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Factors influencing the bat community in vineyards: the role of landscape characteristics, natural structures and management |

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Mestrado em Biologia da Conservação

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Fatores que influenciam a comunidade de morcegos em vinhas: o papel das caraterísticas da paisagem, estruturas naturais e gestão

Resumo

As vinhas são um sistema agrícola muito representado na Europa. Essas áreas apresentam baixos níveis de biodiversidade devido à simplificação da paisagem e ao elevado uso de pesticidas, o que reduz a disponibilidade de insetos e as torna pouco atrativas para morcegos. Nós investigámos o efeito da gestão, do tipo de uso do solo e das estruturas naturais na atividade e riqueza de morcegos em vinhas a duas escalas espaciais: 500 m (escala de vinha) e 1500 m (escala de paisagem). Os resultados demonstraram que as estruturas e os habitats naturais foram mais importantes para os morcegos do que a gestão da vinha. Nós sugerimos que as prioridades de conservação devem ser criar ou manter vegetação ripária e áreas de montado. Essas estruturas naturais são uma componente chave na gestão para promover o uso das vinhas por morcegos, aumentando o seu potencial como reguladores de pragas agrícolas.

Palavras-chave: Escalas espaciais, Habitats ripários, Montado; GLM

Factors influencing the bat community in vineyards: the role of landscape characteristics, natural structures and management

Abstract

Vineyards are one of most represented agricultural systems in European landscape. These areas can present low biodiversity levels due to simplification of landscape and the high input of pesticides, which reduce insect availability and makes them unattractive for bats. We assessed the effect of farming management, land use type and natural structures on bat activity and species richness in vineyards at two spatial scales: 500 m (vineyard scale) and 1500 m (landscape scale). Our results demonstrate that natural structures and habitats were more important to the bat community than vineyard management. We suggest that conservation priorities should be to create or maintain riparian vegetation – near streams or small dams - and areas of “montados”. These natural structures are important for bat populations within or near vineyards, and a key component of agricultural management to promote bat use of vineyards, enhancing their role as pest regulators.

Keywords: Spatial scales, Riparian habitats, “Montado”, GLM

Framework

The conversion of natural ecosystems to agriculture, along with the intensification of management practices, which includes the use of pesticides, affects ecosystems and biodiversity worldwide (Tilman *et al*., 2001; Foley *et al*., 2005; Tscharntke *et al*., 2005).

In the north hemisphere (Europe and United States), landscapes are dominated by agricultural areas and the decline of biodiversity is mainly related to intensification of management practices (Donald *et al*., 2001; Tscharntke *et al*., 2005; Norris, 2008). Particularly in Europe, intensification of land use and extension of agricultural fields in the last century have caused drastic changes in the landscape matrix (Andrén, 1994; Stoate *et al*., 2001), and several habitats have been lost (Hutson *et al*., 2001). In this region, the permanent crops represent the third most predominant agricultural system (Iglesias *et al*., 2012) and within these cultures the vineyards are one of the most common, occupying in the European Union (EU), approximately, 45% of world's total area (Eurostat, 2017). In 2015, Spain, France, Italy and Portugal were the principal wine-grower Member State with 80.2% of the total EU area occupied by vineyards (Eurostat, 2017). Specifically, Portugal is a country rich in agriculture, mainly traditional agriculture (Altieri and Nicholls, 2002) and vineyards are one of the most represented agricultural systems, occupying 178.844 ha of the territory in 2017 (PORDATA, 2018). Although the area under vines in the EU (Eurostat, 2017) and in Portugal (PORDATA, 2018) has decreased over time, these agricultural landscapes represent a potential threat to the local biodiversity caused by the replacement of native habitats and simplification of the surrounding landscape structure and composition (Benton *et al*., 2003; Viers *et al*., 2013; Rodríguez-San Pedro *et al*., 2018). Indeed, these agricultural areas exhibit low levels of biodiversity (Altieri and Nicholls, 2002), and are among the least preferred habitats for vertebrate species (Pithon *et al*., 2016; Di Salvo *et al*., 2009). Furthermore, vineyards present a simplified structure which does not make them attractive for bats (Altieri and Nicholls, 2002), mainly because of the declines in insect abundance and diversity associated with these areas. Additionally, the loss of adjacent vegetation likely has important implications for bat foraging and roost availability (Di Salvo *et al*., 2009; Rodríguez-San Pedro *et al*., 2018). In fact, bats are a group species affected by agricultural intensification through of degradation and/or destruction of foraging habitats, as well roost availability limitation (Mickleburgh *et al.*, 2002; Rodríguez-San Pedro *et al*., 2018). Other problems associated to the intensification of agriculture is the increased use of agrochemicals, namely pesticides, which cause insect biodiversity declines (McLaughlin and Mineau, 1995; Geiger *et al*., 2010). Specifically, and with regards to bats, pesticides reduce the number and diversity of insects-prey which consequently can affect the bat population (Hutson *et al*., 2001; Williams-Guillén *et al*., 2016).

From the point of view of conservation, bats are a relevant group because several species are threatened (Mickleburgh *et al*., 2002). In mainland Portugal 25 bat species are known, belonging to four distinct families: Molossidae, Miniopteridae, Vespertilionidae e Rhinolophidae. All bat species are protected by the Bern Convention and the Born Convention. Furthermore, all bat species are included in Annex IV of "Habitats Directive" (92/42/CEE) and ten in Annex II. According to the Vertebrates Red Book of Portugal (Cabral *et al*., 2005), nine of the bat species are classified as Critically Endangered (CR), Endangered (EN) or Vulnerable (VU). In Europe there is The Agreement on the Conservation of Populations of European Bats – EUROBATS – that aims to protect all 53 European bat species.

Bats have been considered as suitable ecological and environmental indicators because they are distributed worldwide, positioned at high trophic levels, easily identifiable and monitored, functional and taxonomically diverse, and sensitive to several environmental factors (Jones *et al*., 2009). Additionally, insectivorous bats play critical roles as primary predators in many ecosystems. Since bats are the most important natural controllers of night flying insects, they contribute to the suppression of insect populations, such as agricultural pest species, in both natural and human-altered landscapes, and therefore contribute to the maintenance of ecosystem stability (Hutson *et al*., 2001; Kunz *et al*., 2011). Furthermore, bats potentially provide economic value by being agents of pest-control services, i.e. reduced the pesticide application and avoid crop from damage by insect-pests (Boyles *et al*., 2011).

It is recognized that many insectivorous bats use agricultural landscapes as foraging areas and are affected by changes in their management system (Wickramasinghe *et al*., 2003; 2004). So, it is important to understand how we can improve the landscape to increase the abundance and species richness of bats in vineyards. It is recognized that bats benefit from agricultural landscape heterogeneity and the presence of landscape elements particularly those contain water and/or vegetation (Park, 2015). It is known that in intensely managed agricultural habitats, landscape elements such as forest patches, linear vegetation structures (i.e. hedgerows and tree lines) and water bodies, are important for wildlife (Heim *et al*., 2018). Moreover, vegetation structures (i.e. forest edges and linear structures) are important for many species of bats, since they provide foraging habitats, are used as flyways and provide protection against predators and/or wind (Limpens and Kapteyn, 1991; Verboom and Huitema, 1997; Mickleburgh *et al.*, 2002; Fukui *et al*., 2006). So, a landscape approach is thus required to preserve and improve those features which may play a main role in sustaining bat richness and activity. Furthermore, it is also essential to evaluate the importance of different scales analysis because organisms select habitat at different spatial scales (McGarigal *et al*., 2016).

Our study evaluates the importance of management, the different land use and the natural structures in activity and richness of bats in Mediterranean vineyards at two spatial scales: vineyard scale (500 m) and landscape scale (1500 m). This article also intends to find ways to enhance agricultural landscapes for increase crop pest reduction by bats in vineyards.

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

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Research paper

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Abstract

Vineyards are one of most represented agricultural systems in European landscape. These areas can present low biodiversity levels due to simplification of landscape and the high input of pesticides, which reduce insect availability and makes them unattractive for bats. We assessed the effect of farming management, land use type and natural structures on bat activity and species richness in vineyards at two spatial scales: 500 m (vineyard scale) and 1500 m (landscape scale). Our results demonstrate that natural structures and habitats were more important to the bat community than vineyard management. We suggest that conservation priorities should be to create or maintain riparian vegetation – near streams or small dams - and areas of “montados”. These natural structures are important for bat populations within or near vineyards, and a key component of agricultural management to promote bat use of vineyards, enhancing their role as pest regulators.

1. Introduction

The current global biodiversity crisis is caused by global changes, which include converting natural habitats into agricultural areas and intensifying agriculture practices (Tilman *et al*., 2001; Foley *et al*., 2005). Both processes occur across the globe and result in losses or degradation of ecosystems leading to biodiversity losses worldwide (Tilman *et al*., 2001; Tscharntke *et al*., 2005). In Europe, the conversion of large areas into agricultural fields and pastures have caused drastic landscape changes in recent decades, resulting in the widespread loss of natural habitats (Andrén, 1994; Hutson *et al*., 2001; Stoate *et al*., 2001). As a consequence, in European landscapes, almost half of the land surface is dedicated to agriculture (Stoate *et al*., 2009). Field crops and grazing livestock are the most important farming systems, followed by permanent crops (Iglesias *et al*., 2012), which include vineyards. European vineyards account for approximately 45% of world's total area (Eurostat, 2017) making the continent the most relevant for this agricultural product. Within Europe, the distribution of vineyards is highly concentrated in the southern countries. Spain, France, Italy and Portugal were the main wine-grower member states representing 80.2% of the total area occupied in Europe by vineyards in 2015 (Eurostat, 2017).

Vineyards may pose a threat to biodiversity because of the conversion of native habitats and simplification of the surrounding landscape structure (Benton *et al*., 2003; Viers *et al*., 2013; Rodríguez-San Pedro *et al*., 2018). Both the simplified ecological structure and homogeneous landscape support low levels of biodiversity (Altieri and Nicholls, 2002) and can make vineyards one of the least preferred habitats for several groups of vertebrate species (Pithon *et al*., 2016; Di Salvo *et al*., 2009).

Although many insectivorous bat species use agricultural landscapes for foraging (Wickramasinghe *et al*., 2003), vineyards are among the less used, probably because of their simplified structure (Altieri and Nicholls, 2002). Most vineyards are also intensively managed with high inputs of agrochemicals and pesticides, which cause severe declines in insect abundance and diversity, decreasing the availability of insect-prey (McLaughlin and Mineau, 1995; Geiger *et al*., 2010). Commonly, near these areas natural vegetation is also lost resulting in a reduced tree cover and roost availability (Mickleburgh *et al.*, 2002; Di Salvo *et al*., 2009; Rodríguez-San Pedro *et al*., 2018). As a result, bat activity is limited in these areas and bat populations can be severely affected (Hutson *et al*., 2001; Williams-Guillén *et al*., 2016).

One of the main strategies to reduce the input of agrochemicals in agricultural landscapes is to use biological controllers. Natural pest regulation is an important ecosystem service in these areas provided by several organisms: pathogens, parasitoids or predators. For example, fungal entomopathogens can infect insect pests (Shahid *et al*., 2012); wasps parasitize insects also contributing to pest control (Zhang *et al*., 2007); and spiders and Coccinellids consume large numbers of insect pests being widely used in biological control (Obrycki and Kring, 1998; Chatterjee *et al*., 2012). Vertebrate species, such as insectivorous bats and birds, can also contribute decisively to natural pest regulation (Maas *et al*., 2016; Puig-Montserrat *et al*., 2015; Barbaro *et al*., 2016).

In fact, insectivorous bats are important insect predators in many ecosystems (Hutson *et al*., 2001). Since bats are one of the most important natural controllers of night flying insects, they can contribute to the suppression of insect populations, such as agricultural pests, in both natural and human-altered landscapes, and to the maintenance of ecosystem stability (Hutson *et al*., 2001; Kunz *et al*., 2011). So, bats can deliver economic value of pest-control services, i.e. reduced the pesticide application and avoid crop from damage by insect-pest (Boyles *et al*., 2011). All species of insectivorous bats are potentially important as insect prey consumers (Hutson *et al*., 2001) but common bat species are more likely to exert a significant reduction of insect pest populations (Lindell *et al*., 2018) because of the large number of individuals. The combined high biomass of common species within the overall community, and their flexible use of the landscape will enable these bats to be more relevant in the provisioning of the pest regulation ecosystem service, even in agricultural areas.

Thus, it is important understand how we can improve the landscape features to increase the abundance and species richness of bats in vineyards. It is known that in intensely management agricultural habitats landscape elements, such as forest patches, linear vegetation structures (i.e. hedgerows and tree lines) and water bodies, are important for wildlife (Heim *et al*., 2018). Moreover, vegetation structures (i.e. forest edges and linear structures) are important for many species of bats, since they provide foraging habitats, are used as flyways and can provide protection against predators and/or wind (Limpens and Kapteyn, 1991; Verboom and Huitema, 1997; Mickleburgh *et al.*, 2002; Fukui *et al*., 2006). Therefore, a landscape approach is thus required to preserve those features which may play a main role in sustaining bat richness and activity. Although several studies describe the importance of tree cover and natural structures for bats in intensely management agricultural habitats (Heim *et al*., 2015; Kalda *et al*., 2015; Toffoli, 2016; Heim *et al*., 2018), little is known about these structural features in vineyards (Froidevaux *et al*., 2017; Rodríguez-San Pedro *et al*., 2018). But this information is key to promote bat use of vineyards and to potentially increase pest reduction by these flying vertebrates.

