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SAVING TREES FOR SAVING BATS: TREE-LIKE FEATURES AS KEY FORAGING HABITATS FOR INSECTIVOROUS BATS IN INTENSIVELY FARMED AGRICULTURAL LANDS.

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"Não há nenhum caminho tranquilizador à nossa espera. Se o queremos, teremos de construi-lo com as nossas próprias mãos."

José Saramago

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Abstract

The loss of natural vegetation remnants and homogenization of agricultural landscapes have detrimental effects on bat occurrence. As bats are efficient pest controllers, it is important to understand the mechanisms underlying their persistence in agricultural landscapes. By comparing structural features of increasing complexity (open fields, single trees, tree lines and woodlands), we investigated the patterns of bat species richness, flight and feeding activities; and the potential effect of prey availability on these patterns. Open fields were significantly less bat rich and had lower levels of flight and feeding activities than treed features, which were differently used by distinct bat guilds. These differences were not driven by prey availability, which was similar across structural feature complexity. We conclude that the occurrence of different structural elements within agricultural landscapes provide a variety of commuting and feeding habitats for bat species with different requirements, reinforcing the importance of landscape heterogeneity to bat occurrence and species richness in agricultural landscapes.

KEYWORDS: insectivorous bats, activity patterns, prey availability, trees, agricultural landscapes.

PRESERVAR ÁRVORES PARA CONSERVAR MORCEGOS: ESTRUTURAS COM ÁRVORES COMO HABITATS DE ALIMENTAÇÃO CHAVE PARA MORCEGOS INSECTÍVOROS EM ÁREAS DE AGRICULTURA INTENSIVA.

RESUMO

A perda de vegetação natural e a homogeneização das paisagens agrícolas tem efeitos negativos na ocorrência de morcegos. Devido ao importante serviço de controlo de pragas providenciado pelos morcegos, importa perceber os mecanismos subjacentes à sua persistência nestas paisagens. Neste estudo investigámos os padrões de riqueza específica e de actividade de voo e alimentação de morcegos em estruturas de complexidade crescente (campos abertos, árvores isoladas, linhas de árvores e bosques); assim como o potencial efeito da disponibilidade de alimento sobre esses mesmos padrões. Os campos abertos apresentaram menor riqueza específica e actividades de voo e alimentação em comparação com as restantes estruturas, que foram distintamente usadas por diferentes grupos funcionais. A ocorrência de morcegos não foi influenciada por diferenças de disponibilidade de alimento entre estruturas. Os resultados da nossa investigação sugerem que estruturas com distintos graus de complexidade providenciam uma variedade de habitats que facilitam a deslocação e oferecem oportunidades de alimentação para espécies com diferentes requisitos, corroborando a importância da heterogeneidade da paisagem para a ocorrência e riqueza de espécies de morcegos em paisagens agrícolas.

PALAVRAS-CHAVE: morcegos insectívoros, padrões de actividade, disponibilidade de alimento, árvores, paisagens agrícolas.

Framework

Land conversion to agricultural purposes and intensification of management practices are the main drivers of biodiversity loss worldwide (Tilman et al., 2001), not only due to soil erosion, contamination and salinization; siltation of nearby water bodies; and contamination of superficial and ground waters by agrochemicals and fertilizers; but mainly due to alteration, fragmentation and loss of natural habitats (Czech et al., 2000; Tilman et al., 2001)

According to FAO (Food and Agriculture Organization of the United Nations), 38% of worlds terrestrial surface is explored for agricultural purposes – crops and pastures (FAOSTAT, 2016). While in the south hemisphere (Central and South America, Africa and Southeast Asia) agriculture expansion and intensification is causing great loss of natural habitats and the decline of traditional farming practices, in the North hemisphere (Europe and United States) most of the areas are already dominated by agricultural landscapes and the decline of biodiversity is mainly related to intensification of management practices (Donald et al., 2001; Tscharntke et al., 2005; Norris, 2008).

The amount of biodiversity that agricultural production systems are able to retain is different from the original natural habitat. Agroforestry and silvo-pastoral systems in particular can retain significant fractions of the original forest biodiversity; while others, such as intensively farmed crop lands retain considerably less (Norris, 2008).

Different species have different responses to land conversion for agricultural purposes (Pocock & Jennings, 2008). Smaller and generalist species (short life cycles, adapted to open habitats) benefit from the rise of feeding opportunities derived from crop production, increasing their populations; while specialist species, with habitats more restricted to forested areas, see their population number decrease with land conversion to agricultural purposes and landscape homogenization. However, more species are negatively affected by agriculture than benefited, particularly among species with small ranges (Burel et al., 1998; Phalan et al., 2011; Ameixa & Kindlmann, 2011). Because of that, land conversion and intensification of management practices leads to decreasing species richness, with the replacement of high conservation status species by least threatened ones on local species assemblages (Waltert et al., 2004; Aratrakorn et al., 2006).

Landscape heterogeneity and connectivity are of much importance to mitigate managing practices effects on local biodiversity, as landscape complexity attenuates biodiversity loss in intensively managed farm lands. Thus, biodiversity levels on complex farmed landscapes tend to be similar, regardless if they include extensive or intensive systems (Tscharntke et al., 2005). Hedgerows,

forest edges, natural vegetation remnants and fallow lands, among others, offer commuting pathways, shelter, feeding and breeding opportunities for many species, promoting their mobility and persistence in agricultural landscapes (Boughey et al., 2011).

Biodiversity and the biological processes underlying are important, not only because they provide food, raw materials, energy and income; but they are also the main drivers of ecosystem services such as nutrient cycling, microclimate and local hydrological processes regulation, seed dispersal, polinization and pest control (Altieri, 1999, Bianchi et al., 2006). Thus contributing to ecosystems resilience (Elmqvist et al., 2003).

The effects of land conversion to agricultural purposes and of intensification management practices on charismatic groups, such as birds, have been extensively studied (Opdam et al., 1985; Wiens, 1995; Fuller et al., 1997; Donald et al., 2001; Wolff et al., 2001; Waltert et al., 2004; Heikkinen et al., 2004; Whittingham & Evans, 2004; Herzog et al., 2005; Aratrakorn et al., 2006; Harvey et al., 2006; Sekercioglu et al., 2007; Haslem & Bennett; 2008). Nonetheless, those effects on bats are less understood, with most of the studies being conducted in tropical areas (Estrada et al., 2004; Harvey et al., 2006; Medina et al., 2007; Williams-Guillén & Perfecto, 2011), Australia (Lumsden & Bennett, 2005; Lentini et al., 2012); North, Center or Eastern Europe (Russ & Montegomery, 2002; Downs & Racey, 2006; Lesiński et al., 2007; Frey-Ehrenbold et al., 2013; Fuentes-Montemayor et al., 2013; Kalda et al., 2014; Heim et al., 2015); North America (Wolcott & Vulinec, 2012); and in less extent in the Mediterranean region (Davy et al., 2007; Herrera et al., 2015)

Many insectivorous bat species use agricultural landscapes as foraging ground and, like other species, are also affected by changes in land use and management practices (Wickramasinghe et al., 2003, 2004; Williams-Guillén & Perfecto, 2011), with habitat destruction and modification being considered one of the main threats to bats (Mickleburgh et al., 2002). They benefit from agricultural landscape heterogeneity and the occurrence of landscape elements particularly those consisting in water and/or vegetation (Park, 2015). As trees provide roosting opportunities to many bat species (Russo et al., 2004; Hohti et al., 2011; Altringham, 2011), different landscape elements (e.g. single trees, tree lines, small woodland patches, forest edge and riparian galleries) are also used as foraging sites or as landmarks in their commuting routes (Verboom & Spoelstra, 1999; Downs & Racey, 2006). These elements offer protection from high wind speeds, reducing energy costs associated with flight, particularly for small species, while favouring the occurrence of insects and offering protection against predators (Verboom & Huitema, 1997; Verboom & Spoelstra, 1999).

Studies on the importance of different agricultural landscape features for bats highlighted the value of even small and isolated habitat components such as scattered trees as foraging habitats for bats (Lumsden & Bennett, 2005). Within agricultural landscapes, bat abundance and species richness seems to increase with increasing tree density (Lumsden & Bennett, 2005; Lentini et al., 2012), tree cover (Heim et al., 2015), forest remnants size (Lesiński et al., 2007; Lentini et al., 2012) and landscape connectivity (Frey-Ehrenbold et al., 2013), with higher species richness (Heim et al., 2015) and activity (Downs & Racey, 2006; Wolcott & Vulinec, 2012) occurring in the proximity of treed features. Several studies also consistently reported low bat activity levels in open or low tree density lands (Russ & Montegomery, 2002; Estrada et al., 2004; Lumsden & Bennett, 2005; Downs & Racey, 2006; Medina et al., 2007; Lentini et al., 2012; Wolcott & Vulinec, 2012; Frey-Ehrenbold et al., 2013), and suggested that fields closer to forest remnants might be better buffered against outbreaks of agricultural pest insects due to higher species richness and bat activity (Heim et al., 2015).

Bat species assemblages have also been reported to differ according to tree density (Lumsden & Bennett, 2005; Williams-Guillén & Perfecto, 2011), forest remnant size (Lesiński et al., 2007) and forms of tree cover (Harvey et al., 2006). Species adapted to forage in more cluttered environments and with relatively low mobility are particularly sensitive to increasing agricultural intensification (Williams-Guillén & Perfecto, 2011) and decreasing connectivity (Frey-Ehrenbold et al., 2013), with local woodland characteristics being more important than the landscape context to relatively low mobility species, whereas the opposite is true for higher mobility species (Fuentes-Montemayor et al., 2013).

However, little is known about the relative importance of structural features of increasing complexity to bats (Kalda et al., 2014) specially their potential distinct importance to different bat foraging guilds (William-Guillén & Perfecto, 2011; Frey-Ehrenbold et al., 2013), particularly in the Mediterranean region.

With this in mind, we saw in the landscape of "Lezíria do Tejo" (Tagus river floodplain, Center Portugal) an opportunity to investigate the patterns of species richness, flight and feeding activities of bats – divided by the three main foraging guilds – along a gradient of structural features complexity: open fields, single trees, tree lines and small woodland patches; in Mediterranean intensively managed agricultural lands.

The results of our investigation are presented in the scientific article that follows.

Scientific article

Saving trees for saving bats: Tree-like features as key foraging habitats for insectivorous bats in intensively farmed agricultural lands

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Abstract

Land conversion for agricultural purposes and the intensification of management practices, are the major drivers of the global biodiversity decline. The loss of natural vegetation remnants and homogenization of agricultural landscapes have detrimental effects on many species, including bats. As they are important pest controllers, it is important to understand the mechanism underlying their persistence in agricultural landscapes. By comparing structural features of increasing complexity (open fields, single trees, tree lines and woodlands), we investigated the patterns of bat species richness, flight and feeding activities of the three main foraging guilds; and the potential effect of prey availability on these patterns; in a Mediterranean intensively managed agricultural landscape located in Tagus River flood plain ("Lezíria do Tejo"), Centre Portugal. Bats were surveyed by acoustic methods and arthropods by using light traps, during the summer of 2014. Overall we recorded 16197 bat passes, 3449 bat "feeding buzzes", and collected 3643 arthropods. More than 85% of bat passes recorded belong to the edge foragers *Pipistrellus pipistrellus*, *P. pygmaeus* and *P. kuhlii;* and to the open-space foragers *Eptesicus serotinus / E. isabellinus* and *Nyctalus leisleri*. Our results showed that open fields were significantly less bat rich and had lower levels of flight and feeding activities. Treed features were differently used by distinct bat guilds: open-space foragers were more abundant, and foraged preferentially above woodlands; edge foragers activities were higher in tree lines; and narrow-space foragers were more abundant near single trees. Differences on bat activities patterns were not driven by prey availability (measured as arthropods abundance), which was similar across structural feature complexity. We conclude that the occurrence of different structural features within agricultural landscapes provide a variety of commuting and feeding habitats for bat species with different requirements, reinforcing the importance of landscape heterogeneity to bat occurrence and species richness in agricultural landscapes.

