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Cattle-driven forest disturbances impact ensemble composition and activity levels of insectivorous bats in Mediterranean wood pastures

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Abstract Forests can be modified by fine-scale disturbances such as those prompted by cattle grazing, but their impacts on biodiversity are far from being understood. Here, we investigate the response of insectivorous bats to cattle-driven forest disturbances, using a savanna-like Mediterranean agroforestry system, the Portuguese *montado*, as study system. In doing so, we compared bat ensemble composition and activity levels of bats across sites that differed in how frequently they were used by free-ranging cattle. Specifically, we selected sites regularly used by cattle (central places) and sites seldom used (grazing sites). We found strong between-site differences in both bat species composition and activity levels, with lower diversity and activity in central places compared to grazing sites. These response patterns, corresponded to marked between-site differences in tree cover, seemingly driven by cattle use given the lower levels of tree regeneration and vegetation productivity in central places compared to grazing sites. Our work therefore demonstrates that it is not only severe forest loss and fragmentation that has an impact on insectivorous bats, but also when these processes operate at fine spatial scales. We thus suggest that fine-scale forest disturbances, particularly those driven by recurrent cattle use, cannot be neglected in the conservation management of agroforestry systems. In this context, we propose some management strategies aimed at counteracting the impact of cattle-driven disturbances on biodiversity in general, and on insectivorous bats in particular.

Keywords Cattle grazing · Conservation management · Forest loss and fragmentation · Insectivorous bats · Vegetation regeneration

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Introduction

Human activities are triggering unprecedented impacts on natural forests worldwide (Hansen et al. 2013; Keenan et al. 2015). These impacts are disproportionately eroding global terrestrial biodiversity (Betts et al. 2017), with often serious ecological consequences, and are also the drivers behind the major themes of severe forest loss and fragmentation in conservation and management research (Fischer and Lindenmayer 2007). Forests, however, can also be impacted at fine spatial scales (e.g. Peres et al. 2006; Gatti et al. 2015; Ondei et al. 2017). Far from being trivial, many studies have reported widespread alterations in the distribution patterns of forest-associated species in response to fine-scale forest disturbances (i.e., Gray et al. 2006; Kirika et al. 2008; Wilcove et al. 2013; Alroy 2017). Nevertheless, the effects of this widespread but insidious fine scale disturbance have received comparatively less attention in scientific literature (Fischer and Lindenmayer 2007). Studies investigating the effects of fine-scale forest disturbances on biodiversity therefore make a valuable contribution to forest conservation and management research.

Grazing by livestock is one process that disturbs forests at fine-spatial scales, ultimately affecting biodiversity (Mata-González et al. 2007; Rainho et al. 2010; Alkemade et al. 2013; Almeida et al. 2016; Listopad et al. 2018). By affecting the establishment and survival of seedlings, free-ranging cattle have been widely reported to exert a considerable impact on the composition and spatial configuration of both tree and understory shrub cover (e.g. Dufour-Dror 2007; Mayer et al. 2009; Kaufmann et al. 2014; Almeida et al. 2016). Cattle, however, do not make use of the available space homogeneously, and instead commonly use more frequently those sites that provide the best access to key resources such as water and shaded areas (Zengeya et al. 2014; von Müller et al. 2017). This non-random space use exhibited by cattle undoubtedly determines a spatially aggregated impact on vegetation structure, with stronger impacts in those sites consistently used compared to those seldom used (Sutter and Ritchison 2005; Lezama et al. 2015). Grazing by livestock therefore provides a good opportunity to study the impact of fine-scale forest disturbances on both species- and ecosystem processes.

The effects of cattle-driven disturbances on forest-associated species and, to some degree, ecosystem processes, have been mostly reported using birds as case studies (e.g. Martin and Possingham 2005; Nelson et al. 2011; Piana and Marsden 2014; Alhering and Merkord 2016). However, a burgeoning research literature suggests that determining the effects of this form of disturbance is equally challenging for the conservation of other flying vertebrates such as bats (Mendes et al. 2017; García-Morales et al. 2017; Ancillotto et al. 2017). To a large extent, this is because an increasing number of studies are reporting the impact that forest management has on the composition and activity of bat communities (Bouvet et al. 2016; Ancillotto et al. 2017; García-Morales et al. 2017). From a conservation point of view, bats are indeed particularly important as they exhibit a broad range of dietary habits (from species that feed on insects and other arthropods to those that feed on fruit and nectar), thereby providing valuable ecosystem services such as seed dispersal, pollination and pest suppression (Kunz et al. 2011). Thus, changes in the species composition and activity levels of bats could breakdown key ecological functions which support and sustain both natural and managed forest systems (Muscarella and Flemming 2007; Boyles et al. 2011).

