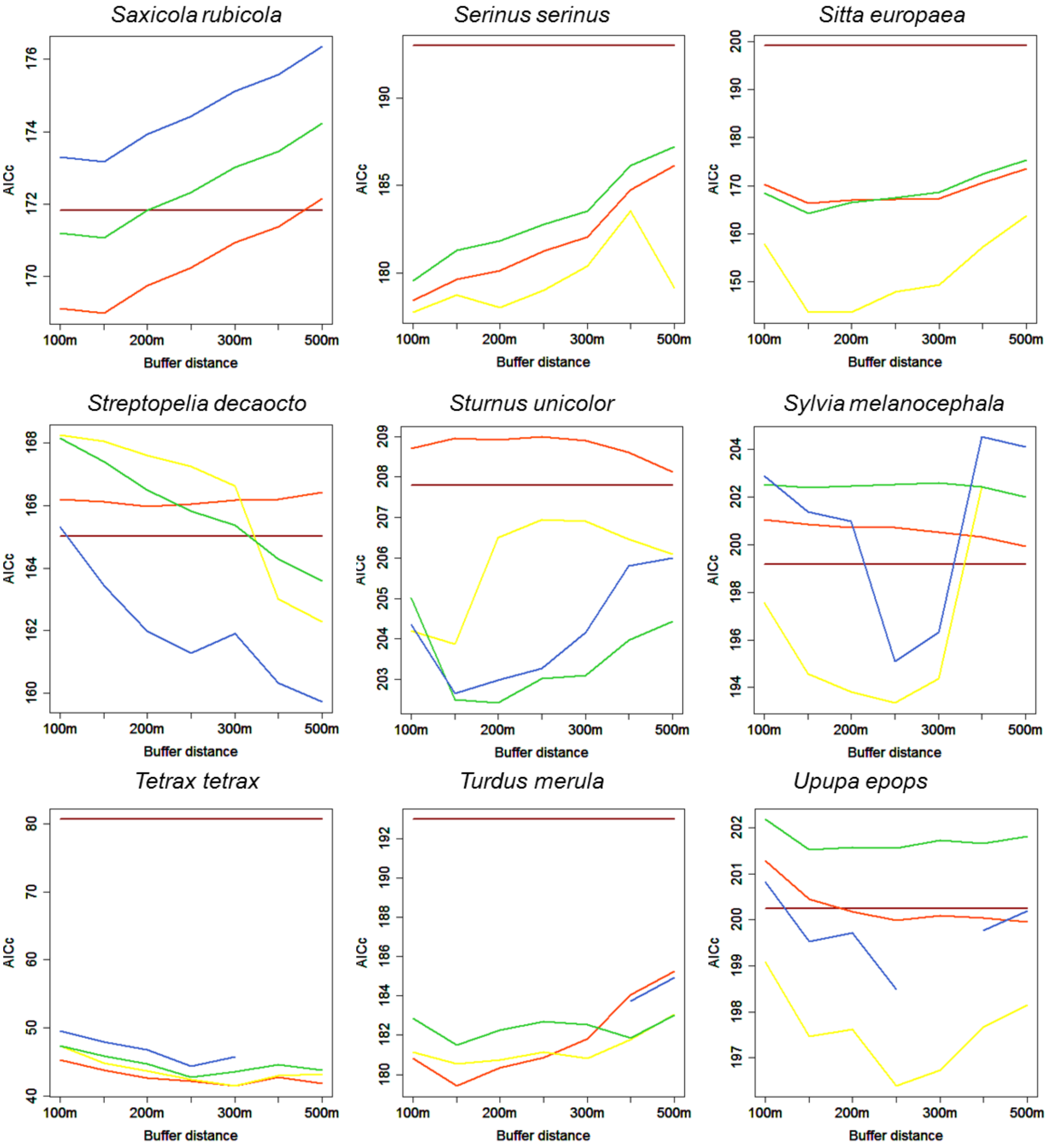

Figure III.B1 (cont.) – AICc scores for each HOF model type (I – dark red; II – orange; III – yellow; IV – green; V – blue) considering the seven buffer distances used to test scale effects (100m; 150m; 200m; 250m; 300m; 400m; 500m).

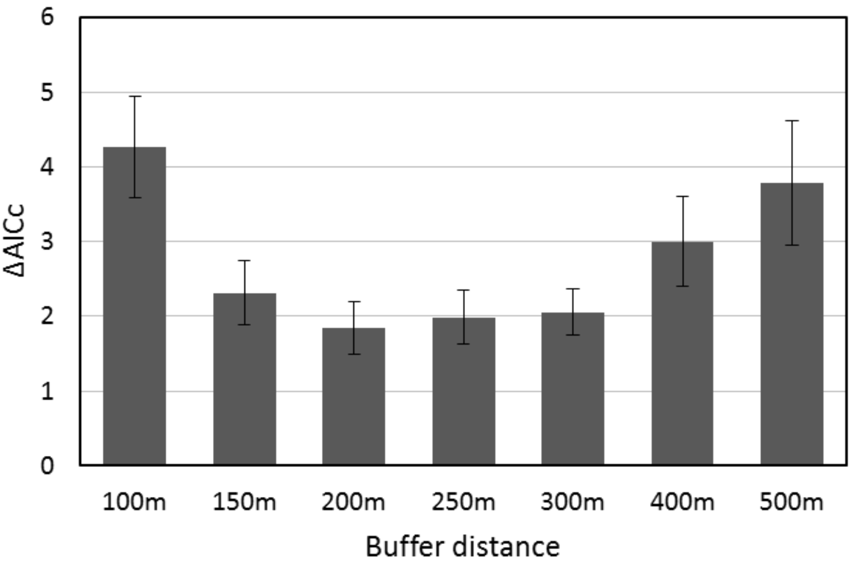

Figure III.B2 – Mean ΔAICc scores (and respective SE) between the different buffer distances tested. ΔAICc scores were calculated for all species considering its specific response (HOF model selection). The 200m buffer distance showed an overall lower AIC deviation.

Table III.B1 – AICc values of the selected HOF model obtain for the optimal buffer distance by species. ∆AICc marks the difference between the optimal buffer distance and the selected buffer distance in subsequent analyses (200m).

		Optimal buffer distance		200m Buffer distance	
Species	Model	Buffer distance	AICc	AICc	∆AICc
Alectoris rufa	II	150m	82.49	82.73	0.24
Carduelis cannabina	II	250m	87.62	88.03	0.41
Carduelis carduelis	V	150m	203.70	204.97	1.27
Certhia brachydactyla	III	250m	151.17	151.86	0.69
Chloris chloris	V	100m	153.14	155.54	2.40
Cisticola juncidis	II	300m	155.62	157.43	1.81
Columba palumbus	III	150m	91.40	91.60	0.20
Coturnix coturnix	II	400m	150.76	152.70	1.94
Cuculus canorus	III	300m	151.22	152.59	1.38
Cyanistes caeruleus	III	200m	89.92	89.92	0.00
Dendrocopos major	III	250m	73.65	74.16	0.51
Emberiza calandra	II	150m	108.22	109.02	0.80
Fringilla coelebs	III	250m	69.76	69.87	0.10
Galerida spp.	II	200m	141.67	141.67	0.00
Hippolais polyglota	II	500m	91.20	91.51	0.31
Lanius meridionalis	III	500m	105.84	110.58	4.74
Lanius senator	V	300m	149.17	150.77	1.60
Lophophanes cristatus	III	200m	87.94	87.94	0.00
Lullula arborea	III	400m	184.24	187.75	3.51
Luscinia megarhyncos	II	500m	184.85	186.13	1.28
Parus major	III	150m	164.61	166.35	1.74
Passer domesticus	V	400m	112.26	121.69	9.42
Passer hispaniolensis	III	250m	136.99	137.14	0.15
Pica pica	IV	500m	46.68	53.90	7.21
Saxicola rubicola	II	150m	168.97	169.74	0.77
Serinus serinus	III	100m	177.72	178.02	0.30
Sitta europaea	III	150m	143.54	143.67	0.13
Streptopelia decaocto	V	500m	159.71	161.98	2.27
Sturnus unicolor	IV	200m	202.41	202.41	0.00
Sylvia melanocephala	III	250m	193.34	193.82	0.47
Tetrax tetrax	II	300m	41.52	42.61	1.09
Turdus merula	III	150m	180.55	180.75	0.20
Upupa epops	III	250m	196.38	197.62	1.23

Appendix III.C: Species responses

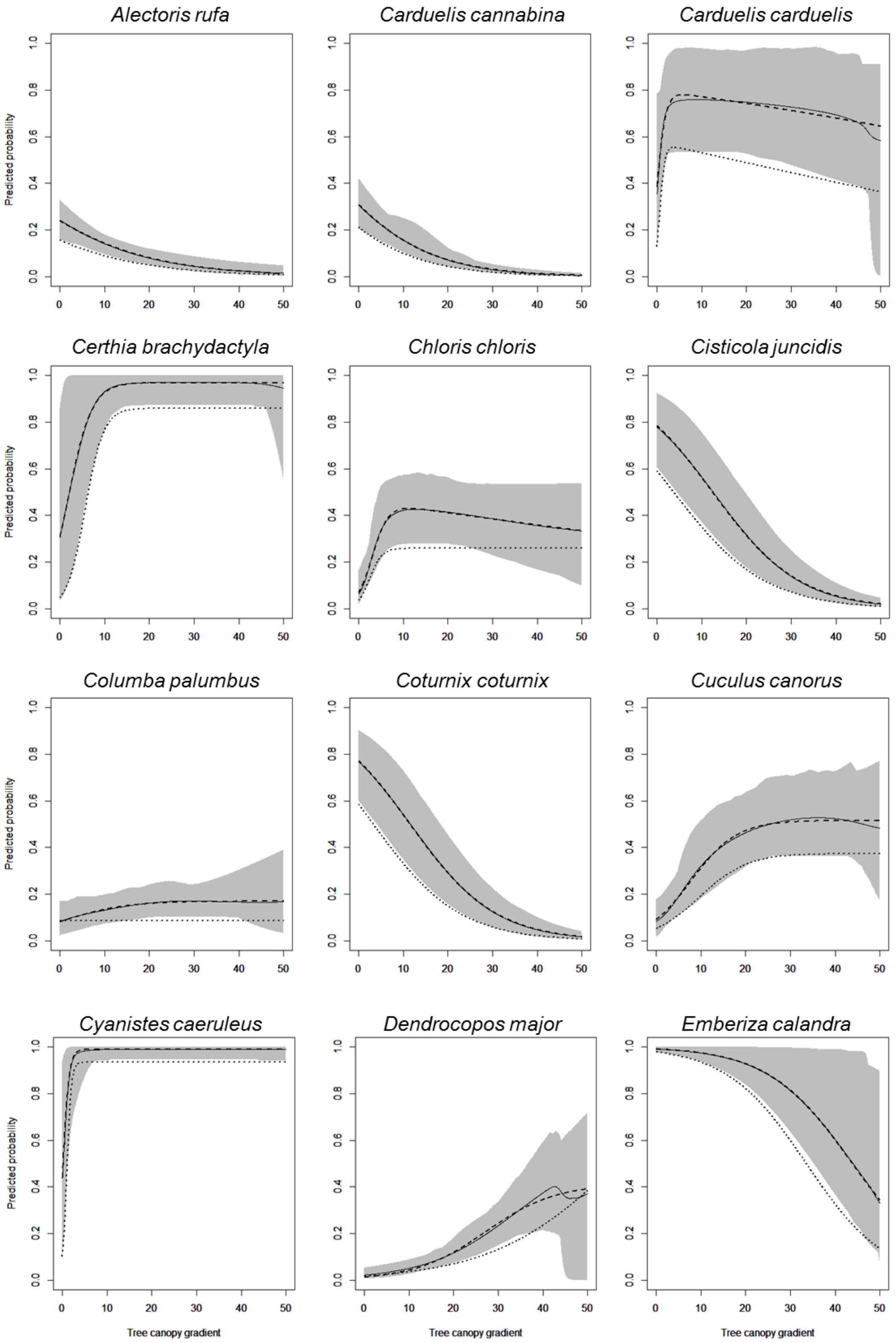

Figure III.C1 – Fitted HOF models to each species. Dotted line shows response curve using raw data. Grey area limits the 100 runs using the predicted probability of occupancy models to correct for putative false absences on bird data, and black line the mean curve response of all simulations. Dashed line marks the final HOF model fitted to the mean curve response of all simulations.

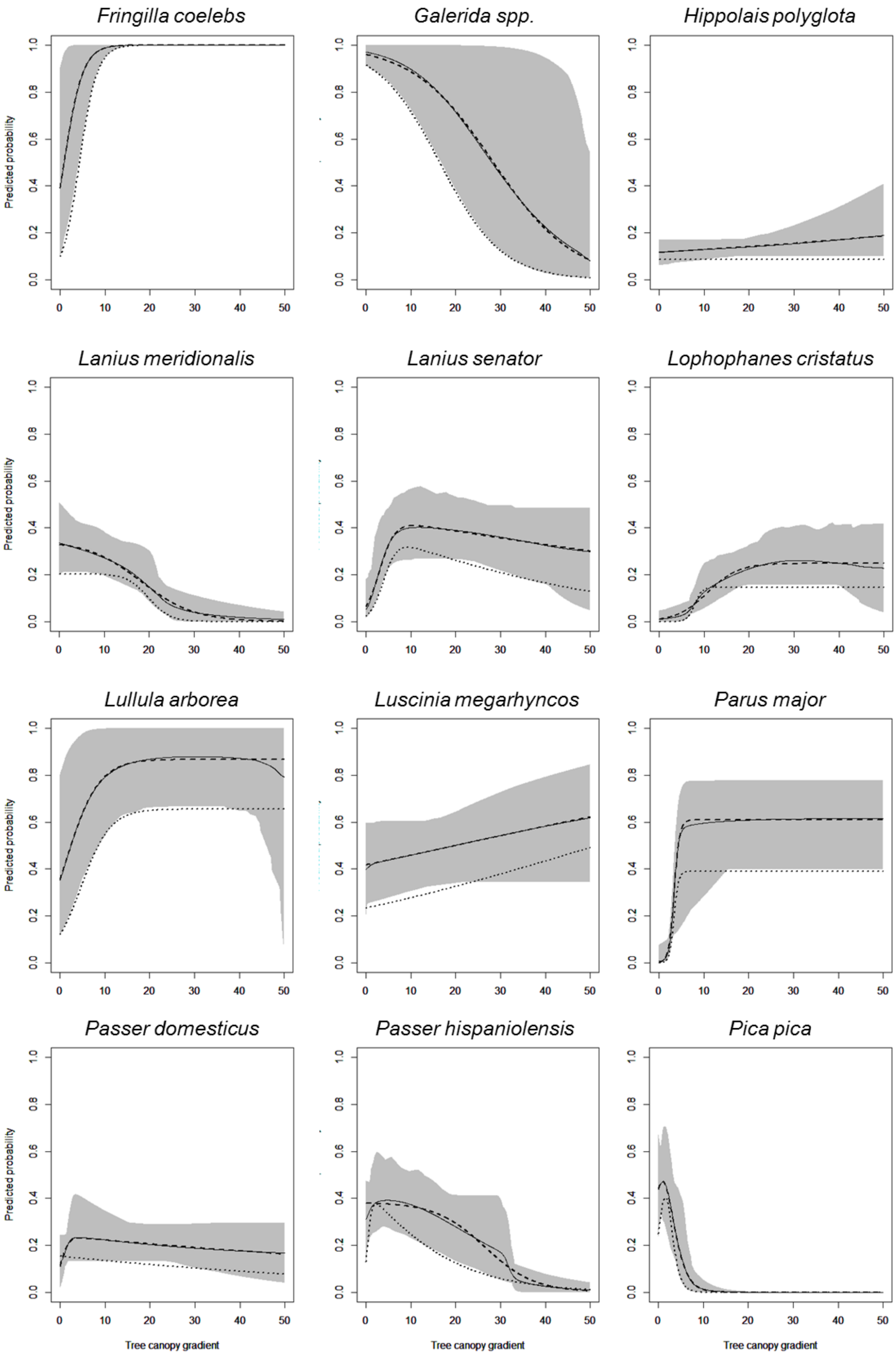

Figure III.C1 (cont.) – Fitted HOF models to each species. Dotted line shows response curve using raw data. Grey area limits the 100 runs using the predicted probability of occupancy models to correct for putative false absences on bird data, and black line the mean curve response of all simulations. Dashed line marks the final HOF model fitted to the mean curve response of all simulations.