Introduction

Agricultural land covers a large and increasing part of the terrestrial surface with recent data showing that almost 40% of the land surface is already devoted to this human activity (FAOSTAT 2016). Both land conversion for agricultural purposes and the intensification of management practices, are the major drivers of the global biodiversity decline (Tilman et al., 2001, Foley et al., 2005), since the high impact activities, such as the increasing use of agrochemicals, the loss, modification and fragmentation of natural habitats, and the reduction of landscape heterogeneity (Tscharntke et al., 2005, Foley et al., 2005) led to the depletion of refuge zones for biodiversity and consequent declines of many plants (Rich & Woodruff, 1996), invertebrates (Hendrickx et al., 2007) and vertebrates (Siriwardena et al., 1998; Donald et al., 2001; Haslem et al., 2008). However, embedded in these modified landscapes some structural features, such as scattered trees, tree lines and forest remnants may act as biological legacies of the natural vegetation cover (Manning et al., 2006; Fisher et al., 2010; Herrera & Garcia, 2009; Rudolphi et al., 2014) and can support high diversity by providing dispersal pathways, food resources, shelter, breeding and roosting opportunities (Manning et al., 2006; Sekercioglu et al., 2007).

Intensification of agriculture management practices have also a negative impact on bat occurrence in simplified agricultural landscapes (Herrera et al., 2015; Park, 2015), as landscape heterogeneity is often referred as the most important factor to support bat diversity (Vaughan et al., 1997a; Russ and Montgomery, 2002; Frey-Ehrenbold et al., 2013), both locally and at regional scale (Kalda et al., 2014).

From the conservation point of view, bats are a relevant group because several species are threatened (Mickleburgh et al., 2002). Additionally, they have been referred as suitable ecological and environmental indicators, because they are distributed worldwide, easily identifiable, easy to monitor, taxonomically stable and sensitive to several environmental factors, to which they respond in a predictable way (Jones et al., 2009; Park, 2015). They also provide valuable ecosystem services such as regulating insect populations, including those that damage crops, to a greater extent than other groups such as birds (Williams-Guillén et al., 2008; Kalka et al., 2008). For that, in recent years there has been an increasing focus on pest control service provided by bats (Agosta & Morton, 2003; Cleveland et al., 2006; Federico, et al., 2008; Boehm et al., 2011; Boyles et al., 2011; Kunz et al., 2011; McCracken et al., 2012; Maas et al., 2013; Riccucci & Lanza, 2014; Wanger et al.,

2014; Puig-Montserrat et al., 2015; Maine & Boyles, 2015), highlighting the importance of understanding the mechanisms underlying their persistence in agricultural landscapes.

Insectivorous bat activity is also commonly linked to insects abundance, as their nightly activity patterns match those of their prey (Erkert, 1982; Taylor & Oneill, 1988). Many bat species are opportunistic foragers that exploit prey swarms (Swift & Racey, 1983; Marques et al., 2004) including those of pests (McCracken et al., 2012; Puig-Montserrat et al., 2015). Further, invertebrate occurrence is also influenced by structural features, such is the case of treed sites that, by providing microhabitats, increase invertebrate abundance and diversity (Oliver et al., 2006; Winter & Moller, 2008; Lacoeuilhe et al., 2016), including for Lepidoptera (Merckx et al., 2012), which is the preferred prey of several common European species, such as *Tadarida teniotis* (Mata et al., 2016) and *Plecotus* spp. (Ashrafi et al., 2011), as well as of many threatened bats (e.g. *Rhinolophus mehelyi* (Salsamendi et al., 2008) *Rhinolophus euryale* (Goiti et al., 2004) and *Barbastella barbastellus* (Rydel et al., 1996).

Several studies have described bat species habitat preferences (Russ & Montgomery, 2002; Fuentes-Montemayor et al., 2013; Kalda et al., 2014) and some recognized the occurrence of different species assemblages across a structural gradient in agricultural landscapes (Lumsden & Bennet, 2005; Lesinski et al., 2007). Nevertheless, little is known about the relative importance of structural features of increasing complexity to species and to different foraging guilds (William-Guillén & Perfecto, 2011; Frey-Ehrenbold et al., 2013), particularly in the Mediterranean agricultural landscapes.

Therefore, the overall aim of this study is to contribute to the knowledge about the structural drivers that enhance bat occurrence in intensively managed agricultural landscapes. We investigated patterns of species richness, flight and feeding activities of the three main foraging guilds of insectivorous bats (open-space, edge and narrow-space foragers) along a gradient of structural features complexity (open fields, single trees, tree lines and woodlands), in the agricultural landscape of Tagus river alluvial plain, Center Portugal. Our specific objectives were: (1) to assess the relative importance of different structural features of increasing complexity to bat species richness, flight and feeding activities analysed separately for species and for foraging guilds; and (2) to assess if potential differences in bat activity patterns are influenced by dissimilarities of prey abundance between structural features.

We hypothesize that bat species richness, flight and feeding activities are higher in treed sites than in open fields; that structural features of different complexity influence guilds activities in different ways; and that bat occurrence is positively influenced by prey availability.

Material and methods

Study area and sampling design

This study was carried out in "Lezíria do Tejo", a periodically flooded agricultural region located at Tagus river alluvial plain in the district of Santarém, Central Portugal (39º6-29'N – 08º21-49W) (Fig. 1a). The climate is mild south Mediterranean, characterized by mild winters and hot dry season from June to September. The regional topography is plain with altitude inferior to 25m a.s.l. (Figure 1). The landscape is dominated by an intensively managed agricultural matrix mainly composed of annual irrigated crops (e.g. maize - *Zea mays*, tomato - *Solanum lycopersicum* and muskmelon - *Cucumis melo*) and, to a lesser extent, permanent crops including grape (*Vitis vinifera*), olive (*Olea europaea*) and orange (*Citrus* spp.) (*ca*. 16 % of regional land surface; authors' unpublished data). The scarce (less than 5%; authors' unpublished data) natural and semi-natural treed habitats occur in the form of scattered trees, hedgerows, small woodland patches as well as tree lines along rural paths and riparian vegetation from Tagus river and other smaller streams and ponds.

To investigate for differences on bat occurrence and prey availability in different structural features, we selected six clusters throughout the study region (Fig. 1a), spaced at least 1.6 km from each other (mean 6.66 ± 2.24 SE). Within each cluster, we selected four sampling sites (*n* = 24) corresponding to four different structural features of increasing complexity: open fields (open crop or pasture fields in which the nearest tree-cover was at least 80 m (mean 136.83 ± 17.05 SE) apart from the sampling site; Fig1b); single trees (single trees in which nearest tree-cover was at least 50 m (mean 88.00 ± 20.03 SE) apart from the sampling site; Fig1c); tree lines (lines of trees of at least 250 m (mean 390.50 ± 47.51 SE) in length; Fig1d); and woodland (small woodland patches with at least 0.27 ha (mean 0.53 ± 0.12 SE); Fig1e). The dominant tree species composing treed habitats at all study sites were black poplar (*Populus nigra* L.) and white poplar (*P. alba* L.) as well as narrow-leafed ash (*Fraxinus angustifolia* Vahl) and Willow (*Salix* spp.), all in quite similar height range (*ca*. 5-7 meters) (Table A1, Appendix A). Sampling sites were located at least 240 m (mean 568 ± 48 SE) from riparian habitats to reduce confounding effects on bat occurrence patterns across structural feature complexity (Down & Racey, 2006).
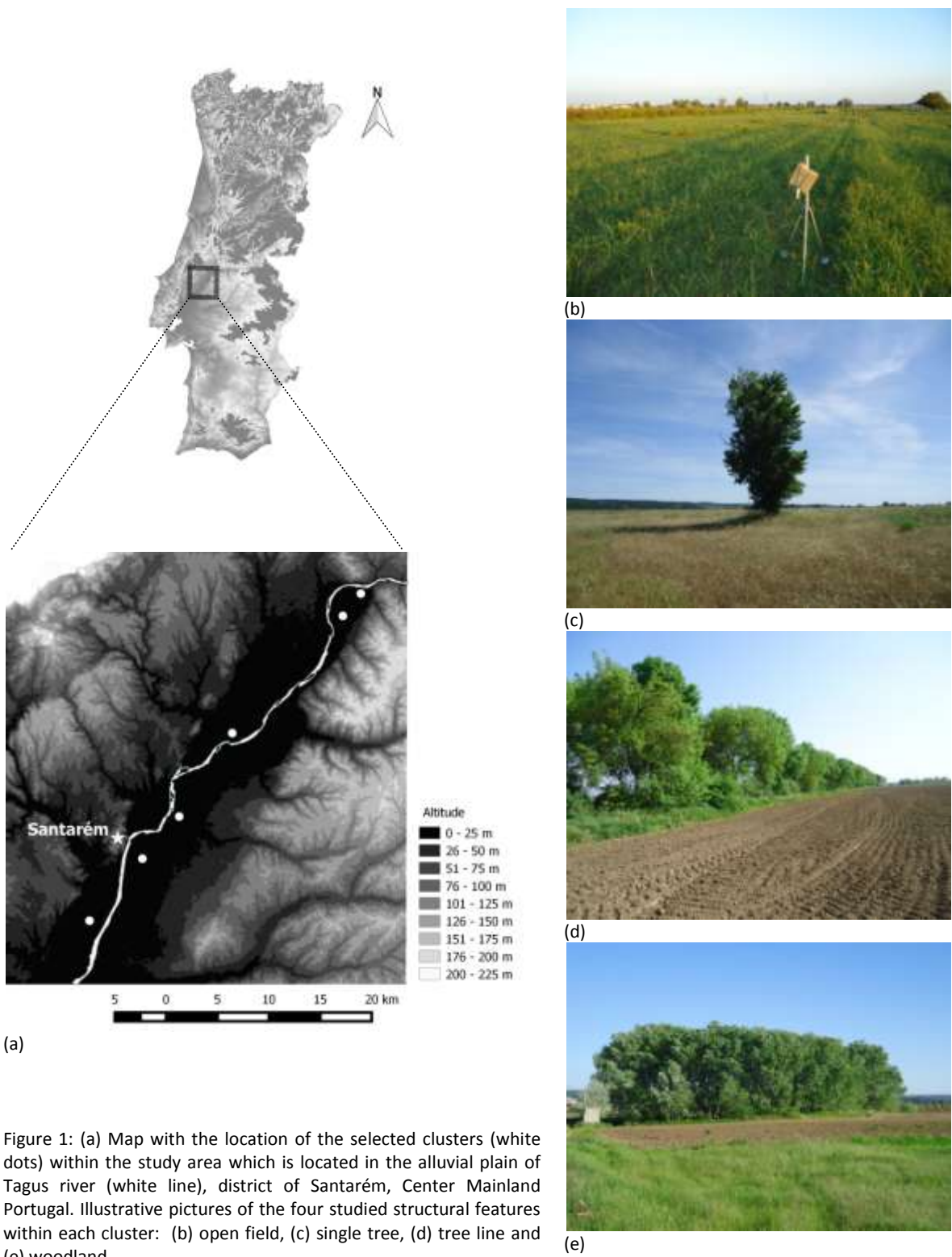
(a)

(b)

(c)

(d)

(e)

Figure 1: (a) Map with the location of the selected clusters (white dots) within the study area which is located in the alluvial plain of Tagus river (white line), district of Santarém, Center Mainland Portugal. Illustrative pictures of the four studied structural features within each cluster: (b) open field, (c) single tree, (d) tree line and (e) woodland.

To control for potential differences in the surrounding landscape of each structural feature a set of landscape-related variables (i.e., distance to water, amount of urban areas, tree cover and water surface) were determined from a 1000 m circular buffer from sampling sites using the open source geographical information system QGIS version 2.8.2 Wien (http://www.qgis.org/). This was made because these factors are widely suggested to influence both ensemble composition and activity levels of insectivorous bats (Rainho & Palmeirim, 2011; Davidai et al., 2015; Heim et al. 2015; Jung & Threlfall, 2016), something that ultimately might drive the relative effect of the structural features under study. Specifically, tree cover include total tree canopy; water surface include rivers, lakes, pools and irrigation tanks surface; and urban comprise all edified areas. Landscape variables were estimated from information available on Land Cover (CORINE 2007), updated with recent aerial photographs from Bing maps. No statistical differences were found between structural features and landscape-context attributes (ANOVA, p >0.199, Table B1, Appendix B) confirming that structural features were comparable with respect to this characteristics.