Here we investigated the spatial distribution patterns of insectivorous bats in a savanna-like Mediterranean agroforestry system, the Portuguese *montado*, which is classified as a Type 1 High Nature Value farming system by the European Environmental Agency (Keenleyside et al. 2014; Ferraz-de-Oliveira et al. 2016). More specifically, we sought to investigate the effects of cattle-driven forest disturbances by comparing the composition and activity levels of bats between sites consistently used by cattle and sites seldom used. Between-site differences in vegetation structure were investigated in order to determine the potential environmental mechanisms underlying the effects of grazing by cattle on bats. Our overall hypothesis is that grazing by cattle will produce between-site differences in vegetation structure, leading to a significant negative impact on bat ensemble composition and activity levels.

Materials and methods

Study site and sampling design

This study was carried out in summer (late June—mid August) of 2014 in the Special Area of Conservation (SAC) of Monfurado, a Site of Community Importance included in the Natura 2000 network (code PTCON0031), and located in South-Eastern Portugal (Fig. 1a). The site of Monfurado comprises around 24,000 ha of well-preserved savanna-like forests of cork (*Quercus suber* L.) and holm-oak (*Q. rotundifolia* L.) trees in varying densities, composing the characteristic Portuguese *montado* (see Pinto-Correia et al. 2011 for a detailed description of the system) (Fig. 1b). The *montado*—known as *dehesa* in Spain—is considered a High Nature Value (HNV) farming system according to the European Environmental Agency (Paracchini et al. 2008). Overall, the *montado/dehesa* agroforestry system covers an area of over four million hectares in the South-Western Iberian Peninsula, highlighting its ecological relevance in the European context (Rigueiro-Rodríguez et al. 2009). Extensive livestock, together to cork extraction, is one of the most important direct production activity of the *montado* system. Thus, natural pastures are an essential structural component in the understory of this type of agroforestry system, although perennial shrubs (mainly belonging to the family Cistaceae such as *Cistus salviifolius* L., *C. crispus* L., *Cistus monspeliensis* L. and *C. ladanifer* L.) are also present, and may be locally abundant.

Within the SAC of Monfurado (centroid 38°28′–38°38′N and 8°18′–8°0′W; WGS84), we selected a