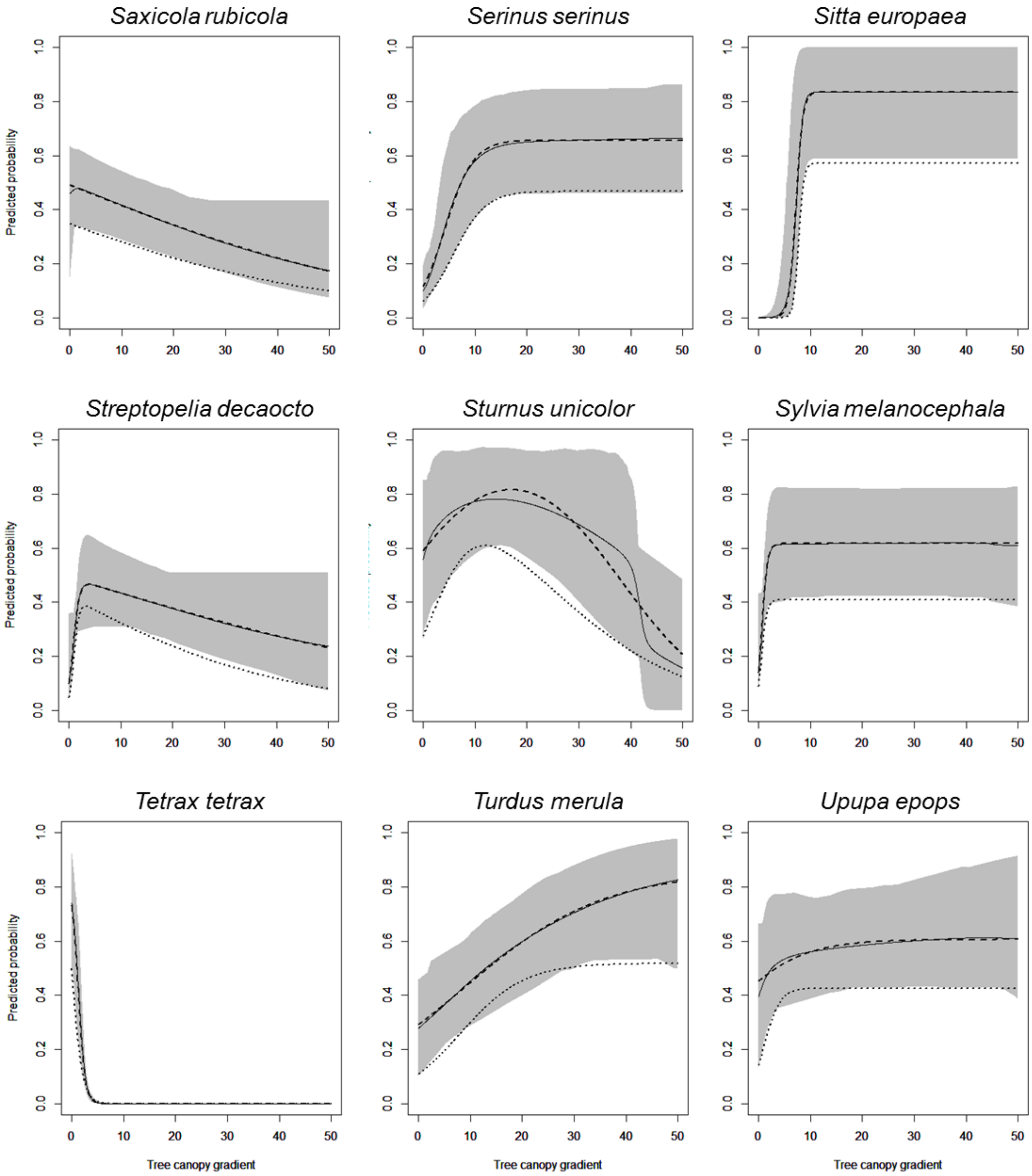

Figure III.C1 (cont.) – Fitted HOF models to each species. Dotted line shows response curve using raw data. Grey area limits the 100 runs using the predicted probability of occupancy models to correct for putative false absences on bird data, and black line the mean curve response of all simulations. Dashed line marks the final HOF model fitted to the mean curve response of all simulations.

Chapter IV

Multispecies landscape functional connectivity enhances local bird species' diversity in a highly fragmented landscape

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Pedro A. Salgueiro[1,2,5], Francesco Valerio[1,3,5], Carmo Silva[1,4,5], António Mira[1,4,5], João E. Rabaça[2,4,5], Sara M. Santos[1,4,5]

[1]UBC – Conservation Biology Lab;

[2]LabOr – Laboratory of Ornithology;

[3]CIBIO-UE – Research Center in Biodiversity and Genetic Resources, Pole of Évora – Research Group in Applied Ecology;

[4]MED — Mediterranean Institute for Agriculture, Environment and Development, Instituto de Investigação e Formação Avançada;

[5]Department of Biology, University of Évora. Mitra, 7002-554 – Évora, Portugal.

IV.1. ABSTRACT

Local species assemblages are likely the result of habitat and landscape filtering. However, there is still limited knowledge on how landscape functional connectivity complements habitat in mediating local species assemblages in real-world fragmented landscapes. In this study, we set up a non-manipulative experimental design in a standard production forest to demonstrate how functional connectivity determines the spatial distribution of a bird community. We test single- and multispecies spatially explicit, landscape functional connectivity models framed within the circuit theory, considering also patch attributes describing habitat amount and quality, to weight their effects on species occurrence and community assemblage. We found that single-species functional connectivity effects contributed positively for occurrence of each species. However, they rarely provided competing alternatives in predicting community parameters when compared to multispecies connectivity models. Incorporating multispecies connectivity showed more consistent effects for all community parameters than single species models, since the overlap between species' dispersal abilities in the landscape shows poor agreement. Habitat amount and quality, though less important, were also determinant in explaining community parameters while possibly relating to the provision of suitable nesting and foraging conditions. Both habitat and landscape filters concur to govern community assembly, though likely influencing different processes: while landscape connectivity determines which species can reach a patch, habitat quality determines which species settle in the patch. Our results also suggest that surrogating multispecies connectivity from single species has potential to source bias by assuming species perceive landscape and its barriers similarly. Inference on this issue must be gathered from as much species as possible.

IV.2. KEYWORDS

Community assemblage; Metacommunity; Production forests; Forest management; Habitat quality; Landscape filtering.

IV.3. INTRODUTION

The ongoing erosion of biological diversity in present landscapes is mostly driven by the loss and fragmentation of habitats (Haddad *et al.*, 2015). Consequently, natural or semi-natural habitats patches are increasingly scattered and isolated, with wildlife populations becoming weakly connected in the remnant suitable patches.

Landscape connectivity relates to both the capacity of the landscape to hold viable routes for dispersal through an inhospitable matrix (structural connectivity, Calabrese and Fagan, 2004), and the ability of a species to engage in such dispersal movements (functional connectivity, Tischendorf and Fahrig, 2000). Enhancing and restoring landscape connectivity (Taylor *et al.*, 1993) may facilitate dispersal movements (Haddad *et al.*, 2003), the colonization of newly available patches (Haddad *et al.*, 2015), and gene flow between populations (Whitlock *et al.*, 2000), thus preventing from local extinction (Gonzalez *et al.*, 1998; Bennett *et al.*, 2006; Staddon *et al.*, 2010). Yet, the assessment of functional connectivity remains challenging (Correa Ayram *et al.*, 2016). In particular, there is still limited insight on how landscape connectivity mediates local multispecies assemblages in highly fragmented landscapes (Ryberg and Fitzgerald, 2015; Fletcher *et al.*, 2016).

Identifying the mechanisms governing multi-species assemblages may allow ecologists to understand the spatial and temporal variation of the diversity and composition of local communities (Cornell and Harrison, 2014). These mechanisms may be dependent on a set of habitat filters that operate locally, determining the set of species likely to occur at a given patch. Regarding birds, these features are often related with vegetation structure (*e.g.*, Lindenmayer *et al.*, 2012; Martin and Proulx, 2015; Salgueiro *et al.*, 2018a), interspecific interactions (Klingbeil and Willig, 2016), or human disturbance (*e.g.*, herbicide use, Kroll *et al.*, 2017). However, landscape effects are expected to also play a relevant role in a context of high fragmentation or isolation (Fahrig, 2002). Because landscapes offer different permeability to different species, local assemblages in isolated patches should vary according to species dispersal ability (Liu *et al.*, 2018) and sensitivity to barriers (Breckheimer *et al.*, 2014). If patches are highly connected for most species, we should expect higher species richness or diversity, as most species are able to reach those patches. Otherwise, landscape will filter out species for which the unsuitable matrix restricts their movements, and the number of species will be a subset of the regional pool of species. Yet, disentangling the effects of landscape connectivity from other key factors for species occurrence (*e.g.*, habitat quality) is still lacking in literature (Fletcher *et al.*, 2016).

Some studies already examined how landscape connectivity influences local communities' diversity. Generally, they acknowledge a positive effect (Fletcher *et al.*, 2016), though others show equivocal influence when compared to other factors (*e.g.*, Ryberg and Fitzgerald, 2015; Lindenmayer *et al.*, 2020). Nonetheless, many studies on multispecies connectivity struggle with limitations and much of the evidence today is unclear (Frey-Ehrenbold *et al.*, 2013; Kang *et al.*, 2015), and mostly relying on indirect inference (Jønsson *et al.*, 2016). For instance, studies often approach landscape structural connectivity to measure how it shapes the spatial structure of metacommunities (*e.g.*, Velázquez *et al.*, 2019; Lindenmayer *et al.*, 2020). Since these approaches solely lie on the spatial arrangement of habitat elements, they often assume that different species have the same ability to move between patches of suitable habitat, which offers a simplified and sometimes unrealistic view of the effects of connectivity.

In this study, we set up a non-manipulative experimental design taking advantage of the patchiness of a landscape subjected to long-standing forestry activity. The main aim is to demonstrate how functional connectivity determines the spatial distribution of a bird community inhabiting a fragmented landscape. We focus on a single most scattered habitat and its distinctive bird community to test single- and multispecies connectivity models on species occurrence and community assemblage. By depicting habitat amount and quality from all patches and mapping landscape attributes, we compare habitat features and landscape filtering effects on local communities. We expect that functional connectivity will be able to define species-specific dispersal abilities, thus proving effective predictors of spatial distribution for species. We hypothesize that local community composition and diversity will hence respond to the cumulative ability of the species (multispecies connectivity) to reach a patch (landscape filtering hypothesis). We test this hypothesis by confronting models accounting for multispecies connectivity and models retaining only single-species connectivity or neglecting this component. Overall, we envision the effectiveness of multispecies connectivity over single-species approaches, as most species show different dispersal abilities or habitat requirements.

IV.4. METHODS

IV.4.1. Study area

The study was carried out in Centre-West Portugal (centroid: 39°38’N 9°02’W), covering an area of 11,121 ha (Figure IV.1). Landscape is dominated by standard production forest involving intensive forestry activities (*e.g.*, logging, plantation, thinning, understory management) of maritime pine (*Pinus pinaster*) and non-native plantations (*Eucalyptus* sp.). Each patch is managed under a rotational scheme of clear-cut patches where shrubs prevail (normally persisting for 5 years; ~11.1% cover), newly planted forests subjected to regular thinning (~18.0% cover), and old-growth forests (with stands reaching 50 to 80 years for pines – ~ 41.7% cover; and 9-10 years for eucalypts – ~7.6% cover). This resulted in a heterogeneous landscape mosaic of well-defined even-aged stands, which vary in composition, density, and age with neighbouring patches. Since forestry is the main activity dominating the landscape, open-shrub patches exhibit a scattered distribution embedded within the forest matrix (Figure IV.1), thus being highly susceptible to fragmentation and isolation effects. Furthermore, they sustain a specialized community of shrubland birds confined to such habitats, and may perceive forest as a barrier to dispersal due to visual obstruction (e.g., Prevedello et al., 2010).

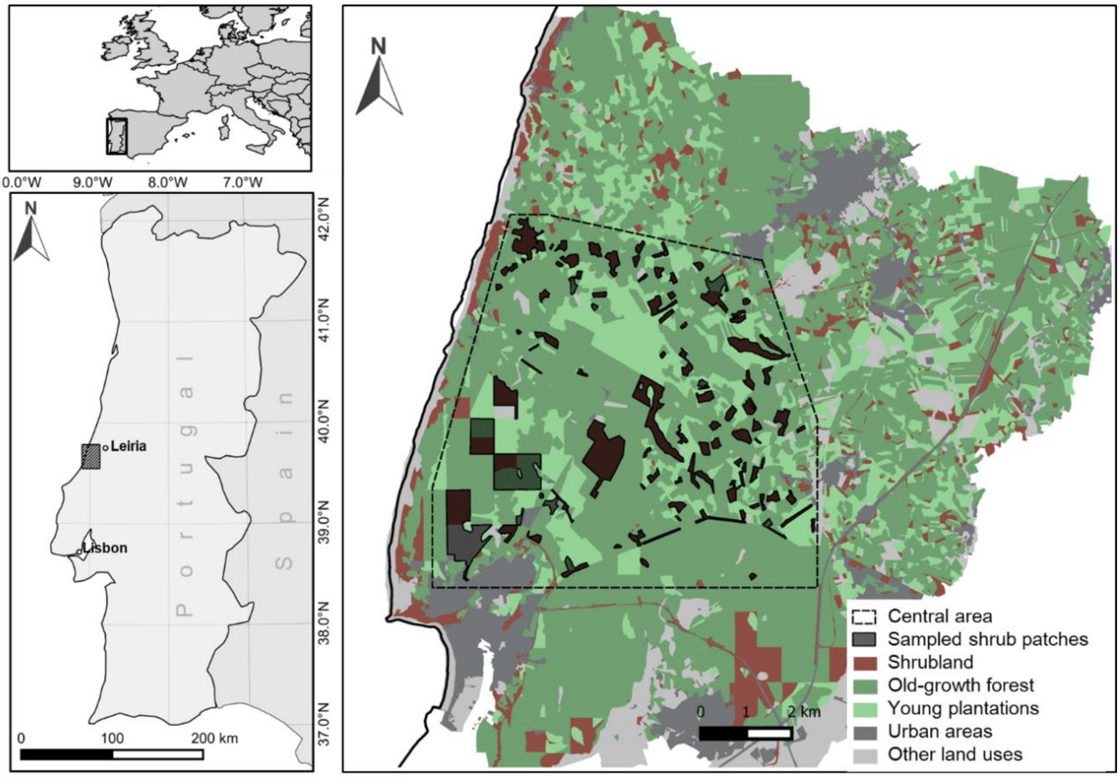

Figure IV.1 – Location and detailed land uses of the total and central study areas where open shrubland habitats are embedded in a forest dominated matrix.

IV.4.2. Focal species surveys

We focused our effort in sampling the shrubland bird community. Bird data was obtained through 10 min point counts (Bibby *et al.*, 2000) with a distance limit of 100 m. A total of 203 point counts were performed on the most representative land uses within the study area, 120 of which covered every open-shrub patch (minimum patch size: 0.226 ha) located at the centre of the study area (central area totalling 3,500 ha, Figure IV.1).

Sampling took place during the breeding season (between April and May 2014) when both resident and migratory species are more conspicuous. Surveys were carried out during the period of highest detectability (6:00–11:00 a.m., Palmeirim and Rabaça, 1994) and with favourable weather conditions (Bibby *et al.*, 2000). All bird species seen or heard were recorded, but fly-over individuals were not included in the analysis.

In order to enhance the statistical power and representativeness of the study area, we chose to visit each point once, investing on a larger number of sampled sites at the expense of a higher survey effort per site (*e.g.*, Loos *et al.*, 2015). To avoid bias from false absences, we calculated the detectability by means of single visit occupancy models

(Lele *et al.*, 2012) using the package “detect” (Solymos *et al.*, 2016) (see details in Appendix IV.A). After this procedure, we retained four bird species for subsequent analyses showing high detectability and representativeness in the study area: Linnet (*Linaria cannabina*), Stonechat (*Saxicola rubicola*), Dartford Warbler (*Sylvia undata*) and Wren (*Troglodytes troglodytes*).

IV.4.3. Environmental variables

We used two types of environmental variables: a set of spatially explicit landscape variables, and another set of local vegetation structure and composition to assess habitat quality (see Appendix IV.B for a detailed description).

Landscape variables relate to topographic characteristics acquired from GIS software (version 2.2., Quantum GIS Development Team 2013). A patch-based conceptualization was used since it provides a suitable and informative description of landscape attributes (Salgueiro *et al.*, 2018b). We produced a thorough land use map (minimum patch size: 100 m^2) using Bing Maps aerial photography (year: 2014; resolution: 30 cm) with field ground validation.

We extracted variables describing both landscape composition and configuration. Compositional parameters regarded the proportions of the main land uses (open shrubland, old-growth pine forest, non-native forest, and young plantations) and Euclidean distances to other land uses (urban areas) or roads. Configuration patterns were determined by calculating the Shannon’s landscape diversity index, number of patches and edge length (considering different edge contrast between the vertical structures of the vegetation of adjacent patches; Ries *et al.*, 2004). Each candidate variable (except for distances) was measured in two buffer widths from the point count (100 m and 250 m) to consider different spatial scales to which species may respond (Morelli *et al.*, 2013).

We described habitat quality as the characteristics of the patch (habitat amount) and vegetation that relate with the provision of appropriate environmental conditions for the species at each site (*sensu* Mortelliti *et al.*, 2010a) regarding the adequacy for nesting and foraging purposes. Density (cover) and structure (height and variation of height) of vegetation layers (shrubs and trees) were sampled from field measurements. Additionally, we identified shrub and tree species occurring at each site, thus providing information on the composition of vegetation. We applied a hierarchical clustering technique weighing trait similarity among plant species using package “vegan” (Oksanen *et al.*, 2017) to reduce the amount of plant species with similar traits into groups providing similar ecological functions to birds (Söderström *et al.*, 2001). We estimated vegetation density by pooling together all species belonging to the same group, the most relevant being: Trees, Calluna-Erica heath shrublands, Thick thorny shrubs, Sand dunes shrubs.

IV.4.4. Functional connectivity modelling

IV.4.4.1. Species distribution models

We built spatially explicit, functional connectivity models for each species based on circuit theory (McRae *et al.*, 2008). We relied on species distribution models (SDM) to infer landscape permeability. This approach has been proved to perform well as a cost-effective method to build functional connectivity models when data on movement or dispersal ability is lacking (Keeley *et al.*, 2016; Ahmadi *et al.*, 2017; Valerio *et al.*, 2019).

For SDM, we modelled the occurrence (presence/absence) of each of the four focal species in response to the set of spatially explicit landscape variables (GLM with binomial error distribution, logistic link function). All variables were standardized (mean of 0 and standard deviation of 1) in order to reduce the order of magnitude between them and have comparable regression coefficients. Each variable fit was initially screened individually (univariated models) while considering the linear and quadratic predictor for each of the two buffer distances. We also evaluated interactions between shrub understory height and main land uses, since we expected that responses would change according to understory’s vertical structure. Modelling selection was based upon a stepwise approach where the most parsimonious model (lowest AICc) was selected. The model ran on a training subset of data (66%) and was tested on the remaining subset. The area under the curve (AUC) was calculated in the testing subset for model validation. We repeated this procedure 100 times and averaged the results (coefficients) of all models. All four species showed a close relation to shrubland habitats, as we found positive responses of the species to either shrub cover or height (see Appendix IV.D). The spatially explicit SDM (10 m resolution) was then developed by fitting the averaged predicted values for the entire landscape.