Bat surveys and species identification

Bat surveys were conducted in 2014, from late June to early October, the period of highest activity for bats in Mediterranean Region (Amorim et al., 2012). Each site was sampled four times, in different periods: early summer (late June / early July), summer (July), late summer (August), early autumn (late September / early October). Cluster 3 was not sampled in early summer. To allow for valid comparisons, all structural features within a cluster were sampled simultaneously for a complete night, starting half an hour before sunset and ending at sunrise. Hence, sampling was conducted in similar moonlight, wind and temperature conditions, thereby standardizing the effect of light levels and climatic conditions in bat assemblage composition and activity (Lang et al, 2006; Lawer & Darkoh, 2016). Further, surveys only took place on mild, calm and rainless nights, when weather conditions were favourable to bats (Erickson & West, 2002; Battersby, 2010).

We surveyed bats through acoustic monitoring. Bat echolocation calls were recorded with automatic bat detectors (D500x Pettersson Elektronik AB, Uppsala, Sweden) equipped with microphones with a sensitivity range from 10 to 190 kHz. This sensitivity range allowed us to cover the complete range of species-specific echolocation calls from the regional bat assemblage as a whole (Rainho et al., 2011). An auto-recording mode setting for 3 s without pre-trigger was used. Recordings were digitized at 300 kHz with a resolution of 16 bits. To standardize conditions and to maximize the number and quality of bat recordings, bat detectors were set at 1.2 meter above the ground, with the microphone facing upwards at a 45º angle, and placed at 5 meters from tree

trunks, in a parallel position to the edge of tree lines and woodland sites, or facing single trees. To minimize the multiple edge effects, bat detectors were placed in the middle of the edge of tree lines and woodland patches (see Jantzen & Fenton, 2013 for a similar procedure).

Echolocation calls sequences were used to determine the identity, flight activity and feeding activity of occurring bat species. These sequences were identified to species level or assigned to single or multi–genus complexes using a semi-automatic classification system prototype developed by *Plecotus – Estudos Ambientais Unip. Lda* (Silva et al., 2014) followed by a user validation as recommended by Russo & Voigt (2016) using published data on bat calls (Rainho et al., 2011). A detailed description of this system is presented by Silva et al. (2013, 2014). This system identifies and measures 19 spectral and temporal parameters of bat echolocation calls trough a custom built R script and identifies them by comparison with a reference database using assemblages of neural networks. The database used is extensive and includes 16000 individual calls from more than 1400 bats of 24 species captured and recorded in Mainland Portugal. Currently the classification system is able to identify bat species or assemblages of species with 95% mean sensitivity and a 4% mean error. Bat calls which could not be identified to species level with certainty were assigned to sonotype categories (Table 1).

To test for differences in the effect of structural features on bat species showing distinct ability to forage in different cluttered habitats, we classified them in three foraging guilds according to species morphological, echolocation and behavioural characteristics (Norberg & Rayner, 1987; Schnitzler & Kalko, 2001; Denzinger & Schnitzler, 2013): Open space bats exploit resources of airborne insects flying far from background targets and catch their prey in the "aerial" mode high above the ground or tree canopy. Edge space bats include aerial and trawling foragers that exploit airborne prey found near the edges of buildings and vegetation, in gaps, or above the ground and water surfaces, and catch their prey in the "aerial" mode. Finally, narrow-space bats include flutter detecting and passive gleaning foragers. Bats foraging in "narrow space" exploit animal prey which is positioned on or near background objects like vegetation or the ground (Table 1).

Because it was not always possible to identify bats to species level, bat species richness was defined as the minimum number of possible bat species, i.e. a higher taxonomical level than species was counted only in the instance that none of the species belonging to this group was identified (e.g. if a site had recordings identified as *Nyctalus leisleri* and *Nyctalus leisleri / Eptesicus* spp., the latter was not included; see Kalda et al., 2014 for similar procedure).

Bat passes were defined as sequences of at least two successive echolocation calls, and were used to contrast relative flight activity between structural features. Bat flight activity was measured in bat passes per hour.

Call sequences were also screened for prey capture attempts, i.e. "feeding buzzes" and bat feeding activity was measured by counting the number of "*feeding buzzes*" that occurred during each sampling night. "*Feeding buzzes*" are specific call sequences with a rapid increasing repetition rate associated with aerial prey capture, therefore indicating feeding activity (Simmons et al. 1979). The number of "*feeding buzzes*" were thus used to contrast feeding activity (feeding buzzes per night) between structural features.

Arthropods sampling and identification

We used light traps to determine prey availability (arthropods taxa richness, abundance, and biomass) associated to each structural feature. Light traps consisted of a 25 L bucket supporting a white plastic cone leading to a punctured recipient containing a sponge soaked with insecticide (Bio Kill – Jesmond Holding A. G.), and a cross shaped flight interception plate assembled above the cone. An 8 watt actinic lamp was positioned in the centre of the cone, to attract photosensitive nocturnal flying arthropods (Figure 2).

Figure 2: Light trap used to capture arthropods during this study.

Light traps were placed at ground level. In single trees, tree lines and woodland sites, they were positioned beneath the outer edge of the tree canopy, so that the cone of light shone partially into

the canopy (see Lumsden & Bennet, 2005 for a similar procedure). Similarly to bat sampling, arthropods were sampled four times along the study period. To allow for valid comparisons, all structural features were sampled simultaneously starting at sunset and ending four hours later. Arthropod sampling was carried out in separate, but consecutive nights to bat sampling, to prevent any potential interference on bat activity, particularly in single trees sampling sites; as some bat species exploit prey swarm around street lights (e.g. *Pipistrellus pipistellus*; Rydell, 1992, a behaviour also observer around light traps during this study. The tree line from cluster 1 and the open field from cluster 2 were not sampled in late June / early July, due to light trap malfunction. Samples were collected and stored in the freezer at -5ºC until processing and identification. Arthropods with less than 2 mm in length were discarded since they are smaller than the size range of prey items that bats species that occur in the study region are able to detect (Denzinger & Schnitzler, 2013). The number of arthropods from each sample was counted and used as measure of arthropod abundance. Whenever possible, specimens were identified to the family level, except for the orders Aranae and Opiliones (identified only to the order level), Lepidoptera (divided into Macrolepidoptera and Microlepidoptera) and Diptera (identified only to the sub-order level) (Barrientos, 1988; Chinery, 1993). When identification was not possible because of missing parts or uncertainty on the identification, arthropods were classified as "unidentified" and left out of the analysis of arthropods taxa richness. Some arthropods were identified to a higher taxonomical level than family. Hence, similarly to bats, arthropods taxa richness was defined as the minimum number of taxa. After arthropods identification, samples were oven-dried at 70ºC for 24 hours and weighed using a laboratory scale with an accuracy of 0.0001 g to obtain their dry weight, used as a measure of arthropods biomass.

Statistical analysis

All statistical analysis was performed with "R" software, version 2.15.1 (http://www.r-project.org) based on the methods described by Zuur et al. (2009)

To investigate differences of bat occurrence (species richness; flight activity and feeding activity, including from open-space and edge foragers guilds) between structural features (open field, single tree, tree line, and woodland) we used generalized linear mixed models (GLMMs), according to the distribution providing the best fit (glmer and lmer; R-package "lme4"; Bates et al., 2013). Poisson distribution was thus used in the model aimed to investigate differences of bat species richness between structural features, and Gaussian distributions in the models built to explore differences of bat flight and feeding activities between structural features. Since arthropods abundance,

biomass, and taxa richness were highly correlated (Spearman correlation $r > 0.70$ in all pairwise correlations), we selected arthropods abundance (as an estimate of prey availability) to be included in bat GLMMs as fixed effect, thus considering potential effect of prey availability on bat occurrence. Sampling session was used as fixed effect to account for seasonal variability on bat activity (Ciechanowski et al, 2010), which also occurred across samplings in this study (ANOVA, $df = 3$, $F = 5.27$, $p = 0.002$). To account for the variation of bats flight and feeding activities, and for prey availability, across the study area (see overall results section), cluster was included as random factor in all models. Post-hoc pairwise comparisons based on Tukey's tests (Gaussian GLMMs) and contrast analysis (Poisson GLMM) were undertaken to compare tree-like features when significant differences between treed sites and open fields were found (glht; R-package "multcomp"; Horthorn et al., 2008).The fit of the GLMMs was evaluated by calculating Pseudo R^2 values (r.squaredGLMM; R package "MuMIn"; Barton, 2013) and by visual inspection of residuals plots.

Due to the low number of bat encounters of narrow-space foragers and the skewed distribution, which persisted after transformation, a Kruskal-Wallis test (kruskal.test; R Core team, 2012) was used to test for significant differences of flight activity between structural features.

Overall bat flight and feeding activities are usually referred as being strongly correlated (O´Donnell, 2000; Heim et al., 2015). Spearman correlation tests confirmed that such is also the case in our study (Spearman correlation, $n = 92$, $r = 0.89$; $p < 0.01$) including the open-space foragers (Spearman correlation, $n = 92$, $r = 0.61$; $p < 0.01$) and edge foragers (Spearman correlation, $n = 92$, $r = 0.91$; $p < 0.01$) activities. Nevertheless, to search for different patterns between structural features, both flight and feeding activities were analysed.

ANOVA tests were used to investigate for significant patterns of bats (bat species richness, flight and feeding activities) and prey availability (arthropods abundance) across the study area, by testing differences between clusters. Differences of prey availability across structural features were also tested using ANOVA. All ANOVA tests were performed using aov function from R-package "stats" (R Core Team, 2012).

For statistical analysis purpose, except for bat species richness and narrow-space foragers activity, variables were transformed to reduce skewness and the influence of extreme values (Table A2, Appendix A); and missing values were replaced by the mean values of the samplings conducted at the same site.

Spatial autocorrelations of bat related variables were assessed through visual inspection of spline correlograms (spline.correlog function; R-package "ncf"; Bjornstad, 2013) and the results showed

that none of the variables under study are spatially auto correlated (Figure B1: Appendix B), supporting that our sampling sites where spatially independent.

Unless otherwise indicated, average values are reported as mean ± SE (standard error) throughout the text.

Results

Overall results

During 937 hours of acoustic surveys we recorded a total of 16197 bat passes. Of these, 13781 (85.1%) were identified to species level while 2416 (14.9%) were assigned to single or multi–genus complexes. Overall, we potentially detected 20 bat species in our study area. However, five species or groups of species accounted for 86.8% of all bat passes: *Pipistrellus pipistrellus* (40.3%), *P. pygmaeus*, (20.1%), *P. kuhlii* (10.1%), *Eptesicus* spp. (8.6%) and *Nyctalus leisleri* (7.7%) (Table 1). Species richness (as measured by the minimum number of bat species) at each sampling site ranged between 1 and 11. Nevertheless, bat species richness was not significantly different between clusters (ANOVA; *df* = 5, *F* = 0.912, *p* = 0.477), ranging from cluster 2 (*n* = 16; 5.5 ± 0.52) to cluster 6 (*n* =16; 6.81 ± 0.53).

Bat passes were unevenly distributed across guilds: 3227 (19.9%) belonged to open-space foragers, 12849 (79.3%) to edge foragers and only 121 (0.8%) to narrow-space foragers. The most common open-space foragers were *Eptesicus* spp. and *Nyctalus leisleri*, both corresponding to 93.3% of open-space foragers passes. More than 90% of edge foragers passes belonged to *Pipistrellus* spp. and 81% of narrow-space foragers passes were from *Myotis myotis / M. blythii and Plecotus* spp. species complexes (Table 1).

A total number of 3449 "*feeding buzzes"* were recorded. Like bat passes, "*feeding buzzes*" were unevenly distributed across guilds: 3278 (95.0%) belonged to edge foragers, 170 (4.9%) to open-space foragers and only one to narrow-space foragers. Regarding open-space foragers, most feeding activity (95.9%) belonged to *Eptesicus* spp (42.4%) and *Nyctalus leisleri* (53.5%). On the other hand, 88.7% of edge foragers feeding activity was from *Pipistrellus* spp., with *Pipistrellus pipistrellus* being the species that forages more frequently in the study area, representing a total of 66.6% of edge foragers feeding activity and 63.3% of total feeding activity observed (Table 1).

Overall bat flight and feeding activities were strongly influenced by edge foragers that total nearly 80% of all bat passes and 95% of all "*feeding buzzes*" registered (Table 1).