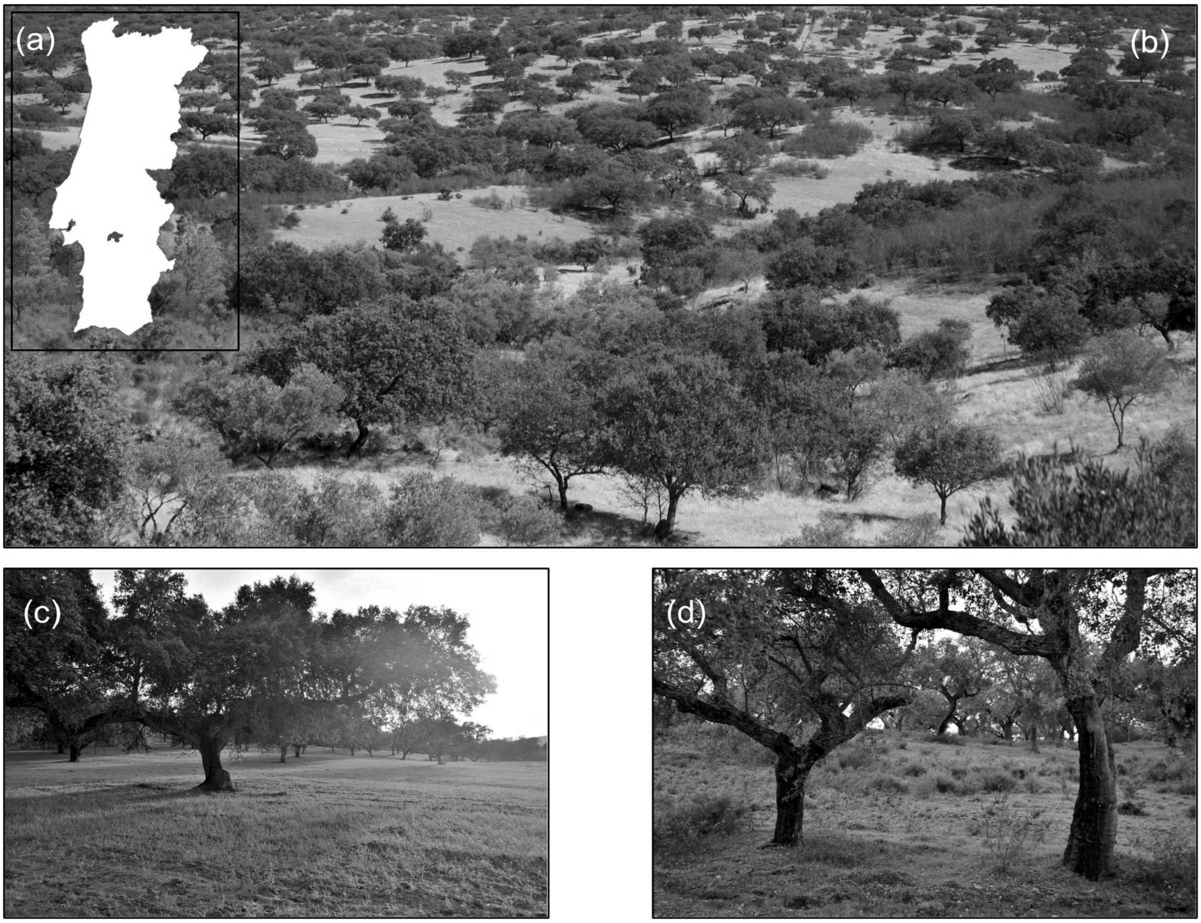

Fig. 1 **a** The location of the Monfurado site within Portugal (shaded area). **b** A photograph illustrating the Portuguese *montado* showing its characteristic savanna-like structure. **c** and **d** show, respectively, an example of a central place and a grazing site where bat acoustic monitoring was performed

total of 21 pastures exclusively devoted to extensive livestock, particularly bovine (*Bos taurus* L.) and, to a much lesser extent, ovine (*Ovis aries* L.). Mean area of individual pastures was 51.61 ± 5.44 ha (range: 21.75–97.35 ha) and mean pairwise distance between them (using the centroids of the polygons generated for each paddock as reference points) was 10 111.73 ± 291.04 meters (range: 592.0–20 671.0 m). To determine the effect of consistent use of a space by cattle on bat ensemble composition and activity levels, we identified within each paddock two types of sites with different frequencies of cattle use ($N = 42$); that is, sites consistently used by cattle (Fig. 1c) and sites seldom used by cattle (Fig. 1d). This distinction was made following the expert advice of farm owners/managers, which was obtained by means of face-to-face interviews in the field. During the interview, each owner/manager was asked to identify within his/her pasture those sites which were more or less frequently used by cattle over the last 10 years, irrespective of the season of the year. The spatial location of these sites were georeferenced using a Global Positioning System (GPS; Garmin GPSMap 62S®; Accuracy: 2 m) and incorporated into a Geographic Information System (GIS; QGIS version 2.18). Frequently used sites were mainly associated with the presence of drinking troughs. This is not surprising as water is a key limiting resource in our study region, particularly during summer when the temperature may reach 45° C. This type of site will henceforth be referred to as *central places*, as water availability is expected to determine foraging range (Coppolillo 2001). Seldom used sites were mainly used for grazing purposes and henceforth will be referred as *grazing sites*.

Mean pairwise distance between central places and grazing sites within each individual paddock was 458.6 ± 19.6 meters (range: 322.1–656.1 m). We used Moran's I correlograms to test for the presence of any potential spatial trend in the distribution of the two types of site (Legendre and Legendre 1998). Moran's I index calculates the similarity between observations from pairs of locations, for each distance class and for each explanatory variable (in our particular case, pairwise distances between the two types of site). The number of equidistant distance classes was calculated following Sturge's rule ($N_{\text{classes}} = 1+3.3 \log n$). Moran's I correlograms did not produce significant coefficients at any distance class ($P > 0.05$ in all pair comparisons), suggesting that both types of site were homogeneously distributed throughout the regional landscape. As such, we ensured a suitable spatial framework to test between-site differences in bat ensemble composition and activity levels irrespective of any spatial constraints in the distribution of sampled sites.

Site characterization

Between-site differences in vegetation structure were investigated. We selected a set of structural features of local vegetation typically shown to be affected by regular cattle use, including proportion of tree canopy, as well as shrub cover and height (Kaufmann et al. 2014). We digitized tree cover in a 50 m radius buffer from the centroid of each site using a GIS platform and orthophotos at a pixel resolution of 0.5 m. The proportion of tree canopy was then calculated as the proportion of the buffer area occupied by forest cover. The proportion and average height of shrub cover (mainly *Cistus* spp.) was determined in the field. The proportion of shrub cover was visually determined in a 10 m radius buffer from the centroid of each site. Average shrub height was determined by measuring shrub height of at least five shrubs within the 10 m radius. In-farm metrics were always obtained by the same researcher, in order to avoid any potential observer bias.

Simultaneous with the acoustic monitoring of bats, we measured the availability of aerial prey insects at each site using light-sticky traps attached to tree branches. Each trap was placed 50 m away from the bat recording site in order to avoid potential interference on bat-call recording, and was suspended approximately two meters above ground. The light-sticky traps consisted in plastic sheets (625 cm^2) coated with adhesive and back-lit with a flashlight (model: EFL07, Ø100 × 150 × 175 mm, 285 g, Tooland/Perel, Gavere, Belgium) attached to the back of the plastic sheet. Traps were activated for one night at each site between sunset and sunrise. At the end of the trapping session, the sum of captures was recorded for each trap to estimate the site-specific availability of insect food-resources for bats.