All models revealed a reasonably high ability to predict species occurrence (AUC_{Linnet} = 0.86 ± 0.06; $AUC_{Stonechat}$ = 0.84± 0.05; $AUC_{DWarbler}$ = 0.82 ± 0.04; AUC_{Wren} = 0.74 ± 0.04), thus indicating that selected variables were good predictors in describing potential suitable areas for each species.

IV.4.4.2. Landscape resistance estimation

Landscape resistance (the degree to which a landscape restricts movements) was computed as an inverse linear function of the SDM. However, since such approaches are generally too conservative and species tend to be less demanding when dispersing, we additionally considered two negative exponential functions to transform SDM into a resistance matrix, following Trainor *et al.* (2013):

$$R = 100 - 99 * \frac{1 - e^{-c*H}}{1 - e^{-c}}$$

The resistance (R) is an exponential transformation of the predicted probability of occurrence from the SDM (H) determined by a factor (*c*) which defines the non-linearity of the relation between resistance and habitat suitability. As c increases, the steepness of the curve increases, meaning that resistance is low at lower suitability values. We generated three resistance surfaces for each species using three transformation values: *c*=0.25 for a linear inverse proportion, *c*=2 for a slight non-linear relation, and *c*=8 for a steeper non-linear relation (*e.g.*, Valerio *et al.*, 2019).

IV.4.4.3. Modelling procedure

We created dispersal models based on circuit theory, which represents animal movement in the form of an electrical network (McRae *et al.*, 2008) by simulating multiple pathways for movement between nodes over a resistance surface.

For connectivity modelling purposes, we defined the nodes independently from our samples by depicting the patches from the SDM with higher probability of occurrence. This avoided high estimates of current density around point samples, which could bias our results. We initially determined the cut-off point by looking for the threshold that maximized the percentage of correct classifications (presence/absence) (Manel *et al.*, 2001; Liu *et al.*, 2005). We then extracted the core areas – high quality habitat patches, excluding patches greatly subjected to edge effects due to their shape (*e.g.*, elongated patches; Lindenmayer, 1994). We followed Puddu and Maiorano (2016) on these calculations by operating a Morphological Spatial Pattern Analysis on the cut-off map in the Guidos software (Vogt, 2016). The resulting habitat patches were transformed into centroids while retaining the patch size attribute. Minimum patch size was set as the minimum area needed to hold a bird's territory (see Appendix IV.C).

Before connectivity modelling, we filtered the number of possible node interactions to reduce overestimation of connectivity by neglecting unlikely links. We inferred functional distances constrained by each of the resistance matrices using package "gdistance" (van Etten, 2017) and used them to calculate the probability of connectivity (PC, Saura and Pascual-Hortal, 2007) between all pairs of nodes using the 'distance' parametrization in the Conefor software (version 2.2, Saura and Torné, 2009). Node location weighed by its size, and median distance of dispersal of each bird species (Appendix IV.C) were used as set-ups for the calculation of PC. All pairwise nodes showing PC ≥ 0.5 were considered connected, *i.e.*, we assumed that a node was reachable from its pair. All remaining links (PC < 0.5) were discarded from further analysis.

Finally, to map species-specific functional connectivity we used the Gflow software (version 0.1.7, Leonard *et al.*, 2017). Current was set to flow between each pair of connected nodes while weighing the conductance (the inverse of resistance matrices). After the combinations of likely connected nodes were calculated, current density was summed into a single cumulative map representing the probability of successful dispersal of an organism (McRae *et al.*, 2008, Koen *et al.*, 2014). This procedure was performed for each of the four focal species times the three resistance matrices (exponential functions), leading to a total of 12 functional connectivity models.

IV.4.5. Data analysis

Firstly, we compared the effectiveness of the three functional connectivity scenarios for each species in explaining their distribution. At this stage, we focused on bird abundance data gathered from open-shrub patches within the central area (Figure IV.1). By considering a smaller central area within the modelling range, we avoided several misconceptions of landscape connectivity occurring at the limits of study areas (Koen *et al.*, 2010; Liu *et al.*, 2018).

We performed GLMs (Poisson error distribution, log link function) to determine the effects of each functional connectivity scenario on bird abundance in comparison with habitat quality descriptors. Four models were obtained for each of the four focal species, one just composed of habitat quality descriptors, and three others additionally holding a functional connectivity scenario for each considered *c*. For each species we compared AIC, explained deviance and r-squared values to assess the fit of the models and determine which scenario improved the model ability to predict bird abundance. Additionally, we calculated the relative importance of each variable through a model averaging approach (Burnham and Anderson, 2002).

Afterwards, we determined if connectivity would influence shrubland bird community-level parameters by testing its effects on species richness, overall abundance, dominance of the 1st ranked species, and Simpson's diversity. The effectiveness of single- and multispecies connectivity models was tested for each case using GLM (Poisson error distribution for the first two, and Gaussian for both the later). Single-species connectivity models consisted on the best resistance scenarios selected from the previous species-specific analyses. Multispecies connectivity model was defined as the joint cost of shrubland bird species to cross a cell, obtained by averaging the values of the best single-species connectivity scenarios (the values were normalized to confer the same weight regardless of the species). We also tested the influence of the coefficient of variation between all four connectivity models to check the effects of uneven values on community parameters. Lower values indicate that all four species perceived a given cell with the same cost; otherwise, the cells offered different resistance. We used the same modelling procedure and analysed the same parameters as for single species models.

We further examined species spatial overlap to ascertain if species showed similar dispersal abilities. For two species sharing similar dispersal abilities, a higher probability of having overlaid conductance paths is expected, and thus a higher proportion of spatial overlap. We measured spatial overlap firstly by calculating the correlation between pairs of the single-species functional connectivity model (our proxy for dispersal ability, Jacobson and Peres-Neto, 2010) using Pearson correlation coefficients. Secondly, we determined the spatial overlap by calculating the proportion of area (cells) shared by two species in relation to the total amount of area covered by both species, above a given conductance threshold. We have only considered cells above the normalized 0.5 value for the multispecies functional connectivity model. We compared the observed spatial overlap coefficient for each pair of species with a set of 100 random permutations of the data, ranging the conductance threshold between 0.2 and 1 (the lower and higher species-specific normalized values of conductance for all species). If two species agree on the same locations for dispersal at a given threshold, then the observed spatial overlap will be above the expected random simulations, and species show synergistic relation (Breckheimer *et al.*, 2014). Otherwise, species may show conflicting dispersal ability, *i.e.*, the dispersal routes for one species do not fit the other and observed overlap will be below the expected. If spatial overlap is the same as random, then both species show an independent relation.

All modelling procedures were performed in R (version 3.0.2., R Development Core Team, 2013).

IV.5. RESULTS

IV.5.1. Connectivity effects on single-species distribution

In almost every model, the inclusion of functional connectivity improved its ability to predict the occurrence of each of the four shrubland bird species, regardless of the exponential function used to describe it (Table IV.1). Nevertheless, the magnitude of exponential transformation weighed differently for some species. For Stonechat and Wren, functional connectivity based on a resistance matrix with a linear inverse proportion ($c = 0.25$) provided the best-fitted results, while for Linnet and Dartford Warbler, a slight non-linear relation ($c = 2$) offered a better outcome. Steeper non-linear relations ($c = 8$) consistently provided lower fit and less parsimonious models with ΔAIC > 4 for all species. Among the most conservative approaches (c = 0.25 and c = 2) only minor differences were detected (ΔAIC < 2 for all species), either providing good alternatives as the best model.

Table IV.1 – Parameter estimates used to evaluate the fit of species abundance models (Akaike's information criterion – AIC, and respective variation – ΔAIC; proportion of explained deviance – ExpDev; and r-squared value – Rsq). Values in bold signal the best model.

Model parameters	Habitat	Habitat + FCM (c=0.25)	Habitat + FCM (c=2)	Habitat + FCM (c=8)
Linnet				
AIC	175.130	157.84	**157.560**	166.38
ΔAIC	17.570	0.280	**0.000**	8.820
ExpDev	0.159	0.310	**0.312**	0.243
Rsq	0.101	0.300	**0.306**	0.157
Stonechat				
AIC	170.350	**155.460**	155.560	156.650
ΔAIC	14.890	**0.000**	0.100	1.190
ExpDev	0.230	**0.370**	0.370	0.370
Rsq	0.188	**0.296**	0.279	0.255
Dartford Warbler				
AIC	234.61	229.99	**228.81**	233.2
ΔAIC	5.800	1.180	**0.000**	4.390
ExpDev	0.379	0.432	**0.442**	0.406
Rsq	0.382	0.462	**0.475**	0.413
Wren				
AIC	258.090	**250.750**	251.400	258.41
ΔAIC	7.340	**0.000**	0.650	7.660
ExpDev	0.115	**0.200**	0.194	0.130
Rsq	0.151	**0.256**	0.238	0.162

Bird species response to functional connectivity (FCM) was unequivocally positive in all cases (Figure IV.2). In fact, this was the only variable present at all single species models, while revealing high relative importance as well (mean RVI = 0.99, see Appendix IV.E for detailed results on model estimates).

Other variables included in the models regarded specific requirements of the species. The amount of habitat (PatchArea) was not relevant for Wren only, while all other species benefited from increasing patch size. Regarding habitat quality, Stonechat occurred in patches with lower shrub height or even in areas with tall shrubs if alternatively shrub height was heterogeneous (interaction between ShrbHeight and ShrbHeightCV). Dartford Warbler, however, was more abundant in patches with homogeneous shrub height. Shrub cover (either as a single factor or in interaction) showed a positive, but equivocal, relation to Dartford Warbler and Wren abundances. Linnet did not show any particular relation to the structure of the shrub layer, being related mostly to its composition. Shrub patches dominated by Calluna/Erica

(HeathShrb) and species typical dune vegetation (DuneShrb) tended to have negative effects on Linnet abundance. Nevertheless, this species was positively favoured when thick, thorny shrubs prevailed (ThornyShrb, namely *Genista*, *Stauracanthus*, and *Ulex* species). In fact, the positive effects of this group of plants extended to other species such as the Wren and Dartford Warbler.

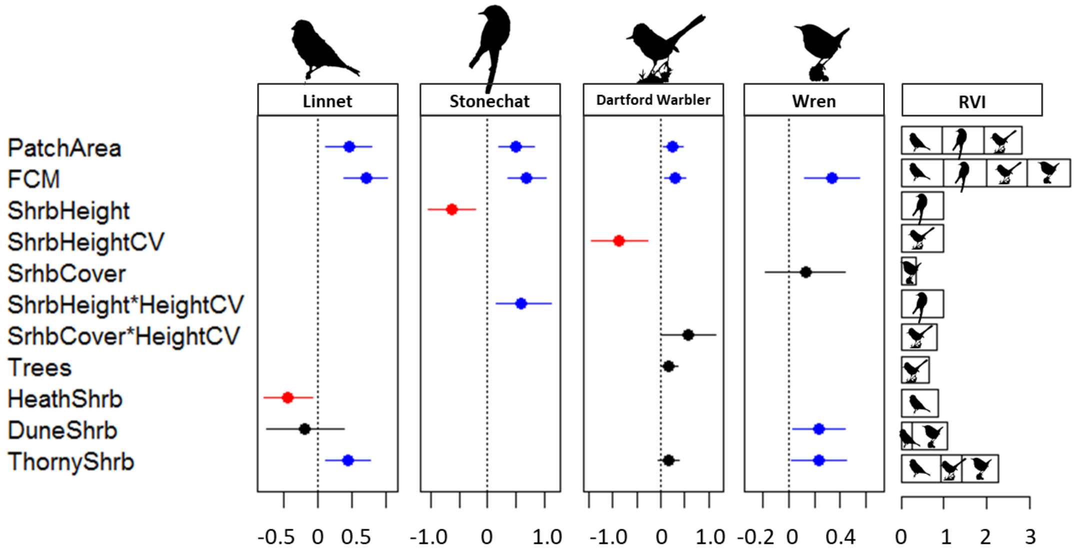

Figure IV.2 – Regression coefficients (dots) and respective confidence interval at 95% (horizontal lines) for the best fit model (considering the best functional connectivity model for each case). Unequivocal responses (whenever the confidence interval does not cross the zero limit) are shown in blue for positive relations, and in red for negative. Otherwise, equivocal responses are drawn in black. The plot on the right shows the cumulative stacking of the relative importance (RVI) of each variable for each of the species.

IV.5.2. Connectivity effects on community assemblages

Adding multispecies functional connectivity to habitat-only models improved the ability to predict total abundance, species richness, 1st rank dominance and Simpson's diversity values (Table IV.2). Single-species functional connectivity rarely provided competing alternatives to the multispecies approach, as single models consistently produced higher AIC values (ΔAIC > 4 in most cases) and lower fit. Stonechat and Linnet showed the best results among single-species functional connectivity, even though its influence was not consistent for all parameters: while Stonechat functional connectivity could compete as an alternative for multispecies connectivity model for total abundance, Linnet outperforms in all other parameters. Both Dartford Warbler and Wren functional connectivity were poor predictors, lowering the fit of the model, in some cases to similar levels as the habitat-only model.

Table IV.2 – Estimated values for each of the parameters used to determine the fit of the model to community's parameters (Akaike's information criterion – AIC, and respective variation – ΔAIC; proportion of explained deviance – ExpDev; and r-squared value – Rsq). Values in bold signal the best model.

Model Parameters	Habitat	Habitat + FCM_{Linnet}	Habitat + $FCM_{Stonechat}$	Habitat + $FCM_{D.Warbler}$	Habitat + FCM_{Wren}	Habitat + $FCM_{Multispecies}$
Total abundance						
AIC	419.70	408.65	406.82	413.12	420.78	**403.88**
ΔAIC	15.82	4.77	2.94	9.24	16.90	**0.00**
ExpDev	0.209	0.308	0.321	0.274	0.216	**0.359**
Rsq	0.203	0.308	0.317	0.274	0.206	**0.360**
Species richness						
AIC	342.72	335.76	337.21	338.58	344.23	**333.34**
ΔAIC	9.38	2.42	3.87	5.24	10.89	**0.00**
ExpDev	0.153	0.293	0.270	0.249	0.161	**0.331**
Rsq	0.154	0.305	0.272	0.253	0.157	**0.339**
1st rank dominance						
AIC	16.64	8.72	10.42	15.17	13.68	**5.53**
ΔAIC	11.11	3.19	4.89	9.64	8.16	**0.00**
ExpDev	0.102	0.183	0.169	0.131	0.144	**0.207**
Rsq	0.102	0.183	0.169	0.131	0.144	**0.207**
Simpson's diversity						
AIC	32.91	26.83	27.20	31.86	30.64	**23.33**
ΔAIC	9.59	3.51	3.88	8.53	7.31	**0.00**
ExpDev	0.148	0.210	0.207	0.172	0.181	**0.235**
Rsq	0.148	0.210	0.207	0.172	0.181	**0.235**

Multispecies functional connectivity (FCM) showed consistent results for all parameters, exhibiting unequivocal positive effects on total abundance, species richness and Simpson's diversity (Figure IV.3). Concurrently, it also revealed a negative effect on 1st rank dominance. The coefficient of variation of the single-species functional connectivity models (FCM_cv) signalling the discrepancy of conductance between species, was only selected in the total abundance model, but with an equivocal meaning and a poor predictive power. The abundance of dune (DuneShrb) and thorny shrubs (ThornyShrb) were also consistent between parameters, revealing the same trends as functional connectivity. However, functional connectivity singled out as the most important variable (RVI = 1.00 in all parameters, Appendix IV.F) while dune shrubs exhibited lower importance (RVI ranged between 0.73 and 0.85) and thorny shrubs showed less consistent values (RVI = [0.87, 1.00]). The amount of habitat (PatchArea) was also an important feature (RVI = [0.46, 1.00]) explaining community parameters, though it showed inconsistency for species richness.

All other variables related to shrub structure (height, heterogeneity and cover) and composition (abundance of trees and Calluna/Erica heath species) showed equivocal (near-zero) effects. Accordingly, their relative importance for the models was modest, overall ranging between 0.24 and 0.46.

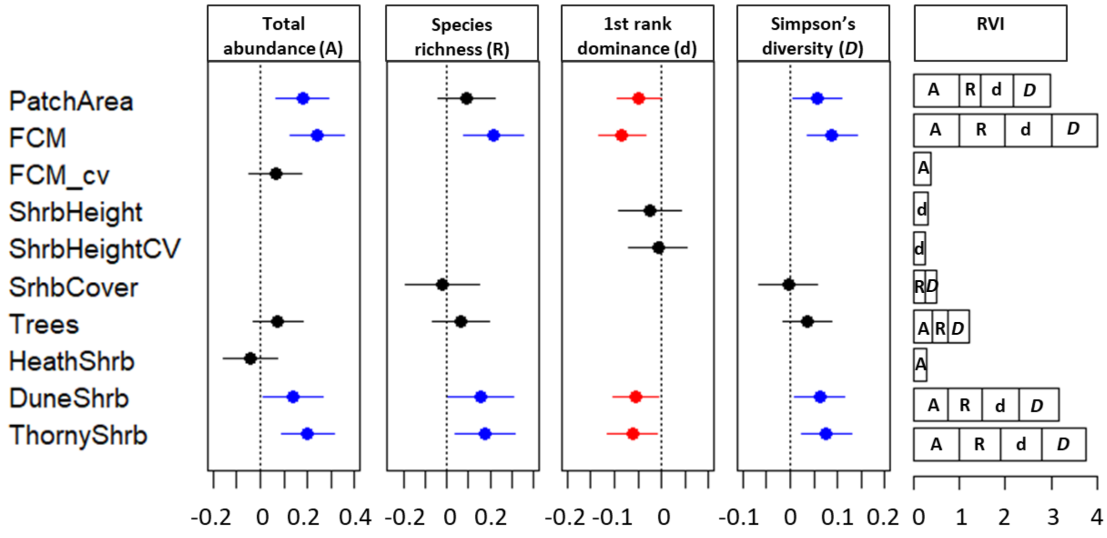

Figure IV.3 – Regression coefficients (dots) and respective confidence interval at 95% (horizontal lines) for the best-fit model (considering the multispecies connectivity model for each case) for community parameters. Unequivocal responses (whenever the confidence interval does not cross the zero limit) are shown in blue for positive relations, and in red for negative. Otherwise, equivocal responses are drawn in black. The plot on the right shows the cumulative stacking of the relative importance (RVI) of each variable for each community parameter.