Despite standardized recording efforts (mean 10.6 ± 0.1 hours per cluster), we found significant differences of overall bat flight and feeding activities between clusters (ANOVA: *df* = 5, *F* = 3.408, *p* = 0.007 and *df* = 5, *F* = 4.626, *p* < 0.001, respectively). Overall bat flight activity ranged from cluster 1 (*n* = 16; 4.68 ± 1.78) to cluster 4 (*n* = 16; 32.09 ± 7.87) followed by cluster 6 (*n* = 16; 30.94 ± 15.16). Bat feeding activity also follows a similar behaviour across the study area, ranging from cluster 1 (*n* = 16; 4.06 ± 1.07) to cluster 4 (*n* = 16; 113.13 ± 49.96) followed by cluster 6 (*n* = 16; 67.88 ± 43.37) (Figure 3).
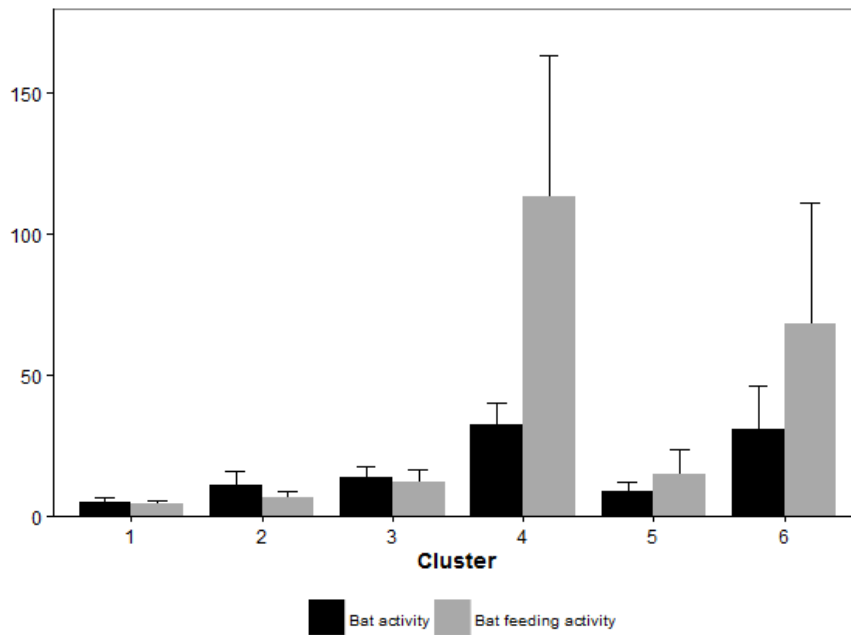

Figure 3: Mean (± SE), bat flight activity (passes/hour: black bars) and bat feeding activity (feeding buzzes/night: grey bars) recorded at the different clusters.

Table 1: Total bat passes (Pass.) and *"feeding buzzes"* (FB) recorded by species or species complexes. Mean (± SE) bat flight activity (passes/h) and mean bat feeding activity (feeding buzzes/night) at different structural features: open field (*n* = 23), single trees (*n* = 23), tree lines (*n* = 23) and small woodland patches (woodland; *n* = 23).

Species	Pass.	FB	Mean ± SE Open field Flight	Feeding	Single tree Activity	Feeding	Tree line Activity	Feeding	Woodland Activity	Feeding
Open-space foragers										
Eptesicus spp.[x]	1393	55	0.17 ± 0.04	-	1.13 ± 0.40	0.22 ± 0.11	0.68 ± 0.15	0.30 ± 0.19	4.05 ± 1.92	1.87 ± 0.88
Nyctalus leisleri[1]	1244	91	0.23 ± 0.07	0.04 ± 0.04	1.31 ± 0.43	0.22 ± 0.11	0.84 ± 0.22	0.61 ± 0.35	2.97 ± 3.11	3.09 ± 2.13
N. lasiopterus[1] / *N. noctula*[1]	7	0	-	-	0.03 ± 0.01	-	-	-	-	-
Nyctalus spp.[#]	37	0	0.03 ± 0.01	-	0.05 ± 0.02	-	0.03 ± 0.01	-	0.04 ± 0.02	-
N. leisleri[1] / *Eptesicus* spp.[x]	375	17	0.05 ± 0.01	0.04 ± 0.04	0.46 ± 0.21	0.04 ± 0.04	0.18 ± 0.05	0.04 ± 0.04	0.95 ± 0.41	0.61 ± 0.32
Tadarida teniotis[1]	171	7	0.03 ± 0.02	-	0.30 ± 0.02	-	0.23 ± 0.14	0.04 ± 0.04	0.35 ± 0.32	0.26 ± 0.26
Subtotal	3227	170	0.51 ± 0.10	0.09 ± 0.06	3.02 ± 1.01	0.48 ± 0.19	1.88 ± 0.44	1.00 ± 0.49	8.36 ± 3.71	5.83 ± 3.25
Edge foragers										
Myotis daubentonii[2]	18	2	-	-	0.02 ± 0.01	0.22 ± 0.52	0.03 ± 0.01	0.30 ± 0.19	0.03 ± 0.01	1.87 ± 0.88
Barbastella barbastellus[1]	203	12	0.03 ± 0.01	-	0.07 ± 0.02	-	0.46 ± 0.16	0.13 ± 0.07	0.30 ± 0.11	0.39 ± 0.23
Pipistrellus pipistrellus[2]	6543	2183	0.94 ± 0.54	0.83 ± 0.41	4.60 ± 1.49	6.09 ± 1.96	12.03 ± 3.43	65.39 ± 30.11	9.61 ± 6.09	22.61 ± 19.05
P. pygmaeus[2]	3251	525	1.21 ± 0.78	1.30 ± 0.83	2.39 ± 0.73	5.09 ± 2.07	4.41 ± 1.62	9.22 ± 3.26	5.31 ± 2.34	7.22 ± 4.29
P. kuhlii[2]	1634	141	0.42 ± 0.20	0.13 ± 0.07	2.81 ± 1.19	3.30 ± 1.51	1.17 ± 0.35	1.35 ± 0.59	2.29 ± 1.02	1.35 ± 0.51
Miniopterus schreibersii[3]	700	233	0.09 ± 0.06	0.09 ± 0.09	0.33 ± 0.12	0.52 ± 0.34	1.62 ± 0.64	6.83 ± 3.76	0.89 ± 0.54	2.70 ± 2.39
Pipistrellus spp.*	177	60	0.07 ± 0.04	-	0.10 ± 0.04	0.17 ± 0.08	0.29 ± 0.08	1.70 ± 0.81	0.28 ± 0.13	0.74 ± 0.45
Pipistrellus spp. / *M. schreibersii*[3+]	323	122	0.04 ± 0.02	0.09 ± 0.06	0.13 ± 0.04	0.30 ± 0.17	0.69 ± 0.23	3.48 ± 2.04	0.48 ± 0.24	1.43 ± 1.09
Subtotal	12849	3278	2.81 ± 1.41	2.43 ± 1.08	10.45 ± 3.33	15.48 ± 4.29	19.32 ± 5.00	88.13 ± 35.73	19.19 ± 8.98	36.48 ± 27.19
Narrow-space foragers										
Rhinolophus ferrumequinum[3]	14	0	0.004 ± 0.004	-	0.004 ± 0.004	-	0.004 ± 0.004	-	0.05 ± 0.03	-
M. myotis[3] / *M. blythii*[5]	55	0	-	-	0.17 ± 0.16	-	0.05 ± 0.02	-	0.02 ± 0.01	-
M. emarginatus[1] / *M. bechsteinii*[4]	2	0	-	-	0.004 ± 0.004	-	0.003 ± 0.003	-	-	-
Myotis escalerai[3]	3	0	-	-	0.004 ± 0.004	-	0.003 ± 0.003	-	0.004 ± 0.004	-
Plecotus spp.[˙]	47	1	0.004 ± 0.004	-	0.11 ± 0.06	0.04 ± 0.04	0.04 ± 0.02	-	0.04 ± 0.02	-
Subtotal	121	1	0.009 ± 0.006	-	0.29 ± 0.17	0.04 ± 0.04	0.11 ± 0.04	-	0.11 ± 0.05	-
Total	16197	3449	3.32 ± 1.50	2.52 ± 1.08	13.76 ± 3.39	16.00 ± 4.25	22.77 ± 5.41	89.13 ± 36.06	27.67 ± 11.17	42.30 ± 30.12

[#] includes *Nyctalus lasiopterus*, *N. noctula* and *N. leisleri*.
* includes *P. pipistrellus* / *P. pygmaeus* and *P. pipistrellus* / *P. kuhlii* species complexes.
[+] includes *P. pipistrellus* / *P. pygmaeus* / *M. schreibersii* and *P. pygmaeus* / *M. schreibersii* species complexes.
[x] includes *Eptesicus serotinus*[2] and *E. isabellinus*[6].
[˙] includes *Plecotus auritus*[1] and *P. austriacus*[2].
Conservation status for Mainland Portugal (Cabral et al., 2006): [1] Data deficient, [2] Least concern; [3] Vulnerable, [4] Endangered, [5] Critically endangered, [6] Not evaluated.

We collected 3643 arthropods (> 2 mm in length) belonging to 17 taxonomic orders using light traps during 360 sampling hours: 1845 (50.6%) were identified to family, 1051 (28.8%) to sub-order, 68 (1.9%) to order level, and 674 moths (18.5%) were classified into macro or micro Lepidoptera. It was not possible to identify 5 individuals.

The most abundant orders were Diptera (*n* = 1054), Coleoptera (*n* = 954), Lepidoptera (*n* = 674) and Hemiptera (*n* = 424), which together comprised *ca.* 85% of all specimens captured (Table 2, Table A3: Appendix A).

Table 2: Total and mean arthropods abundance (divided by order), arthropods biomass (g) and arthropods taxa richness (± SE) at different structural features: open fields (*n* = 23), single trees (*n* = 22), tree lines (*n* = 22) and woodlands (*n* = 23).

Arthropods	Number of specimens	Mean ± SE			
		Open Field	Single Tree	Tree line	Woodland
Order					
Diptera	1054	18.05 ± 4.80	11.74 ± 4.12	8.05 ± 2.23	9.13 ± 1.97
Coleoptera	954	17.41 ± 11.66	8.78 ± 4.23	7.14 ± 3.22	9.22 ± 3.32
Lepidoptera	674	9.73 ± 1.83	5.17 ± 1.43	8.77 ± 2.16	6.43 ± 1.24
Hemiptera	424	6.00 ± 2.11	4.52 ± 1.56	5.05 ± 1.62	3.35 ± 0.80
Trichoptera	218	2.95 ± 1.45	1.78 ± 1.42	0.82 ± 0.41	4.09 ± 2.32
Hymenoptera	178	3.36 ± 1.35	1.48 ± 0.58	1.41 ± 0.41	1.70 ± 0.46
Neuroptera	57	0.18 ± 0.08	0.35 ± 0.20	1.36 ± 0.53	0.65 ±1.11
Dermaptera	39	0.27 ± 0.18	0.13 ± 0.07	1.18 ± 0.82	0.17 ± 0.14
Araneae	18	0.55 ± 0.23	0.09 ± 0.06	0.05 ± 0.05	0.13 ± 0.07
Opiliones	4	-	0.09 ± 0.09	-	0.09 ± 0.09
Orthroptera	4	0.09 ± 0.09	0.04 ± 0.04	-	0.04 ± 0.04
Dictyoptera	3	-	0.04 ± 0.04	-	0.09 ± 0.06
Plecoptera	3	0.14 ± 0.13	-	-	-
Psocoptera	3	-	-	-	0.13 ± 0.07
Mecoptera	2	-	0.04 ± 0.04	0.05 ± 0.05	-
Strepsiptera	2	-	-	0.05 ± 0.05	0.04 ± 0.04
Ephemeroptera	1	0.05 ± 0.04	-	-	-
Unidentified	5	-	0.04 ± 0.04	0.18 ± 0.13	-
Arthropods abundance	3643	58.77 ± 15.75	34.30 ± 9.03	34.09 ± 8.05	35.26 ± 5.69
Arthropods biomass	-	0.10 ± 0.02	0.07 ± 0.01	0.09 ± 0.03	0.09 ± 0.02
Arthropods taxa richness	-	8.86 ± 0.92	6.87 ± 0.89	7.50 ± 0.88	8.78 ± 0.88

No significant differences of prey availability (arthropods abundance) between structural features were found (ANOVA, *df* = 3, *F* = 1.237, *p* = 0.301), suggesting that prey abundance is similar in all structural features.