Cattle-driven impacts on vegetation regeneration and productivity

To establish the link between the structural properties of individual sites and the impact of cattle on such properties, we determined both tree regeneration patterns and the Normalized Difference Vegetation Index (NDVI) for each individual site, as surrogates of vegetation regeneration and productivity patterns, respectively. To determine site-specific tree regeneration, we counted the total number of saplings below 130 cm in height along a 20 m transect. We selected this sapling height as it is widely accepted to represent a key threshold beyond which survival probabilities significantly increase when cattle is present (Dufour-Dror 2007). Second, to determine site-specific NDVI, we obtained the Landsat-8 images from the US Geological Survey (USGS) Land Processes Distributed Active Center (LP DAAC; http://lpdaac.usgs.gov). The cloud free images of the study area (WRS-2 scene: path 203, row 33, 30 m resolution) that coincided with the study sites during 2014 were examined. All images were put on a common radiometric scale and the radiance values were converted to at-sensor reflectance in order to account for differences in the spectral variability between the images acquired on different dates (Chander et al. 2009). NDVI was calculated for each scene from the corrected reflectance images for Band 4 and Band 5. We used a 50 m radius buffer at each sampling site to extract the NDVI per month, and determine the average for the dry period; that is, between June and October ($N = 4$).

Bat acoustic monitoring and identification

To determine bat ensemble composition and species-specific activity levels at each site, we recorded echolocation calls using acoustic monitoring devices (Petterson D500x; Pettersson Elektronik AB, Uppsala, Sweden). We used real-time recordings (sampling rate 500 kHz, 16 bit) triggered by the sound pressure level at a threshold of − 40 dB SPL. To increase the clarity of bat calls, we used a high-pass frequency filter of 20 kHz in order to decrease recorded sounds coming from insects. During all surveys, we used the same auto-recording mode setting for 3 s without pre-trigger. One monitoring device was placed at every site, on individual trees, approximately 2 m above ground, oriented towards tree canopy gaps and positioned at a 45° angle to minimize the influence of vegetation clutter on the quantity and quality of bat passes registered. Each site was visited once, with the acoustic monitoring starting 30 min before sunset and lasting for 3 h in order to limit the recording time to the period of peak bat activity (Mendes et al. 2017). Bat monitoring was not performed on nights with unfavorable weather conditions (e.g. rain or strong winds), due to their widely recognized impact on bat activity (Ford et al. 2005) and detectability (Dixon 2012).

Before bat call identification, the recordings were scrubbed to remove potential noise and low quality files using the software Kaleidoscope (Wildlife Acoustics, Inc., version 3.1.1). Recordings were then analyzed using the open-source software Audacity 1.3.10 Beta (available at http://audacity.sourceforge.net/). We identified search-phase bat calls through the visual inspection of pulse sequences and assigned the calls to the lowest taxonomic level possible using measurements of key pulse features such as maximum energy (FMaxE), pulse duration (D), inter-pulse interval (IPI) and pulse initial (Fi) and end frequency (Fe). Frequency parameters (FMaxE, Fi and Fe) were measured from spectrograms, whereas time variables (IPI and D) were measured from oscillograms. Identifications were made by individually inspecting pulses and pulse sequences for key features (see above), with a minimum of five pulses required to identify bats with easily recognizable call structures. Bat calls were identified using a reference collection from Portugal (Rainho et al. 2013). In some cases, bat calls were unavoidably classified at genus level as no reference data for differentiating at a lower taxonomic level is currently available. This was the case, for example, for species belonging the genera *Eptesicus* spp. (which potentially included *E. serotinus* and *E. isabellinus*) and *Plecotus* spp. (which potentially included *P. auritus* and *P. austriacus*) (see Herrera et al. 2015 for a similar procedure). Other exceptional cases included the distinction between calls belonging to *Pipistrellus pygmaeus* and *Miniopterus schreibersii,* for which—because their echolocation calls are not distinguishable through the approach we used for species identification—we opted to create a composite category which included both species, i.e., *P. pygmaeus/M. schreibersii*.

Statistical analysis

Separate species accumulation curves and sample-based rarefaction curves were used to compare species richness between central places and grazing sites as well as to assess sampling effort at the two types of site. The sample-based rarefaction curves and their 95% confidence intervals were then rescaled by the number of expected species (Colwell et al. 2004). Inventory completeness was calculated as the percentage of estimated species actually observed (Moreno and Halffter 2000). To test for significant differences in species composition between types of site, we used a two-way Analysis of Similitude (ANOSIM) test, a non-parametric permutation test analogous to ANOVA, but using similarity indices; in our case the Sørensen similarity index (see Herrera et al. 2015 for a similar procedure).