IV.5.3. Species spatial overlap

While comparing dispersal abilities between pairs of species (Figure IV.4), we found that results varied between moderate ($r_s = 0.62$ between Linnet and Stonechat; and rs = 0.60 between Dartford Warbler and Wren) and weak correlations (rs = 0.24 and 0.34 between Wren and both Linnet and Stonechat, respectively). The proportion of spatial overlap also showed poor agreement between dispersal abilities of the species in some cases (Figure IV.4). Wren, for instance, differs from Linnet and Stonechat dispersal abilities, since the observed agreement between their conductances is lower than expected. Dispersal abilities of these species were, therefore, conflicting. Dartford Warbler observed proportion of spatial overlap did not differ greatly from randomized simulations. Yet, Linnet and Stonechat agreed between them, so there is a high chance that cells with high conductance may serve both species. In fact, both species dispersal ability overlap in 50% when considering a threshold of conductance = 0.50. At the same threshold, these species overlapped ca. 40% with Dartford Warbler’s dispersal ability and a modest 20-30% with Wren.

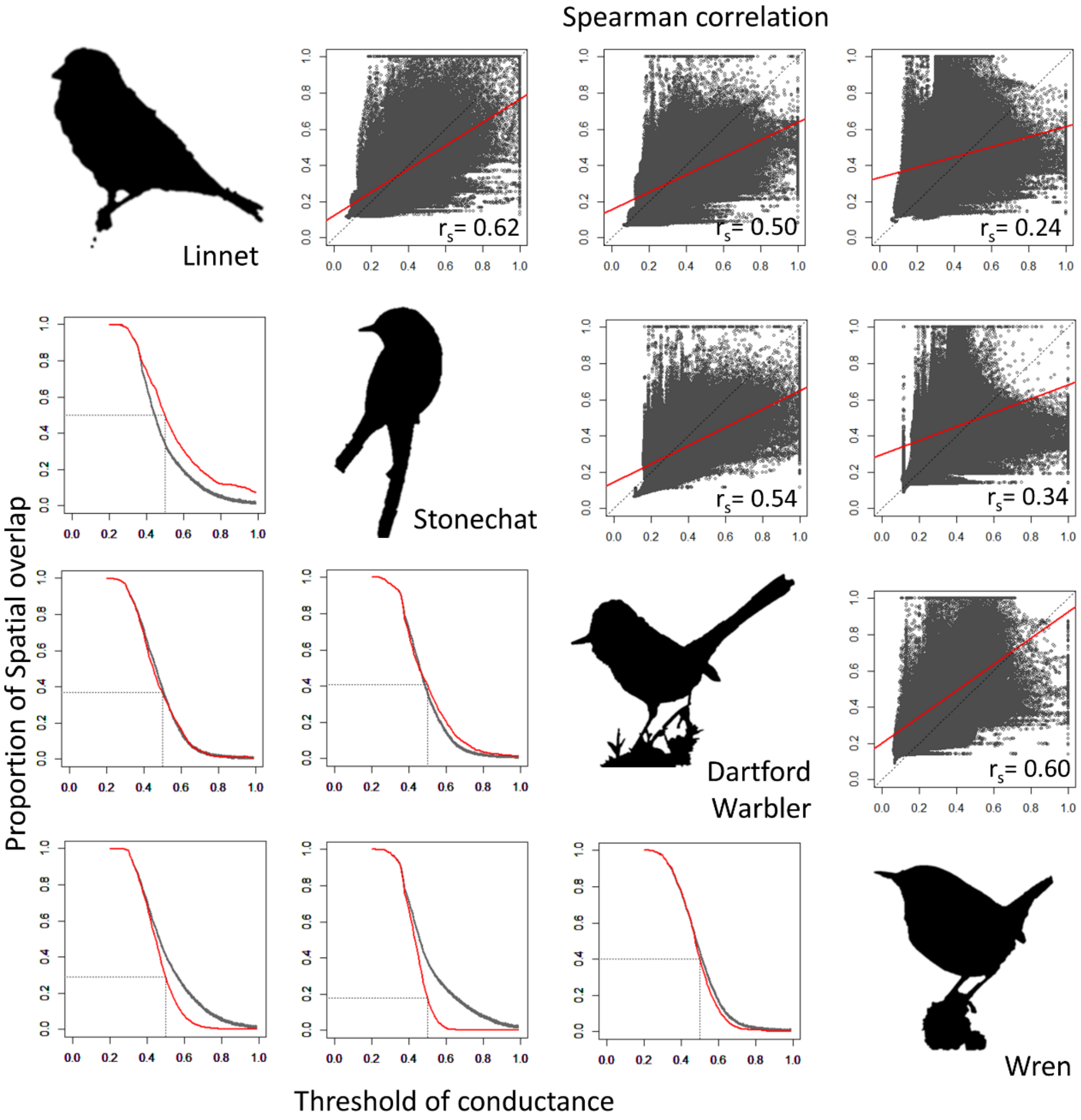

Figure IV.4 – Pairwise comparisons of the dispersal abilities of the four shrubland bird species. Top-right corner plots show the Pearson correlation between the conductances of each pair of species. Bottom-left plots signal proportion of spatial overlap between two species, measured at different thresholds of conductance. Red lines show the observed relation in each case. Dashed lines in spatial overlap plots signal the theoretical relationship expected from a randomized relation. Species show synergistic relation when the red line is above the expected; otherwise, species show conflicting dispersal ability.

IV.6. DISCUSSION

Our results clearly show that multispecies functional connectivity had a strong and positive effect on local community diversity supporting the importance of landscape filtering structuring shrub bird community. Highly connected patches held richer and more diverse communities, in line with most of the evidence (Fletcher *et al.*, 2016). As hypothesized, high landscape connectivity allows birds to move and colonize other suitable patches supporting larger populations and diverse communities (Martensen *et al.*, 2008). Conversely, because low connectivity hinders individuals to move freely within the matrix, isolated patches hold less species. Therefore, they are more likely to be dominated by one or few species for which landscape matrix is more permeable. Most importantly, we found the landscape filtering effect to be very consistent and quite relevant when compared with other measures of habitat amount or quality, largely accounted as utterly important for metacommunity structure (*e.g.*, Ryberg and Fitzgerald, 2015; Lindenmayer *et al.*, 2020).

However, this does not hinder that habitat filtering still plays a significant role in shaping local communities in our landscape. In fact, we also detected similar (though slightly smaller) effects of habitat amount: communities that are more diverse occurred in larger patches. The response was not conclusive for species richness, though a tendency for larger patches to hold more species is noticeable. In a reduced bird community like this it is conceivable that even small patches can hold most of the species. Nonetheless, this effect may relate to the fact that effective patch size may not be restricted to the patch itself, but to the overall network of functionally connected patches (Martensen *et al.*, 2008). Thus, connectivity complements habitat amount, mitigating possible effects derived from small patch size (the fragmentation threshold hypothesis, Fahrig, 2003).

Regarding habitat quality, local bird communities tended to be richer and diverse in patches where dune and thorny shrubs were more abundant. This may be related to the provision of suitable nesting and foraging conditions. For example, concealing nests in thorny or thick shrubs may offer additional protection from nest predation. This relation has been described for other bird communities (Söderström *et al.*, 2001) or species (Svendsen *et al.*, 2015) and was further observed in this study for species usually nesting in such conditions (Linnet, Dartford Warbler and Wren). Conversely, this relation was not detected in ground-nesting species (Stonechat) (Catry *et al.*, 2010; de Juana and Garcia, 2015). Other dune shrubs (*e.g.*, *Corema album*) often provide edible berries, an alternative resource even for mainly insectivorous birds.

Our results also show that despite all four species are sympatric each exploits its niche in different ways. For instance, Linnet is quite adverse to forested areas, while Wren is more tolerant as it also occurs in young pine plantations (Appendix IV.D).

Stonechats usually nest and forage on the ground, thus avoiding patches with tall shrubs, whereas Dartford Warbler uses dense and thick shrubs for nesting (Catry *et al.*, 2010). This could explain the modest overlap between single-species functional connectivity routes. One may argue that using SDM to build resistance surfaces will mostly reflect the occupied niche of each species and may not conveniently capture dispersal habitat characteristics (Revilla and Wiegand, 2008; Vasudev *et al.*, 2015), even though we compensated for such effects by testing several negative exponential transformations. Overlaying data from all species, however, diluted species-specific habitat requirements, empowering the multispecies connectivity model.

IV.6.1. Theoretical implications

Our study provides evidence that community assembly is largely dependent on both landscape connectivity and habitat quality. Both these attributes, however, are likely to influence different processes of the bird assembly (Lindenmayer *et al.*, 2020). While landscape connectivity determines which species are able to reach a patch (colonization), habitat quality determines which species are expected to settle in that patch (occupancy). Thus, the weight that each of these attributes assumes on community assembly will strongly depend on the intrinsic dispersal ability of each species to move across the landscape (functional connectivity), as well as on the capacity of the patch to provide specific resources for the settlement of different species. For instance, while working with mobile species in highly connected landscapes, all of them will have the same ability to reach a patch. Since landscape will not offer enough resistance to filter species, it is unlikely that landscape connectivity will play a significant role in structuring local communities (Poniatowski *et al.*, 2016). The same may hold true for impermeable matrices where all species are filtered and only habitat characteristics will determine which species occur. Conversely, as species exhibit specific requirements while traversing the matrix, the likelihood of each species reaching a patch differs as landscape offers uneven resistance. In this study, as landscape matrix filtered out species with lower capability to reach a suitable patch, the composition of local communities was highly dependent on landscape connectivity.

In this context, endorsing one focal or umbrella species to represent an entire community (*i.e.*, assume multiple species perceive landscape and its barriers similarly;

e.g., Cushman and Landguth, 2012) will hold potential bias, though may seem a cost-efficient solution (but see Dilkina *et al.*, 2016) when empirical data on movement is lacking (Fagan and Calabrese, 2006; Jønsson *et al.*, 2016). Functional connectivity is species-specific (Goodwin, 2003; Jacobson and Peres-Neto, 2010) and a suitable dispersal habitat/corridor for one species may not favour others (Koen *et al.*, 2014; Wang *et al.*, 2018). Our study supports the rationale that umbrella or focal species' connectivity is a poor proxy of multiple species landscape connectivity (McClure *et al.*, 2016; Wang *et al.*, 2018). Although some approaches show compelling evidence on the use of umbrella species, our general recommendation is that approaches dealing with communities should not rely only on measuring and enforcing connectivity for a single species (see also McClure *et al.*, 2016), but rather gather inference from as much species as possible.

IV.6.2. Management implications

Many studies devoted to understand patterns of biodiversity in fragmented landscapes are performed under controlled conditions, using manipulated landscapes (*e.g.*, Haddad *et al.*, 2015; Damschen *et al.*, 2019), while this investigation draws evidence from real-world landscapes. For that reason, our results provide important recommendations for management of production forests (*e.g.*, Viljur and Teder, 2018).

On-the-ground management practices should compromise with both landscape and habitat effects. Habitat conditions should relate to the specific requirements of the species, mainly those related with the provision of nesting/shelter and foraging conditions. In our case, shrubland birds benefited from thick thorny shrubs such as *Genista triacanthos* or *Ulex* sp. on which they may rely for nesting. Larger patches (habitat amount) can hold higher levels of diversity and forest managers should promote them instead of smaller patches, thus avoiding small-estate management. Nevertheless, even smaller patches can hold significant amounts of diversity if properly connected to other suitable patches.

Our landscape is quite dynamic since patches are under a rotational scheme between short fallow periods where shrubs dominate, and elongated periods of forest stand (up to 80 years). For that reason, we suggest that connectivity can be a key factor for landscape management. Maintaining connectivity between patches (independently of their size) may guarantee the persistence of animal communities associated to shrub patches. In this respect, creating and managing long-lasting shrub corridors that compartmentalize landscape should allow the dispersal of species into newly available areas as source patches evolve into forest stands. As a positive side effect, this could also create discontinuities in the landscape that may prevent the control of forest threats such as summer fires.

IV.7. ACKNOWLEDGMENTS

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Appendix IV.A: Single visit occupancy model for estimating detectability of shrubland birds' community

In order to enhance the statistical power and representativeness of the study area, we chose to visit each point once and invest on a larger number of sampled sites at the expense of a higher survey effort per site (*e.g.*, Loos *et al.,* 2015). To avoid bias from false absences we only considered for further analysis highly detectable breeding bird species common in shrublands of Centre-West Portugal. Therefore, we calculated the detectability for Linnet Linaria cannabina, Woodlark Lullula arborea, Iberian Green Woodpecker *Picus sharpei*, Stonechat *Saxicola rubicola*, Sardinian Warbler *Sylvia melanocephala*, Dartford Warbler *Sylvia undata* and Wren *Troglodytes troglodytes*, by means of single visit occupancy models (Lele *et al.*, 2012). Bird occurrence was tested for probability of occupancy in function of patch size, shrub height and number of trees, while accounting for imperfect detection arising from meteorological conditions (temperature and nebulosity), time of day (minutes from sunrise) and time of year (days from Spring equinox) effects. The models were selected following a backward elimination process where the sequential removal of each variable was tested. We selected the most informative model with ΔAIC lower than 4. Occupancy models were performed using the package "detect" (Solymos *et al.*, 2016). After this procedure, we only retained four bird species for subsequent analyses showing higher levels of detectability and representativeness in the study area (Table IV.A.1): Linnet, Stonechat, Dartford Warbler and Wren.

Table IV.A.1 – Single visit occupancy models for each analysed species, estimated detectability (d) and standard error (SE), and representativeness in the sampling sites (%). Variables used for occupancy estimation: patch area (Patch), mean shrub height (Shrbhei) and number of trees (Ntrees). Variables used to estimate detectability: temperature (Temp), cloud cover (Cloud), time of day (minutes from sunrise - ToD) and time of year (days from Spring equinox - ToY).

Species	model (~ occupancy | detectability)	d ± SE	%
Linnet *Linaria cannabina*	~Patch +ShrbHei +Ntrees | Temp +ToY +ToD	0.661±0.034	24.17
Woodlark *Lullula arborea*	~Patch +ShrbHei +Ntrees | Temp +ToY +ToD	0.389±0.008	25.00
Iberian Green Woodpecker *Picus sharpie*	~ShrbHei +Ntrees | Cloud +ToY +ToD	0.742±0.040	10.00
Sardinian Warbler *Sylvia melanocephala*	~ShrbHei +Ntrees | Temp +Cloud +ToD	0.749±0.030	15.83
Stonechat *Saxicola rubicola*	~Patch +ShrbHei +Ntrees | Temp +Cloud +ToD	0.909±0.026	28.33
Dartford Warbler *Sylvia undata*	~Patch +ShrbHei +Ntrees | Temp +Cloud +ToY +ToD	0.756±0.008	55.83
Wren *Troglodytes troglodytes*	~Patch +ShrbHei +Ntrees | Temp +Cloud +ToY	0.763±0.008	59.17

Appendix IV.B: Explanatory variables

Two types of environmental variables were used in analyses: a set of spatially explicit landscape variables, and another set of local vegetation structure and composition to assess habitat quality of the patch.

Landscape variables relate to topographic characteristics acquired from GIS software (QGIS version 2.2, Quantum GIS Development Team, 2013) using a thorough land use map. Extracted variables describe both landscape composition and configuration (see Table IV.B.1 for additional details). Compositional parameters regarded the proportions of the main land uses and Euclidean distances to other less representative land uses or infrastructures. Configuration patterns related to the landscape Shannon's diversity index number of patches and edge length. Since the landscape shows high patchiness, we explored different edge hardness regarding the contrast between the vertical structure of the vegetation of adjacent patches (Ries *et al.,* 2004; Reino *et al.,* 2009). Hard (high contrast) edges were considered to exist between old-growth pine plantations and open shrubland areas, while soft (low contrast) edges were found between old-growth plantations and young plantations, or young plantations and open shrubland areas. Total edge considers the sum of both hard and soft edges.

Habitat quality (sensu Mortelliti *et al.,* 2010) refers to the provision of appropriate environmental conditions that promote individual and population persistence. We depicted characteristics of the patch (habitat amount) and vegetation that relate with density (cover) and structure (height and variation of height) of vegetation layers (shrubs and trees) accounted for from field measurements in 20 random points within 100 m distance from each point count. Additionally, we identified shrub and tree species occurring at each site, thus providing information on the composition of shrubland habitats. Since different plant species showing similar traits may share similar ecological function to birds, we reduced the amount of plant species into functional groups (Söderström *et al.*, 2001). We applied a hierarchical clustering technique weighing trait similarity among plant species (see Table B.2 for further details on plant traits) using package "vegan" (Oksanen *et al.,* 2017). We were able to define seven ecological plant groups for which density was estimated pooling together all species belonging to the same group: Trees, Shrubs producers of fleshy fruits, Calluna-

Erica heath shrublands, Degraded heaths dominated by Cistus spp., Thick thorny shrubs, Sand dunes related shrubs, and Vines (see Figure B.3 for further details).

Table IV.B.1 – Description of the initial set of explanatory variables used in our study. Two sets of variables were considered, according to its source: Landscape variables refer to spatially explicit topographic characteristics acquired from GIS software, while Patch quality variables refer to habitat structure and composition measured on field at each site.