So, our aim was assess the importance of the management of vineyards, of different land uses and of natural structures adjacent and within these agricultural areas for bat activity and richness.

Our specific aims were to (i) determine which bat species use vineyards; and (ii) infer which of the land uses, of natural structures and vineyard management types most influence bat activity and richness. We also investigated this topic for the most abundant species in vineyards, which may have a higher potential of providing pest regulation services. We did these analyses at two spatial scales - vineyard scale (500 m) and landscape scale (1500 m) - in these agricultural lands.

2. Materials and methods

2.1. Study area

The study area was located in southern Portugal, Évora district (38°34N, 7°54W) (Figure 1). This area has a Mediterranean climate with characteristic mild winters and long summers with hot and dry conditions (Rivas-Martinez and Loidoi, 1999) from June to September. It has a low annual rainfall (609 mm) and average annual temperatures range from 9.3 to 23.3º C (IPMA, 2018). In this area, the topography is plain with altitude ranging from 100 to 400 m.

The landscape is dominated by a Mediterranean agro-silvo-pastoral system, the “montado”. This system consisting of tree stands of evergreen cork (*Quercus suber*) and/or holm (*Q. rotundifolia*) oaks intermixed with extensive agricultural areas. Other less represented land uses include meadows, pastures and fallows, olive groves, eucalyptus plantations, vineyards, pine groves, shrubs and small villages (Galantinho and Mira, 2009; Rainho and Palmeirim, 2011; Medinas *et al*., 2013).

In this study, we selected 29 sampling sites in 10 large vineyards, but three were excluded from further analysis due to sampling problems. Mean distance between 26 sampling sites was 1157.36 ± 496.81 m (mean ± SD).

Figure 1: Map of study area in south of Portugal (Évora district) and location of sampling sites in vineyards (n=26) (obtained using QGIS 2.18.14).

2.2. Bat echolocation call recording and identification

Bat call sampling occurred in 2017, from July to August. Each site was sampled during six consecutive nights, taking into account weather conditions favorable to bats: mild, calm and rainless nights (Erickson and West, 2002; Battersby, 2010). On each night sampling started 30 minutes before sunset and lasted until sunrise. Bat echolocation calls were recorded using automatic stationary bat detector systems. We used Pettersson D500x detectors (sampling frequency: 300 kHz). An auto-recording mode setting for 2 seconds was used.

We manually identified each bat pass to species level when possible or assigned to single or multi–genus complexes using Audacity 2.1.2 and a semi-automatic classification system prototype developed by Plecotus – Estudos Ambientais Unip. Lda (Silva *et al*., 2014). This system identifies and measures 19 spectral and temporal parameters of bat echolocation calls through a custom built R script. Call classification is done by using assemblages of neural networks built based on a reference database that includes 16 000 individual calls from more than 1 400 bats of 24 species captured and recorded in mainland Portugal.

This classification system is able to identify bat species or assemblages of species with 95% mean sensitivity and a 4% mean error. The results from the semi-automatic system were reviewed using the "Chave de identificação acústica de morcegos de Portugal continental" (Rainho *et al*., 2011) and other bibliographic references (for example, Russo and Jones, 1999; Russo and Jones, 2002; Obristh *et al*., 2004; Russo and Papadatou, 2014).

A bat pass was defined as a sequence of two or more echolocation calls made as a bat flew past the detector (Thomas and West, 1989). Echolocation calls sequences were used to determine species richness and assess the activity of bats. Bat species richness was defined as the minimum number of possible bat species, because it was not always possible to identify bats to species level. Thus, a higher taxonomical level than species, *i.e.* genus, or phonic group, was counted only when none of the species belonging to this group were previously identified individually. In addition, bat activity was measured as the number of recorded bat passes during the sampling period, six nights.

2.3. Landscape variables

The surrounding landscape of vineyards may have a strong influence on the bat community of these agricultural areas (Froidevaux *et al*., 2017). Hence, we analyzed the effect of land use near vineyards on bat presence and abundance. In this way, we created buffers with radii of 50, 100, 150, 300, 500, 750, 1000 and 1500 m around the center point of each sampling sites to extract landscape characteristics using the open source geographical information system QGIS Desktop 2.18.14. The smallest of these scales (50 m) represents site-specific characteristics of vineyard, whereas the larger scale (1500 m) represents the landscape scale around the vineyards. Within each buffer, we calculated the proportion of land cover categories (i.e., urban area, olive groves, semi-natural habitat or “montado”, waterline and wetland, unproductive area, waterline with trees, tree line, water body, pasture and vineyard – Table 1A in Appendix A) from information available on Land Cover (COS, 2007) and agricultural areas (IFAP, 2016). Although we used detailed land cover data, agricultural areas can be highly dynamic with marked changes on vegetation structure that may impact the bat community. Thus, we further assessed the accuracy of the land cover classification and delimitation using recent aerial photographs (visualized with Bing maps).

We used LecoS (Landscape Ecology Statistics – QGIS-Plugin; Jung, 2016) to analyze the composition and configuration of the 10 land cover categories mentioned above. Specifically, we calculated four landscape metrics: landscape proportion (Lp) - the proportion of the cells from a specific class of the total number of cells of the classified raster; edge length (E_length) - the total length of all patches from a specific class; number of patches (Npatch) - the number of patches identified for each class; and patch density (P_density) - the total density of patches in the landscape across all patch types. In addition, we obtained three landscape indexes: Shannon's Diversity index (DIV_SH) - the proportional abundance of every patch of a certain type, multiplied by that proportion; Shannon's equitability (DIV_EV) - the distribution of the patches within the total area; and Simpson's Diversity index (DIV_SI) - the diversity of the landscape mosaic in terms of the combination of number of patches and extent of each patch type. Finally, we calculated for each sampling site the distance to three known important habitats for bats: (i) semi-natural habitat or "montado", (ii) water bodies, and (iii) waterlines with trees. The description of each variable is present in Table 1.

Table 1: Description of explanatory variables used in models of 500 and 1500 m and the corresponding transformation.

Variable code	**Description**	**Transformation**	
		500 m	**1500 m**
Dist_snatural_habitat	Distance to semi-natural habitats	square root	square root
Dist_water_bodies	Distance to water bodies	square root	square root
Dist_waterline_trees	Distance to waterlines with trees	square root	square root
E_length_olive	Edge length of olive groves and fruit crops	square root	square root

E_length_snatural_habitat	Edge length of semi-natural habitats	-	square root
E_length_urban_area	Edge length of urban areas	square root	-
E_length_vineyard	Edge length of vineyards	✓	-
Lp_olive	Landscape proportion of olive groves and fruit crops	arcsin of square root	-
Lp_pasture	Landscape proportion of pastures	arcsin of square root	-
Lp_snatural_habitat	Landscape proportion of semi-natural habitats	arcsin of square root	arcsin of square root
Lp_treeline	Landscape proportion of tree lines	arcsin of square root	arcsin of square root
Lp_urban_area	Landscape proportion of urban areas	-	arcsin of square root
Lp_vineyard	Landscape proportion of vineyards	✓	-
Lp_water_bodies	Landscape proportion of water bodies	arcsin of square root	-
Lp_waterline_trees	Landscape proportion of waterlines with trees	arcsin of square root	arcsin of square root
Npatch_pasture	Number of patches of pastures	-	square root
Npatch_snatural_habitat	Number of patches of semi-natural habitats	-	square root
Npatch_urban_area	Number of patches of urban areas	square root	-
Npatch_water_bodies	Number of patches of water bodies	square root	square root
Npatch_waterline_trees	Number of patch of waterlines with trees	-	square root
Pdensity_olive	Patch density of olive groves and fruit crops	square root	-

Pdensity_pasture	Patch density of pastures	square root	square root
Pdensity_snatural_habitat	Patch density of semi-natural habitats	square root	square root
Pdensity_urban_area	Patch density of urban areas	square root	square root
Pdensity_vineyard	Patch density of vineyards	✓	-
Pdensity_water_bodies	Patch density of water bodies	square root	logarithm
Pdensity_waterline_trees	Patch density of waterlines with trees	-	logarithm

Note: ✓: variable not transformed; – : variable was not used in final models.

During the exploratory analysis of the landscape variables we found that the buffers of the smaller spatial scales (50, 100, 150 and 300 m) were composed mainly of vineyards, while the other land use categories were absent or occurred infrequently. Therefore, we excluded the spatial scales lower than 500 m from further analysis. From the remaining spatial scales we assessed only the smaller (500 m – vineyard scale) and the larger (1500 m – landscape scale) scales for the sake of simplicity.

2.4. Statistical analysis

To understand the influence of landscape heterogeneity and the natural structures in vineyards on activity and richness of the bat community, we performed several statistical analyses. All statistical analyses were performed with “R” software (Version 3.3.0) based on the methods described by Zuur *et al*. (2009). We used Generalized Linear Models (GLM) which consist of three steps: (i) choosing a distribution for the response variable, (ii) defining the systematic part in terms of covariates, and (iii) specifying the relationship/link between the expected value of the response variable and the systematic part.

Firstly, we did exploratory analysis to detect possible non-linear relationships between the response variables - bat activity, species richness and activity of four common species: *Pipistrellus kuhlii, Pipistrellus pygmaeus, Pipistrellus pipistrellus*, and *Nyctalus leisleri* - and landscape variables. We performed correlations graphics to assess the strength of these relationships and select the best candidate variables for the models. We then created a correlation matrix of all candidate explanatory variables to check for possible collinearity. For each pair of independent variables showing high collinearity (|r|>0,7), we only selected the most biologically meaningful variable for further analysis. The explanatory variables to be included in the model building process were either square root, arcsin of square root or log transformed to approach a normal distribution and reduce the effect of potential outliers (Zuur *et al*., 2007) (Table 1). Because the management of the vineyard most likely has strong implications in the activity and species richness of bats in these areas we included this variable in all models. Using information from surveys applied to the managers and wine producers we coded each sampling site as Integrated Farm Management (IFM – farming system aimed to production sustainability by using agrochemical inputs under a set of rules and application safety periods) or organic (farming system that excludes the use of synthetic fertilizers and pesticides aiming to optimize the productivity and suitability of the agroecosystem).

Because some sampling sites were located in the same large vineyard area we compared two types of models for each response variable (for example: bat activity) to assess the need to incorporate this information in our analyses (Zuur *et al*., 2009). First, we built a Generalized Least Squares model (GLS) and then a Linear Mixed Model (LMM) that included the random factor vineyard area (~ 1 | vineyard) using the nlme package (Pinheiro *et al*., 2016). We then used the Akaike's Information Criterion (AIC) value to identify the best model (model with the lower AIC value). After selecting the model type, we did a variable selection of the fixed components to obtain the final model with command step in case of GLS model. For LMM, we excluded variables until we have a final model with only significant variables. In these cases, we used summary command to inspect the significance of the variables and the anova command to apply sequential testing. We plotted the response curve against the predicted values for all final model variables with significant relations. Finally, we assessed the model assumptions by visual examination of residuals' plots (residuals vs fitted values, normal Q-Q, scale-location, and residuals vs leverage).

3. Results

In total, we recorded 3432 bat passes during the sampling season, which corresponded to an average bat activity of 22 passes/night/site. Of these, 2580 (75.17%) were identified to species level while 850 (24.77%) were assigned to single or multi–genus complexes. Only two bat passes were not identified.

We detected 19 species or groups of species (7 species and 12 groups of species) but more than 90% of the bat activity was concentrated on the genus *Pipistrellus* (Table 2). Specifically, the most common species were *P. kuhlii* (33.19%), *P. pygmaeus* (23.75%), *P. pipistrellus/P. pygmaeus* (13%), *P. pipistrellus* (11.13%), the phonic group *Eptesicus serotinus/E. isabellinus* (3.55%) and *Nyctalus leisleri* (3.32%).

As referred above, the most common species was *P. kuhlii,* which was detected in 25 of the 26 sampling sites surveyed (96.15%). We recorded the two other *Pipistrellus* species, *P. pygmaeus* and *P. pipistrellus*, in 21 of 26 sampling sites (80.77%). Other common bat species were *N. leisleri*, which was present in 18 of 26 sampling sites (69.23%) and *Miniopterus schreibersii*, recorded in 13 sampling sites (50%). We also detected rare bat species or groups of species, such as *Barbastella barbastellus*, *Nyctalus lasiopterus*/*N. noctula*, *Plecotus auritus/P. austriacus* and *Rhinolophus mehelyi*/*R. euryale*. These species were recorded in a low number and in different sampling sites: *B. barbastellus* was present in 2 sampling sites – (7.69% - VIN26 and VIN27), and *N. lasiopterus*/N. *noctula, P. auritus/P. austriacus* and *R. mehelyi*/R. *euryale* were present in only 1 site (3.85% - VIN20, VIN28 and VIN3, respectively).

Species richness peaked in sites VIN26 and VIN27, where we recorded eight bat species, and had the lowest value in VIN2, where we only detected one species.

Table 2: Bat species detected, number of bat passes and number of sampling sites where each bat species was detected.