In line with bat flight and feeding activities, prey availability was also significantly different between clusters. Arthropods abundance (ANOVA; *df* = 5, F = 4.536, P <0.001) ranged from cluster 2 (10.6 ± 3.43) to cluster 6 (71.81 ± 22.12). Arthropods biomass (ANOVA; *df* = 5, *F* = 6.109, *p* <0.001) ranged from cluster 2 (0.03 ± 0.01) to cluster 1 (0.19 ± 0.10). Finally, arthropods taxa richness (ANOVA; *df* = 5, *F* = 4.613, *p* < 0.001) ranged from cluster 2 (4.80 ± 0.67) to clusters 3 (10.25 ± 1.15) and 6 (10.25 ± 1.31).

Bat species richness across structural features complexity

Our results show that species richness (as measured by the minimum number of bat species) was significantly different between structural features. Single trees, tree lines and woodlands were more species rich than open fields (Table 3), however, were similar between them (Figure 4; Table 4). Prey availability had no significant influence in bat species richness and no significant temporal patterns were observed (Table 3).
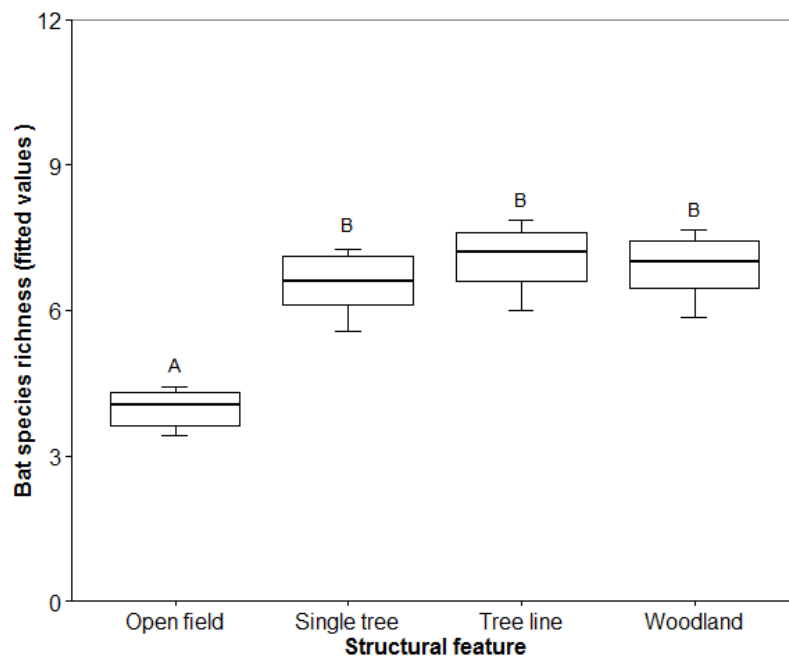
Figure 4: Boxplots showing upper whisker (maximum data point), interquartile range box (top line = 75% of the data ≤ this value; middle line = median; lower line = 25% of the data ≤ this value) and lower whisker (minimum data point) for bat species richness in different structural features (open field, single tree, tree line, and woodland) in agricultural landscapes. Fitted values predicted by GLMM are used. Different capital letters indicate significant differences between structural features ($p \le 0.05$).

Few species were limited to just one structural feature. Most were indeed recorded in all structural features, except in open fields where the presence of many bat species was not registered. Such is the case of the edge forager *M. daubentonii*, the open-space foragers *Nyctalus lasiopterus* / *N. noctula*, but particularly the narrow-space foragers, whose presence was either not confirmed in open fields (*Myotis* spp.) or were extremely rare (*R. ferrumequinum*, *Plecotus* spp.). Overall, this response pattern resulted in a more similar bat community composition between treed habitats, than between them and open fields (Table 1).

Bat flight activity across structural features complexity

Overall flight activity (as measured by the number of bat passes per hour) and the flight activities of open-space and edge foragers were significantly higher in single trees, tree lines and woodlands when compared to open fields (Table 3), but statically similar between them (Table 4). Narrow-space foragers flight activity was also significantly different between structural features (Kruskal-Wallis; df = 3, χ^2 = 12.513, p = 0.006) with higher levels of flight activity occurring also at tree-like features (Table 1). Nevertheless, some differences in flight activity patterns across tree-like features emerged. Open-space foragers were more active in woodland patches (mainly driven by *Eptesicus* spp.), while the activity of edge foragers (mainly driven by *Pipistrellus pipistrellus*) and narrow-space foragers (mainly driven by the *Myotis myotis / M. blythii* and *Plecotus* spp.) were higher in tree lines and single trees, respectively (Figure 5, Table 1).

Temporal patterns also emerged (Table 3): overall and edge foragers flight activities were significantly higher in late summer (sampling 3); on the other hand, open-space foragers flight activity was significantly lower in early autumn (sampling 4). Prey availability had no significant influence in flight activities.

Bat feeding activity across structural features complexity

In line with flight activity, overall bat feeding activity (as measured by number of "feeding buzzes" per night), and that of edge foragers, were significantly higher in single trees, tree lines and woodlands when compared to open fields (Table 3), but no significant differences between them were found (Table 4). However, open-space foragers feeding activity was significantly higher in woodlands when compared to single trees, tree lines and open fields (Tables 3 and 4), with *Nyctalus leisleri* being the main contributor to open-space foragers feeding activity detected in woodland sites (Table 1). Other patterns were noticed: edge foragers feeding activity was higher in tree lines (mainly driven by *Pipistrellus pipistrellus*) (Figure 5; Table 1) and it is worth noting that the only narrow-space forager "feeding fuzz" (from a *Plecotus* spp. specimen) was recorded at a single tree.

Overall and edge foragers feeding activities were significantly higher in late summer (sampling 3) and no significant effect of prey availability was found (Table 3).

Table 3: Summary table showing the influence of structural features (open field, single tree, tree line, and woodland), sampling period and prey availability (arthropods abundance), on bats species richness, flight and feeding activities (including from open-space and edge foragers guilds, considering cluster as random effect. Parameter estimates (± SE) and models goodness of fit (model R^2) are presented. Significance codes: '***' $p \le 0.001$, '**' $p \le 0.01$, '*' $p \le 0.05$, '.' $p \le 0.1$.

Model / Fixed effects	Structural feature			Sampling period			Prey availability	Model R^2
	Single tree	Tree line	Woodland	Sampling 2	Sampling 3	Sampling 4	Arthr. abundance	(%)
Bat species richness	0.50 ± 0.13 ***	0.58 ± 0.13 ***	0.55 ± 0.13***	0.20 ± 0.12 .	0.23 ± 0.12 .	0.12 ± 0.12	-0.004 ± 0.015	30.3[a]
Bat flight activity								
Total	1.22 ± 0.29***	1.51 ± 0.29 ***	1.37 ± 0.29***	0.21 ± 0.29	0.92 ± 0.29**	-0.45 ± 0.29	-0.02 ± 0.04	49.5
Open-space foragers	0.60 ±0.21 **	0.51 ± 0.21*	0.90 ± 0.21***	-0.004 ±0.210	-0.08 ± 0.21	-0.53 ± 0.21*	0.002 ± 0.028	33.3
Edge foragers	0.96 ± 0.29**	1.51 ± 0.29***	1.06 ± 0.29***	0.47 ± 0.29	1.44 ± 0.29***	<0.01 ± 0.29	-0.03 ± 0.04	51.6
Bat feeding activity								
Total	1.20 ± 0.37**	1.88 ± 0.37***	1.36 ± 0.36***	0.35 ± 0.362	1.20 ± 0.36**	0.16 ± 0.36	-0.07 ± 0.05	49.5
Open-space foragers	0.21 ± 0.021	0.28 ± 0.21	0.78 ± 0.21***	0.05 ± 0.20	-0.07 ± 0.20	-0.09 ± 0.20	0.004 ± 0.027	25.1
Edge foragers	1.11 ± 0.38**	1.88 ± 0.38***	1.11 ± 0.37**	0.48 ± 0.37	1.43 ± 0.37***	0.29 ± 0.57	-0.07 ± 0.05	47.5

[a] For the model with a Poisson error distribution, goodness of fit (Model R^2) do not include random effect.

Table 4: Summary table showing pairwise comparisons of bats flight and feeding activities (including from open-space and edger foragers guilds) between tree-like features (single tree, tree line and woodland; post-hoc analysis: Tukey test for Gausian GLMM and contrast analysis for Poisson GLMM). Parameter estimates (± SE) are presented. Significance codes: '***' $p \le 0.001$, '**' $p \le 0.01$, '*' $p \le 0.05$, '.' $p \le 0.1$.

Model	Tree-like features comparison		
	Tree line - Single tree	Woodland – Single Tree	Woodland – Tree line
Bat species richness[a]	0.080 ± 0.111	0.052 ± 0.112	-0.028 ± 0.109
Bat flight activity			
Total[b]	0.29 ± 0.29	0.15 ± 0.29	-0.14 ± 0.29
Open-space foragers[b]	-0.09 ± 0.21	0.30 ± 0.21	0.39 ± 0.21
Edge foragers[b]	0.55 ± 0.29	0.11 ± 0.29	-0.45 ± 0.29
Bat feeding activity			
Total[b]	0.68 ± 0.36	0.17 ± 0.36	-0.51 ± 0.36
Open-space foragers[b]	0.07 ± 0.20	0.57 ± 0.20*	0.50 ± 0.20 .
Edge foragers[b]	0.77 ± 0.37	<0.001 ± 0.37	-0.78 ±0.37

[a] GLMM with Poisson distribution.
[b] GLMM with Gaussian distribution.
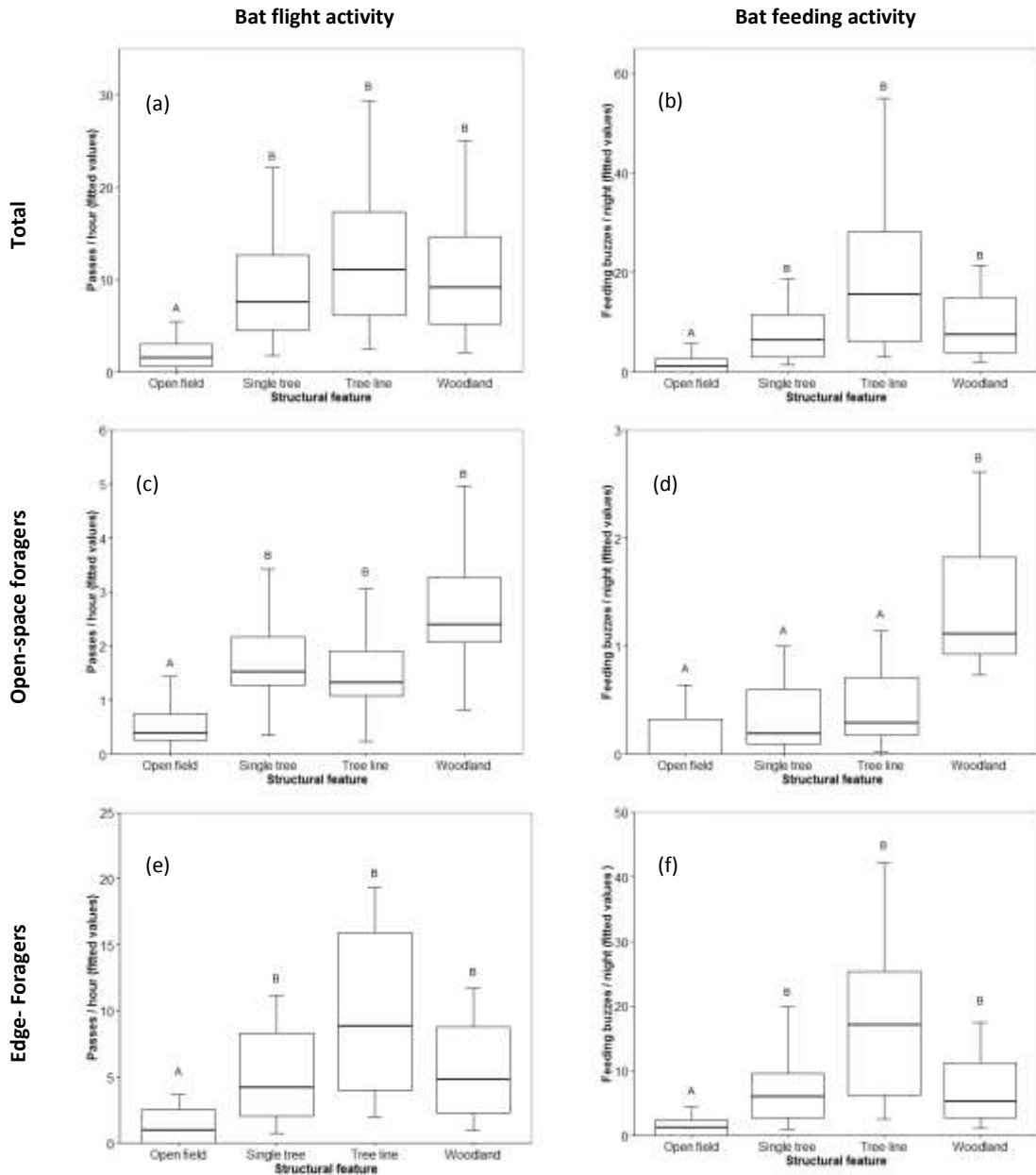
Figure 5: Boxplots showing upper whisker (non outlier maximum data point), interquartile range box (top line = 75% of the data ≤ this value; middle line = median; lower line = 25% of the data ≤ this value) and lower whisker (minimum data point) for (a) bat activity, (b) bat feeding activity, (c) open-space foragers activity, (d) open-space foragers feeding activity, (e) edge foragers activity and (f) edge foragers feeding activity at different structural features (open field, single tree, tree line, woodland) in agricultural landscapes. Fitted values predicted by GLMM are used. Different capital letters indicate significant differences between structural features ($p \leq 0.05$).