Acronym	Description	Units
Landscape		
Dist2Urban	Distance to urban areas	m
Dist2Road	Distance to roads	m
Dist2Edges	Distance to edges	m
Dist2LCEdge	Distance to nearest low contrast edge	m
Dist2HCEdge	Distance to nearest high contrast edge	m
ShDiv	Shannon's diversity index within 100m and 250m	-
NumberHabitats	Number of different land uses within 100m and 250m	-
MeanPatchSize	Mean patch size within 100m and 250m	ha
LengthLCE	Total length of low contrast edges within 100m and 250m	m
LengthHCE	Total length of high contrast edges within 100m and 250m	m
LengthTE	Total length of all edges within 100m and 250m	m
ShMedHei	Medium height shrub undercover within 100m and 250m	ha
ShLowHei	Low height shrub undercover within 100m and 250m	ha
ShTallHei	Tall height shrub undercover within 100m and 250m	ha
OpenShrb	Open shrubland area within 100m and 250m	ha
YoungPlant	Young plantation forest area within 100m and 250m	ha
PineFrst	Old-growth pine forest area within 100m and 250m	ha
Non-nativeFrst	Non-native forest area within 100m and 250m	ha
Patch quality		
PatchArea	Habitat amount provided by the patch size	ha
ShrbHeight	Mean shrub height within the sampling point (<100m)	m
ShrbHeightCV	Coefficient of variation (heterogeneity) of shrub height	-
SrhbCover	Percentage cover of shrubs within the sampling point (<100m)	%
NumbTrees	Number of trees within the sampling point (<100m)	-
Trees	Percentage cover of trees within the sampling point (<100m)	%
HeathShrb	Percentage cover of Calluna-Erica heath shrublands within the sampling point (<100m)	%
DuneShrb	Percentage cover of sand dunes related shrubs within the sampling point (<100m)	%
DegrHeathShrb	Percentage cover of degraded heaths dominated by Cistus spp. shrubs within the sampling point (<100m)	%
ThornyShrb	Percentage cover of thick thorny shrubs (Genista and Ulex) within the sampling point (<100m)	%
FleshFruitShrb	Percentage cover of shrubs producers of fleshy fruits within the sampling point (<100m)	%
Vines	Percentage cover of vines within the sampling point (<100m)	%

Table IV.B.2 – Ecological group defined by hierarchical clustering of the plant species found during field sampling and respective description of plant traits used for analysis. Data on plant traits was gathered from the following databases: Castroviejo *et al.* (1986-2014), Franco (1971, 1984), Franco e Afonso (1994, 1998, 2003), Flora-On (2014), Kleyer *et al.* (2008), Royal Botanic Gardens Kew (2020).

Ecological Group	Scientific name	Biotypes	Growth form	Branching	Height	Fruit	Zoochory	Thorns
Trees	*Acacia* sp.	Phanerophytes	Tree	Compact	>1000cm	Legume	No	No
	Eucalyptus sp.	Phanerophytes	Tree	Open	>1000cm	Dry	No	No
	Pinus pinaster	Phanerophytes	Tree	Medium	>1000cm	Dry	No	No
	Quercus faginea	Phanerophytes	Tree	Compact	>1000cm	Dry	Yes	No
	Quercus suber	Phanerophytes	Tree	Medium	>1000cm	Dry	Yes	No
Shrubs producers of fleshy fruits	*Arbutus unedo*	Phanerophytes	Shrub, Tree	Compact	<1000cm	Fleshy	Yes	No
	Cytisus sp.	Phanerophytes	Shrub, Tree	Medium	<1000cm	Legume	Yes	No
	Myrtus communis	Phanerophytes	Shrub	Compact	<1000cm	Fleshy	No	No
	Olea europea sylvestris	Phanerophytes	Shrub, Tree	Compact	>1000cm	Fleshy	Yes	No
	Pistacia lentiscus	Phanerophytes	Shrub, Tree	Medium	<1000cm	Fleshy	Yes	No
	Rhamnus alaternus	Phanerophytes	Shrub, Tree	Medium	<1000cm	Fleshy	Yes	No
Calluna-Erica heath shrublands	*Calluna vulgaris*	Phanerophytes, Chamaephytes	Shrub	Medium	<200cm	Dry	Yes	No
	Pterospartum tridentatum	Phanerophytes, Chamaephytes	Shrub	Compact	<200cm	Dry	No	No
	Cistus salvifolius	Phanerophytes, Chamaephytes	Shrub	Medium	<200cm	Dry	No	No
	Coronilla glauca	Phanerophytes	Shrub	Open	<200cm	Dry	Yes	No
	Erica sp.	Phanerophytes, Chamaephytes	Shrub, Tree	Medium	<50cm	Dry	Yes	No
	Erica umbellata	Chamaephytes	Shrub	Medium	<50cm	Dry	Yes	No
	Halimium halimifolium	Phanerophytes, Chamaephytes	Shrub	Open	<200cm	Dry	No	No
	Quercus coccifera	Phanerophytes, Chamaephytes	Shrub	Compact	<200cm	Dry	Yes	No
	Rosmarinus officinalis	Phanerophytes, Chamaephytes	Shrub	Medium	<200cm	Dry	No	No
Sand dunes related shrubs	*Carpobrotus edulis*	Chamaephytes	Succulent	Open	<50cm	Fleshy	Yes	No
	Corema album	Phanerophytes	Shrub	Open	<200cm	Fleshy	No	No
	Daphne gnidium	Phanerophytes, Chamaephytes	Shrub	Open	<200cm	Fleshy	Yes	No

Ecological Group	Scientific name	Biotypes	Growth form	Branching	Height	Fruit	Zoochory	Thorns
Degraded heaths dominated by *Cistus* spp	*Phillyrea angustifolia*	Phanerophytes	Shrub	Open	<1000cm	Fleshy	Yes	No
	Ruscus aculeatus	Geophyte	Bush	Open	<200cm	Fleshy	Yes	No
	Cistus crispus	Chamaephytes	Bush	Open	<200cm	Dry	No	No
	Cistus psilosepalus	Phanerophytes	Bush	Medium	<200cm	Dry	No	No
	Halimium calycinum	Phanerophytes, Chamaephytes	Bush	Open	<200cm	Dry	No	No
	Helichrysum stoechas	Chamaephytes	Bush	Open	<200cm	Dry	No	No
	Lavandula sp.	Phanerophytes, Chamaephytes	Bush	Open	<200cm	Dry	No	No
Thick thorny shrubs	*Genista triacanthos*	Phanerophytes, Chamaephytes	Shrub	Medium	<200cm	Legume	No	Yes
	Stauracanthus genistoides	Phanerophytes	Shrub	Compact	<200cm	Legume	No	Yes
	Ulex minor	Chamaephytes	Shrub	Compact	<200cm	Legume	No	Yes
	Ulex sp.	Phanerophytes, Chamaephytes	Shrub	Compact	<1000cm	Legume	No	Yes
Vines	*Rubia peregrina*	Chamaephytes, Scandent	Vine	Open	<1000cm	Fleshy	Yes	No
	Rubus ulmifolius	Chamaephytes, Scandent	Shrub, Vine	Compact	<1000cm	Fleshy	Yes	Yes
	Smilax aspera	Scandent	Vine	Open	<1000cm	Fleshy	Yes	Yes

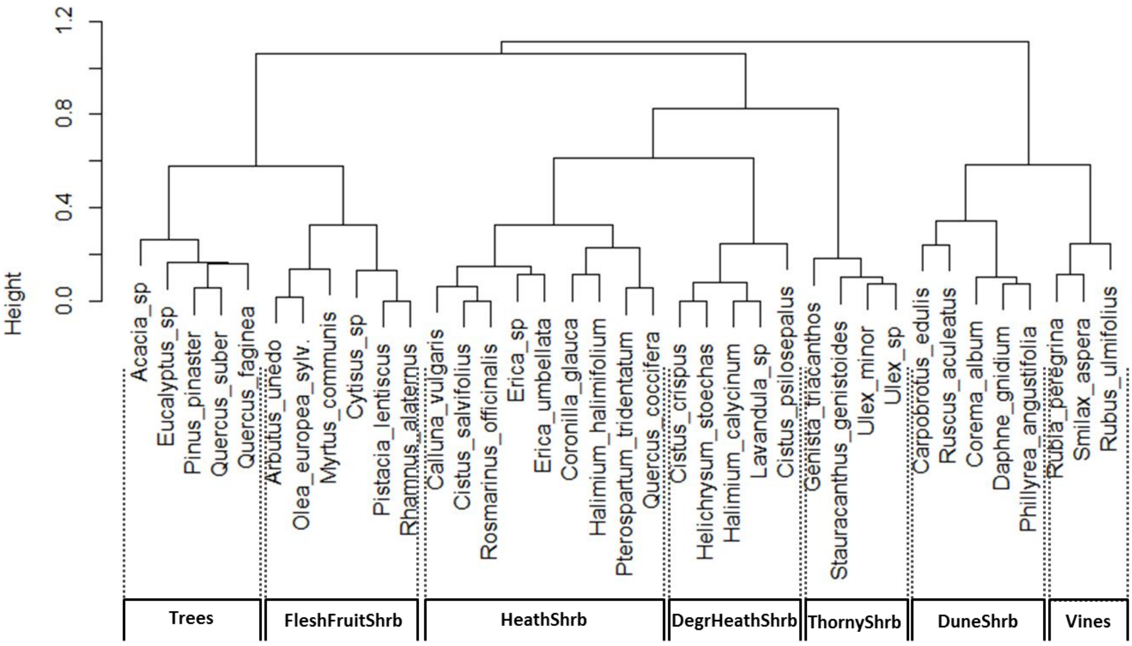


Figure IV.B.3 – Hierarchical clustering results obtained after analysis of trait similarity between plant species found during field sampling, and respective ecological group summarizing key characteristics for each group cluster: Trees, FleshFruitShrb (Shrubs producers of fleshy fruits), HeathShrb (Calluna-Erica heath shrublands), DegrHeathShrb (Degraded heaths dominated by Cistus spp), ThornyShrb (Thick thorny shrubs), DuneShrb (Sand dunes related shrubs), Vines.

Appendix IV.C: Species traits

Table IV.C.1 – Bird species trait data on dispersal ability and minimum size area needed to hold a breeding pair, used to model functional connectivity. Data was gathered from different sources: (a) Prugh *et al.* (2008); (b) Helm *et al.* (2006); (c) Bibby (1979); (d) Paradis *et al.* (1998); (e) Coleiro (2002); (f) Vincze *et al.* (2019); (g) Urbina-Tobias and Fontanilles (2018); (h) Cramp (1988, 1992); and (i) Cramp and Perrins (1994).

Species	Mean Dispersal Distance (km)	Median Dispersal Distance (km)	Wing aspect ratio	Minimum Area (ha)
Linnet *(Linaria cannabina)*	4.4 (a)	1.97 (d)	5.03 (f)	0.02-0.07 (i)
Stonechat *(Saxicola rubicola)*	11.7 (b)	2.2 (b)	4.24 (f)	<0.25 (h)
Dartford Warbler *(Sylvia undata)*	3.3 (c)	2 (e) (*)	4.44 (f) (**)	0.23 (Gascogne); 0.28 (Sardinia) (g,h)
Wren *(Troglodytes troglodytes)*		4.61 (d)	3.82 (f)	0.3, 0.37, 0.48 (England) (h)

(*) no values available, used available values for *S. melanocephala*

(**) no values available, used the mean of other phylogenetically related species: *S. atricapilla*, *S. borin*, *S. curruca*, *S. communis*

Appendix IV.D: Results of species distribution models

All models were checked for possible over-dispersion of our response data (Anderson, 2008) using the package 'AER' (Kleiber and Zeileis, 2008). Spearman correlation ranks were used to detect collinearity and, whenever highly correlated ($rs>0.70$; Tabachnik and Fidell, 1996), we proceeded only with the most ecologically meaningful variable. Variance inflation factors (VIF) where calculated using package 'car' (Fox and Weisberg, 2011) to discard collinearity (VIF scores > 2). We plotted both model residuals and partial residuals to check for model fitting and assess significant influence on model parameters. Residuals were tested for spatial autocorrelation using spline cross-correlograms (package 'ncf', Bjornstad, 2013).

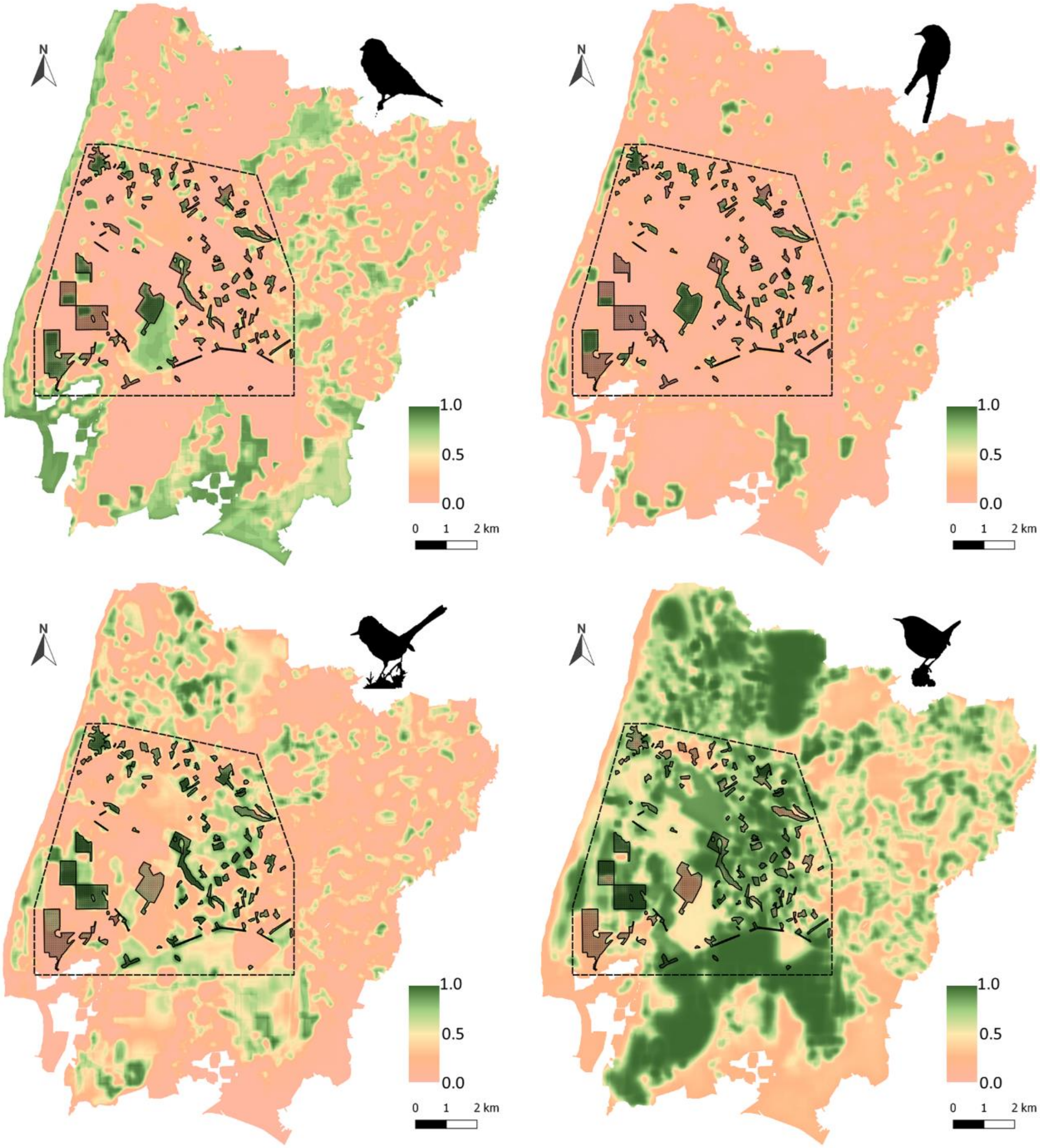


Figure IV.D.1 – Spatially-explicit Species Distribution Models for each of the four analysed species (brown to green gradient signals the probability of occurrence). From top left to bottom right: Linnet (*Linaria cannabina*); Stonechat (*Saxicola rubicola*); Dartford Warbler (*Sylvia undata*); Wren (*Troglodytes troglodytes*). Grey-shaded polygons signal the sampled shrub patches within the central area (delimited by a dashed line).

Table IV.D.2 – Averaging results of species distribution models from the 100 runs from the stepwise approach for model selection. For each species we present the spatial scale to each variable, the coefficient of regression and respective standard deviation, the type of response (l – linear, or q – quadratic), and the number of models where each variable entered (out of 100).