SPECIES	BAT PASSES	OCCURENCE IN SAMPLING SITES (N sites=26)
Barbastella barbastellus	3	2
Eptesicus serotinus/E. isabellinus	122	15
Myotis daubentonii	11	7
Myotis myotis/M. blythii	10	5
Miniopterus schreibersii	115	13
Myotis sp.	2	2
Nyctalus lasiopterus/N. noctula	1	1
Nyctalus leisleri	114	18
N. leisleri/E. serorinus/E. isabellinus	75	17
N. leisleri/N. lasiopterus/N. noctula	54	14
Plecotus auritus/P. austriacus	1	1
Pipistrellus kuhlii	1139	25
Pipistrellus pipistrellus	382	21
P. pipistrellus/P. kuhlii	85	8
P. pipistrellus/P. pygmaeus	446	22
P. pipistrellus/P. pygmaeus/M. schreibersii	10	4
Pipistrellus pygmaeus	815	21
P. pygmaeus/M. schreibersii	44	6
Rhinolophus mehelyi/R. euryale	1	1
Unidentified	2	1

3.1. Bat activity and species richness in vineyards

Total bat activity showed a strong relation with two distinct freshwater habitats, waterlines and small ponds. Our results suggest that bats are more active near waterlines with trees and on sites with a higher proportion of water bodies, within a buffer of 500 m (Table 3). The response curve of distance to waterlines with trees shows that estimated bat activity decreases from this habitat until 1000 m away. Further than this distance the predicted bat activity is close to 0 and there is no relation with distance to waterline with trees (Figure 2a). According to our model, the proportion of water bodies in a 500 m buffer also influences directly the activity of bats (Figure 2b). We estimate that sites with only 10% of water body cover (proportion of) have an activity level of 200 bat passes during six nights. And the only site with 30% proportion of water bodies is predicted to have approximately 800 bat passes. Two other variables were included in this model, but had no significant effect, distance to water bodies (positive relation) and patch density of urban areas (negative relation).

Table 3: Model of bat activity at 500 m scale; model adjusted $R^2 = 52.48\%$; model p-value = 0.0005. Variable p-value codes: ‘***’ $p \leq 0.001$, ‘**’ $p \leq 0.01$.

Variable	**Estimate**	**Std. Error**	**t value**	**p-value**
Intercept	141.228	166.851	0.846	0.4069
Dist_water_bodies	10.137	5.022	2.019	0.0565
Dist_waterline_trees	-9.601	2.805	-3.423	0.0026 **
Lp_water_bodies	1334.581	284.607	4.689	0.0001 ***
Pdensity_urban_area	-50695.616	37569.930	-1.349	0.1916

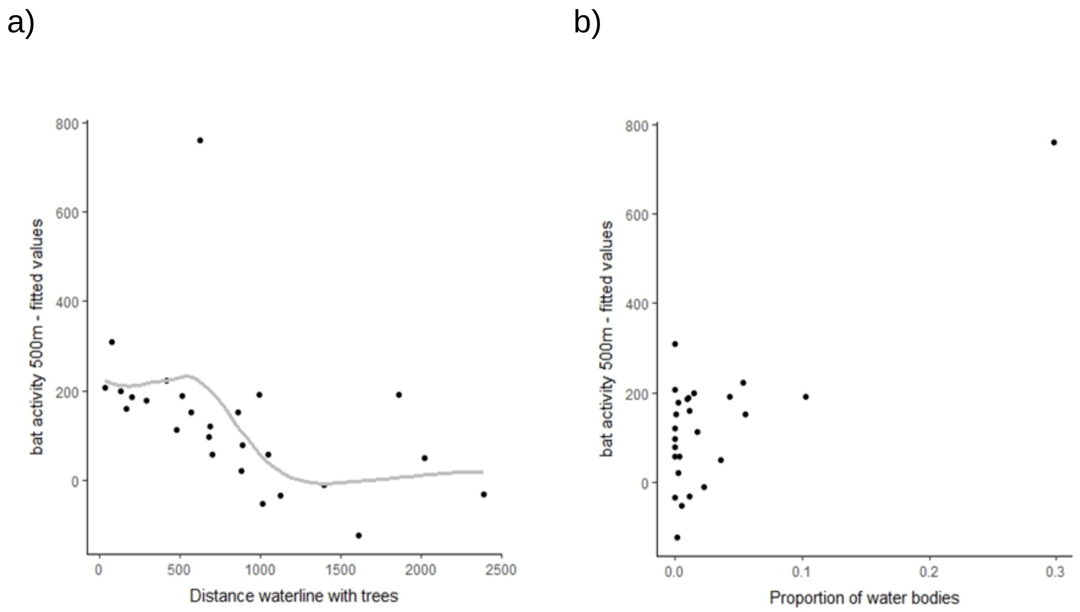


Figure 2: Relationships between bat activity model (500 m scale) and distance to waterline with trees (a) and to proportion of water bodies (b).

Our results revealed that bat species richness also increases with increasing proportion of waterlines with trees (Table 4). The maximum species richness (eight bat species) occurs in sites where the proportion of waterlines with trees also has the highest value (approximately 3%) (Figure 3). Two other landscape variables were included in this model, proportion of water bodies (positive effect) and patch density of vineyards (negative effect), although the relationship with species richness in vineyards was not significant.

Table 4: Model of bat species richness at 500 m scale; model adjusted $R^2 = 39.56\%$; model p-value = 0.0027. Variable p-value codes: ‘***’ $p \leq 0.001$.

Variable	Estimate	Std. Error	t value	p-value
Intercept	5.114	0.691	7.401	< 0.0001 ***
Lp_water_bodies	3.979	2.078	1.915	0.0686
Lp_waterline_trees	21.820	5.508	3.962	0.0007 ***
Pdensity_vineyard	-253300	145700	-1.738	0.0962

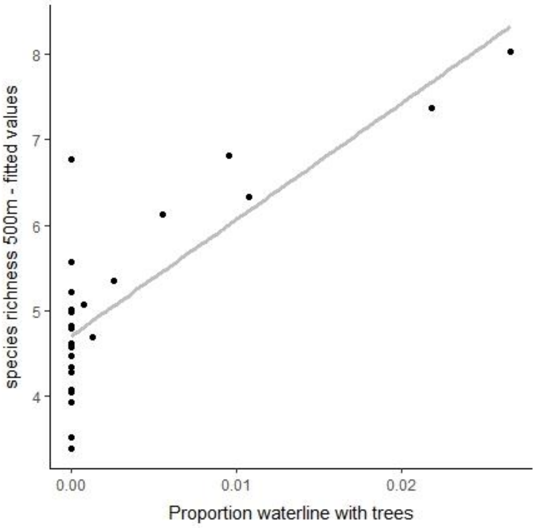


Figure 3: Relationship between fitted values of bat species richness model (500 m scale) and landscape proportion of waterline with trees.

3.2. Activity of common bat species in vineyards

The activity of *P. kuhlii*, the most common bat species in our data set, decreased with distance to the waterlines with trees, while it increased with patch density of water bodies or small dams. However, both these variables had a non-significant relation with the activity of this species (Table 5).

Table 5: Model of *P. kuhlii* activity at 500 m scale; model adjusted R^2 = 11%; model p-value = 0.1003.

Variable	Estimate	Std. Error	t value	p-value
Intercept	65.137	52.391	1.243	0.2263
Dist_waterline_trees	-2.643	1.670	-1.582	0.1272
Pdensity_water_bodies	51135.271	28304.496	1.807	0.0839

The model of *P. pygmaeus* activity had a large number of variables, but none had a significant effect. Landscape proportion of tree line, distance to waterline with trees, landscape proportion of olive groves and semi-natural habitats and number of patches of urban area appear to have a negative effect on the activity of this bat species. On the other hand, patch density of pasture was the only variable which had a positive effect (Table 6).

Table 6: Model of *P. pygmaeus* activity at 500 m scale; model adjusted R^2 = 15.46%; model p-value = 0.1611.

Variable	Estimate	Std. Error	t value	p-value
Intercept	148.353	73.650	2.014	0.0584
Dist_waterline_trees	-2.670	1.452	-1.839	0.0816
Lp_olive	-121.275	67.746	-1.790	0.0894
Lp_snatural_habitat	-72.991	40.805	-1.789	0.0896
Lp_treeline	-1011.010	517.072	-1.955	0.0654
Npatch_urban_area	-33.573	22.494	-1.493	0.1520
Pdensity_pasture	44168.254	23652.984	1.867	0.0774

In case of *P. pipistrellus*, the increasing distance to waterline with trees had a negative effect on the activity. Also the higher proportion of vineyards had a negative effect on the activity of this bat species (Table 7). Figure 4a shows that there is a high activity of *P. pipistrellus* near waterlines and a marked decline in areas further away from this habitat; at 500 m from waterlines we estimate that the activity of this species is halved. Simultaneously, the highest activity levels occur when the proportion of vineyards is less than 15% of the 500 m radius buffer (Figure 4b). Other agricultural areas, such as pastures and olive groves, had a negative effect on *P. pipistrellus* activity, but both these relationships did not reach significance.

Table 7: Model of *P. pipistrellus* activity at 500 m scale; model adjusted R^2 = 39.42%; model p-value = 0.0051. Variable p-value codes: '***' p ≤ 0.001, '*' p ≤ 0.05.

Variable	Estimate	Std. Error	t value	p-value
Intercept	69.789	13.094	5.330	< 0.0001 ***
Dist_waterline_trees	-0.920	0.405	-2.271	0.0338 *
Lp_pasture	-27.868	18.833	-1.480	0.1538
Lp_vineyard	-34.564	15.472	-2.234	0.0365 *
Pdensity_olive	-6631.705	4368.590	-1.518	0.1439

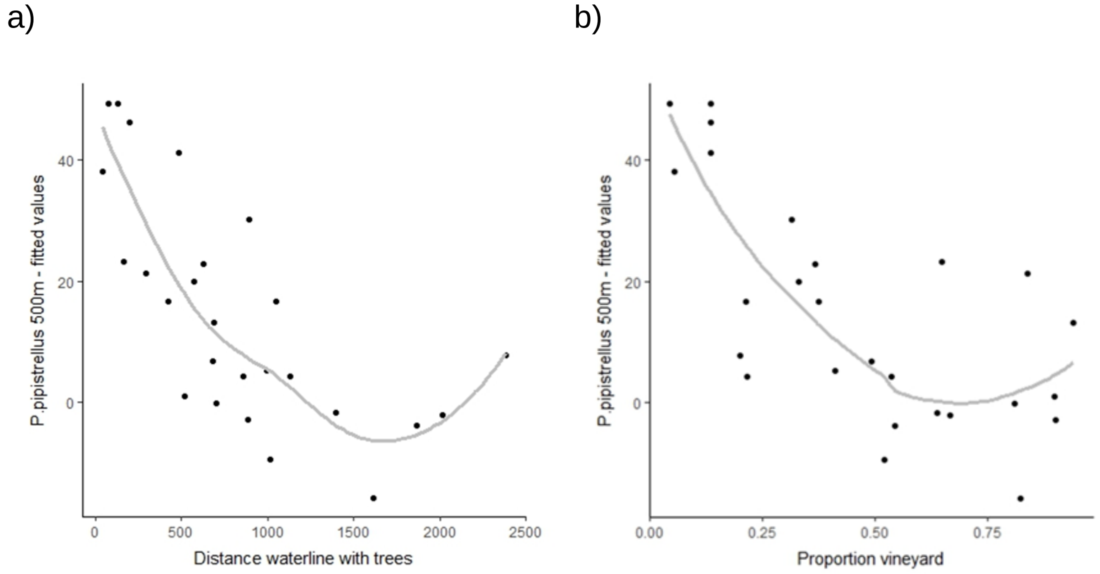


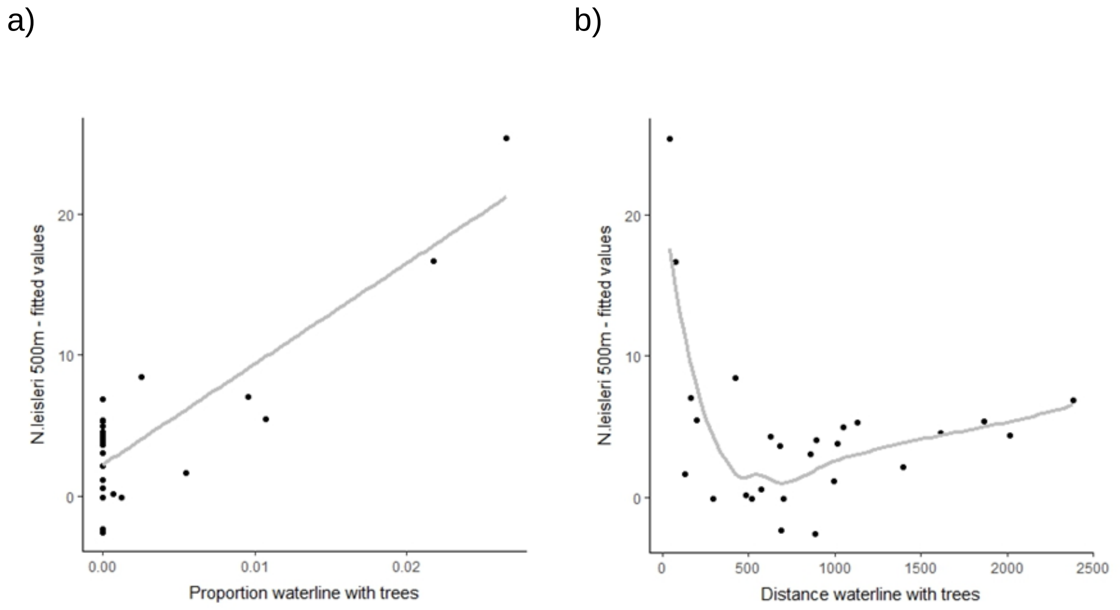
Figure 4: Relationships between fitted values of *P. pipistrellus* model (500 m scale) and distance to waterline with trees (a) and landscape proportion of vineyard (b).