Generalized linear models (GLMs) were used to test for significant between-site differences in the activity level of bats. Because most bat calls recorded belonged to a simple genus (i.e., *Pipistrellus* spp; see Results) we performed a community-level approach to investigate differences in bat activity between central places and grazing sites. Thus we considered the total number of bat passes per site as response variable and site type as fixed factor. GLMs fitted to dependent variables were based on Poisson distributions and *log* link functions. We include both insect availability and the presence of fresh cattle dung as the only covariates. Inferences related to the potential effects of variables related to vegetation structure on bat ensemble composition and activity levels were made ad hoc. Farm identity was included in the models as a random factor.

All statistical analyses were performed in R statistical software, version 3.3.2 (R Development Core Team 2016) using the function specaccum under the package vegan to develop species accumulation and rarefaction curves, vegdist library for glm2 and PSCL to develop ANOSIM and GLM analysis, and spdep to develop Moran's I tests.

Results

Between-site differences in vegetation structure

We found strong between-site differences in tree canopy. Specifically, that tree canopy was significantly higher in grazing sites than in central places ($F_{1,40} = 12.09$; $P < 0.0001$; Fig. 2; Table 1). The number of tree saplings also varied between the two types of site, with the recorded number of saplings $\leq$ 130 cm in height being higher in grazing sites than in central places ($F_{1,40} = 5.47$; $P < 0.05$; Fig. 3; Table 1). Similarly, the NDVI index strongly varied between the two types of site. Specifically, the NDVI index for grazing sites was higher than that for central places ($F_{1,40} = 11.40$; $P < 0.001$; Fig. 3; Table 1). No significant between-site differences were found in either shrub cover ($F_{1,40} = 0.92$; $P > 0.05$) or shrub height ($F_{1,40} = 0.06$; $P > 0.05$) (Table 1).

Between-site differences in bat ensemble composition

A total of 5028 passes were positively identified, belonging to eight bat genera, namely, *Pipistrellus* spp. ($N = 4\ 774$; 94.9%), *Eptesicus* spp. ($N = 101$; 2.0%), *Myotis* spp. ($N = 76$; 1.5%), *Nyctalus* spp. ($N = 19$; 0.4%), *Rhinolophus* spp. ($N = 10$; 0.3%), *Barbastella* spp. ($N = 2$; 0.05%) and *Plecotus* spp. ($N = 1$; 0.02%) (Table 2). Overall, two pipistrelle

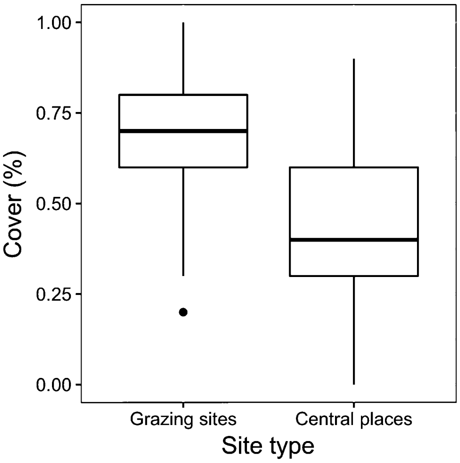

Fig. 2 Box plots showing the between-site (i.e., grazing sites vs. central places) differences in the proportion (%) of tree (*Quercus* spp.) cover

Table 1 Mean ± SE [range: min.–max.] of vegetation-related variables that were considered in terms of explaining between-site differences (Central places vs. Grazing sites) in bat ensemble composition and activity levels of insectivorous bats in a *montado*-dominated landscape in South-Eastern Portugal (Fig. 1)

	Forest cover (%)	Number of saplings	NDVI (index)	Shrub cover (%)	Shrub height (cm)
Central places	45.2 ± 4.7 [20.0–100.0]	55.4 ± 19.0 [0.0–360.0]	0.35 ± 0.0 [0.11–0.47]	20.7 ± 5.9 [0.00–100]	53.8 ± 7.9 [0.0–100.0]
Grazing sites	66.9 ± 4.9 [0.0–90.0]	136.6 ± 29.0 [0.0–490.0]	0.30 ± 0.0 [0.13–0.49]	32.6 ± 5.3 [0.00–90.0]	66.6 ± 7.0 [0.0–120.0]

species, the common pipistrelle *P. pipistrellus* and the Kuhl's pipistrelle *P. kuhlii* were the most frequently recorded species, accounting for about 85% of the total number of bat passes (Table 2). Other frequently recorded bats were the house bats (genus *Eptesicus*, which probably included *E. serotinus* and *E. isabellinus*). A total of 45 calls (0.9%) could not be identified to genus or species level and were thus classified as multi-genus complex or undetermined bats (Table 2).