Discussion

By comparing different structural features of increasing complexity, namely open fields, single trees, tree lines and small woodland patches, we aimed to access their relative use by different bat foraging guilds in an intensively managed agricultural landscape.

As expected, our results show the importance of tree-like features (single trees, tree lines and small woodland patches) for bat species richness, flight and feeding activities, including their distinct importance for different bat guilds. However, contrary to what we hypothesized, prey availability (measured as arthropods abundance) did not influence bat occurrence. Thus, bats higher use of the tree-like features within landscape was not driven by differences on prey availability (measured as arthropods abundance) between these and open fields.

Bat species composition, spatial and temporal patterns

Many bat species were recorded using both open and treed habitats in the agricultural matrix, either for foraging or commuting, but only a few were abundant. The predominance of edge foragers *Pipistrellus* spp. and open-space foragers *Eptesicus* spp. in our records was predictable since they are abundant and widely distributed across mainland Portugal (Rainho et al., 2013). These are generalist and synanthropic species that use many different roosts (e. g. houses, trees, bridges), forage in a wide variety of habitats, including agricultural landscapes, and their occurrence is usually higher near water sites (Rainho, 2007; Dietz et al., 2009; Rainho et al., 2013), which are common and widespread in the study area. Further, the predominance of *Pipistrellus pipistrellus* over *P. pygmaeus* and *P. kuhlii* was expected as *P. pipistrellus* is known to forage in a wide range of habitats (Rainho, et al., 2013), whereas *P. pygmaeus* is a more specialized and selective species that forages and commutes preferentially along riparian habitats (Russ & Montgomery, 2002; Davidson-Watts et al., 2006), not surveyed during this study. The lower occurrence of *P. kuhlii*, also a generalist species (Russo & Jones, 2003; Rainho, 2007; Rainho et al, 2013) suggests that this is the less common of the *Pipistrellus* species in the study area.

The high activity on cluster 4 and 6 may be explained by the occurrence of unknown bat roosts near these sites (i.e. buildings or trees). The selection of clusters of sites was demanding and we did an extensive search in the study area using aerial photographs and field visits. However, we had limited information on the presence of bat roosts, which can influence bat activity levels locally. Such is the case of "Salgueiro Maia" bridge in Santarém, which characteristics make it suitable as roost for several bat species (Amorim et al., 2013) and where *Pipistrellus pygmaeus* individuals were observed roosting (Barreiro, S., pers. obs.). Further, we potentially detected 20 bat species across the study area, but the highest species richness registered was of only 11 species, suggesting differences on bat assemblages across sites. However, we did not explore these differences in our analyses.

As expected, both flight and feeding activities were higher during late summer (sampling 3) when bat activity peaks in Mediterranean areas (Amorim et al., 2012), and the lower records of open-space foragers during early autumn (sampling 4) are probably related to the reduced occurrence of *N. leisleri*, a species with seasonal migrating behaviour, capable of travelling long distances between summer and winter roosts (Hutterer et al., 2005; Dietz et al., 2009). As the winters are mild in the study area, probably most individuals do not hibernate in the region and in the early autumn many have already started their migration for the winter roosts (Shiel & Fairley, 1998; Estók, 2007).

Bat species richness across structural features complexity

Our results highlight the importance of tree-like features for bat species richness in agricultural landscapes, with species richness being almost the double in all tree-like features compared to open fields (Figure 5). These results add to the mounting evidence that treed sites support higher bat species richness (Lumsden & Bennett, 2005; Medina et al., 2007; Fisher et al., 2010; Heim et al., 2015) and indicate that even single trees are important to retain species richness across agricultural landscapes (Heim et al., 2015). This is supported by the rarity or complete absence of some species in open fields such as some narrow-space foragers (e.g. *Rhinolophus ferrumequinum*, *Myotis* spp., *Plecotus* spp.), the open-space foragers *Nyctalus lasiopterus / N. noctula,* or even the edge forager *Myotis daubentonii*. These species are either rare in the study region or restricted to densely wooded habitats such as deciduous forests and riparian galleries (Rainho et al., 2013). Moreover, some species limited detection range (e.g. *R. ferrumequinum*, *Myotis bechsteinii*, *Plecotus* spp.) makes them more sensitive to habitat fragmentation (Frey-Ehrenbold et al., 2013), thus more restricted to wooded habitats. Nevertheless, the low-intensity echolocation calls of these bats makes them difficult to survey by acoustic methods (Fenton, 2003), hence their occurrence and activity may be under recorded. The rarity of the water bat (*Myotis daubentonii*) in the study was expected. Although very common in the study area (Barreiro, S., pers. obs), this species feeds mainly by trawling insects from the surface of calm waters (Norberg & Rayner, 1987) and forages preferentially over water bodies or around riparian vegetation preferring to commute along streams over hedgerows (Rydel et al., 1999; Warren et al., 2000; Down & Racey, 2006). As referred before, sampling sites were chosen at a minimum distance from water habitats, explaining why *M. daubentonii* was rarely detected during this study.

Bat flight and feeding activities across structural features complexity

Our results showed that bat flight and feeding activities, including from the three main foraging guilds, where higher at tree-like features when compared to open fields, indicating bat preferences for treed sites over open habitats. Other authors also found similar results and consistently reported decreasing bat activity with decreasing tree density across agricultural landscapes (Lumsden & Bennett, 2005; Fisher et al., 2010); higher bat activity rates at forest edge and linear treed habitats when compared to open areas (Russ & Montgomery, 2002; Estrada et al., 2004; Downs & Racey, 2006; Medina et al., 2007; Lentini et al., 2012; Wolcott & Vulinec, 2012); and the increase of bat activity in sites closer to forest (Heim et al., 2015). Our results are also in line with the work of Frey-Ehrenbold et al. (2013) that found higher bat activity levels for all three foraging guilds around treed landscape elements, when compared to open control areas. Several hypotheses may explain this behaviour: treed landscape elements provide protection from wind, for both insects and bats foraging near vertical strata; commuting along vegetation edges reduces predation risk especially from predators that hunt using visual cues (e.g. owls), particularly at higher light levels (e.g. dawn and dusk periods or full moon nights); bats use treed landscape features as landmarks and navigation guides (Verboom & Huitema 1997; Verboom & Spoelstra, 1999).

Although open-space foragers flight activity was statistically similar between tree-like features, they showed a preference for woodland patches (mainly due to *Eptesicus* spp.). Feeding activity of this foraging guild, however, was significantly higher on woodlands than any other structural features, mainly due to the contribution of *Nyctalus leisleri*. These differences may be explained by the species specific habitat requirements. While *Eptesicus* spp. are synanthropic and opportunistic bats that forage at canopy level at woodland edges, clearings, and other linear elements (e.g. riparian galleries), preferentially within agricultural landscapes (Zunkal & Gadjosik, 2012; Rainho et al., 2013; Lisón et al., 2014); *N. leisleri* normally forages up to *ca.* 5 km from roosts above woodland, riparian vegetation and pastures, although it seems to avoid intensively farmed areas (Vaughan et al., 1997a; Water et al., 1999; Rainho et al. 2013). Higher levels of *N. leisleri* feeding activity on small woodland patches suggests that preserving these features within agricultural landscapes may retain some of the characteristics that these bats need to forage. This can be further enhanced because all of the woodland sites were located near pastures, which are a preferential foraging habitat for *N. leisleri* (Vaughan et al., 1997a; Vincent et al., 2011).

Edge foragers flight and feeding activities were both similar between tree-like features, although higher at tree lines, especially the feeding activity, mainly due to the contribution of *Pipistrellus*

pipistrellus. These results are consistent with the flight characteristics and foraging ecology of this guild. These species use woodland edges and linear elements to commute between roosts and foraging areas, and can forage along them or in nearby open areas (Verboom & Huitema, 1997; Downs & Racey, 2006; Vincent et al., 2011; Zeale et al., 2012), taking advantage of the protection that they provide including for insect prey (Verboom & Spoelstra, 1999). Despite our results, we cannot assume that edge foragers are less active in woodlands than in tree lines, as they could be using more protected edge sides of the small woodland patches, which were not always possible to survey due to access constraints or the occurrence of "pivot" irrigation systems, mainly on the surrounding maize crops.

Finally, narrow-space foragers activity was higher at single trees, particularly for *Myotis myotis* / *M. blythii* and *Plecotus* spp. Additionally, the only "feeding buzz" of this guild was recorded in a single tree. The occurrence of *Myotis myotis* / *M. blythii* and *Plecotus* spp. mainly on single trees emphasizes the importance of these features as important landscape landmarks for these species, not only for commuting, but also as foraging areas (Entwistle et al., 1996; Geva-Sagiv et al., 2015).

The existence of distinct patterns of flight and feeding activities of the three foraging guilds across tree-like features, are in line with the findings of other researches who reported differences of bat assemblages across tree density (Lumsden & Bennett, 2005; William-Guillén & Perfecto, 2011), forest remnant size (Lesiński et al., 2007) and types of tree cover (Harvey et al., 2006; Medina et al., 2007), and suggest that different structural features provide distinct opportunities for bats with different requirements. Thus emphasizing the importance of landscape heterogeneity to bat occurrence in agricultural landscapes (Park, 2015).

Influence of arthropods availability in bat occurrence

The most abundant insect orders (*Diptera*, *Coleoptera*, *Lepidoptera*, *Hemiptera*) are also the ones mainly consumed by the most common bat species in the study area (*Pipistrellus* spp., *Eptesicus* spp. and *Nyctalus leisleri*) (Vaughan, 1997b; Barlow, 1997; Waters et al., 1999; Goiti et al., 2003; Zunkal & Gadjosik, 2012; Lisón et al., 2015).

Overall prey availability was similar between structural features, supporting the findings of Lentini et al. (2012). These results can be explained by the homogeneity of agricultural practices across sampling sites within each cluster (e.g. crop assemblage, use of agrochemicals, disturbance frequency), as these influence prey availability in agricultural lands (Fahrig & Jonsen, 1998; Wickramasinghe et al., 2004). However, prey availability varied between clusters, probably because

of small differences of land management, crop assemblages and growth stage (Fahrig & Jonsen, 1998) at local scale. Nevertheless, we can assume that management practices are similar at sampling sites within each cluster.

Overall, our results suggest that, in the study area, prey availability is not the main driver of distinct patterns of bat occurrence in the structural features studied and emphasize the importance of treed features to bat flight and feeding activities, when compared to open areas, even when prey availability is at least similar at these sites. Other authors also suggest that landscape features characteristics are of primary importance for bat activity and that prey availability (measured as arthropods abundance) may play a secondary role in shaping bat foraging behaviour (Morris et al., 2010; Rainho, et al., 2010). Although prey abundance is normally used as a measure of prey availability (Lumsden & Bennett, 2005; Lentini et al., 2012), these are distinct parameters that in some circumstances may not even be related. Bats may select their foraging areas considering their prey accessibility and not only their abundance. Depending on bat species and its behaviour, different habitat features can potentially limit bats accessibility to prey and the time and energy they expend to capture it (Rainho et al., 2010).

Conclusions

Considering that bat species richness, flight and feeding activities, including those from the three main foraging guilds, were considerably lower at open areas; our results strongly support that treed habitats are of most importance to bats occurrence in intensively farmed landscapes.