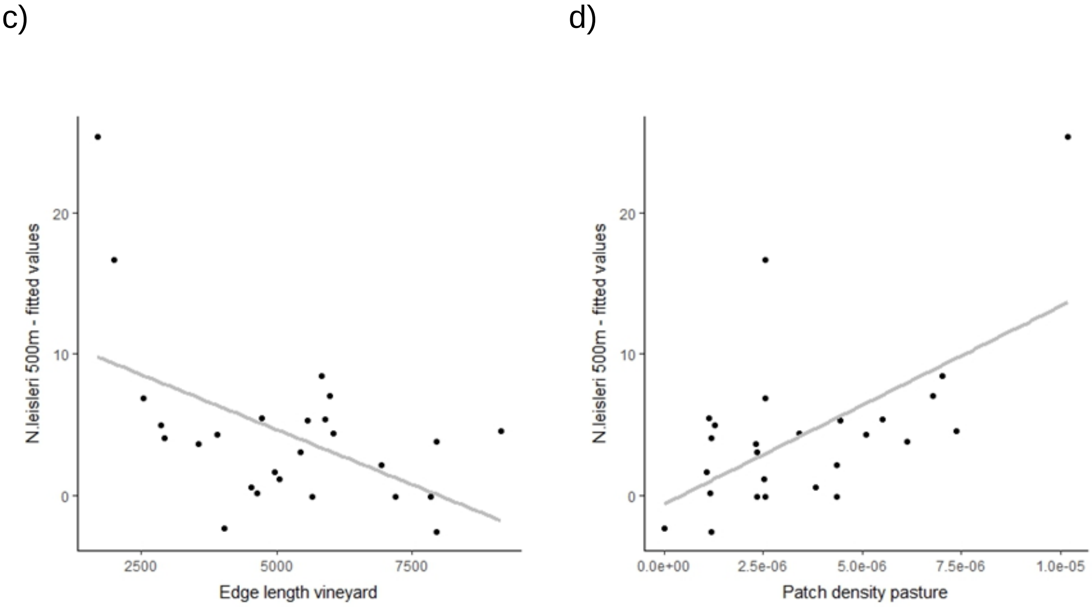
The activity of *N. leisleri* was related to a high number of landscape variables (Table 8). Our model suggests that activity of this species is higher in areas with higher proportion of waterline with trees, which corresponds to approximately 2.8% of the 500 m buffer (Figure 5a). In contrast, the distance to waterlines with trees appears to have a positive influence on the activity, until approximately 500-1000 m the distance of this habitat had a negative effect on the activity of this bat species (Figure 5b). Additionally, the *N. leisleri* activity was higher when edge length of vineyard decreases, and the highest value of activity of this bat species is observed when this variable presents values <2500 m

(Figure 5c). *N. leisleri* activity was also higher when density of patches of pasture and urban area increases. The higher values occur when patch density of pastures or of urban areas is approximately 0.00001 (Figure 5d, Figure 5e). The distance to water bodies appears to positively influence the activity of *N. leisleri*, but this relationship did not reach significance.

Table 8: Model of *N. leisleri* activity at 500 m scale; model adjusted R^2 = 83.72%; model p-value < 0.0001. Variable p-value codes: ‘***’ p ≤ 0.001, ‘**’ p ≤ 0.01, ‘*’ p ≤ 0.05.

Variable	Estimate	Std. Error	t value	p-value
Intercept	-6.814	3.646	-1.869	0.0772
Dist_water_bodies	0.122	0.075	1.605	0.1249
Dist_waterline_trees	0.203	0.078	2.613	0.0171 *
E_length_vineyard	-0.002	< 0.001	-4.152	0.0005 ***
Lp_waterline_trees	74.360	20.620	3.605	0.0019 **
Pdensity_pasture	3702	864.600	4.282	0.0004 ***
Pdensity_urban_area	1909	845.600	2.257	0.0359 *





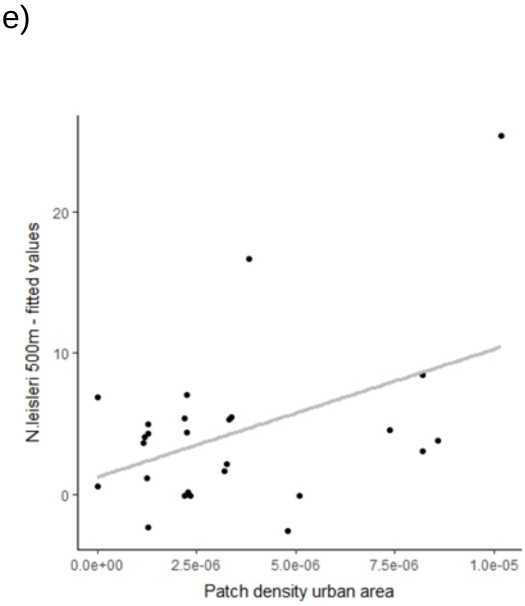


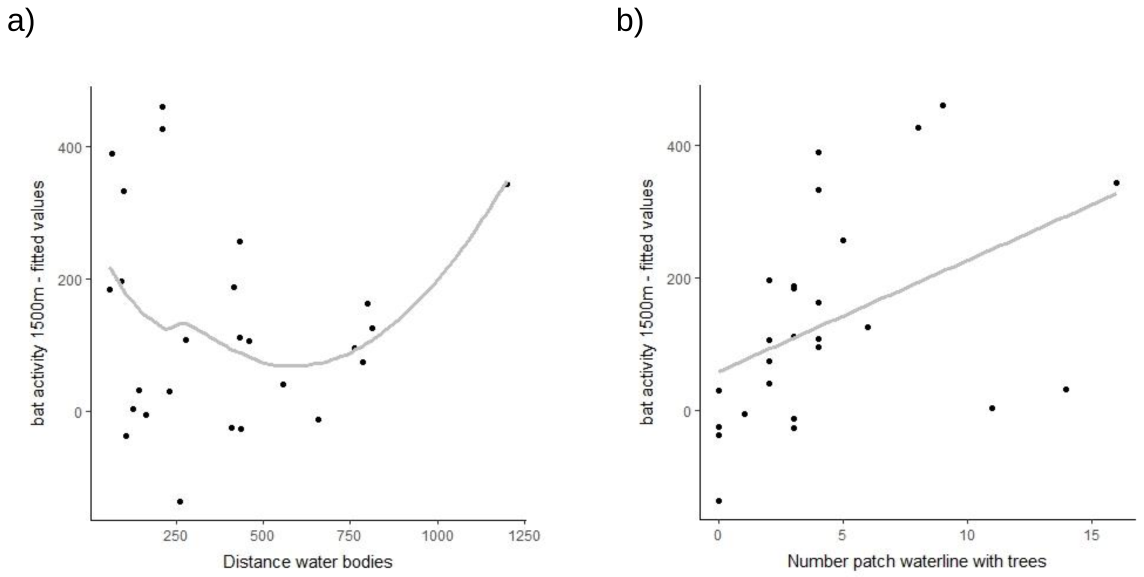
Figure 5: Relationships between fitted values of *N. leisleri* model (500 m scale) and landscape proportion of waterline with trees (a), distance to waterline with trees (b), edge length of vineyard (c), patch density of pasture (d) and urban area (e).

3.3. Bat activity and species richness at landscape scale

In 1500 m scale, the total bat activity was related to the distance and availability of water, more specifically with the distance to water bodies (negative effect) and number of patches of waterline with trees (positive effect) (Table 9). Bat activity peaked next to water bodies and decreased until 750 m away (Figure 6a). The number of waterline with trees patches had a marked effect: vineyard sites with five patches had between 150 and 400 bat passes compared to almost no bat activity in sites without patches of riparian vegetation (Figure 6b). Another variable included in this model was the proportion of urban area, which had a negative effect on bat activity. Higher activity of bats occur when proportion of urban area is close to 0%, while it decreased markedly when urban areas cover 10% or more (Figure 6c).

Table 9: Model of bat activity at 1500 m scale; model adjusted $R^2 = 48.52\%$; model p-value = 0.0005. Variable p-value codes: ‘***’ $p \leq 0.001$, ‘*’ $p \leq 0.05$.

Variable	Estimate	Std. Error	t value	p-value
Intercept	276.025	105.572	2.615	0.0158 *
Dist_water_bodies	-11.409	4.545	-2.510	0.0199 *
Lp_urban_area	-819.165	195.884	-4.182	0.0004 ***
Npatch_waterline_tree	157.948	33.577	4.704	0.0001 ***



c)

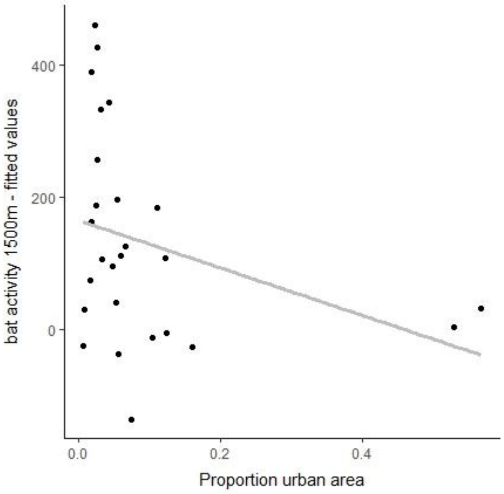


Figure 6: Relationships between fitted values of bat activity model (1500 m scale) and distance to water bodies (a), number of patches of waterline with trees (b) and landscape proportion of urban area (c).

At the landscape scale, the proportion of waterline with trees had a positive effect in bat species richness (Table 10). We recorded a higher species richness in sites with higher proportion of waterline with trees; they had approximately 1.5% of this habitat (Figure 7). Two other variables were included in final model: number of patches of pasture (negative effect) and patch density of water bodies (negative effect). However, both showed a non-significant relation with bat species richness.

Table 10: Model of bat species richness at 1500 m scale; model adjusted R^2 = 41.15%; model p_value = 0.0020. Variable p-value codes: '*' p ≤ 0.05.

Variable	Estimate	Std. Error	t value	p-value
Intercept	-15.627	11.890	-1.314	0.2023
Lp_waterline_trees	19.153	7.526	2.545	0.0185 *
Npatch_pasture	-0.341	0.245	-1.393	0.1775
Pdensity_water_bodies	-1.539	0.817	-1.884	0.0728

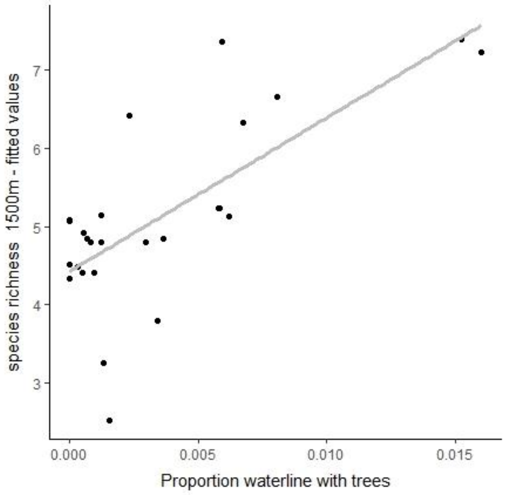


Figure 7: Relationship between fitted values of bat species richness model (1500 m scale) and landscape proportion of waterline with trees.

3.4. Activity of common bat species at landscape scale

The activity of *P. kuhlii* decreased with higher proportion of urban area (Figure 8a), whereas it increased when the density of semi-natural habitats increases (Table 11). The higher activity values occur in sites with relatively high density of semi-natural habitats or “montados” (0.003%) (Figure 8b).

Table 11: Model of *P. kuhlii* activity at 1500 m scale; model adjusted R^2 = 24.15%; model p-value = 0.01596. Variable p-value codes: ‘*’ p ≤ 0.05.

