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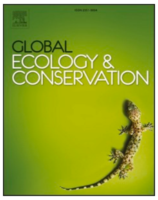

Original research article

Agroforestry systems favor bat conservation but only when old and grazed

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ABSTRACT

As a consequence of agricultural intensification and landscape homogenization, semi-natural elements such as hedges, woodland patches and scattered trees have been removed from many agricultural areas. The resulting habitat loss has led to the decline in the diversity and abundance of many taxa including bats, which are highly dependent on woody plants for foraging, roosting and reproduction. By combining trees with crops (silvoarable systems) or livestock (silvopastoral systems), agroforestry re-integrates structural diversity into agricultural areas that could have beneficial effects on biodiversity. In this study, bat activity was recorded with autonomous sound recorders (AudioMoth) in sixty-five agroforestry and reference sites across western Europe. Bat activity in silvopastoral systems was two times higher than in pastures and orchards and four times higher than in cropland. In addition, social calls and foraging rates of bats were highest in silvopastoral systems. By contrast, bat activity was not higher in silvoarable systems compared to control plots. Tree characteristics affected total bat activity, which was higher with increased tree age and in sites with broad-leaved compared with coniferous trees. Our results show that the combination of old broad-leaved trees and livestock is highly beneficial for bats. Thus, silvopastoral systems deserve more attention in sustainable agriculture and biodiversity conservation.

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However, management should also be considered and especially the implementation of silvopastoral systems with low-intensity grazing and low pesticide input should be supported.

1. Introduction

Agricultural intensification has considerably modified European landscapes. Semi-natural habitats such as hedges and woodland patches as well as scattered trees have been removed, leading to a decrease in landscape diversity (Stoate et al., 2001; Robinson and Sutherland, 2002). The resulting loss of shelters, roosting sites, foraging habitats and food resources has led to severe population declines in farmland biodiversity (e.g. Fahrig, 2003) including insects (e.g. Raven and Wagner, 2021), birds (Donald et al., 2001; Benton et al., 2002) and mammals (Pekin and Pijanowski, 2012). Likewise, bat populations have been affected by land use changes and suffered drastic declines during the 20th century, in part due to reduced roost and prey availability (Mickleburgh et al., 2002; Park, 2015; Treitler et al., 2016). Across Europe, bat conservation is supported by several conventions (e.g. Bern and Bonn conventions (Council of Europe, 1979, United Nations Environment Programme, 1979)), agreements (e.g. EUROBATS Agreement (United Nations Environment Programme/Eurobats/Eurobats/Eurobats, 1991)) and actions plans (e.g. Action Plan for the Conservation of Bat Species in the European Union (European Commission/Eurobats, 2018)) and bats are legally protected in the European Union (Article 12 of the Habitat Directive, 92/43/CEE (European Union, 1992)). However, bat populations remain under pressure from anthropogenic threats, especially in agricultural areas where they face habitat change and roost disturbance (European Commission/Eurobats, 2018; Frick et al., 2019). Their low reproduction rate, long lives and high metabolic requirements make bats sensitive to human activities and environmental change (Jones et al., 2009).

Bat sensitivity, combined with their presence in a wide range of ecosystems, make these mammals important bioindicators of wider biodiversity values (Jones et al., 2009). As insectivorous bats need a large quantity of insect prey to fulfil their energy requirements (Arthur and Lemaire, 2015; Russo et al., 2021), their foraging activity closely correlates with insect availability. The activity of European bats was shown to increase in the presence of cattle and dung, which attract numerous insects (Downs and Sanderson, 2010; Ancillotto et al., 2017). Moreover, previous studies have shown a positive effect of nearby forests, tree lines or isolated trees, hedgerows, tree groves (Boughey et al., 2011; Heim et al., 2015; Finch et al., 2020) on bat activity as well as on species richness. Especially old and broad-leaved trees are known to represent foraging and roosting habitats of higher value for bats compared to younger and coniferous tree stands, often associated to shorter rotation periods (Boye and Dietz, 2005; Russo et al., 2016; Charbonnier, 2016a and 2016b). Dense networks of linear woody features within a landscape represent important landmarks for bats and are used both as commuting routes (e.g. between roosts and foraging areas) and for foraging (Verboom and Huitema, 1997; Heim et al., 2015).