The distinct preferences of species, and foraging guilds, for different tree-like features, regardless prey availability, highlight the importance of preserving the existing, and the reintroduction of new structural features to promote connected and heterogeneous landscapes able to provide a variety of commuting and feeding habitats for bat species with different requirements (Park, 2015). Additionally, as trees can provide roosting opportunities, the conservation of natural remnants with old trees is also of high importance, as they are more likely to offer roost opportunities (Ruczyński et al., 2010), not only for tree dwelling bats (Hohti et al., 2011), but also for other generalist species when choosing roosting places. Thus, the availability of roosting sites within agricultural landscapes is important for bat persistence, particularly of species with short home ranges (Rainho & Palmeirim, 2011).

Considering that bat activity is usually higher in the vicinity of treed features, fields closer to these might be better buffered against outbreaks of agricultural pest insects due to higher species

richness and bat activity (Heim et al., 2015), as pest pressure is usually lower in complex landscapes (Bianchi et al., 2006). Hence, by enhancing landscape heterogeneity and treed habitat quality we will be able to further the pest control services provided by bats. For that, the management of treed habitats within agricultural landscapes should become part of agro-ecosystem schemes.

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Final remarks

With this study we aimed to explore the relative importance of structural features of increasing complexity (open fields, single trees, tree lines and small woodland patches) to bat species richness, flight and feeding activities, including those from the three main foraging guilds (open-space, edge and narrow space foragers) in an intensively managed Mediterranean agricultural landscape. Additionally, we explored if different patterns of bat occurrence were driven by differences of prey availability.

Contrary to what we hypothesize, bat occurrence was not driven by prey availability (measured as arthropods abundance). However prey abundance measured at ground level may not be reflecting real prey availability for species that forage at different vertical strata. For that we suggest that future studies should use an assemblage of different sampling techniques to obtain more accurate data about prey availability for bats with different foraging behaviour.

However, in line with investigations undertaken in other world regions, our results confirmed that bat species richness, flight and feeding activities are higher in treed sites when compared to open fields, and that tree-like features complexity influence the occurrence of different species and foraging guilds, emphasizing the importance of heterogeneity to bats persistence in agricultural landscapes.

"Leziria do Tejo" is historically an important and fertile Portuguese agricultural region that has been suffering a process of managing practices intensification and landscape homogenization throughout time, particularly due to the increasing production of annual crops, such as BT maize to animal feed and tomato to food industry. The decreasing number of crop variety and the enlargement of production areas, in detriment of the still existing natural vegetation remnants, make this region an interesting study area to assess the effects of managing practices intensification on bats. Nonetheless, due to the high degree of landscape transformation it also presents an opportunity to investigate the effects of natural vegetation conservation and restoration measures. We end this work expressing our whish of one day take part in the latter research because that would mean that such measures were being undertaken.

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Appendix A

Table A1: Description of sampling sites (Crops_sur: Crops on the surrounding area; Crops_site: Crops on sampling site; Urban: Urban area (1000m radii); Water: Water surface (1000m radii); Trees: Tree cover (1000m radii); Dist_water: Distance to water, Dist_tree: distance to the nearest tree; Area: woodland canopy area; Length: length of tree lines)

Structural feature	Cluster	Tree species	Crops_site	Crops_sur	Urban (%)	Water (%)	Trees (%)	Dist_water (m)	Dist_tree (m)	Length (m)	Area (ha)
Open field	1	-	pasture	pasture	0.0006	0.0052	0.2242	602	173	-	-
	2	-	pasture	pasture, maize, tomato	0.0005	0.2697	0.0945	551	98	-	-
	3	-	pasture	pasture, maize	0.0003	0.0572	0.1200	243	88	-	-
	4	-	pasture	pasture, vineyards	0.0002	0.0000	0.0119	1216	125	-	-
	5	-	melon	melon, maize	0.0031	0.0002	0.0227	617	208	-	-
	6	-	tomato	tomato	0.0030	0.0005	0.0194	665	129	-	-
Single tree	1	Populus nigra	pasture	pasture, maize	0.0006	0.3493	0.2659	680	77	-	-
	2	Juglans regia	pasture	pasture	0.0145	0.0005	0.1790	760	51	-	-
	3	Fraxinus angustifolia	maize	maize	0.0001	0.0029	0.0399	246	196	-	-
	4	Fraxinus angustifolia	maize	maize	0.0001	0.0175	0.0295	844	61	-	-
	5	Salix sp.	tomato	maize, vineyard	0.0154	0.0600	0.0339	566	68	-	-
	6	Populus nigra	pasture	pasture, wheat	0.0032	0.3×10^{-4}	0.0403	672	75	-	-
Tree line	1	Populus nigra	maize	maize, pasture	0.0005	0.4694	0.3292	381	-	373	-
	2	Populus nigra	pasture	pasture, maize, tomato	0.0006	0.3012	0.0910	409	-	295	-
	3	Fraxinus angustifolia, Salix *spp.*	pasture	Pasture, maize, cabbage	0.3×10^{-4}	0.4002	0.1617	614	-	628	-
	4	Fraxinus angustifolia, Salix *spp.*	tomato	tomato	0.0026	0.1800	0.0955	612	-	375	-
	5	Fraxinus angustifolia	tomato	tomato	0.0029	0.0030	0.0271	902	-	404	-
	6	Fraxinus angustifolia	vineyard	vineyard, maize	0.0067	0.0002	0.0361	514	-	268	-
Woodland	1	Populus nigra	pasture	pasture	0.0010	0.5631	0.3452	287	-	-	0.52
	2	Betula alba	pasture	pasture, maize	0.0045	0.5×10^{-4}	0.1683	308	-	-	0.27
	3	Fraxinus angustifolia, Salix *spp.*	pasture/cabbage	pasture/cabbage, maize	0.3×10^{-4}	0.4699	0.1730	612	-	-	1.13
	4	Fraxinus angustifolia, Salix *spp.*	maize	maize	0.0006	0.4004	0.0495	345	-	-	0.40
	5	Populus alba	pasture	pasture, maize	0.0264	0.0625	0.0625	633	-	-	0.54
	6	Populus nigra, Fraxinus angustifolia, Salix *spp.*	pasture	pasture, tomato	0.0050	0.3×10^{-4}	0.0440	357	-	-	0.29

Table A2: Discription, unities, transformations and summary statistics (Mean ± SD) of transformed variables under study (Bats, Landscape and Arthropods).

Variables	Unit	Description	Transformation	Mean ± SD	Range
Bats					
Bat species richness	species	Minimum number of bat species	Not transformed	6.10 ± 2.43	1 - 11
Bat flight activity	encounters /h	Mean number of bat encounters per hour	Logarithmic	0.82 ± 0.17	0.30 - 1.08
Open-space foragers flight activity	encounters /h	Mean number of open-space foragers encounters per hour	Logarithmic	0.38 ± 0.38	0 - 1.87
Edge foragers flight activity	encounters /h	Mean number of edge foragers encounters per hour	Logarithmic	0.70 ± 0.60	0 - 2.29
Narrow-space foragers flight activity	encounters /h	Mean number of narrow-space foragers encounters per hour	Not transformed	0.13 ± 0.45	0 - 3.89
Bat feeding activity	feeding buzzes	Mean number of bat "feeding buzzes" per night	Logarithmic	0.83 ± 0.73	0 - 2.86
Open-space foragers feeding activity	feeding buzzes	Mean number of open-space foragers "feeding buzzes" per night	Logarithmic	0.17 ± 0.34	0 - 1.85
Edge foragers feeding activity	feeding buzzes	Mean number of edge foragers "feeding buzzes" per night	Logarithmic	0.78 ± 0.74	0 - 2.80
Narrow-space foragers feeding activity	feeding buzzes	Mean number of narrow-space foragers "feeding buzzes" per night	Not transformed	0.01 ± 0.10	0 - 1
Landscape					
Urban area (1000 m)	%	Proportion of edified area in a buffer area with radii 1000 m	Angular	0.05 ± 0.04	0.005 - 0.163
Water surface (1000 m)	%	Proportion of water surface in a buffer area with radii 1000 m	Angular	0.29 ± 0.30	0 - 0.85
Distance to water	meters	Minimum distance to water	Logarithmic	2.73 ± 0.18	2.39 - 3.09
Tree cover (1000 m)	%	Proportion of canopy area in a buffer area with radii 1000 m	Angular	0.31 ± 0.15	0.11- 0.63
Prey availability					
Arthropods taxa richness	families	Minimum number of arthropods families	Not transformed	8.00 ± 4.25	0 - 20
Arthropods abundance	arthropods	Number of arthropods	Square-root	5.53 ± 3.16	0 - 19
Arthropods biomass	g	Arthropods dry weight	Square-root	0.26 – 0.14	0 - 0.78

Table A3: Arthropod taxa and mean (±SE) abundance at different structural features in an agricultural landscape: open field (*n* = 23), single trees (*n* = 22), tree lines (*n* = 22) and woodland (*n* = 23).

Taxa	Number	Mean ±SE			
		Open field	Single tree	Tree line	Woodland
Araneae	18	0.55 ± 0.23	0.09 ± 0.06	0.05 ± 0.05	0.13 ± 0.07
Subtotal	18	0.55 ± 0.23	0.09 ± 0.06	0.05 ± 0.05	0.13 ± 0.07
Coleoptera					
Alleculidae	1	-	-	-	0.04 ± 0.04
Anobiidae	1	-	-	-	0.04 ± 0.04
Anthicidae	18	0.36 ± 0.23	0.26 ± 0.22	0.09 ± 0.09	0.09 ± 0.09
Aphodiidae	5	0.09 ± 0.06	-	0.14 ± 0.10	-
Byrrhidae	1	0.05 ± 0.04	-	-	-
Carabidae	436	3.82 ± 2.03	6.30 ± 3.49	3.86 ± 2.35	5.30 ± 2.51
Cebrionidae	25	0.45 ± 0.33	-	0.50 ± 0.45	0.17 ± 0.10
Cerambicidae	1	-	-	-	0.04 ± 0.04
Coccinellidae	1	0.05 ± 0.04	-	-	-
Dermestidae	3	-	0.09 ± 0.09	0.05 ± 0.05	-
Dryopidae	5	-	0.22 ± 0.22	-	-
Dytiscidae	3	0.09 ± 0.09	0.04 ± 0.04	-	-
Elateridae	6	0.14 ± 0.13	-	0.09 ± 0.09	0.04 ± 0.04
Helodidae	9	0.05 ± 0.04	-	0.05 ± 0.05	0.30 ± 0.19
Heteroceridae	1	-	-	0.05 ± 0.05	-
Hygrobiidae	1	0.05 ± 0.04	-	-	-
Lagriidae	1	-	-	-	0.04 ± 0.04
Lampiridae	91	0.41 ± 0.18	0.57 ± 0.23	1.27 ± 0.64	1.78 ± 0.62
Leiodidae	11	0.45 ± 0.26	-	0.05 ± 0.05	-
Melandryidae	1	-	-	-	0.04 ± 0.04
Mycetophagidae	245	9.27 ± 8.79	0.70 ± 0.71	0.68 ± 0.59	0.43 ± 0.25
Nitidulidae	25	0.86 ± 0.68	0.04 ± 0.04	0.05 ± 0.05	0.17 ± 0.10
Ptinidae	1	-	-	-	0.04 ± 0.04
Scarabaeidae	3	-	0.04 ± 0.04	-	0.09 ± 0.09
Scolytidae	1	-	-	-	0.04 ± 0.04
Staphylinidae	55	1.27 ± 0.76	0.48 ± 0.18	0.18 ± 0.11	0.52 ± 0.31
Throgidae	2	-	0.04 ± 0.04	0.05 ± 0.05	-
Unidentified	1	-	-	0.05 ± 0.05	-
Subtotal	954	17.41 ± 11.66	8.78 ± 4.23	7.14 ± 3.22	9.22 ± 3.32
Dermaptera					
Carcinophoridae	1	-	0.04 ± 0.04	-	-
Labiduridae	34	0.14 ± 0.13	0.04 ± 0.04	1.18 ± 0.82	0.17 ± 0.14
Labiidae	4	0.14 ± 0.07	0.04 ± 0.04	-	-
Subtotal	39	0.27 ± 0.18	0.13 ± 0.07	1.18 ± 0.82	0.17 ± 0.14
Dictyoptera					
Polyphagidae	1	-	0.04 ± 0.04	-	-
Blattidae	2	-	-	-	0.09 ± 0.06
Subtotal	3	-	0.04 ± 0.04	-	0.09 ± 0.06
Diptera					
Brachycera	469	9.23 ± 3.27	7.22 ± 2.79	1.82 ± 0.45	2.61 ± 0.90
Nematocera	582	8.73 ± 2.25	4.52 ± 1.53	6.24 ± 1.99	6.48 ± 1.38
Unidentified	3	0.09 ± 0.09	-	-	0.04 ± 0.04
Subtotal	1054	18.05 ± 4.80	11.74 ± 4.12	8.05 ± 2.23	9.13 ± 1.97
Ephemeroptera					
Myirtacidae	1	0.09 ± 0.04	-	-	-
Subtotal	1	0.09 ± 0.04	-	-	-

Table A3 (continuation): Arthropod taxa and mean (±SE) abundance at different structural features in an agricultural landscape: open field (*n* = 23), single trees (*n* = 22), tree lines (*n* = 22) and woodland (*n* = 23).