Variable	Estimate	Std. Error	t value	p-value
Intercept	-69.860	60.27 0	-1.159	0.2583
Lp_urban_area	-206.730	93.690	-2.206	0.0376 *
Pdensity_snatural_habitat	145471.300	51849.700	2.806	0.0100 *

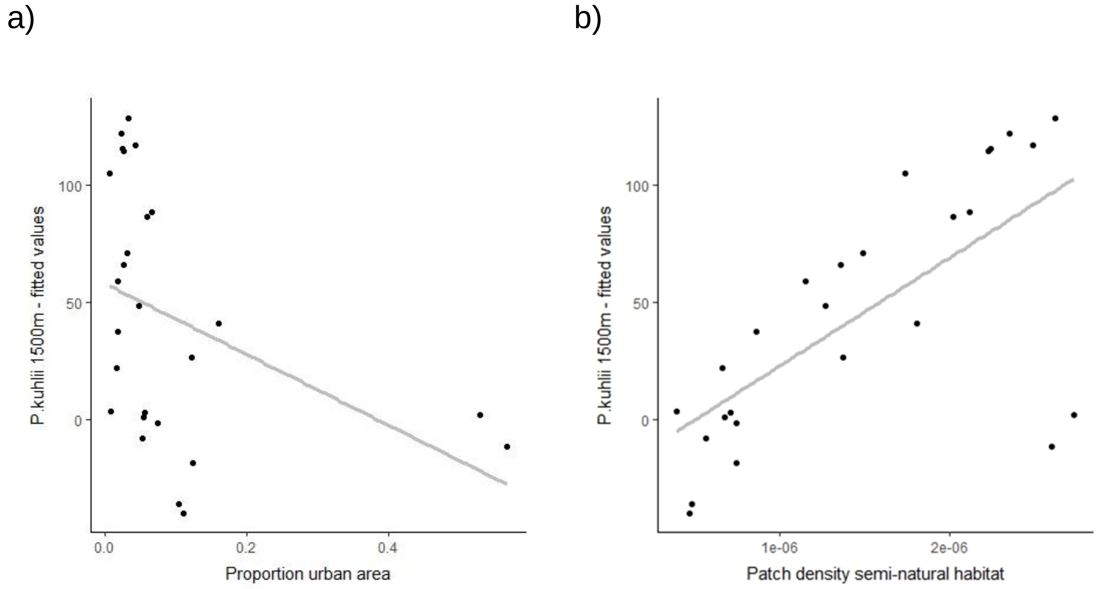


Figure 8: Relationships between fitted values of *P. kuhlii* model (1500 m scale) and landscape proportion of urban area (a) and patch density of semi-natural habitat (b).

The activity of *P. pygmaeus* was higher when the number of semi-natural habitat patches increased, and peaked when there were approximately 20 patches of "montado" (Figure 9). Patch density of urban area (negative effect) was also included in the final model, but had a non-significant relation with the activity of this species (Table 12).

Table 12: Model of *P. pygmaeus* activity at 1500 m scale; model adjusted R^2 = 15.21%; model p_value = 0.05745. Variable p-value codes: '*' $p \leq 0.05$

Variable	Estimate	Std. Error	t value	p-value
Intercept	-6.302	54.190	-0.116	0.9084
Npatch_snatural_habitat	45.588	18.513	2.462	0.0217 *
Pdensity_urban_area	-91743.210	45646.338	-2.010	0.0563

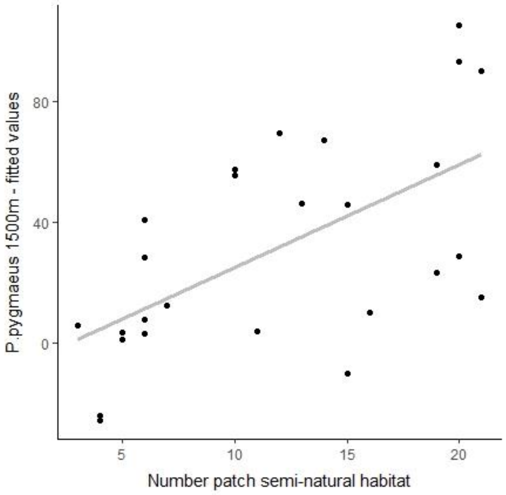


Figure 9: Relationship between fitted values of *P. pygmaeus* model (1500 m scale) and number of patches of semi-natural habitat.

P. pipistrellus activity was higher in sites with higher proportion of waterline with trees and semi-natural habitats (Table 13). The highest values occur when the proportion of waterline with trees is 1.5% (Figure 10a) and in areas with more than 75% of "montados" surrounding the vineyard (Figure 10b).

Table 13: Model of *P. pipistrellus* activity at 1500 m scale; model adjusted R^2 = 47.62%; model p-value = 0.0002259. Variable p-value codes: '*' p ≤ 0.05.

Variable	Estimate	Std. Error	t value	p-value
Intercept	-16.310	7.330	-2.226	0.0361 *
Lp_snatural_habitat	26.290	11.560	2.274	0.0326 *
Lp_waterline_trees	340.240	123.530	2.754	0.0113 *

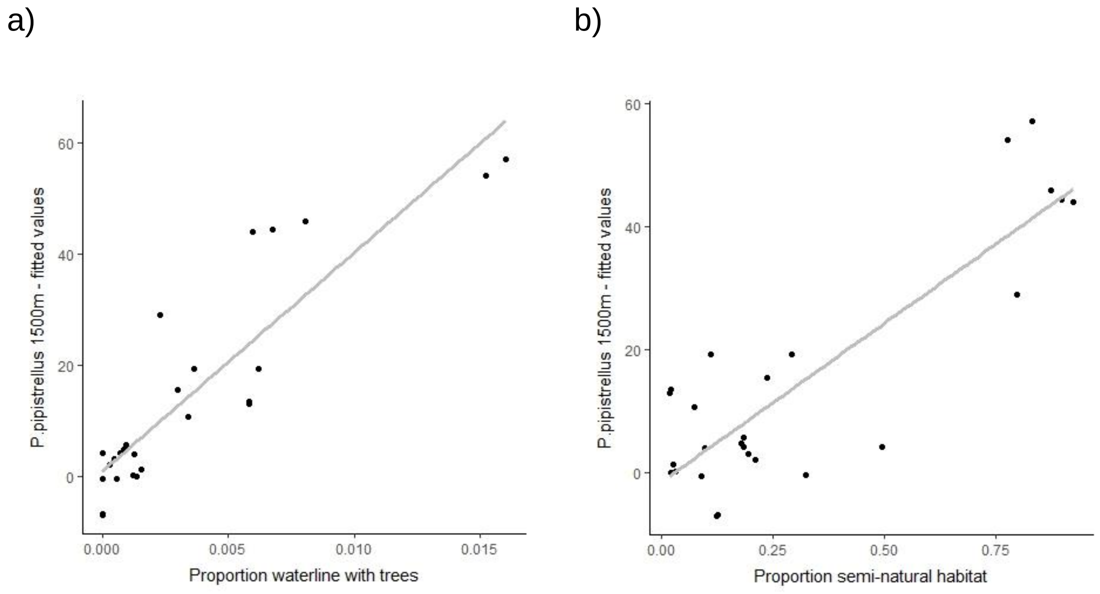


Figure 10: Relationships between fitted values of *P. pipistrellus* model (1500 m scale) and landscape proportion of semi-natural habitat (a) and landscape proportion of waterline with trees (b).

The model of *N. leisleri* activity was the only which included the random factor vineyard, hence we used the mixed model approach. In this case, the distance to semi-natural habitat had a positive effect in activity of *N. leisleri* and distance to water bodies had a negative effect (Table 14). The slope for distance to semi-natural habitat was -0.279, which means that activity of *N. leisleri* in proximity of semi-natural habitats is higher than away of this habitat. The higher value of activity of *N. leisleri* occurs when distance to semi-natural habitats is approximately 80 m (Figure 11a). The slope for distance to water bodies was 0.300, indicating that activity of *N. leisleri* was lower in proximity of water bodies. The higher activity of *N. leisleri* (> 20 bat passes) occur when distance to water bodies is approximately 825 m (Figure 10b).

Table 14: Model of *N. leisleri* activity at 1500 m scale. Variable p-value codes: ‘*’ p ≤ 0.05.

Variable	Value	Std. Error	t-value	p-value
Intercept	4.108	3.266	1.256	0.2290
Dist_snatural_habitat	-0.279	0.134	-2.081	0.0563
Dist_water_bodies	0.300	0.123	2.435	0.0289 *

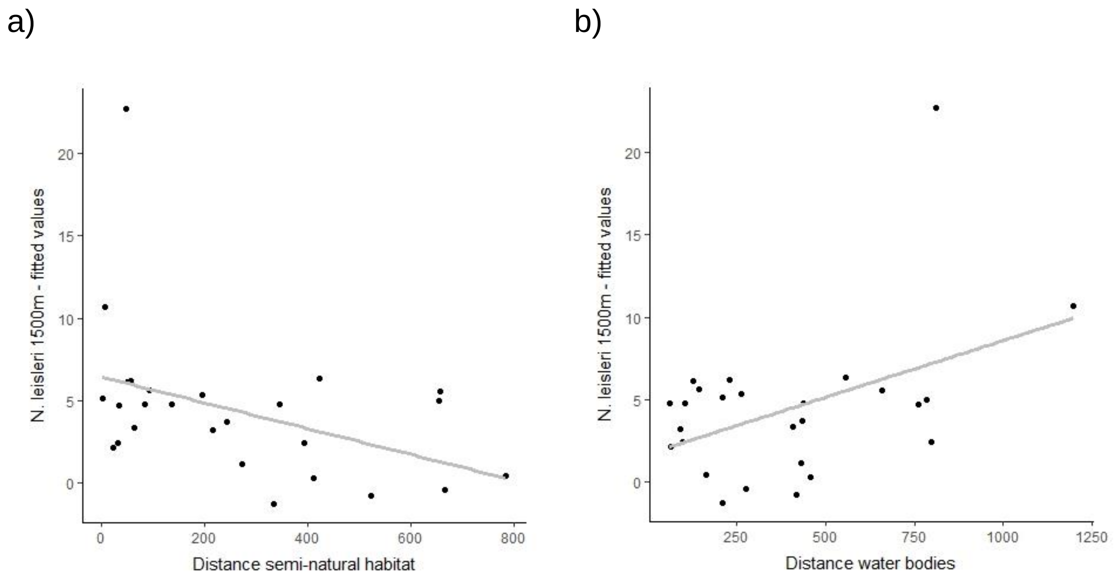


Figure 11: Relationships between fitted values of *N. leisleri* model (1500 m scale) and distance to semi-natural habitat (a) and distance to water bodies (b).

In Table 15 it is possible observe the summary of the final models at vineyard (500 m) and landscape scale (1500 m).

Table 15: Summary table of the final models for the two spatial scales (500 and 1500 m). Variable p-value codes: ‘***’ p ≤ 0.001, ‘**’ p ≤ 0.01, ‘*’ p ≤ 0.05.

Variables	**500m**			**1500m**		
ACTIVITY	**Coefficient**	**Std. Error**	**p-value**	**Coefficient**	**Std. Error**	**p-value**
Dist_water_bodies	10.137	5.022	0.0565	-11.409	4.545	0.0199 *
Dist_waterline_trees	-9.601	2.805	0.0026 **	-	-	-
Lp_urban_area	-	-	-	-819.165	195.884	0.0004 ***
Lp_water_bodies	1334.581	284.607	0.0001 ***	-	-	-
Npatch_waterline_trees	-	-	-	157.948	33.577	0.0001 ***
Pdensity_urban_area	-50695.616	37569.930	0.1916	-	-	-
SPECIES RICHNESS	**Coefficient**	**Std. Error**	**p-value**	**Coefficient**	**Std. Error**	**p-value**
Lp_water_bodies	3.979	2.078	0.0686	-	-	-
Lp_waterline_trees	21.820	5.508	0.0007 ***	19.153	7.526	0.0185 *
Npatch_pasture	-	-	-	-0.341	0.245	0.1775
Pdensity_vineyard	-253300	145700	0.0962	-	-	-
Pdensity_water_bodies	-	-	-	-1.539	0.817	0.0728
P. KUHLII	**Coefficient**	**Std. Error**	**p-value**	**Coefficient**	**Std. Error**	**p-value**
Dist_waterline_trees	-2.643	1.670	0.1272	-	-	-
Lp_urban_area	-	-	-	-206.730	93.690	0.0376 *
Pdensity_snatural_habitat	-	-	-	145471.300	51849.700	0.0100 *
Pdensity_water_bodies	51135.271	28304.496	0.0839	-	-	-
P. PYGMAEUS	**Coefficient**	**Std. Error**	**p-value**	**Coefficient**	**Std. Error**	**p-value**
Dist_waterline_trees	-2.670	1.452	0.0816	-	-	-
Lp_snatural_habitat	-72.991	40.805	0.0896	-	-	-
Lp_treeline	-1011.010	517.072	0.0654	-	-	-
Lp_olive	-121.275	67.746	0.0894	-	-	-
Npatch_snatural_habitat	-	-	-	45.588	18.513	0.0217 *
Npatch_urban_area	-33.573	22.494	0.1520	-	-	-

Pdensity_pasture	44168.254	23652.984	0.0774	-	-	-
Pdensity_urban_area	-	-	-	-91743.210	45646.338	0.0563
P. PIPISTRELLUS	**Coefficient**	**Std. Error**	**p-value**	**Coefficient**	**Std. Error**	**p-value**
Dist_waterline_trees	-0.920	0.405	0.0338 *	-	-	-
Lp_snatural_habitat	-	-	-	26.290	11.560	0.0326 *
Lp_waterline_trees	-	-	-	340.240	123.530	0.0113 *
Lp_pasture	-27.868	18.833	0.1538	-	-	-
Lp_vineyard	-34.564	15.472	0.0365 *	-	-	-
Pdensity_olive	-6631.705	4368.590	0.1439	-	-	-
N. LEISLERI	**Coefficient**	**Std. Error**	**p-value**	**Coefficient**	**Std. Error**	**p-value**
Dist_snatural_habitat	-	-	-	-0.279	0.134	0.0563
Dist_waterline_trees	0.203	0.078	0.0019 *	-	-	-
Dist_water_bodies	0.122	0.075	0.1249	0.300	0.123	0.0289 *
Lp_waterline_trees	74.360	20.620	0.0019 **	-	-	-
E_length_vineyard	-0.002	< 0.001	0.0005 ***	-	-	-
Pdensity_pasture	3702	864.600	0.0004 ***	-	-	-
Pdensity_urban_area	1909	845.600	0.0359 *	-	-	-

4. Discussion

We aimed to investigate how the management and the natural structures, within and adjacent to vineyards, influence the bat community of these agricultural areas. We focused on bat activity, species richness and activity of the four most common species at two spatial scales: vineyard and landscape.