As suggested by species accumulation and sample-based rarefaction curves, the minimum and maximum number of species occurring was higher in grazing sites ($N = 12$ and $N = 13$, respectively) than in central places ($N = 7$ and $N = 8$, respectively) (Table 2; Fig. 4). Overall, species accumulation and sample-based rarefaction curves reached an asymptote, suggesting we adequately sampled insectivorous bats in both types of site (Fig. 4). Considering the community of bats as a whole, all species and species complexes were present at grazing sites. At central places, in contrast, a number of species were absent, specifically: three species (namely, *Myotis bechsteinii*, *Barbastella barbastellus* and *Tadarida teniotis*) as well as two single-genus complexes (namely, *Rhinolophus* spp., which potentially included four species: *R. mehelyi*, *R. hipposideros*, *R. ferrumequinum* and *R. euryale*, and *Plecotus* spp., which belonged either to *P. auritus* or *P. austriacus*) (Table 2). Between-site differences in species composition were found to be statistically significant by ANOSIM test, as assessed by the Sørensen's index ($P < 0.001$).

Between-site differences in bat activity levels

In line with species richness, the activity of the bat community as a whole was significantly higher in grazing sites than in central places (Table 2; Fig. 5). More specifically, bat activity was four fold higher in grazing sites (190.80 ± 49.63 passes per night; $N = 4007$) than in central places (48.14 ± 11.30 passes per night; $N = 1\ 011$) (Table 2). Overall, the activity levels of most species (including highly generalist species such as those belonging to the genus *Pipistrellus*) was higher in grazing sites compared to those in central places, with the exception of those recorded from *Myotis escalerai* Kaup, 1829 and the multi-genus complex *Eptesicus* spp./*Nyctalus* spp. (Table 1). Bat activity recorded in central places was in fact almost exclusively attributed to pipistrelle

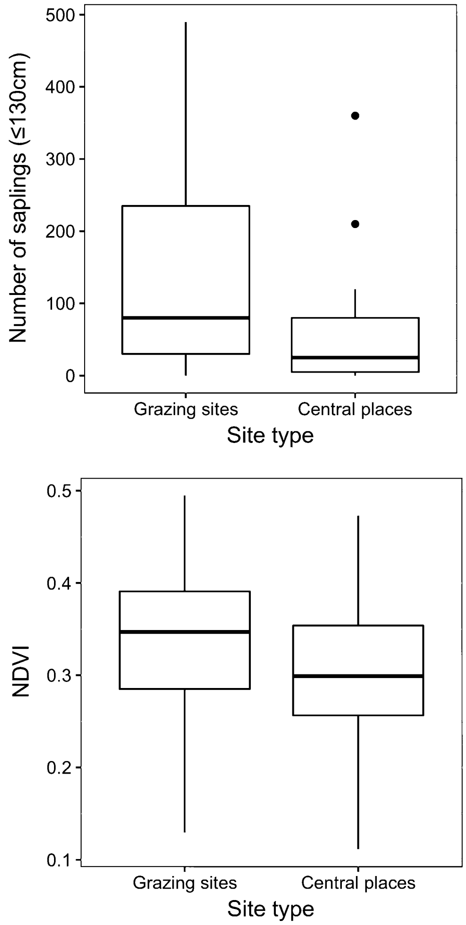

Fig. 3 Box plot showing the differences in the number of saplings of at least 130 cm in height (upper panel) and the NDVI index between grazing sites and central places (lower panel)

species, which accounted for almost 90% of the total bat activity in such sites (Table 2). No significant effect of insect availability was found on either flight activity or species richness (Table 3).

Discussion

Our work suggests that, through their non-random use of the whole available area, free-ranging cattle cause strong between-site differences in vegetation structure, namely tree cover density. More importantly, it demonstrates that these cattle-driven fine-scale forest disturbances drive noticeable between-site differences in the community composition and activity levels of insectivorous bats. Our work therefore demonstrates that loss of forest cover has an impact on insectivorous bats even when operating at fine spatial scales. Because many bat species are of high conservation concern (including some of those which we recorded in the current work; IUCN 2017) and play a pivotal ecological role in forests worldwide (Kunz et al. 2011), we suggest that fine-scale forest disturbances must not be neglected in the conservation management of forest systems, both natural and managed.

The response patterns exhibited by bats found in this study are in line with previous studies focused on other flying vertebrates like birds (Martin and Possingham 2005; Nelson et al. 2011; Alhering and Merkord 2016). In accordance with these other studies, the number of bat species recorded in highly-disturbed sites (i.e., central places) was significantly lower than that recorded in less-disturbed sites (grazing sites). Indeed, the bat community in central places was composed almost exclusively by highly generalist species such as those belonging to the genus *Pipistrellus* which accounted for up to 90% of total bat pulses. Moreover, the level of activity of the bat community as a whole was four-fold lower in central places than in grazing sites. On the basis of existing research literature, two mechanisms could be behind this response pattern. On the one hand, vegetation ground cover is widely recognized to influence the activity of forest-associated bats through determining the availability and accessibility of prey insects (e.g. Rainho et al. 2010; Cruz et al. 2016). Hence between-site differences in bat ensemble composition and activity levels might potentially be explained by cattle-driven alterations in the structure of the understory layer. However, despite shrub cover tending to be lower in central places, we found no significant between-site differences in either shrub cover or shrub height, something that ultimately explains the similar insect prey availability in both types of site.