By deliberately combining trees with crops (silvoarable systems) or livestock (silvopastoral systems) on the same land, agroforestry adds structural diversity to farmland (Nair, 1993). The biophysical interactions between the woody and non-woody components support ecosystem services (Jose, 2009; Mosquera-Losada et al., 2009; Palma et al., 2007) such as water retention (Joffre and Rambal, 1988) or nutrient cycling (Nair, 2007; Torralba et al., 2016) and can result in both economic and ecological advantages. The high heterogeneity due to the presence of trees and/or shrubs in agroforestry also benefits biodiversity by providing shelter, food, roosting and breeding opportunities for many organisms (Jose, 2009; McAdam and McEvoy, 2009; Torralba et al., 2016; Mupepele et al., 2021). Agroforestry has been shown to benefit arthropods (Boinot et al., 2019; Pardon et al., 2019), birds (Edo et al., 2024) and mammals (Klaa et al., 2005; Gonçalves et al., 2012) all of which can promote ecosystem services such as pest control (Boinot et al., 2019; Staton et al., 2019). Although it has been demonstrated that agroforestry supports biodiversity and that bat activity is higher if linear elements and grazing animals are present in the landscape (Ancillotto et al., 2017), to our knowledge, no previous studies have specifically focused on bats in agroforestry systems at a European scale. Therefore, this study aims to elucidate the effects of agroforestry on bat richness and activity to inform and adapt conservation strategies for these European-wide protected mammals and in turn derive potential benefits to agriculture, since bats play a major role in the control of pest insects (Boyles et al., 2011; Kunz et al., 2011; Ancillotto et al., 2017).

We predict that bat activity is higher in agroforestry systems, due to higher structural heterogeneity, compared with open agriculture (cropland and pastures) as well as compared with orchards. Given that grazing livestock attract numerous insects and that low-intensity grazing also contributes to habitat heterogeneity, we predict that grazing has a positive effect on bat activity. Overall, we predict bat activity to increase in grazed habitats (pastures and silvopastures) and in plots associated with woody elements (forests, agroforestry), as bats often depend on vegetation structures for both commuting and foraging. Hence, we predict more positive effects of silvopastoral than of silvoarable systems on bat activity. We predict that coniferous and broad-leaved trees will differently affect bat activity and we expect an increase of bat activity with tree age as both increasing age and broad-leaved trees are known to represent roosting and foraging habitats of high value for bats.