4.1. Bat activity and species richness in vineyards

Bat activity in vineyards was higher near to waterlines with trees and in sites with a high proportion of water bodies. Moreover, the positive effect of this habitat on bat activity extends into the adjacent areas of vineyards; bat activity peaks next to riparian vegetation and decreases until 500 m from it. Bat species richness also increased in sites with higher area covered by waterlines with trees. This strong link is evident even when there is a small area occupied by this habitat. Bat species richness peaked in vineyards with only 2% of riparian vegetation, where we recorded seven or eight species, compared to an average of four species in sites with no riparian vegetation. Water-related habitats are very important in Mediterranean regions because of the scarcity of water resources across the landscape (Carmel and Safriel, 1998; Russo and Jones, 2003; Rainho, 2007). Specifically, riparian habitats are important for many insectivorous bats because they fulfill several ecological functions: they are highly used for foraging due to the high abundance of insect prey (Hutson *et al*., 2001; Fukui *et al*., 2006; Russo and Jones, 2003; Korine *et al*., 2016), and for commuting between roosts and feeding areas (Limpens and Kapteyn, 1991; Mickleburgh *et al.*, 2002; Heim *et al*., 2018). Riparian habitats also provide shelter from wind and predators (Limpens and Kapteyn, 1991; Verboom and Huitema, 1997; Fukui *et al*., 2006) and an abundant source of fresh water for bats (Rainho and Palmeirim, 2011; Korine *et al*., 2016). This important relationship between bats and riparian vegetation that we observed in vineyards, has also been documented across several natural (Russo and Jones, 2003, Amorim *et al*. 2018) and urbanized landscapes (Boughey *et al*., 2011; Heim *et al*., 2015).

Other types of wetlands – small dams and ponds - are also important for bat activity, as revealed in our analyses. The activity of bats increased linearly and peaked at 30% cover of water bodies, although this was a noisy relationship. Similarly to waterlines these wetlands provide numerous foraging opportunities and high water availability (Stahlschmidt *et al*., 2012; Sirami *et al*., 2013, Korine *et al*., 2016, Heim *et al*., 2018).

4.2. Activity of common bat species in vineyards

Two of the four bat species that we analysed yielded overall significant models at the vineyard scale: *P. pipistrellus* and *N. leisleri.* The activity of *P. pipistrellus* was higher in proximity to waterlines with trees and in sites with low proportion of vineyard. These bats' preference for tree lines has been reported by several authors (Downs and Racey, 2006; Dietz *et al*., 2009). *P. pipistrellus* bats prefer to fly along tree lines than in open farmland fields, presumably because of the high abundance of Diptera that congregate near these windbreaks (Pocock and Jennings, 2008). Riparian vegetation provides a much higher abundance of insect-prey than tree lines because it adds the numerous individuals emerging from the water surface (Fukui *et al*., 2006). In contrast, low *P. pipistrellus* activity was observed in sites of high vineyard cover. This agricultural system consists of a homogeneous, simplified structure (Altieri and Nicholls, 2002), which does not make it attractive for bats (Di Salvo *et al*., 2009). Moreover, the use of pesticides in vineyards decreases the overall insect-prey availability by reducing their abundance and diversity (Rodríguez-San Pedro *et al*., 2018). Additionally, sites with high cover of vineyards tend to be placed in central areas of the farms, further from the farm edges and from semi-natural habitats. Eight sites had more than 60% cover of vineyards within a 500 m radius, including three sites that had more than 90% cover. Conversely, sites near the edges of vineyards, which include other semi-natural habitat areas and their edges, seem to be preferred by these bats. Rodríguez-San Pedro *et al*. (2018) report a high bat feeding activity in vineyard edges, demonstrating the importance of these interfaces even when adjacent to homogeneous areas. This pattern was also observed in other intensively managed agricultural landscapes, where *P. pipistrellus* bats usually commute and feed along natural edges (Downs and Racey, 2006; Pocock and Jennings, 2008).

The waterlines with trees influences the activity of *N. leisleri* in contrasting ways. On the one hand, it was higher when the proportion of waterlines with trees increases in vineyards. But, the activity of *N. leisleri* was also lower near waterlines with trees. So, these bats prefer areas with riparian vegetation although they might not use these waterlines for foraging or follow them closely for commuting. Surprisingly, the activity of this bat species was higher in sites with higher density of urban areas. The response of bats to urbanization is species-specific: most species are negatively affected but open space foragers and bats with flexible roosting requirements can tolerate urban areas (Russo and Ancillotto, 2015; Jung and Threlfall, 2018). *N. leisleri* usually forages above the tree canopy, in the medium and high air space, and can also roost in buildings (Waters *et al*., 1999). These traits clearly indicate that although described as a mainly forest species (Dietz *et al*., 2009; Marques, 2013) it can also use urban areas. Additionally, the activity of this species also increases in locations with high density of pastures, which is one of its preferred foraging habitats (Dietz *et al*., 2009; Marques, 2013). Finally, the edge length of vineyards can be negative to *N. leisleri* activity. This may due to the fact of edge length of vineyards can decrease the edge length of highly used foraging habitats such as forest edges (Dietz *et al*., 2009).

The activity two most common bat species in our data set - *P. kuhlii* and *P. pygmaeus* - increased near riverine habitats, which agrees with the habitat preferences of both (*e. g.* Rainho, 2007). Despite the abundant data, the two final models were uninformative and these results should be carefully evaluated.

4.3. Bat activity and species richness at landscape scale

In the scale of 1500 m, hereafter termed landscape scale, the overall bat activity was higher in the vicinity of water bodies and in locations with high number of patches of waterline with trees, but lower in areas with high proportion of urban area. Species richness also increased markedly in areas with high proportion of waterlines with trees. Therefore, both distance to and the availability of water sources are of utmost importance for bats (*e. g*. Salvarina, 2016), also for this spatial scale. We found evidence that waterlines with trees, although covering very small areas, are used by a large number of bat species of the community.

Therefore, the same factors that influence at the landscape scale, the ecological factors concerning bat foraging, commuting and water drinking, also influence the number of bat species using vineyards. Finally, our results indicate that vineyards with urban areas occupying more than 10% of the surrounding area have lower bat activity compared to those that have no urban areas nearby. This pattern is probably a result of the negative effect of urbanization on bat activity (Jung and Threlfall, 2018). It is likely that this negative effect spills over into the adjacent vineyards.

4.4. Activity of common bat species at landscape scale

At the landscape scale, all the four most common bat species had meaningful models. *P. kuhlii*, had lower activity in sites with high proportion of urban areas, while it was higher in vineyard sites with high density of "montados". As referred above, bats are usually affected negatively by urban areas (Jung and Threlfall, 2018), however, *P. kuhlii* is often found in built up areas (Rainho, 2007; Dietz *et al*., 2009; Líson and Calvo, 2013), where it feeds on abundant insect-prey in gardens, parks and around streetlamps. This concentration of activity in the urban areas may induce the low level of activity in the nearby vineyards. Also, vineyards surrounded by areas with high density of "montados" were most used by *P. kuhlii*. This generalist species is also often found in forested areas of the Iberian Peninsula (Líson and Calvo, 2013), including oak woodlands (Rainho, 2007). "Montados" provide a high availability of tree roosts to bats, either tree holes or the spaces between the cork and the trunk. It also provides abundant insect prey particularly in areas with understory shrubs (Rainho, 2007). The good conditions of these mediterranean woodlands for bat species is reflected on the positive relationship with the other three species of bats, *P. pygmaeus*, *P. pipistrellus* and *N. leisleri*.

Additionally, the higher *P. pipistrellus* activity in sites with great proportion of waterlines with trees may be related with its foraging strategy: this bat species patrols along linear structures to capture prey (Dietz *et al*., 2009). Moreover, our results are in agreement with other studies which demonstrated that *P. pipistrellus* foraged mostly above riparian vegetation (Carmel and Safriel, 1998) and shows a great preference for linear aquatic habitats (Líson and Calvo, 2013).

In the case of *N. leisleri*, the activity decreased in the vicinity of water bodies, demonstrating that distance to water is not important for this bat species. It is surprising, since in Europe bats have a clear affinity for aquatic habitats, even in areas with great proportion of water sources (Downs and Racey, 2006; Boughey *et al*., 2011).

4.5. Comparing vineyard and landscape scales

Our results suggest that the activity of bats is influenced by different structures and habitats at 500 or 1500 m however, the distance to water sources – waterlines with trees, and water bodies – was selected for the two spatial scales. Bat species richness had a similar pattern, which reinforces that the availability of water or freshwater habitats is very important for bats both at the vineyard and landscape scale. For *P. kuhlii* and *P. pygmaeus,* the two most common species, only the models at the landscape scale – larger scale of study - were informative. In contrast, the activity of *P. pipistrellus* was influenced by the presence of the same habitat – riparian vegetation – at both spatial scales. Finally, *N. leisleri* activity was related to different sets of variables at the two spatial scales, and often had contrasting relationships. This bat usually forages over large areas (7.4 - 18.4 km^2, Waters *et al*., 1999), flying over the canopy in the medium layer of the airspace. Therefore, both the 500 m and 1500 m scales may be suboptimal to model this species (Jackson and Fahrig, 2015).

In conclusion, although bat activity and species richness had similar patterns over the two analysed scales, the two most common bat species only had good models at the landscape scale. So, it is likely that there is a mismatch between the scale at which bats respond to the changes of the landscape and the scale at which managers may act. This potential gap can be filled with the coordination of groups of vineyard farmers or with the strong involvement of the regional planning authorities.

4.6. The relative contribution of vineyard practices and natural structures for bat communities

In our study the type of vineyard management was included in only a few final models but none of the relationships yielded significant results (Appendix B), suggesting there are no differences of bat activity, species richness and the activity of the four most common bat species between vineyards under Integrated Farm Management (IFM) or organic management. Bat activity and species richness are presumably higher in organic compared to conventional farms because of the lack of synthetic pesticides in the organic areas (e. g. Wickramasinghe *et al*. 2003). So, our results may be related with the period of the bat surveys, which took place between the end of July and end August. When we started the surveys several weeks had passed since farmers last sprayed pesticides in the vineyards. Hence, the potential differences between the insect prey availability of two types of vineyards may have been reduced, abating the impact of the vineyard management system on the whole bat community.

However, the reports of higher bat activity and species richness in organic farms has been subject to debate; several authors have reported this pattern (Wickramasinghe *et al*. 2003; Rodríguez-San Pedro *et al*., 2018), but others did not find it (Froidevaux *et al*., 2017; Olimpi and Philpott, 2018). An explanation for these apparently contrasting results is that the landscape features may play a decisive role on the bat activity and richness in agricultural areas. Our results also support this conclusion; we showed that there is an interaction between vineyard management and natural structures, but that the latter are more important for bats. Froidevaux *et al*. (2017) also found that bat activity and species richness was mainly influenced by landscape features regardless of the vineyard management, organic or conventional. Moreover, in a study encompassing several farming systems the authors did not find differences either in bat activity or diversity between conventional and organic farms (Olimpi and Philpott, 2018).

It is noteworthy that organic farms show a higher availability of insects compared to conventional farms (*e. g*. Wickramasinghe *et al*., 2004) and as a consequence, these are apparently contrasting results. One likely explanation is the link between species mobility and higher influence of landscape features compared to the management. An example of this probable link within bats is reported by Fuentes-Montemayor *et al*. (2013) and Pocock and Jennings (2008) but there is scant information in the literature. However, we can test this argument by assessing which factor, agricultural management or landscape features, influences most the abundance and species richness of animal groups with different mobility levels. Weibull and Ostman (2003) demonstrated that plants and carabids were most affected by farm management comparatively to landscape features. Additionally, Froidevaux *et al*. (2017) reported the same pattern for arachnids, which were more abundant in organic vineyards. In contrast, for butterflies, one of the invertebrate groups with higher mobility, the landscape structure and landscape features seemed to be more important than the farming system for high species diversity and composition (Weibull *et al*., 2000; Weibull and Ostman, 2003). Together with the examples of bats referred above, the higher influence of landscape features and heterogeneity over that of farm management is also observed in highly mobile vertebrate species, such as insectivorous birds (Piha *et al*., 2007; Smith *et al*., 2010). In conclusion, less mobile species, such plants, carabids, and arachnids, are less affected by landscape features and more influenced by farm management, while the effect of landscape features is stronger for the mobile invertebrate and vertebrate species, including bats.

4.7. The potential contribution of common and rare bat species for pest regulation services

Insectivorous bats play critical roles as primary predators in many ecosystems. They are the most important natural controllers of night flying insects, contributing to the suppression of insect populations, including agricultural pest species, in both natural and human-altered landscapes (Hutson *et al*., 2001; Kunz *et al*., 2011). Therefore, bats may provide economic value of pest-control services, *i. e.* reduce the pesticide application and avoid crop damage by insect-pests, contributing to ecosystem stability (Boyles *et al*., 2011; Kunz *et al*., 2011). Lindell *et al*. (2018) refer that common predator species are more likely to reduce pest populations than less common groups, probably due to their large combined biomass. Because of the very high numbers of individuals of common predator species, they are able to reduce pest populations even when their individual consumption is low. However, rare or threatened bat species increase functional diversity (Mouillot *et al*., 2013) and can contribute decisively to natural pest regulation. Several agricultural pests are moths and some rare or threatened bat species feed mostly on these insects, such as horseshoe bats (*Rhinolophus* spp.) and Barbastelles (*Barbastella barbastellus*).