Variables	Linnet (*Linaria cannabina*)				Stonechat (*Saxicola rubicola*)				Dartford Warbler (*Sylvia undata*)				Wren (*Troglodytes troglodytes*)			
	Scale	Coef. ±SD	Rp	#mod	Scale	Coef.	Rp	#mod	Scale	Coef.	Rp	#mod	Scale	Coef.	Rp	#mod
PineFrst	**100m**	**-5.76±1.6**	**(l)**	**96**												
YoungPlant	**100m**	**-7.72±2.43**	**(q)**	**94**	100m	-2.76±1.35	(q)	34	250m	2.94±0.56	(l)	30	**100m**	**3.35±0.75**	**(l)**	**100**
Non-nativeFrst													250m	2.77±0.63	(l)	48
OpenShrb	**100m**	**3.74±1.25**	**(l)**	**8**	**100m**	**3.96±0.69**	**(l)**	**100**	**100m**	**2.93±0.77**	**(l)**	**100**	250m	-2.57±0.45	(l)	8
ShMedHei									**100m**	**2.71±0.72**	**(l)**	**94**				
ShTallHei					100m	-4.44±3.12	(l)	86	**100m**	**4.05±0.87**	**(l)**	**100**	**100m**	**3.96±1.12**	**(l)**	**99**
ShLowHei:PineFrst	250m	4.81±1.35	(l)	7					100m	-2.16±2.84	(l)	9				
ShMedHei:PineFrst													**250m**	**6.46±1.54**	**(l)**	**100**
MeanPatchSize	100m	-9.56±3.72	(l)	74	100m	1.9±2.63	(l)	13	100m	4.07±0.64	(q)	10	**250m**	**2.56±0.68**	**(l)**	**88**
NumberHabitats	250m	-4.6±0.91	(l)	46					250m	-4.41±1.32	(q)	58	250m	-1.01±3.86	(l)	7
Dist2Urban										**2.22±0.59**	**(l)**	**73**				
Dist2Road										-1.99±0.35	(l)	8		-1.84±0.41	(l)	28
Dist2LCEdge										-16.06±5.13	(q)	100				
Dist2HCEdge										1.95±5.26	(l)	10		-7.76±2.25	(q)	3
LengthHCE					250m	2.05±1.07	(l)	27	**100m**	**2.88±0.75**	**(l)**	**91**	250m	2.08±0.47	(l)	44
LengthTE	100m	-2.2±1.83	(l)	19												

Appendix IV.E: Results of functional connectivity models

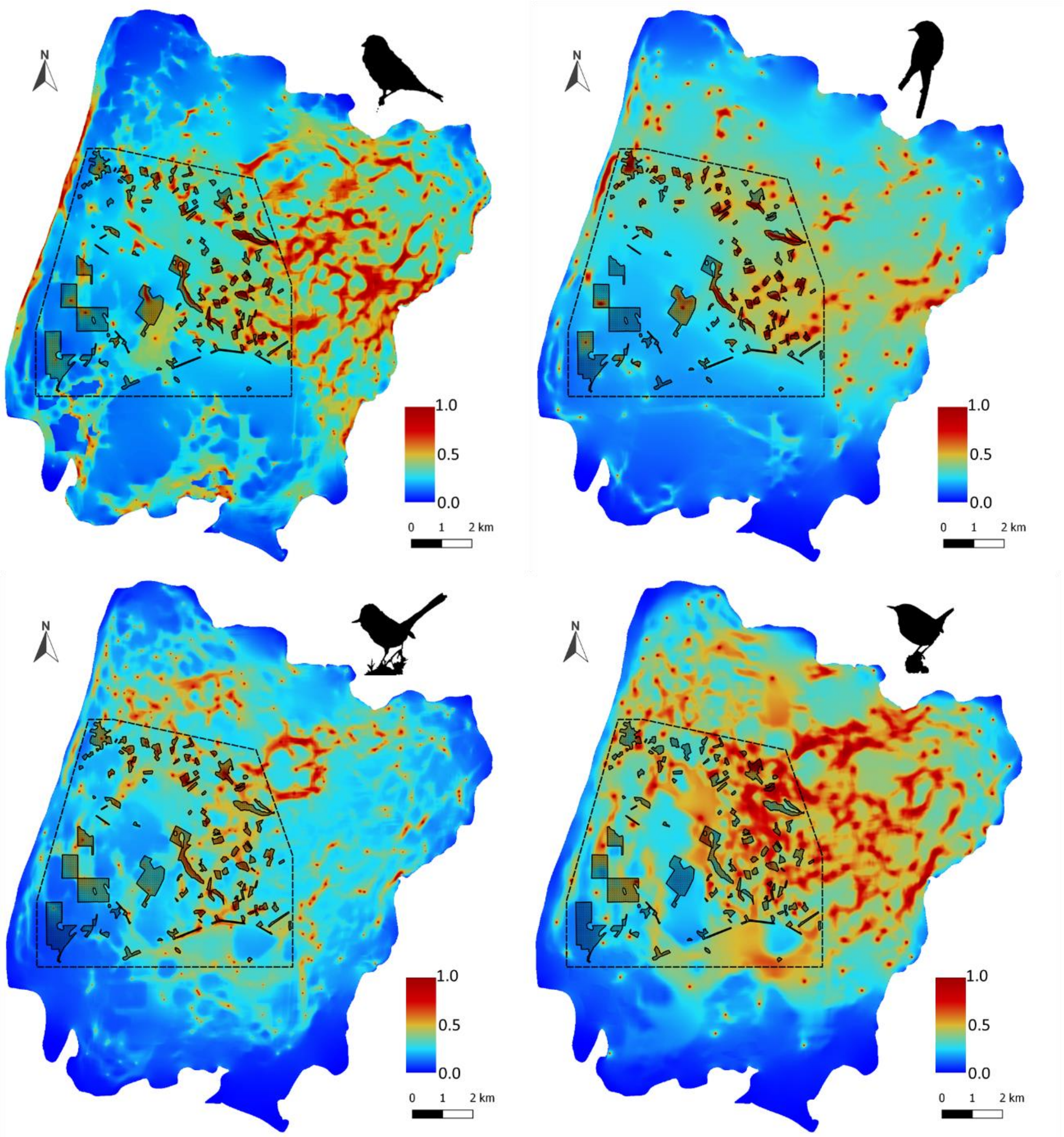


Figure IV.E.1 – Functional connectivity models derived from circuitscape for each of the four analysed species. From top left to bottom right: Linnet (*Linaria cannabina*); Stonechat (*Saxicola rubicola*); Dartford Warbler (*Sylvia undata*); Wren (*Troglodytes troglodytes*). Red shading signal the areas of higher connectivity for each species, while blue shading mark areas of greater resistance to movement. Grey-shaded polygons signal the sampled shrub patches within the central area (delimited by a dashed line).

Table IV.E.2 – Model coefficients for each of the species-specific tested models considering habitat-only characteristics, or adding functional connectivity models with different transformation factor (c). The confidence interval at 95% (CI95%), P value (P: ‘.’ for P < 0.1; ‘*’ for P < 0.05; ‘**’ for P < 0.01; ‘***’ for P < 0.001) and relative variable importance (RVI) from model averaging are also shown.

	Habitat				Habitat + FCM (c=0.25)				Habitat + FCM (c=2)				Habitat + FCM (c=8)			
Variables	Coef.	CI95%	P	RVI	Coef.	CI95%	P	RVI	Coef.	CI95%	P	RVI	Coef.	CI95%	P	RVI
Linnet																
(Intercept)	-1.32	[-1.73;-0.92]	***		-1.56	[-2.02;-1.10]	***		-1.59	[-2.07;-1.11]	***		-1.48	[-1.94;-1.03]	***	
PatchArea	0.41	[0.10;0.71]	**	0.94	0.44	[0.11;0.77]	**	0.91	0.46	[0.13;0.8]	**	0.95	0.48	[0.16;0.82]	**	0.97
ThornyShrb	0.21	[-0.10;0.51]		0.45	0.43	[0.10;0.75]	*	0.94	0.44	[0.11;0.76]	**	0.94	0.38	[0.05;0.71]	*	0.82
HeathShrb	-0.52	[-0.86;-0.18]	**	1.00	-0.41	[-0.77;-0.04]	*	0.83	-0.43	[-0.79;-0.06]	*	0.87	-0.47	[-0.82;-0.12]	**	0.97
DuneShrb	-0.35	[-0.88;0.18]		0.45	-0.14	[-0.71;0.43]		0.26	-0.18	[-0.75;0.39]		0.26	-0.22	[-0.77;0.33]		0.30
FCM					0.68	[0.38;0.98]	***	1.00	0.71	[0.40;1.02]	***	1.00	0.58	[0.21;0.94]	**	1.00
Stonechat																
(Intercept)	-0.90	[-1.28;-0.57]	***		-1.27	[-1.78;-0.84]	***		-1.28	[-1.79;-0.85]	***		-1.31	[-1.85;-0.87]	***	
PatchArea	0.36	[0.09;0.63]	**	1.00	0.51	[0.20;0.82]	**	1.00	0.50	[0.20;0.81]	**	1.00	0.57	[0.25;0.91]	***	1.00
ShrbHeight	-0.56	[-0.96;-0.20]	**	1.00	-0.62	[-1.05;-0.23]	**	1.00	-0.64	[-1.07;-0.24]	**	1.00	-0.65	[-1.09;-0.25]	**	1.00
ShrbHeight:ShrbHeightCV	0.65	[0.26;1.12]	**	1.00	0.59	[0.15;1.12]	*	1.00	0.58	[0.15;1.11]	*	1.00	0.53	[0.14;1.02]	*	1.00
FCM				1.00	0.69	[0.36;1.03]	***	1.00	0.70	[0.36;1.05]	***	1.00	0.75	[0.37;1.17]	***	1.00
Dartford Warbler																
(Intercept)	-0.31	[-0.65;0.02]	.		-0.41	[-0.78;-0.04]	*		-0.42	[-0.78;-0.05]	*		-0.34	[-0.69;0.01]	.	
PatchArea	0.20	[0.01;0.40]	*	0.73	0.24	[0.02;0.44]	*	0.81	0.26	[0.04;0.47]	*	0.86	0.26	[0.03;0.49]	*	0.84
ShrbHeightCV	-0.96	[-1.56;-0.35]	**	1.00	-0.90	[-1.49;-0.31]	**	1.00	-0.86	[-1.44;-0.28]	**	1.00	-0.96	[-1.56;-0.35]	**	1.00
SrhbCover:ShrbHeightCV	0.64	[0.05;1.23]	*	0.97	0.58	[-0.01;1.17]	.	0.85	0.57	[-0.01;1.15]	.	0.84	0.64	[0.04;1.26]	*	0.94
Trees	0.19	[0.01;0.37]	*	0.73	0.17	[-0.02;0.35]	.	0.64	0.17	[-0.01;0.36]	.	0.66	0.18	[0.00;0.36]	*	0.70
ThornyShrb	0.13	[-0.08;0.35]		0.40	0.16	[-0.06;0.38]		0.46	0.16	[-0.06;0.38]		0.49	0.14	[-0.08;0.36]		0.42
FCM					0.27	[0.07;0.47]	**	0.92	0.30	[0.08;0.53]	**	0.96	0.26	[-0.03;0.46]	.	0.59

	Habitat				Habitat + FCM (c=0.25)				Habitat + FCM (c=2)				Habitat + FCM (c=8)			
Variables	Coef.	CI95%	P	RVI	Coef.	CI95%	P	RVI	Coef.	CI95%	P	RVI	Coef.	CI95%	P	RVI
Wren																
(Intercept)	-0.30	[-0.52;-0.09]	**		-0.35	[-0.58; -0.13]	**		-0.36	[-0.58;-0.13]	**		-0.31	[-0.52;-0.09]	**	
SrhbCover	0.25	[-0.04;0.54]	.	0.71	0.13	[-0.18; 0.44]		0.35	0.14	[-0.17;0.45]		0.35	0.24	[-0.06;0.54]		0.62
ThornyShrb	0.22	[-0.01;0.45]	.	0.68	0.24	[0.03; 0.45]	*	0.83	0.26	[0.04;0.47]	*	0.87	0.24	[0.01;0.47]	*	0.74
DuneShrb	0.18	[-0.024;0.39]	.	0.66	0.24	[0.03; 0.44]	*	0.83	0.25	[0.04;0.46]	*	0.86	0.21	[-0.01;0.43]	.	0.67
FCM					0.34	[0.13; 0.54]	**	1.00	0.34	[0.11;0.57]	**	1.00	0.14	[-0.11;0.38]		0.38

Appendix IV.F: Results of multispecies functional connectivity model

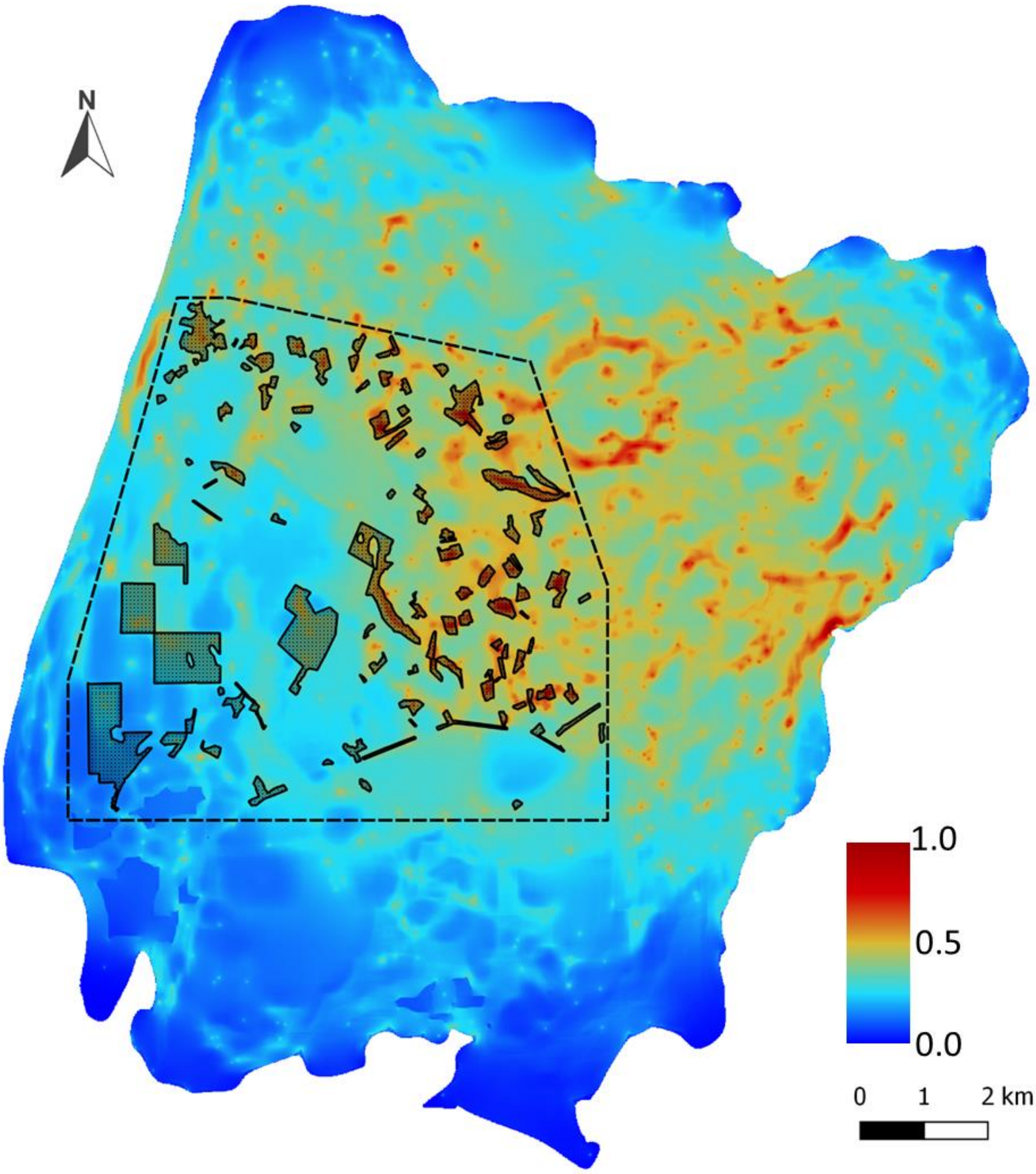


Figure IV.F.1 – Multispecies functional connectivity model. Red shading signal the areas of higher connectivity for all species, while blue shading mark areas of greater resistance to movement. Grey-shaded polygons signal the sampled shrub patches within the central area (delimited by a dashed line).

Table IV.F.2 – Model coefficients for each of the community parameters tested models considering habitat-only characteristics, or adding single-species or multispecies functional connectivity models. The confidence interval at 95% (CI95%), P value (P: '.' for P < 0.1; '*' for P < 0.05; '**' for P < 0.01; '***' for P < 0.001) and relative variable importance (RVI) from model averaging are also shown.

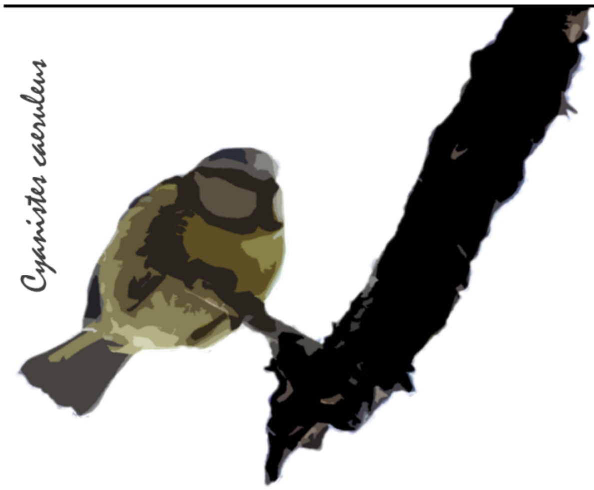
	Habitat				Habitat + FCM$_{Linnet}$				Habitat + FCM$_{Stonechat}$			
Variables	Coef.	CI95%	P	RVI	Coef.	CI95%	P	RVI	Coef.	CI95%	P	RVI
Total abundance												
(Intercept)	1.16	[1.05;1.27]	***		0.70	[0.42;0.99]	***		0.69	[0.42;0.96]	***	
PatchArea	0.15	[0.04;0.25]	**	0.98	0.15	[0.05;0.25]	**	1.00	0.17	[0.06;0.27]	**	1.00
Trees	0.10	[0;0.2]	.	0.69	0.10	[-0.01;0.2]	.	0.63	0.07	[-0.04;0.17]		0.38
ThornyShrb	0.17	[0.06;0.28]	**	1.00	0.22	[0.11;0.34]	***	1.00	0.19	[0.08;0.3]	***	1.00
HeathShrb	-0.04	[-0.15;0.08]		0.29	-0.01	[-0.12;0.11]		0.23	-0.05	[-0.16;0.06]		0.30
DuneShrb	0.08	[-0.05;0.2]		0.43	0.12	[0;0.25]	.	0.66	0.14	[0.01;0.27]	*	0.77
FCM					0.96	[0.43;1.49]	***	1.00	0.90	[0.44;1.35]	***	1.00
FCMcv												
Species richness												
(Intercept)	0.87	[0.74;0.99]	***		0.44	[0.1;0.78]	*		0.50	[0.15;0.85]	**	
PatchArea	0.07	[-0.05;0.2]		0.38	0.06	[-0.07;0.19]		0.34	0.08	[-0.05;0.21]		0.39
SrhbCover	0.03	[-0.13;0.2]		0.27	0.02	[-0.15;0.19]		0.27	0.01	[-0.17;0.18]		0.26
Trees	0.10	[-0.03;0.22]		0.53	0.08	[-0.05;0.21]		0.42	0.07	[-0.07;0.2]		0.35
ThornyShrb	0.14	[0;0.27]	*	0.75	0.18	[0.05;0.32]	**	0.92	0.16	[0.02;0.29]	*	0.83
DuneShrb	0.09	[-0.05;0.23]		0.36	0.14	[-0.01;0.29]	.	0.63	0.15	[0;0.3]	.	0.67
FCM					0.91	[0.28;1.53]	**	0.99	0.73	[0.18;1.28]	**	0.96
1st rank dominance												
(Intercept)	0.61	[0.56;0.66]	***		0.77	[0.65;0.89]	***		0.73	[0.59;0.87]	***	
PatchArea	-0.04	[-0.09;0.01]		0.56	-0.04	[-0.09;0.01]		0.53	-0.04	[-0.09;0.01]	.	0.60
ShrbHeight	-0.04	[-0.1;0.02]		0.43	-0.04	[-0.11;0.02]		0.46	-0.04	[-0.11;0.02]		0.44
ShrbHeightCV	0.02	[-0.04;0.09]		0.30	0.01	[-0.06;0.07]		0.27	0.00	[-0.07;0.07]		0.25
ThornyShrb	-0.05	[-0.11;0]	.	0.67	-0.06	[-0.12;-0.01]	*	0.81	-0.06	[-0.11;0]	*	0.76