2. Material and methods

2.1. Study sites

The study was carried out in eight different geographical regions. In each region we selected an agroforestry farm (in the following referred as “site”) including either silvoarable agroforestry (combination of trees and crops) or silvopastoral agroforestry systems (combination of trees and livestock) and nearby control plots. The sites were located in seven countries across Europe: England, Switzerland, France (two sites) Germany, Italy, Portugal, and Spain (Fig. 1). We assessed bat diversity and activity in one to three agroforestry fields per site (hereafter termed as "plots"). In total we sampled seven silvoarable plots located in Southern France, Switzerland and England and thirteen silvopastoral plots located in Spain, Portugal, Italy, Central France and Germany. For each agroforestry plot, two to three control plots with the same woody or agricultural components were sampled. Thus, in addition to the silvoarable systems, a total of seven croplands (with the same crop as in the agroforestry system), ten forests and four orchards (with the same tree species as in the agroforestry system) were sampled. Similarly, 13 open pastures, 16 forests and five orchards were sampled as control plots for the silvopastoral systems. We defined the forests as areas with more than 10 percent tree cover over at least 0.5 ha and with part of the trees aged more than 30 years, but excluding trees of agricultural production systems (FAO Food and Agriculture Organization of the United Nations, 2018). Fruit or nut orchards (n = 9) were sampled if the trees in the agroforestry system were fruit or nut trees (i.e. in Germany, Switzerland, in Southern France and in Portugal). Agroforestry and control plots of a same site were located nearby, to minimize the variation of e.g. climate, soil, and the surrounding landscape (coordinates of each plot are given in Supporting Table A1). The minimum distance between plots of the same site was 200 m, to avoid any overlap of the bat call recordings. We selected mature agroforestry and orchard plots with trees planted at least 12 years ago. Hereafter, the time since planting will be referred to as "tree age", irrespective of age of the trees at the time of planting which is not always known. The trees of the silvoarable plots in Switzerland (*Malus domestica, Prunus avium*), England (mixed broad-leaved tree stands) and Southern France (*Juglans regia, Pinus* spp.) were at least 12, 25 and 27 years old, respectively. The trees of the silvopastoral plots were 20 (Germany, *Malus domestica*), 25 (Portugal, *Pinus* spp.), 35 (Central France, *Acer pseudoplatanus*, *Fraxinus excelsior* and *Prunus avium*), 90 (Italy, *Quercus* spp.) and 175 (Spain, *Quercus* spp.) years old. The control orchards and forests were stocked with trees of the same species and of approximatively the same age as those in the respective agroforestry site. Information on management, environmental parameters, tree species and crops associated to each plot as well as sampling dates can be found in Supporting Table A1.

2.2. Data collection

We assessed bat activity via analysis of the echolocation calls they use to detect prey and for orientation, and analysis of social calls. Autonomous sound recorders (AudioMoth V1.1.0, Open Acoustic Devices, firmware version 1.7., configuration app version 1.6.0; Hill et al., 2019) were mounted on a thin pole at a height of 1.5 m, with the microphone oriented towards the respective plot's centre. In each plot one AudioMoth was set up three times between March and July in 2021 (England, Germany, Switzerland and Central France) and 2022 (Southern France, Italy, Portugal and Spain). See Supporting Table A1 for the detailed sampling dates. Recorders were placed at least 20 m from the plot's edge to record only individuals active within the studied habitat (Fuentes-Montemayor et al., 2013) and rotated between plots for each sampling to reduce possible hardware bias. AudioMoths were wrapped in a single layer of clingfilm to protect them from humidity and dust. We conducted surveys during calm and dry weather (i.e., wind force between 0 and 1 on the Beaufort scale and no precipitation), as bat activity is strongly reduced during wind or rain (Arthur and Lemaire, 2015). During each of the three samplings, the AudioMoths were set to record continuously from ninety minutes before sunset until ninety minutes after sunrise. Full night recordings with continuous sampling allow the detection of more species and can account for varying activity of bats during the night (Skalak et al., 2012). Devices were programmed to record at medium gain, a recording duration of 3595 s and sleep