On the other hand, tree cover density is another landscape-related attribute widely recognized to influence the activity of forest-associated bats through determining foraging behavior (e.g. Patriquin and Barclay 2003). We found strong between-site differences in tree cover, with central places showing a lower tree cover density than did grazing sites. These differences seem to be related to the stronger pressure exerted by cattle on vegetation regeneration, as both the number of tree saplings and productivity was lower in central places compared to grazing sites. The deleterious impact of cattle on tree cover has been

Table 2 Flight activity (passes per hour) (mean ± SE) in sites identified as frequently used by cattle (central places; $N = 21$) and less frequently used by cattle (grazing sites; $N = 21$) within *montado* farms in the Special Area of Conservation (SAC) of Monfurado, Southern Portugal

Level		Conservation status[a]	Mean passes per night (± SE)	
			Grazing sites	Central places
Species	*Pipistrellus pipistrellus* Schreber, 1774	LC	22.24 ± 7.61 (467)	6.14 ± 1.74 (129)
	Pipistrellus kuhlii Kuhl, 1817	LC	20.33 ± 4.98 (427)	6.00 ± 1.86 (126)
	Nyctalus leisleri Kuhl, 1817	LC	0.62 ± 0.27 (13)	0.29 ± 0.21 (6)
	Myotis daubentonii Kuhl, 1817	LC	0.81 ± 0.34 (17)	0.14 ± 0.10 (3)
	Myotis escalerai Cabrera, 1904	NE[b]	0.14 ± 0.08 (3)	0.29 ± 0.24 (6)
	Barbastella basbastellus Schreber, 1774	VU	0.10 ± 0.1 (2)	– (0)
Single-genus complex	*Pipistrellus* spp. Kaup, 1829	–	118.81 ± 35.37 (2495)	27.81 ± 8.02 (584)
	Eptesicus spp. Rafinesque, 1820	–	3.00 ± 1.03 (63)	1.81 ± 0.81 (38)
	Myotis spp. Kaup, 1829	–	0.90 ± 0.42 (19)	0.38 ± 0.25 (8)
	Rhinolophus spp. Gray, 1825	–	0.48 ± 0.43 (10)	– (0)
	Plecotus spp. Geoffroy, 1818	–	0.05 ± 0.05 (1)	– (0)
	Myotis myotis Borkhausen, 1797/*M. blythii* Tomes, 1857	LC/CR	0.67 ± 0.24 (14)	0.14 ± 0.10 (3)
	Myotis bechsteinii Kuhl, 1817/*M. emarginatus* Geoffroy, 1806	VU/NE	0.14 ± 0.1 (3)	– (0)
Multi-genus complex	*Pipistrellus pygmaeus* Leach, (1825)/*M. schreibersii* Kuhl 1817[b]	LC/NT	21.86 ± 9.70 (459)	4.14 ± 1.39 (87)
	Eptesicus spp/*Nyctalus* spp.[c]	–	0.62 ± 0.26 (13)	1.00 ± 0.71 (21)
	Undetermined bats	–	0.29 ± 0.12 (6)	0.24 ± 0.10 (5)
Total			191.10 ± 49.63 (4013)	48.38 ± 11.32 (1016)

Numbers in parentheses indicate the total number of passes recorded

[a] IUCN (2017), *NT* near threatened, *LC* least concern, *VU* vulnerable, *NE* not evaluated

[b] This double category was created because both species have overlapped calls

[c] Probably includes *E. serotinus* (Schreber, 1774) and *E. isabellinus* (Temminck, 1839)

widely demonstrated (Dufour-Dror 2007; Mayer et al. 2009; Kaufmann et al. 2014; Almeida et al. 2016), although the impact of cattle-driven forest disturbances on insectivorous bats is poorly documented. The response pattern of bats we found in this study apparently contradicts the hypothesis that cattle have a direct positive influence on the occurrence and activity levels of insectivorous bats through attracting suitable prey such as dipterans and coprophagous beetles (Downs and Sanderson 2010; Rainho et al. 2010; Ancillotto et al. 2017). As an explanation, we believe that the negative, long-term and indirect influence of cattle on bats through the impact on tree cover density is probably stronger than the positive, immediate and direct influence of the presence of cattle favoring the occurrence of prey insects. In this context, we suggest that further research should be conducted which aims to disentangling the direct and indirect effects of cattle on biodiversity in general, and on bats in particular. If not, we are in danger of not fully understanding the actual role that free-ranging cattle play in the conservation management of forest systems.