	Habitat				Habitat + FCM_{Linnet}				Habitat + $FCM_{Stonechat}$			
Variables	Coef.	CI95%	P	RVI	Coef.	CI95%	P	RVI	Coef.	CI95%	P	RVI
DuneShrb	-0.03	[-0.08;0.02]		0.41	-0.05	[-0.09;0]	.	0.65	-0.05	[-0.11;0]	*	0.74
FCM					-0.35	[-0.6;-0.11]	**	1.00	-0.27	[-0.49;-0.05]	*	0.91
Simpson’s diversity												
(Intercept)	0.43	[0.38;0.48]	***		0.27	[0.13;0.42]	***		0.28	[0.14;0.43]	***	
PatchArea	0.05	[-0.01;0.1]	.	0.64	0.04	[-0.01;0.1]	.	0.59	0.05	[0;0.1]	.	0.7
SrhbCover	0.02	[-0.05;0.09]		0.31	0.02	[-0.05;0.08]		0.27	0.01	[-0.06;0.07]		0.25
Trees	0.05	[-0.01;0.1]	.	0.59	0.04	[-0.01;0.1]		0.55	0.04	[-0.02;0.09]		0.46
ThornyShrb	0.07	[0.01;0.12]	*	0.91	0.08	[0.03;0.14]	**	0.98	0.07	[0.08;0.55]	**	0.95
DuneShrb	0.04	[-0.01;0.1]		0.52	0.05	[0;0.11]	*	0.73	0.06	[0.02;0.13]	*	0.83
FCM					0.36	[0.1;0.62]	**	0.96	0.31	[0.01;0.12]	**	0.94

Table IV.F.2 (cont.) – Model coefficients for each of the community parameters tested models considering habitat-only characteristics, or adding single-species or multispecies functional connectivity models. The confidence interval at 95% (CI95%), P value (P: '.' for P < 0.1; '*' for P < 0.05; '**' for P < 0.01; '***' for P < 0.001) and relative variable importance (RVI) from model averaging are also shown.

	Habitat + FCM$_{DWarbler}$				Habitat + FCM$_{Wren}$				Habitat + FCM$_{Multispecies}$			
	Coef.	CI95%	P	RVI	Coef.	CI95%	P	RVI	Coef.	CI95%	P	RVI
Total abundance												
(Intercept)	0.70	[0.33;1.07]	***		1.10	[0.81;1.39]	***		1.13	[1.02;1.25]	***	
PatchArea	0.17	[0.07;0.28]	**	1.00	0.15	[0.05;0.25]	**	0.98	0.18	[0.07;0.29]	**	1.00
Trees	0.09	[-0.02;0.19]		0.56	0.10	[0;0.2]	.	0.68	0.07	[-0.03;0.18]		0.43
ThornyShrb	0.18	[0.07;0.29]	***	1.00	0.17	[0.06;0.27]	**	0.99	0.20	[0.09;0.31]	***	1.00
HeathShrb	-0.05	[-0.17;0.06]		0.33	-0.04	[-0.15;0.07]		0.29	-0.04	[-0.16;0.07]		0.28
DuneShrb	0.09	[-0.03;0.22]		0.48	0.08	[-0.05;0.2]		0.41	0.14	[0.01;0.27]	*	0.76
FCM	0.99	[0.32;1.67]	**	0.98	0.40	[-0.43;1.23]		0.34	0.24	[0.13;0.36]	***	1.00
FCMcv									0.06	[-0.05;0.18]		0.38
Species richness												
(Intercept)	0.48	[0;0.95]	*		0.84	[0.57;1.11]	***		0.84	[0.72;0.97]	***	
PatchArea	0.09	[-0.04;0.22]		0.45	0.07	[-0.05;0.2]		0.390	0.09	[-0.04;0.22]		0.46
SrhbCover	0.01	[-0.16;0.18]		0.26	0.03	[-0.13;0.2]		0.270	-0.02	[-0.19;0.15]		0.26
Trees	0.08	[-0.05;0.21]		0.43	0.10	[-0.03;0.22]		0.51	0.07	[-0.06;0.2]		0.34
ThornyShrb	0.15	[0.02;0.28]	*	0.82	0.13	[0;0.27]	*	0.730	0.17	[0.04;0.31]	*	0.91
DuneShrb	0.10	[-0.04;0.25]		0.47	0.09	[-0.06;0.23]		0.390	0.16	[0.01;0.31]	*	0.73
FCM	0.93	[0.15;1.72]	*	0.88	0.24	[-0.75;1.23]		0.250	0.22	[0.08;0.35]	**	1.00
1st rank dominance												
(Intercept)	0.69	[0.51;0.86]	***		0.76	[0.54;0.97]	***		0.61	[0.56;0.66]	***	
PatchArea	-0.04	[-0.09;0.01]	.	0.61	-0.05	[-0.11;0]	*	0.74	-0.05	[-0.1;0]	.	0.72
ShrbHeight	-0.03	[-0.1;0.04]		0.37	-0.03	[-0.09;0.04]		0.34	-0.02	[-0.09;0.04]		0.32
ShrbHeightCV	0.01	[-0.05;0.08]		0.26	0.01	[-0.05;0.07]		0.25	-0.01	[-0.07;0.06]		0.25
ThornyShrb	-0.06	[-0.11;0]	*	0.76	-0.05	[-0.1;0]	.	0.66	-0.06	[-0.11;-0.01]	*	0.87

	Habitat + FCM$_{DWarbler}$				Habitat + FCM$_{Wren}$				Habitat + FCM$_{Multispecies}$			
	Coef.	CI95%	P	RVI	Coef.	CI95%	P	RVI	Coef.	CI95%	P	RVI
DuneShrb	-0.03	[-0.08;0.01]		0.46	-0.03	[-0.08;0.01]		0.46	-0.05	[-0.1;-0.01]	*	0.82
FCM	-0.27	[-0.59;0.04]	.	0.61	-0.42	[-0.82;-0.02]	*	0.79	-0.08	[-0.13;-0.03]	**	1.00
Simpson’s diversity												
(Intercept)	0.36	[0.18;0.54]	***		0.32	[0.09;0.54]	**		0.43	[0.38;0.48]	***	
PatchArea	0.05	[0;0.1]	.	0.68	0.06	[0;0.12]	*	0.78	0.06	[0.01;0.11]	*	0.80
SrhbCover	0.02	[-0.05;0.08]		0.29	0.01	[-0.06;0.08]		0.27	0.00	[-0.07;0.06]		0.24
Trees	0.04	[-0.01;0.1]		0.55	0.05	[-0.01;0.1]		0.58	0.04	[-0.02;0.09]		0.46
ThornyShrb	0.07	[0.01;0.13]	*	0.93	0.06	[0.01;0.12]	*	0.86	0.08	[0.02;0.13]	**	0.98
DuneShrb	0.04	[-0.01;0.1]		0.55	0.04	[-0.01;0.1]		0.55	0.06	[0.01;0.12]	*	0.85
FCM	0.28	[-0.06;0.62]		0.57	0.40	[-0.03;0.83]	.	0.67	0.09	[0.03;0.14]	**	1.00



Chapter V

General conclusions

Land-use conversion and intensification are at the origin of most human driven landscape modifications (Newbold *et al.*, 2015) including habitat loss and fragmentation (Lindenmayer *et al.*, 2008; Hooper *et al.*, 2012; Driscoll *et al.*, 2013). Such landscape modifications threat global biodiversity (Fischer and Lindenmayer, 2007, Hooper *et al.*, 2012) and erode genetic diversity (Bruggeman *et al.*, 2010), leading species to the brink of extinction and depleting ecosystem services (Haddad *et al.*, 2015; Mitchell *et al.*, 2015). As landscapes worldwide experience these untamed changes, ecologists need to respond with concrete environmental tools and strategies to guide land-use policies and propose effective management alternatives aiming sustainable practices (Balmford *et al.*, 2003). Understanding the complex interactions between animal communities and human-induced landscape changes is pivotal to support these goals.

This thesis aims at determining the role of structural and functional landscape traits and connectivity in mediating the spatial distribution of bird communities inhabiting fragmented areas. In order to explore the specific objectives of the thesis as well as to depict concrete implications of the studies, we focused on real-world landscapes most representative of the Portuguese forestry context, yet largely subjected to human intervention. The studies here presented build upon several theoretical considerations of the fragmentation research to test their assumptions as applied to our specific landscape contexts, uncover the ecological thresholds at which changes in species and communities occur, and determine the effects of functional connectivity on the spatial distribution of species and the processes governing community assembly.

The following sections address the main conclusions gathered from the outputs of the studies in this thesis. Arising from our findings, we unfold the main contributions to the current knowledge and outline further research needed to better understand the effects of landscape fragmentation and functional connectivity on bird communities.

V.1. SUMMARY OF THE MAIN FINDINGS

V.1.1. Assessing patterns of landscape structure in human-modified landscapes

Inappropriate representations of the landscape can strongly bias species response to structural elements, as different conceptualizations of the same landscape differently capture its spatial heterogeneity. Chapter II offers a valuable insight on this issue, testing the response of several bird species in the two structurally different landscapes to measure the adequability of alternative landscape conceptualizations based on competing theories (*e.g.*, patch-based approaches derived from the island biogeography theory by MacArthur and Wilson, 1967; and gradient-based approaches supported by the continuum concept by Austin, 1985; Fischer and Lindenmayer, 2006).

We concluded that the adequability of a conceptualization relates to trade-offs between the landscape structure and the way species perceive it, namely, how their resources are distributed. We found patch-based models to provide suitable conceptualizations in both mosaic and variegated landscapes. In mosaic landscapes, because patches are internally homogeneous (Bennett *et al.*, 2006), species tended to respond similarly as they perceive the landscape structure likewise (Didham *et al.*, 2012). However, patch-based conceptualizations neglect within patch heterogeneity often present in variegated landscapes. In these circumstances, if they are not species-oriented (*i.e.*, depicting suitable patches from inhospitable matrix for a given species), they will likely fail to capture important resources and species responses to their availability. Gradient-based approaches, on the other hand, depict spatial heterogeneity in a way not achievable by patch-based models, thus better reflecting the spatial distribution of resources (*e.g.*, food, nest, shelter). Those models are particularly important to understand responses of specialist species to landscape traits (Fischer and Lindenmayer, 2006; Price *et al.*, 2009; Stoddard 2010).

In a nutshell, patch-based models offer a simplified perception of landscape heterogeneity suitable for species with broad requirements (*e.g.*, generalist species), since they describe wide attributes of the landscape (*e.g.*, non-forest vs. forest cover). Gradient-based models are able to capture spatial heterogeneity, hence providing information on the allocation of specific resources, being appropriate for species with narrower ecological requirements.

These results are in agreement with our first hypothesis of the thesis, which states that the adequacy of a model to describe species responses to landscape structure depends on both landscape topography and species perception.

These findings imply that species will better respond to landscape models that approximate to its own perception of the landscape, and the model that better discriminates species-specific resources will be ecologically more meaningful. Since different species look for specific resources, their perception of the landscape differs, resulting in highly individualistic responses to landscape conceptualization. As corollary, artificial landscape classifications despite being able to detect structural landscape elements may not serve all species. By overlooking spatial heterogeneity within patches we may neglect landscape permeability provided, for instance, by the presence of small clusters or scattered trees in large farmland patches (Fischer and Lindenmayer, 2002) that can operate as stepping-stones (Saura *et al.*, 2014).

V.1.2. Critical thresholds of the bird community in a highly fragmented landscape

The variegated structure of the Mediterranean landscape derived from the fuzzy tree cover pattern translates into an uneven distribution of resources that change gradually and spatially. Therefore, the increasing cover of trees benefits bird species seeking for forest habitat conditions providing them with good resources to nest and forage, while open farmland birds have the amount and quality of suitable habitat reduced in these circumstances. In a landscape where these changes are gradual, we expected that species-specific and community-level thresholds occurred along a resource gradient of tree canopy cover, determining the spatial patterns of species richness, turnover and assemblages (third hypothesis of the thesis; the fragmentation threshold hypothesis by Fahrig, 2003).

The study presented in Chapter III agrees with the hypothesis by reporting strong changes in bird composition occurring between 1% and 10% tree canopy cover, explicitly marking the turnover between well-defined assemblages of open-farmland and forest-dependent birds. However, as many species show some tolerance to low canopy cover, open woodlands of sparse tree cover (1 to 25%) favours the co-occurrence of farmland, transition and forest species due to the higher habitat heterogeneity (see also, Tellería, 2001; Sanderson *et al.*, 2009; Bonthoux *et al.*, 2013). This has driven species richness to peak at 10% canopy cover.

Furthermore, our results also revealed a segregation of species assemblages with different species clumping at distinct ranges of the gradient. This segregation was somewhat linked to higher levels of specialization (narrower niche width) that constraint species to occur at very specific ranges. For instance, farmland species only occurred at tree cover canopy densities below 10%, and some of the most emblematic species of these systems (*e.g.*, Little Bustard) occurred preferably at densities below 1%. Transition species peaked between 1% and 25% canopy cover, suggesting that specialization also occurred at intermediate levels of tree canopy cover (Tellería, 2001; Bonthoux *et al.*, 2013). In contrast, forest species showed a broader distribution within the forest range (larger niche width), reflecting the strong plasticity and tolerance of these species by also occupying islets of isolated trees and areas of scant tree cover (see also Bonthoux *et al.*, 2013). Nevertheless, the probability of occurrence of other forest specialist species, which are generally absent in low covered areas, is favoured with increasing tree canopy density.

While aiming at defining the ranges of tree cover most vulnerable to species loss, and which best fulfil the requirements for conservation purposes, we face competing alternatives that will inevitably result in winners and losers. Managing for 10% tree cover may uphold higher bird diversity but may be inadequate to protect other specialist species. Because different canopy cover assists different species assemblages, prioritizing a single management practice to benefit a single assemblage, may imperil the persistence of others in the landscape. Conversely, the traditionally extensive agro-forestry management resulting from centuries of traditional human activities (*e.g.*, agriculture, cattle grazing and forestry; Blondel *et al.*, 2010) that promoted the characteristic large scale variegated landscape (Pinto-Correia *et al.*, 2011), may sustain a balanced trade-off between species assemblages, as long as isolation effects do not hinder the ability of species reaching suitable habitats.

V.1.3. Spatial distribution of bird community driven by functional connectivity

Landscape functional connectivity strongly and positively influences local community diversity by governing the ability of a species to reach a patch while dispersing. In Chapter IV we focused this issue by testing the role of single- and multispecies landscape connectivity on species' spatial distribution (fourth hypothesis), and local community composition and diversity (fifth hypothesis), following the metacommunities theory by Leibold *et al.* (2004).

We found that landscape functional connectivity plays a consistent role in determining the spatial distribution of species even when compared with descriptors of habitat amount or quality whose influence on distribution is largely accounted in the literature (*e.g.*, Ryberg and Fitzgerald, 2015; Lindenmayer *et al.*, 2020). We also concluded that highly connected patches hold richer and more diverse local communities, allowing birds to move and colonize other suitable patches (see also Martensen *et al.*, 2008; Fletcher *et al.*, 2016 for similar conclusions). On the other hand, less permeable matrices hinder species movement, amplifying the isolation effects of patches embedded on them. As a consequence, local communities in more isolated patches are less diverse and often dominated by a single species for which landscape remains more permeable.

Further investigating the effectiveness of single-species connectivity to predict community composition and diversity, we found that the use of umbrella or focal species provided limited information to be used as proxies of multispecies landscape connectivity. Because dispersal ability is a species-specific trait (Goodwin, 2003; Jacobson and Peres-Neto, 2010) little agreement was found between most species, thus concluding that suitable corridors for one species may not favour others (Cushman and Landguth, 2012; Koen *et al.*, 2014; Wang *et al.*, 2018). While using a single umbrella or focal species one assumes that multiple species perceive landscape and its barriers similarly, which will hold potential bias. Although endorsing one single-species can provide a cost-efficient solution in some cases (*e.g.*, Cushman and Landguth, 2012;

Breckheimer *et al.*, 2014), our general recommendation is that community approaches should gather inference from as much species as possible.

V.2. CONTRIBUTION TO THE EXISTING BODY OF KNOWLEDGE

Our findings contribute to the growing and timely research devoted to understand non-random spatial patterns of bird distribution and abundance in fragmented landscapes. This investigation provides theoretical and practical contributions from real-world landscapes, detaching from studies performed in manipulated landscapes under controlled conditions, which offer a limited insight while neglecting the casuistic topology of the landscapes and the interplay between different drivers governing community assembly. Here, we build upon the results of the three studies performed in the framework of this thesis to explore their implications to the ecological theory and report the contributions for the management of forest landscapes.

V.2.1. Theoretical and conceptual considerations

V.2.1.1. Individualistic continuum vs. community-unit concept?

Do organisms respond independently to change (species-specific), or is there an interdependence (dynamic synchrony) effect among organisms occurring at the same environmental conditions? The conceptualization of communities as coherent and functional assemblages, or the sheer sum of species coincidently occurring in space and time, is still a non-consensual topic of discussion. The implications of this topic relate to the integration of individual responses in complex community dynamics, and to what extent the resulting arrangement surrogates discrete assemblages.