4.8. Management implications

Considering the decline of bat populations and their potential role in the regulation of insect pests in agricultural ecosystems, it is necessary to provide effective management recommendations that attract bats to and promote their use of vineyards. So, for land owners, managers and conservationists it is very important to understand which landscape elements are relevant and efficient to enhance species richness and thus vital ecosystem function in agricultural areas.

Our results suggest that conservation actions to benefit bats should be to create or maintain linear features with trees, mainly those linked to water, either riparian vegetation or small agricultural dams. These landscape structures are important for bat populations within or near vineyards, and the small areas covered by them can increase markedly the suitability of landscapes for bats. Therefore, the restoration of riparian habitats should be a key component of agricultural management to promote bat conservation and increase their potential role as pest consumers. Patches of semi-natural habitats, such as “montados”, were also important for the activity of the most common bat species. Thus, keeping a landscape mosaic of vineyards and semi-natural habitats will also increase the suitability of these for bats. Heterogeneous landscapes that combine vineyards, riparian vegetation lines and patches of “montados” will be able to support large populations of bats and host a high species richness.

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6. Appendix A

Table 1A: Description of each land cover categories.

Land cover categories	Description
Urban area	Settlements, cities, roads, houses, and other human infrastructures
Olive groves	Olive groves, fruit crops, and orchards
Semi-natural habitat	“Montado”, forestry agricultural systems, and forests
Unproductive area	Quarries, and mines
Waterline and wetland	Runoff lines, and wetlands
Waterline with tree	Riparian habitats, and areas along rivers and stream corridors with vegetation
Tree line	Lines of trees
Water body	Water courses, rivers, lakes, and damns
Pasture	Pastures and non-cultivated open agricultural areas
Vineyard	Vine crops

7. Appendix B

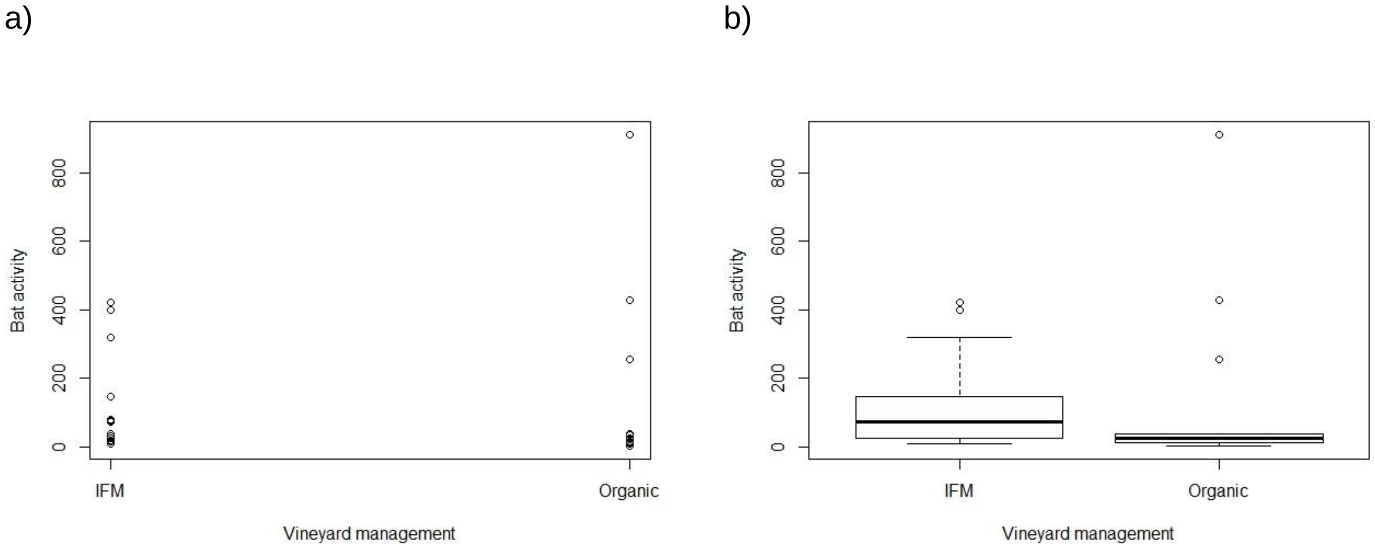

Figure 1B: Plot (a) and boxplot (b) of relationship of bat activity and vineyard management: IFM (Integrated Farm Management) and Organic.

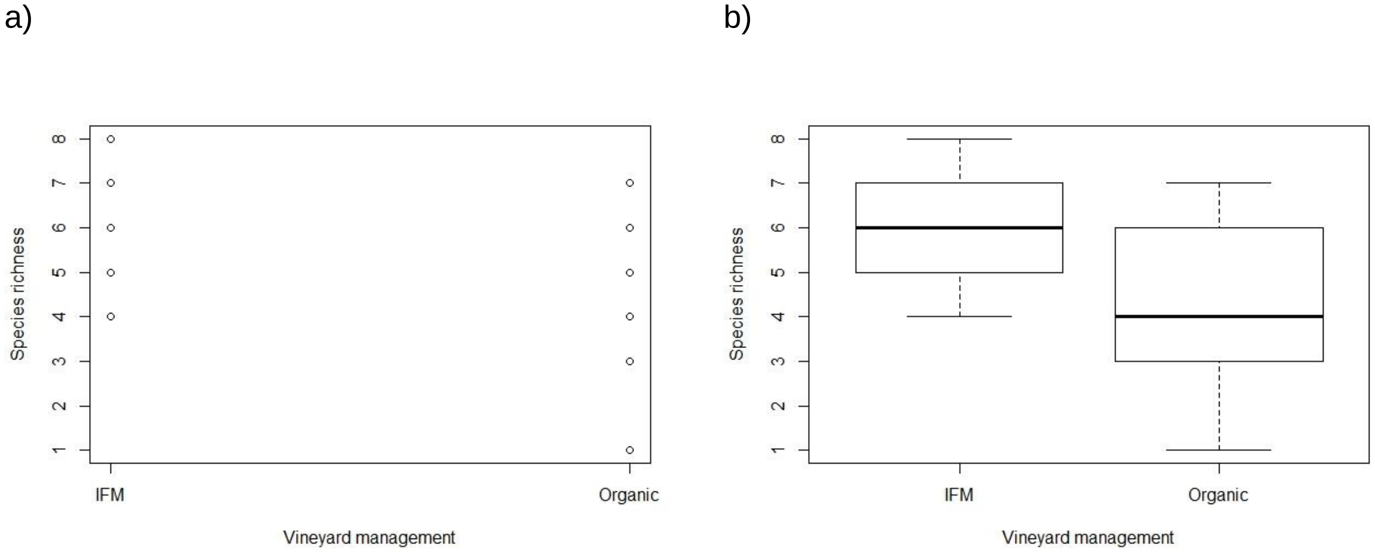

Figure 2B: Plot (a) and boxplot (b) of relationship of bat species richness and vineyard management: IFM (Integrated Farm Management) and Organic.

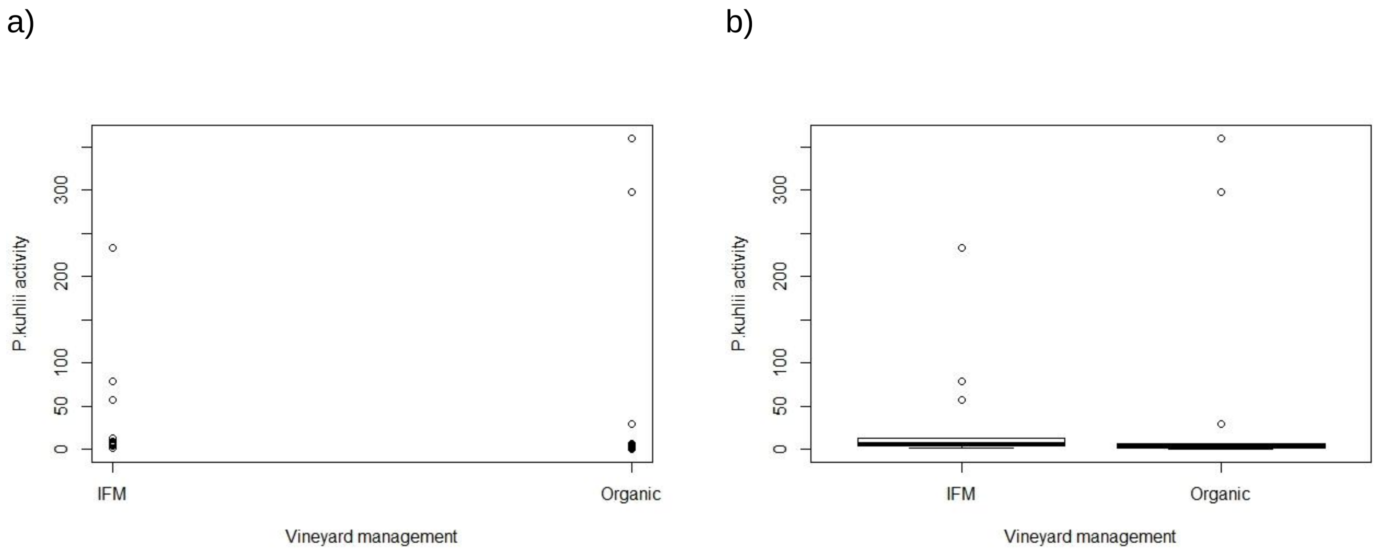

Figure 3B: Plot (a) and boxplot (b) of relationship of *P. kuhlii* activity and vineyard management: IFM (Integrated Farm Management) and Organic.

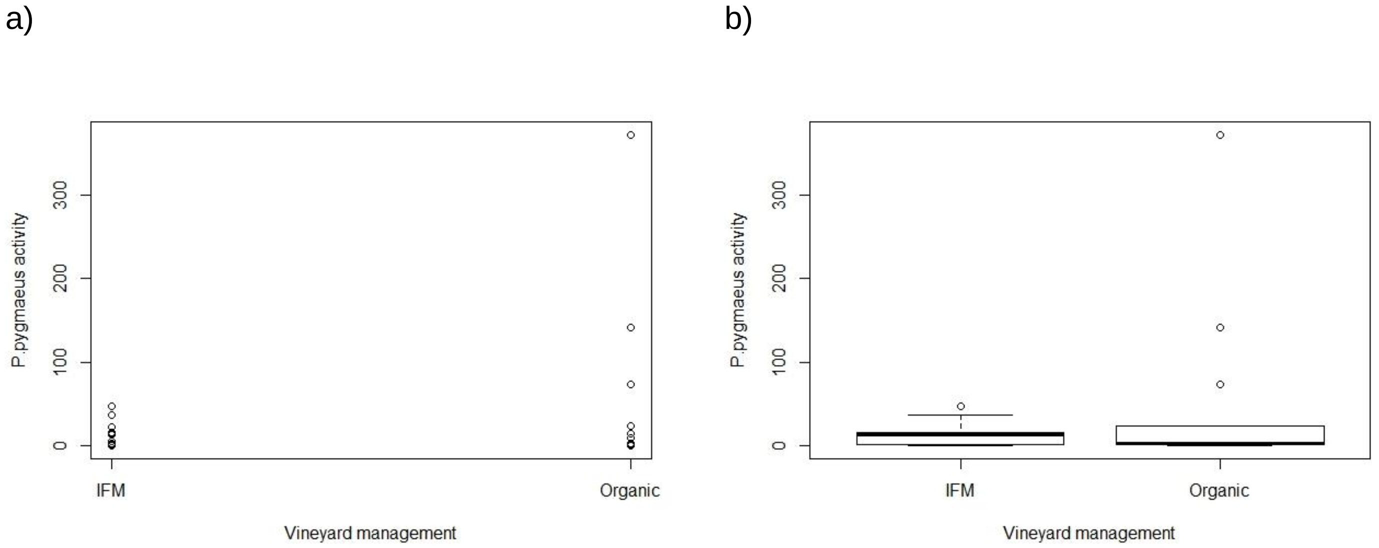

Figure 4B: Plot (a) and boxplot (b) of relationship of *P. pygmaeus* activity and vineyard management: IFM (Integrated Farm Management) and Organic.