It should be noted that our conclusions are particularly important for our study system, the *montado*/*dehesa* agroforestry system. This is because the characteristic savanna-like structure of the *montado* could lead to anticipate a limited impact of reduced tree cover density on forest-associated flying species

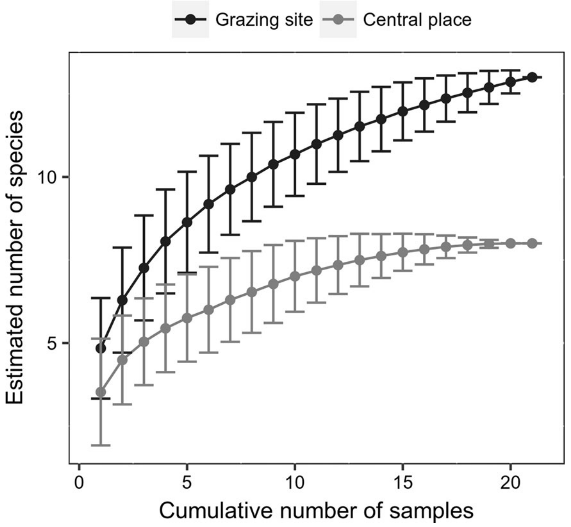

Fig. 4 Species accumulation curves used to compare species richness between central places and grazing sites, as well as to assess sampling effort at the two types of site. The cumulative number of bat species (*y*-axis) is plotted as a function of the cumulative number of samples (*x*-axis). Box plots indicate the expected species richness and its standard deviation from central places (gray dots), and grazing places (black dots)

Fig. 5 Box plot showing differences in flight activity (mean number of passes per hour) of the bat community as a whole between grazing sites and central places

such as birds and bats (Godinho and Rabaça 2011). However, our results lead this theoretical preconception to be null. Indeed, our results suggest that fine-scale changes in tree cover density strongly impacts not only ensemble composition but also activity levels of insectivorous bats, potentially threatening the biocontrol services they provide, including pest control services. In line with this, the consideration of fine-scale forest disturbances seems crucial for the conservation management of the *montado*/*dehesa* for High Nature Value (Ferraz-de-Oliveira et al. 2016). This is particularly relevant if we consider that livestock farming is one of the main production activities in, and the main economic incentive of, the *montado*/*dehesa* agroforestry system (Pinto-Correia et al. 2011). Moreover, a generalized decline in this particular system has been reported throughout the Mediterranean region, especially in Portugal, Spain, Morocco, France and Italy, with most of this decline associated with failures in juvenile tree regeneration due to livestock browsing, among others factors (Almeida et al. 2016; Godinho et al. 2016). While our work has direct implications for the conservation management of our study system, its conclusions are also of interest for other forest systems around the world since fine-scale forest disturbances—prompted by cattle grazing, selective logging or fires– are widespread, their consequences on biodiversity in general and on bats in particular are poorly understood.

Counteracting the impact of cattle-driven fine-scale forest disturbance

The sites frequently used by cattle (i.e. central places) were those mainly associated with the presence of water and feeding troughs, whereas those less often used by cattle (i.e. grazing sites) were mainly used for grazing purposes. This suggests that water availability and food supply might be amongst the main mechanisms underlying the strong between-site differences in space use exhibited by cattle (Salvarina 2016 and references therein). The influence of these pivotal resources (i.e., water and food) indeed appears to be of such significance as to lead cattle to select sites of lower tree crown coverage, even in summer when temperatures in our study region commonly reached 40 °C. In the face of the strong impact cattle have on vegetation structure and its concomitant influence on the composition and activity of insectivorous bats, we propose periodic changes in the location of both water and feeding troughs as a potential management action (Ryan and Getz 2005). These periodic rotations would increase the likelihood of vegetation regeneration including that of tree-like species such as *Q. rotundifolia* and *Q. suber*. Ultimately, this would allow

Table 3 Results of generalized linear models (GLMs) to test for significant between-site differences in the activity level of bats

	Estimate	S.E.	t value	Significance
Flight activity				
Intercept	− 3.441	0.247	13.900	0.000
Site type (Central places)	− 1.125	0.323	− 3.482	**0.001**
Insect availability	0.086	0.890	0.096	0.924
Species richness				
Intercept	1.586	0.109	14.608	0.000
Site type (Central places)	− 0.333	0.154	− 2.159	**0.031**
Insect availability	0.114	0.381	0.300	0.764

We considered the number of bat passes per hour as response variable and site type as fixed factor. Farm identity was included in the models as a random factor. Significant variables ($P < 0.05$) are in bold

insectivorous bats to become distributed throughout the whole landscape without the restrictions imposed by the shortage of tree cover. Other alternatives would include fenced exclosures in order to increase the establishment and survival of tree seedlings and, in turn, forest regeneration.

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