Taxa	Number	Mean ±SE			
		Open field	Single tree	Tree line	Woodland
Hemiptera					
Acanthosomatidae	1	0.05 ± 0.04	-	-	-
Anthocoridae	3	0.09 ± 0.06	-	0.05 ± 0.05	-
Aphididae	1	-	-	-	0.04 ± 0.04
Cicadellidae	119	0.86 ± 0.03	1.74 ± 1.28	1.68 ± 1.06	1.00 ± 0.38
Corixidae	10	0.23 ± 0.22	0.09 ± 0.06	0.09 ± 0.09	0.04 ± 0.04
Cydnidae	1	-	-	0.05 ± 0.05	-
Delphacidae	5	-	0.04 ± 0.04	0.09 ± 0.06	0.09 ± 0.06
Dictyopharidae	1	-	-	-	0.04 ± 0.04
Lygaeidae	3	-	0.04 ± 0.04	0.09 ± 0.09	-
Mesoveliidae	2	0.05 ± 0.04	-	-	0.04 ± 0.04
Miridae	255	4.45 ± 2.08	2.17 ± 0.56	2.77 ± 1.06	2.00 ± 0.66
Nabidae	6	0.05 ± 0.04	0.09 ± 0.06	0.09 ± 0.09	0.04 ± 0.04
Notonectidae	1	-	-	-	0.04 ± 0.04
Reduviidae	9	0.09 ± 0.06	0.22 ± 0.13	0.09 ± 0.06	-
Tigidae	1	0.05 ± 0.04	-	-	-
Veliidae	4	0.09 ± 0.06	0.09 ± 0.06	-	-
Unidentified	2	-	0.04 ± 0.04	0.05 ± 0.04	-
Subtotal	424	6.00 ± 2.11	4.52 ± 1.56	5.05 ± 1.62	3.35 ± 0.80
Hymenoptera					
Bethylidae	1	-	0.04 ± 0.04	-	-
Braconidae	72	1.50 ± 0.77	0.57 ± 0.26	0.77 ± 0.24	0.39 ± 0.12
Ceraphronidae	1	-	-	-	0.04 ± 0.04
Diapriidae	3	0.05 ± 0.04	-	0.05 ± 0.05	0.04 ± 0.04
Eulophidae	3	-	0.09 ± 0.09	0.05 ± 0.05	-
Evaniidae	1	-	-	-	0.04 ± 0.04
Formicidae	48	1.18 ± 1.16	-	0.45 ± 0.26	0.52 ± 0.29
Gasteruptiidae	1	-	0.04 ± 0.04	-	-
Ichneumonidae	18	0.27 ± 0.15	0.09 ± 0.06	0.05 ± 0.05	0.39 ± 0.17
Mutillidae	26	0.32 ± 0.27	0.61 ± 0.53	0.05 ± 0.05	1.17 ± 0.10
Myrmaridae	1	-	-	-	0.04 ± 0.04
Pompilidae	1	0.05 ± 0.04	-	-	-
Sphecidae	1	-	-	-	0.04 ± 0.04
Unidentified	1	-	0.04 ± 0.04	-	-
Subtotal	178	3.36 ± 1.35	1.48 ± 0.58	1.41 ± 0.41	1.70 ± 0.46
Lepidoptera					
Macro-lepidoptera	111	0.73 ± 0.22	1.96 ± 0.72	1.18 ± 0.39	1.04 ± 0.34
Micro-leptidoptera	563	9.00 ± 1.74	3.22 ± 0.86	7.57 ± 2.09	5.39 ± 1.20
Subtotal	674	9.73 ± 1.83	5.17 ± 1.43	8.77 ± 2.16	6.43 ± 1.24
Mecoptera					
Batticidae	2	-	0.04 ± 0.04	0.05 ± 0.05	-
Subtotal	2	-	0.04 ± 0.04	0.05 ± 0.05	-
Neuroptera					
Berothidae	1	-	-	0.05 ± 0.05	-
Chrysopidae	42	0.14 ± 0.07	0.26 ± 0.15	1.18 ± 0.48	0.30 ± 0.15
Coniopterygidae	4	-	-	-	0.17 ± 0.17
Hemerobiidae	9	0.05 ± 0.04	0.09 ± 0.06	0.14 ± 0.07	0.13 ± 0.10
Myrmeleontidae	1	-	-	-	0.04 ± 0.04
Subtotal	57	0.18 ± 0.08	0.35 ± 0.20	1.36 ± 0.53	0.65 ± 0.23
Opiliones	4	-	0.09 ± 0.09	-	0.09 ± 0.09
Subtotal	4	-	0.09 ± 0.09	-	0.09 ± 0.09
Orthroptera					
Gryllidae	4	0.09 ± 0.09	0.04 ± 0.04	-	0.04 ± 0.04
Subtotal	4	0.09 ± 0.09	0.04 ± 0.04	-	0.04 ± 0.04

Table A3 (continuation): Arthropod taxa and mean (±SE) abundance at different structural features in an agricultural landscape: open field (n = 23), single trees (n = 22), tree lines (n = 22) and woodland (n = 23).

Taxa	Number	Mean ±SE			
		Open field	Single tree	Tree line	Woodland
Plecoptera					
Capniidae	1	0.05 ± 0.04	-	-	-
Taeniopterygidae	3	0.09 ± 0.09	-	-	-
Subtotal	3	0.14 ± 0.13	-	-	-
Psocoptera					
Ectopsocidae	1	-	-	-	0.04 ± 0.04
Psocidae	1	-	-	-	0.04 ± 0.04
Unidentified	1	-	-	-	0.04 ± 0.04
Subtotal	3	-	-	-	0.13 ± 0.07
Strepsiptera					
Callipharixenidae	1	-	-	-	0.04 ± 0.04
Mengeide	1	-	-	0.05 ± 0.05	-
Subtotal	2	-	-	0.05 ± 0.05	0.04 ± 0.04
Trichoptera					
Beraeidae	2	0.09 ± 0.06	-	-	-
Hydropsychidae	20	0.18 ± 0.10	0.26 ± 0.18	-	0.43 ± 0.25
Hydroptilidae	36	1.05 ± 0.67	0.04 ± 0.04	0.05 ± 0.05	0.48 ± 0.48
Leptoceridae	4	0.05 ± 0.04	-	0.14 ± 0.14	-
Philopotamidae	2	-	-	0.05 ± 0.05	0.04 ± 0.04
Psychomyiidae	116	0.68 ± 0.35	1.43 ± 1.29	0.18 ± 0.13	2.78 ± 1.95
Unidentified	38	0.91 ± 0.52	0.04 ± 0.04	0.41 ± 0.26	0.35 ± 0.19
Subtotal	218	2.95 ± 1.45	1.78 ± 1.42	0.82 ± 0.41	4.09 ± 2.32
Unidentified	5	-	0.04 ± 0.04	0.18 ± 0.13	-
Total	3643	58.77 ± 15.75	34.30 ± 9.03	34.09 ± 8.05	35.26 ± 5.69

Appendix B

Table B1: Results of ANOVA comparisons between landscape variables (urban area, water surface and tree cover, at buffer areas with radii 1000 m) and structural features in an agricultural landscape: open field (n = 6), single trees (n = 6), tree lines (n = 6) and woodland (n = 6).

Landscape variables	Df	F	p-value
Urban area	3	0.719	0.552
Water surface	3	1.527	0.238
Distance to water	3	1.137	0.358
Tree cover	3	0.482	0.699

Bat flight activity **Bat feeding activity** **Bat species richness**

Total

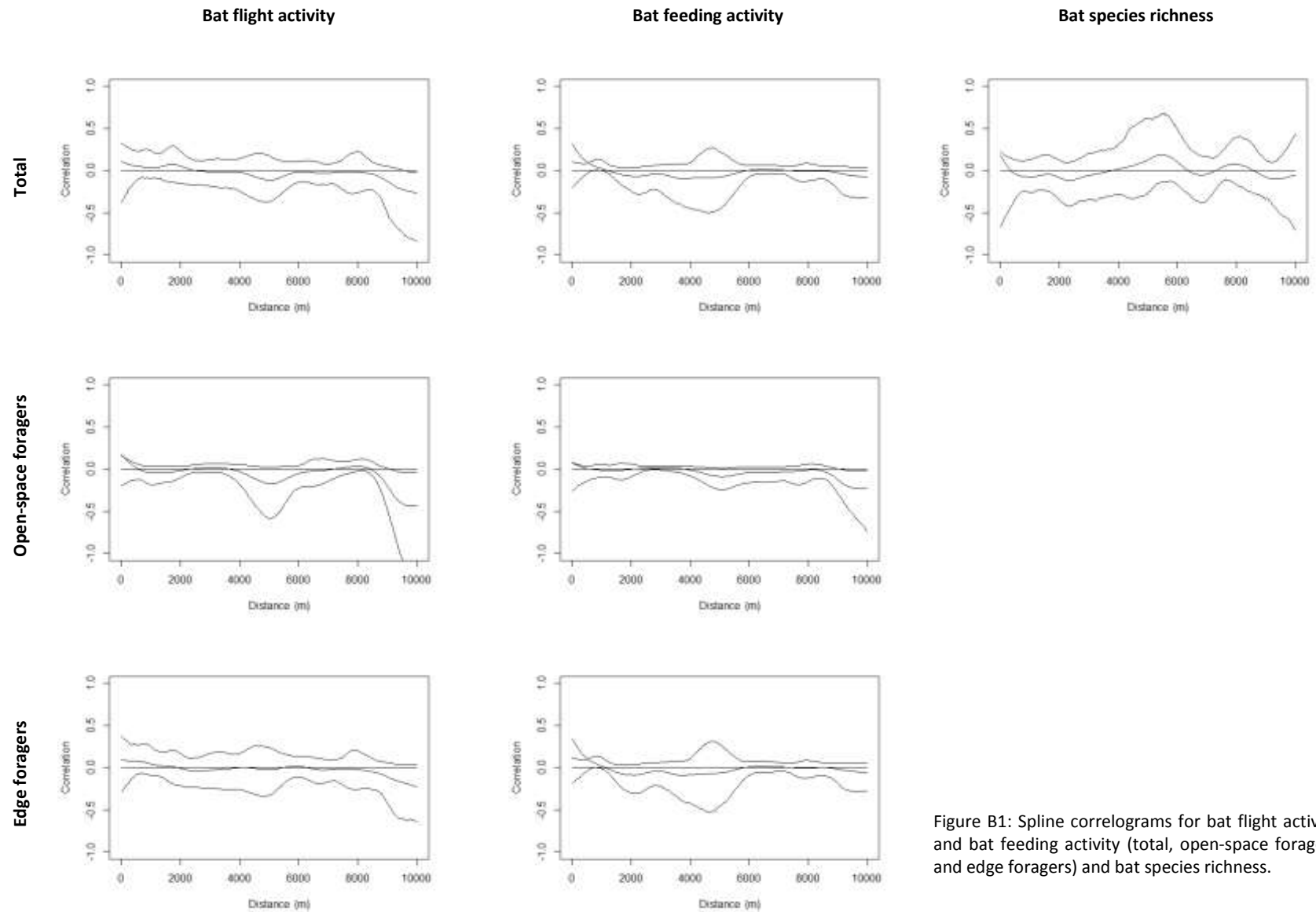

Open-space foragers

Edge foragers

Figure B1: Spline correlograms for bat flight activity and bat feeding activity (total, open-space foragers and edge foragers) and bat species richness.