Throughout the thesis this topic was recursively addressed because we expected species to perceive and respond to landscape change uniquely and differently (second hypothesis) according to their ecological requirements. This hypothesis arose from two main concerns, enunciated in Chapter II. Firstly, species exploit multi-dimensional niches, and the way multiple resources are spatially distributed hardly comply with an explicit categorization of landscape heterogeneity into suitable/unsuitable habitat patches. Secondly, patch delimitation forces species to perceive landscape (and resources within) similarly, which may originate biased results (Fischer and Lindenmayer, 2006; Lindenmayer *et al.,* 2008).

All three papers presented in this thesis (Chapters II to IV) offer, to some extent, insights upon this topic. In Chapter II, we analysed species responses to landscape conceptualizations. We assumed that, if species perceive landscape similarly, a consistent agreement around a given conceptualization should be expected. We found that patch-based conceptualizations accurately captured the structure of mosaic landscapes (such as standard production pine forests), thus supporting the Clementsian hypothesis (community-unit). Yet, some species perceived landscape differently, and their occurrence is better explained by conceptualizations that provided information about important microhabitat resources (*e.g.*, stand characteristics). As we further investigated in Chapter IV, shrubland species, though bounded by the same habitat, showed very different requirements in terms of habitat amount and quality, which further echoed in the ability of the species to disperse, and on the cues they follow to find suitable habitat patches. Since functional connectivity differed among species, the use of umbrella or a focal species to surrogate the whole community is a potential source of bias.

In Mediterranean oak woodlands the differences were more marked since the variegated structure of the landscape challenges human-oriented patch delimitation (Fischer and Lindenmayer, 2002; Dunn and Majer, 2007). In such landscape, gradient-based conceptualizations were able to capture highly detailed and ecologically meaningful information on resource allocation for species with specific requirements, while species with broad requirements responded better to simplified patch-based conceptualizations (see Chapter II). Chapter III provides a comprehensive approach on this topic specifically applied to Mediterranean oak woodlands. We found that many species distributed continuously along the forest cover range adjusting their optima or tolerance ranges to avoid niche overlap (Austin, 1999), which is compatible with the Gleasonian perspective (individualistic continuum). However, the patterns related to both richness and turnover rates do not assume a clear constant variation along the gradient as expected, showing at least one distinct peak, which agrees with the Clementsian hypothesis. Thus, species non-randomly overlap within their niche ranges suggesting that the bird community is also structured in well-defined assemblages, *e.g.*, a marked change in community composition occurs between open grassland and forest assemblages.

Strong discontinuities in the landscape (*e.g.*, open grassland or forest) generate discontinuities in species distribution (*e.g.*, farmland vs forest species), whereas in gradients with low patch contrast species tend to distribute individualistically shaping their realised niche in the presence of competitors exploring the same resources (Austin, 1999). Species traits related to their plasticity in using environmental resources (*e.g.*, generalist vs specialist) seem to be key to acknowledge this hypothesis. Yet, our results are in agreement with the "integrated community concept" proposed by Lortie *et al.* (2004) which recognizes the synergistic effects between the strength and direction (positive or negative) of the interspecific relations and species-specific tolerance that will influence the cohesiveness of an ecological assemblage.

V.2.1.2. Filtering processes and community assembly

It is well established in literature and widely considered that local community composition and structure are driven by a set of processes able to hierarchically filter species from a regional pool of competitors (Cadotte and Tucker, 2017).

In Chapter IV we investigated the contributions of both landscape and habitat filters to provide evidence that community assembly largely depended on both landscape connectivity and habitat amount and quality. As both these attributes likely influence different processes of bird assembly (Lindenmayer *et al.*, 2020), the weight each attribute assumes depends on the species response regarding the composition and configuration of the landscape (functional connectivity), and the suitability of the patch to provide appropriate resources for each species integrating the community.

We found that the composition of local communities was highly dependent on landscape connectivity as landscape offered uneven resistance. Since the four bird species exhibited different requirements while traversing the unsuitable forest matrix, the likelihood of each species reaching a specific patch varied. To a lesser extent, habitat filtering (habitat amount and patch quality) also played a significant role in shaping local communities. Local communities tended to be more complex in larger patches, possibly holding more heterogeneous conditions regarding vegetation structure and composition, which may provide suitable nesting and feeding conditions for a larger number of species (Söderström *et al.*, 2001; Svendsen *et al.*, 2015).

Chapter III also offers some insight on the effects of habitat filtering on bird communities. Tree canopy by changing gradually along the landscape acted like a filter: as conditions altered some species were benefited and others impaired. Following the ecological niche theory, species' distributions behaved non-linearly to the gradient following unimodal (Gaussian) responses (Austin, 2007). Species, thus, presented an optima range where they thrived, and beyond which the likelihood of occurrence decayed as the conditions farther apart from it deteriorated, reflecting the process of habitat filtering. However, because species showed an individualistic behaviour within assemblages, adjusting their optima or tolerance ranges to avoid niche overlap (Austin 1999), we can likely argue that competition also played a role in shaping local communities. The issue here is that the species response patterns do not result from independent habitat filtering effects, but from the interplay between habitat and interaction filters. This means that the effects of both filters may be indivisible from each other, and only by measuring the species persistence in the absence of competitors will one determine the isolated effects of habitat filtering (Kraft *et al.*, 2015; Cadotte and Tucker, 2017).

However, since the investigation of competition was beyond the scope of this thesis, we can only speculate about the combined effects between filters and the extent to which they independently contribute to shape local communities. Nevertheless, our results suggest that the contribution of combined filtering processes may outmatch the classical overview of independent isolated filters acting at different temporal and spatial scales in community assembly. Further theoretical and conceptual considerations, as well as studies addressing these issues, should consider the interplay between different filters and bridge the combined effects between them.

V.2.2. Practical contributions

V.2.2.1. Management practices of production pine forests

Landscapes dominated by production pine forests are quite dynamic since patches are under a rotational scheme between short fallow periods where shrubs dominate and large periods of forest stands (up to 50-80 years). This causes major constraints to birds as overall landscape is continuously changing and some habitat patches are somewhat ephemeral in their suitability. Landscape dynamics has two major consequences: (1)

changes in the suitability of patches potentiate a habitat filtering effect that will affect the likelihood of a species to occupy a patch, and (2) modifications in the permeability of the involving matrix may impede or enable the dispersal of a species, thus reflecting a landscape filtering effect that influences the probability of a species reaching a patch. As the processes governing bird community assembly in production pine forests is subjected to both habitat and landscape filters, on-the-ground management practices should compromise with both effects.

Habitat filtering effects report the constraints driven by habitat amount and quality. Regarding habitat amount, we found that larger patches were, in general, able to hold a higher diversity of birds as predicted by the species-areas relationships theory (Arrhenius, 1921). As a standard practice, larger patches should prevail over smaller ones; yet, patch size may not be restricted to the patch itself and a network of functionally connected small patches may alternatively retain and promote high levels of diversity (effective patch size, see Martensen *et al.*, 2008). Habitat quality reflects the conditions provided by patches that may or may not comply with the ecological requirements of each species, namely the provision of nesting/shelter and foraging conditions. Our results show that both the structure (*e.g.*, cover, height) and the composition of the vegetation determine the ability of a species to settle in a patch. However, because species preferences did not agree regarding vegetation structure, the results for the overall community parameters were not often consistent among species. Still, our findings point out to a consistent positive effect of thick thorny shrubs (such as *Genista triacanthos* or *Ulex* sp.) which provide safe nesting places, and of shrubs producing fleshy fruits (*e.g.*, *Corema album*) that often provide edible berries.

Landscape filtering effects, on the other hand, mainly relate to the quality (*i.e.*, permeability) of the matrix instead of the patch. We show that maintaining connectivity between patches (independently of their size) facilitated the persistence of bird communities associated to shrub patches. Therefore, beyond the patch, a strategic approach to forest management at the landscape-scale is also required to effectively address sustainable exploitation. One possible practice relates to keeping shrub corridors or stepping stones patches with diverse characteristics allowing the dispersal of different species into newly available areas as patches evolve to other habitats. In addition, maintaining long-standing, high quality habitat patches in the landscape can harbour a large number of species and supply species to the neighbouring habitats.

V.2.2.2. Management practices of Mediterranean oak woodlands

Current management practices are driving Mediterranean agro-ecosystems to either management intensification or land abandonment (Pinto-Correia and Mascarenhas, 1999; Plieninger and Schaar, 2008). As a consequence, the characteristic savannah-type structure and high landscape heterogeneity often associated with the tree cover gradient may be at risk as the extreme ranges of the open grassland-to-forest gradient are presently being favoured.

Nevertheless, our results suggest that bird specialization occurs along different ranges of the gradient, highlighting the potential of the variegated system to hold high bird diversity. For instance, species richness can be enhanced by maintaining a low forest cover density (≈10% tree canopy cover), complying with the ranges where transition species find their optima. Although many forest species are tolerant to low tree canopy cover, forest specialist species are rarer, benefiting mostly from dense forests. However, farmland birds would benefit from tree cover below 10%, preferably at about 1%. The forest cover thresholds found in our study can be used as indicators of this specific resource marking the limits of species occurrence where populations may be more sensitive to forest cover management. Local management practices should focus, therefore, on optimizing the potential of an area by adjusting tree cover to more effective conservation targets. However, opting for a heterogeneous tree cover management scheme (with areas of very low tree cover intermixed with higher tree cover areas) will result in higher species richness at the regional level.

Furthermore, since both farmland and forest bird species show some tolerance to low tree canopy cover, functional connectivity of the landscape may be facilitated by its variegated structure or by the existence of small suitable areas that can be used as 'stepping stones' (Fischer and Lindenmayer, 2002; Saura *et al.*, 2014). This hypothesis was explored by Herrera and co-authors (2018) who have corroborated that heterogeneous forests (with low or uneven canopy cover) were more likely to provide linkage habitats for different bird assemblages, even though such habitats may detach from the generally conceived requirements of each species.

The multi-functional structure of the Mediterranean woodlands allows the existence of a more complex community exploring different niches provided by the heterogeneity of the landscape (Mulatu *et al.*, 2016). In addition, the same heterogeneity supported by the variegated structure, or the existence of small patches, facilitates functional connectivity for various species assemblages (Herrera *et al.*, 2018). The intensification of the system promoted by agro-environmental policies privileging intensive livestock density may result in the breaking of this structure (Pinto-Correia and Mascarenhas, 1999), imperilling bird diversity, as well as hindering ecological processes.

V.3. FUTURE DIRECTIONS

In the last thirty years we have witnessed a considerable and timely advance in the field of landscape ecology. Fuelled by the increasing human pressure driving the modification of natural landscapes, the awareness of several sectors of the society has now joined the concerns of ecologists in preventing these changes and their pervasive effects on overall biodiversity and ecosystem services. Within these years, several seminal or highly impacting studies have provided innovative and outstanding perspectives in the study of habitat fragmentation (Andrén, 1994; McIntyre and Hobbs, 1999; Fahrig, 2001-2003; Fischer and Lindenmayer, 2007; Haddad *et al.*, 2015), connectivity (Taylor *et al.*, 1993; Tischendorf and Fahrig, 2000; Fletcher *et al.*, 2016), and community ecology (Austin, 1999, Leibold *et al.*, 2004; Lortie *et al.*, 2004). Especially in the last decade many tools have been developed and are now available to explore the effects of both structural and functional connectivity and its implications for the conservation of species and habitats (*e.g.*, McRae *et al.*, 2008; Saura and Tomé, 2009; McGarigal *et al.*, 2012). These tools offer a large set of indices and methods specifically designed for that purpose based on graph (*e.g.*, Saura *et al.,* 2011; Luque *et al.,* 2012) or circuit theories (McRae *et al.*, 2008).

As these tools are continuously being updated to produce more precise and informative outcomes, the demand for finer-resolution data also grows in order to feed the increasingly complex algorithms. Unfortunately, movement-tracking devices have not accompanied the rate of development of the analytical tools, at least for small bird species, or at affordable costs. Consequently, quantifying functional connectivity is still a major concern in current approaches. Ideally, landscape functional connectivity should rely on empirical movement or dispersal data (Zeller *et al.*, 2012). Although birds are still on the upper percentile of the most studied *taxa* regarding connectivity (due to the rapid and feasible accessibility of occurrence data), information on species movement, dispersal or genetics still bores significant constraints when studying such small animal species in spatially scattered populations (Jacobson and Peres-Neto, 2010). The use of resistance surfaces based on habitat use or species niche is one of the most considered alternatives (*e.g.*, Ahmadi *et al.*,2017; Valerio *et al.*, 2019), but it possibly leads to overestimate resistance to movements. Because dispersal is often a short time event and generally occurs in non-habitat patches (Clobert *et al.*, 2012) such models may not conveniently capture dispersal habitat characteristics (Revilla and Wiegand, 2008; Vasudev *et al.*, 2015). Building scenarios considering non-linear parameterizations of the inversion of habitat models has demonstrated potential to produce more credible landscape connectivity measures (*e.g.*, Trainor *et al.*, 2013) as it allows accounting for larger portions of the landscape enabling dispersal (Keeley *et al.*, 2016). Yet, the lack of robust and reliable movement data hampers the development of further research and the attainment of evidence-based results over broader and finer scales to tackle the already pressing impacts of fragmentation and habitat loss in human-altered landscapes (Virkkala *et al.*, 2013). The amount of effort and investment in logistics needed to gather such information is still overwhelmingly inaccessible, thus more research and development of such technologies is necessary to advance (Engler *et al.*, 2017).

Still on technological grounds, the use of unsupervised methods of landscape characterization holds enormous potential to monitor landscape and biodiversity changes at larger scales. As several approaches available can extract the same type of information, with inevitable differences, the consequences can be dramatic when determining exact thresholds marking changes in the occurrence of species. Mainly for that reason, the adoption of such measures in conservation should always be regarded as preventive, and managers should avoid managing too close to the thresholds. More detailed and precise information is thus needed addressing the different dimensions of the niche and how they interact with each other. Satellite remote sensing, LiDAR and other very high-resolution optical information have been made available in recent years, offering innovative and unique data to assess spatiotemporal dynamics of vegetation productivity and landscape heterogeneity (e.g., Nagendra et al., 2013; Valerio et al., 2020). The acquisition of this information, still struggles with constraints of remote sensing technology in acquiring highly detailed habitat structures (Bruton *et al.*, 2015), especially regarding the vertical complexity of vegetation, or the logistics and financial cost of applying over large areas in case of LiDAR technology. Nonetheless, these technologies are already, and will most likely continue, to revolutionize the field of landscape ecology.

On another subject, most fragmentation and connectivity-related studies target topics addressing species distribution, movement and demography, or community change and assembly processes (see also Chapter I). Yet, the net impact of habitat fragmentation and landscape connectivity can extend well beyond species-specific and community attributes, and rebound in ecological processes where they are involved in, *i.e.*, the provision of ecosystem services. Theory suggests that ecosystem service provision can be negatively affected by increasing habitat fragmentation (Bovo et al., 2018) and reduced landscape connectivity, since it depends on the flow of organisms and matter (Mitchell *et al.*, 2013). By imposing constraints to flow, landscapes filter both species and matter, thus controlling the likelihood of biotic and abiotic interplay (Mitchell *et al.*, 2015). In other words, the ability of species to move throughout the landscape will determine the provision of ecosystem services able to occur at any given space and time. Though pressing this issue may be, evidence-based approaches are notably lacking in literature (Mitchell *et al.*, 2013), and the topics yet to explore are plentiful. Overall, it will be necessary to determine how the functional diversity is conditioned by landscape composition and configuration, and how it relates to the disruption of connectivity and, concomitantly, to the loss or rewiring (if it occurs) of interaction networks. Understanding the trade-offs between connectivity change and ecosystem services in fragmented landscapes will endow researchers and practitioners with improved tools for landscape planning and management (Mitchell *et al.*, 2013). As consequence of the improved benefits associated with those services, greater awareness on the importance of managing landscape connectivity will be gathered by the overall society. Birds are already well acknowledged as ecosystem service providers by pollinating plants (Traveset *et al.*, 2015), dispersing seeds (Costa *et al.*, 2018), autoregulating food webs (Lourenço *et al.*, 2018) and ecosystems (namely, crop pests:

Rey Benayas *et al.*, 2017), which makes this group a suitable model to explore these issues.

As a final plea, increasing landscape connectivity has the potential to minimize or reverse fragmentation effects (Diniz *et al.*, 2020) by improving and restoring the permeability of the landscape (Taylor *et al.* 1993). This can potentially buffer against the negative (and synergistic) effects of landscape and climate change (Krosby *et al.*, 2010), though assisted by other measures such as the increase of habitat amount and quality (Hodgson *et al.*, 2009). Landscape managers and policy-makers increasingly address ecologists and conservation researchers demanding for concrete solutions to reverse connectivity loss, to prevent further biodiversity loss and restore ecosystems services (Villard and Jonsson, 2009; Lindenmayer *et al.*, 2008; Driscoll *et al.*, 2013). Yet, the effective use of landscape connectivity as a tool in conservation planning is still very limited, mainly due to poor communication among the several actors. Communicating the outcomes of the research should be a growing commitment of the ecologists to promote effective on-the-ground manageable practices accessible to planners, managers, policy-makers and the public.

This thesis attempted to grasp over these objectives. The topics addressed concur with both the theoretical frameworks and practical concerns while advancing on the current agenda guiding landscape and community ecology, and ultimately contributing to the conservation of the natural assets in the two main forest landscapes in Portugal. For that reason, the main findings addressed in each chapter are intended to report concrete and clear management options, outlining novel and alternative perspectives to approach these landscapes. This thesis is, nonetheless, only a small window looking at a limited range of the fragmentation panchreston. In a world in change, many issues remain unsolved for the uneasy and questioning mind of the ecologist.

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UNIVERSIDADE DE ÉVORA
INSTITUTO DE INVESTIGAÇÃO
E FORMAÇÃO AVANÇADA

Contactos:

Universidade de Évora

Instituto de Investigação e Formação Avançada - IIFA

Palácio do Vimioso | Largo Marquês de Marialva, Apart. 94

7002-554 Évora | Portugal

Tel: (+351) 266 706 581