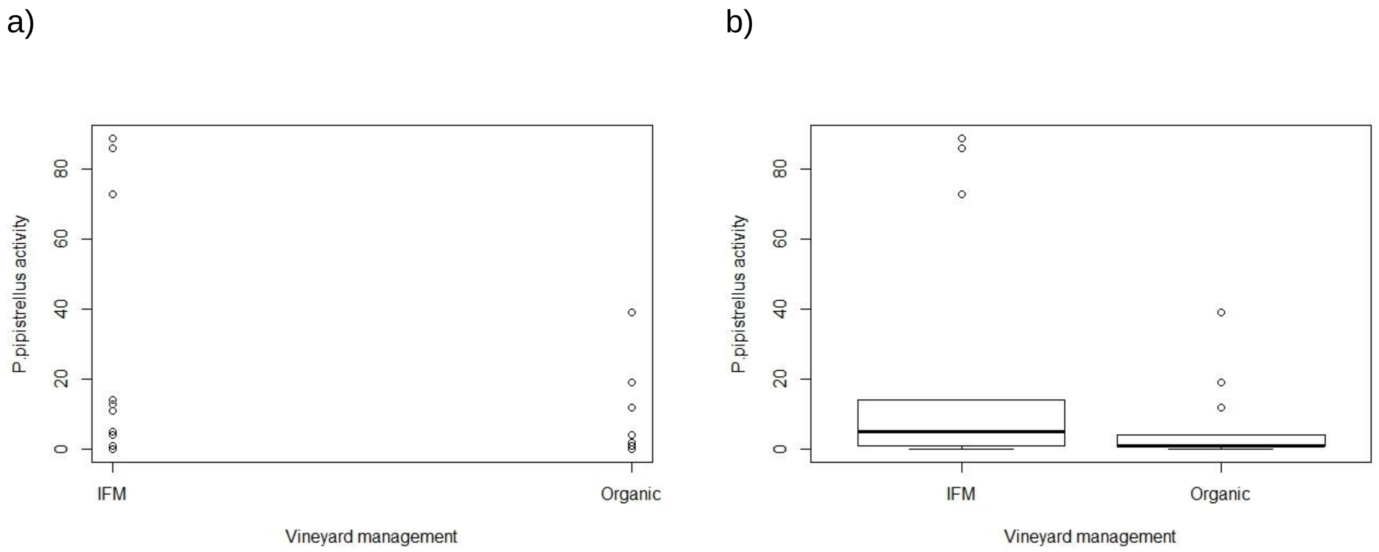

Figure 5B: Plot (a) and boxplot (b) of relationship of *P. pipistrellus* activity and vineyard management: IFM (Integrated Farm Management) and Organic.

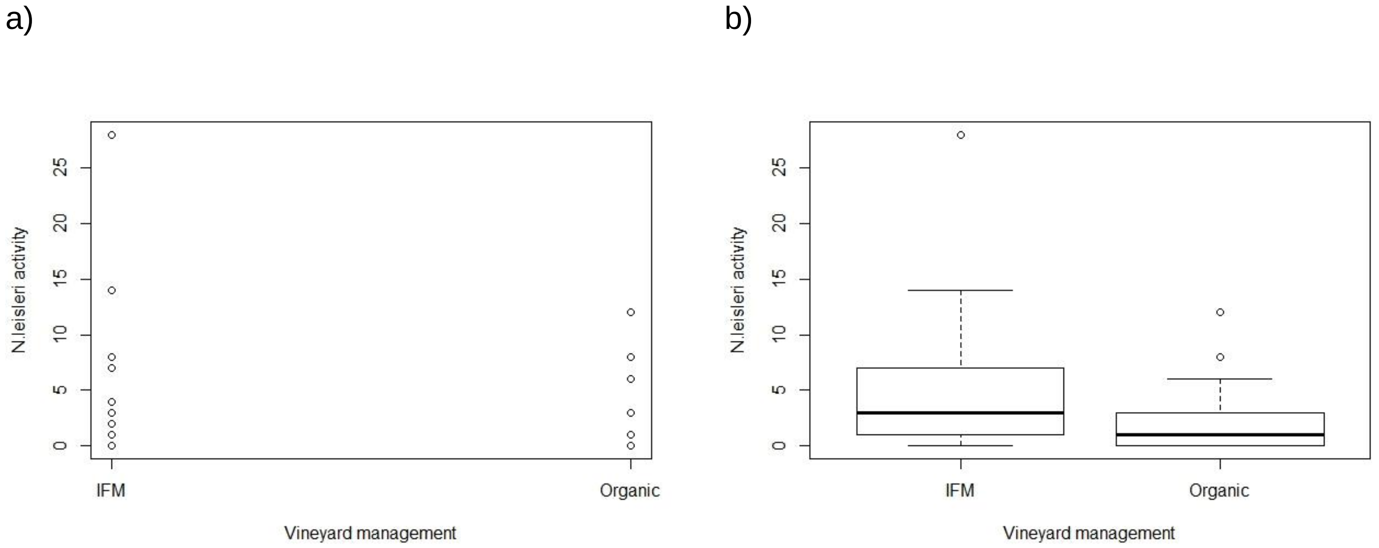

Figure 6B: Plot (a) and boxplot (b) of relationship of *N. leisleri* activity and vineyard management: IFM (Integrated Farm Management) and Organic.

Table 1B: Model of bat activity at 500 m scale with exploratory variable 'management'; model adjusted $R^2 = 50.71\%$ and p-value = 0.0003. Variable p-value codes: '***' $p \leq 0.001$, '**' $p \leq 0.01$, '*' $p \leq 0.05$.

Variable	**Estimate**	**Std.Error**	**t value**	**Pr (>|t|)**
Intercept	18.491	142.462	0.130	0.8980
Dist_water_bodies	10.614	5.102	2.080	0.0493 *
Dist_waterline_trees	-8.581	2.751	-3.119	0.0050 **
Lp_water_bodies	1343.326	289.792	4.635	0.0001 ***

Table 2B: Model of bat species richness at 500 m scale with exploratory variable 'management'; model adjusted $R^2 = 39.56\%$ and p-value =0.0027. Variable p-value codes: '***' $p \leq 0.001$.

Variable	**Estimate**	**Std.Error**	**t value**	**Pr (>|t|)**
Intercept	5.114	0.691	7.401	< 0.0001 ***
Lp_water_bodies	3.979	2.078	1.915	0.0686
Lp_waterline_trees	21.820	5.508	3.962	0.0007 ***
Pdensity_vineyard	-253300	145700	-1.738	0.0961

Table 3B: Model of *P. kuhlii* activity at 500 m scale with exploratory variable 'management'; model adjusted $R^2 = 11\%$ and p-value = 0.1003.

Variable	**Estimate**	**Std.Error**	**t value**	**Pr (>|t|)**
Intercept	65.137	52.391	1.243	0.2263
Dist_waterline_trees	-2.643	1.670	-1.582	0.1272
Pdensity_water_bodies	51135.271	28304.496	1.807	0.0839

Table 4B: Model of *P. pygmaeus* activity at 500 m scale with exploratory variable ‘management’; model adjusted R^2 = 15.46% and p-value = 0.1611.

Variable	Estimate	Std.Error	t value	Pr (>|t|)
Intercept	148.353	73.650	2.014	0.0584
Dist_waterline_trees	-2.670	1.452	-1.839	0.0816
Lp_olive_fruit	-121.275	67.746	-1.790	0.0894
Lp_snatural_habitat	-72.991	40.805	-1.789	0.0896
Lp_treeline	-1011.010	517.072	-1.955	0.0654
Npatch_urban_area	-33.573	22.494	-1.493	0.1520
Pdensity_pasture	44168.254	23652.984	1.867	0.0774

Table 5B: Model of *P. pipistrellus* activity at 500 m scale with exploratory variable ‘management’; model adjusted R^2 = 39.42% and p-value = 0.0051. Variable p-value codes: ‘***’ p ≤ 0.001, ‘*’ p ≤ 0.05.

Variable	Estimate	Std.Error	t value	Pr (>|t|)
Intercept	69.789	13.094	5.330	< 0.0001 ***
Dist_waterline_trees	-0.920	0.405	-2.271	0.0338 *
Lp_pasture	-27.868	18.833	-1.480	0.1538
Lp_vineyard	-34.564	15.472	-2.234	0.0365 *
Pdensity_olive_fruit	-6631.705	4368.590	-1.518	0.1439

Table 6B: Model of *N. leisleri* activity at 500 m scale with exploratory variable ‘management’; model adjusted R^2 = 85.26% and p-value < 0.0001. Variable p-value codes: ‘***’ p ≤ 0.001, ‘**’ p ≤ 0.01, ‘*’ p ≤ 0.05.

Variable	Estimate	Std.Error	t value	Pr (>|t|)
Intercept	-4.871	3.236	-1.505	0.1496
Dist_waterline_trees	0.266	0.008	3.333	0.0037 **
Lp_snatural_habitat	-2.839	1.718	-1.653	0.1157
Lp_waterline_trees	108.800	25.470	4.274	0.0005 ***
E_length_vineyard	0.002	0.0004	-5.781	< 0.0001 ***
Pdensity_pasture	2645	919.100	2.878	0.0100 **
Pdensity_urban_area	1804	803.800	2.244	0.0376 *
Management	2.188	1.226	1.785	0.0910

Table 7B: Model of bat activity at 1500 m scale with exploratory variable ‘management’; model adjusted $R^2 = 53.99\%$ and p-value = 0.0013. Variable p-value codes: ‘***’ $p \leq 0.001$, ‘**’ $p \leq 0.01$, ‘*’ $p \leq 0.05$.

Variable	Estimate	Std.Error	t value	Pr (>|t|)
Intercept	-2087.341	1483.150	-1.407	0.1755
Dist_snatural_habitat	7.703	5.064	1.521	0.1467
Dist_water_bodies	-13.572	4.475	-3.033	0.0068 **
Lp_urban_area	-978.405	197.660	-4.950	< 0.0001 ***
Npatch_waterline_trees	184.384	34.742	5.307	< 0.0001 ***
Pdensity_water_bodies	-152.416	101.981	-1.495	0.1515
Management	116.623	63.508	1.836	0.0820

Table 8B: Model of bat species richness at 1500 m scale with exploratory variable ‘management’; model adjusted $R^2 = 41.69\%$ and p-value = 0.0018. Variable p-value codes: ‘*’ $p \leq 0.05$.

Variable	Estimate	Std.Error	t value	Pr (>|t|)
Intercept	-19.230	10.361	-1.863	0.0759
Lp_waterline_trees	12.775	8.110	1.575	0.1295
Pdensity_water_bodies	-1.811	0.722	-2.510	0.0199 *
Management	-0.881	0.600	-1.469	0.1559

Table 9B: Model of *P. kuhlii* activity at 1500 m scale with exploratory variable ‘management’; model adjusted $R^2 = 24.15\%$ and p-value = 0.0160. Variable p-value codes: ‘*’ $p \leq 0.05$.

Variable	Estimate	Std.Error	t value	Pr (>|t|)
Intercept	-69.860	60.270	-1.159	0.2583
Lp_urban_area	-206.730	93.690	-2.206	0.0376 *
Pdensity_snatural_habitat	145471.300	51849.700	2.806	0.0100 *

Table 10B: Model of *P. pygmaeus* activity at 1500 m scale with exploratory variable ‘management’; model adjusted R^2 = 11.10% and p-value = 0.0990.

Variable	Estimate	Std.Error	t value	Pr (>|t|)
Intercept	-44.840	45.940	-0.976	0.3392
Pdensity_treeline	-47090000	25320000	-1.860	0.0758
Management	66.300	32.410	2.046	0.0524

Table 11B: Model of *P. pipistrellus* activity at 1500 m scale with exploratory variable ‘management’; model adjusted R^2 = 47.62% and p-value = 0.0002. Variable p-value codes: ‘*’ p ≤ 0.05.

Variable	Estimate	Std.Error	t value	Pr (>|t|)
Intercept	-16.310	7.330	-2.226	0.0361 *
Lp_snatural_habitat	26.290	11.560	2.274	0.0326 *
Lp_waterline_trees	340.240	123.530	2.754	0.0113 *

Table 12B: Model of *N. leisleri* activity at 1500 m scale with exploratory variable 'management'. Variable p-value codes: ‘*’ p ≤ 0.05.

Variable	Estimate	Std.Error	t value	Pr (>|t|)
Intercept	4.108	3.266	1.256	0.2290
Dist_snatural_habitat	-0.279	0.134	-2.081	0.0563
Dist_water_bodies	0.300	0.123	2.435	0.0289 *

Final remarks

With this study we aimed to infer which land uses types, presence of natural structures and management that most influence the activity and species richness of bats in Mediterranean vineyards. Additionally, we explored these relationships at two different spatial scales (500 and 1500 m).

Relatively to natural structures, we observed that these features within and surrounding the vineyards are important for bats. From the studied landscape structures, the waterlines with trees appears to be the most important bats. Additionally, "montados" were the most important habitat for bat activity.

In general, bat community appears to be influenced at the two spatial scales analysed (500 and 1500 m), although we observed that the 1500 m scale has more influence on the bat community. With exception of bat activity, all other models were better at the landscape scale (1500 m), demonstrating that stronger relationships between land use and species richness, *P. kuhlii*, *P. pygmaeus* and *P pipistrellus* activity were found at this scale. In case of *N. leisleri* activity, the final models had contrasting relationships, suggesting that both the 500 m and 1500 m scales may be suboptimal to analyse the activity of this species.

Contrary to our expectations, the management variable did not present significant results, suggesting that there was no significant differences in bat activity, species richness and in the activity of four most common species between IFM and organic vineyards. Apparently, the organic management of the agricultural parcels appears to be more influence in the increase of activity and species richness of vertebrates in homogeneous landscapes (i.e. Wickramasinghe *et al*., 2003; Rodríguez-San Pedro *et al*., 2018). Although our landscape is still somewhat heterogeneous, with different land uses, there seems to be an ongoing homogenization of the landscape. If this trend continues, it is expected that the management of agricultural areas will have a greater importance for the activity and species richness of bats in vineyards.

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