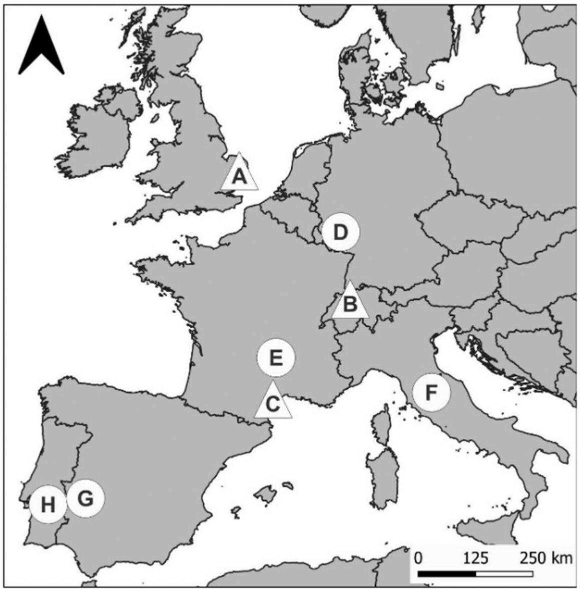

Fig. 1. Geographic location of the silvoarable (A-C) and silvopastoral (D-H) study sites.
Triangles = silvoarable systems, circles = silvopastoral systems, A = Wakelyns (UK), B = Eulenhof and Sursee (CH), C = Restinclières (FR), D = Bannmühle (DE), E = Lamartine (FR), F = Tenuta di Paganico (IT), G = Dehesa de Majadas (ES), H = Moinhos de Vento (PO).

duration of 5 s. The sampling rate of 192 kHz was suited to record all bat species of the study region except for *Rhinolophus euryale and R. hipposideros*. Recordings were saved as.wav files and stored on memory cards (SanDisk Corporation, Milpitas, California, USA). The same recordings, but different time windows were used to study birds in a previous study (Edo et al., 2024), which is the reason why the sampling took place in spring.

2.3. Species identification

The audio recordings from each site were split into one-minute files and pre-classified using the software Kaleidoscope Pro (version 5.4.8; Auto-ID: Bats of Europe classifier version 5.4.0 with European region database corresponding to each country; Wildlife Acoustics Inc., Concord, MA, USA). The software Kaleidoscope detects bat signals with a frequency range between 8 and 120 kHz, a pulse length in the range of 2 and 500 ms and a maximum of 500 ms inter-syllable gap. Files without any detected bat signals following these criteria were filtered out as "noise files" by the software and were not further analyzed. Files containing three (or fewer) bat calls recognized by the software as well as files misidentified by the software (e.g. vocalization of birds, orthoptera, anthropogenic noise) were manually assigned to "noise files". Spectrogram parameters used were an FFT (Fast Fourier Transform) size of 512 and a Win size of 128 in an overlapping Hann window.

All one-minute files associated with a bat species or associated with the label "No-ID" were manually verified to avoid errors due to automatic identification (Russo and Voigt, 2016; Rydell et al., 2017). Each bat pass (defined as three or more echolocation calls recognized by Kaleidoscope within one second of each other) was identified at species level for *Barbastella barbastellus*, *Hypsugo savii, Pipistrellus pipistrellus*, *Rhinolophus ferrumequinum* and *Tadarida teniotis.* Due to the similarities in call structures and frequencies and difficulties to distinguish between species especially in cluttered environments, we assigned several bat species to species groups/sonotypes: *Pipistrellus nathusii/P. kuhlii*, *Pipistrellus pygmaeus/Miniopterus schreibersii*, *Myotis* spp., *Plecotus* spp. and Nyctaloid sonotype (Schnitzler and Kalko, 2001; Heim et al., 2015; Russo and Voigt, 2016; Rydell et al., 2017). The Nyctaloid sonotype potentially included the species *Eptesicus isabellinus, E. nilssonii, E. serotinus, Nyctalus lasiopterus, N. leisleri, N. noctula* and *Vespertilio murinus. Myotis spp.* and *Plecotus spp.* potentially included all *Myotis* and *Plecotus* species from the study area. We identified the different bat species on the basis of their calls' shape, regularity, recurrence, and signal structure as well as signal measurements such as maximum energy frequency, bandwidth, call duration, start and end frequency, maximum and minimum frequency, characteristic frequency, and inter-pulse interval (Barataud, 2020; Russ, 2021; Skiba, 2009; Jamault et al., 2018).

In addition to the total activity (total number of active minutes for each species), we counted feeding buzzes in the final approach towards prey before capture, as well as social calls, used for intra- and inter-species communication (Russ, 2021). A maximum of one individual per bat species, one feeding buzz and one social call was counted per one-minute file. We quantified bat activity during the sampling period by summing the total number of minutes containing bat passes ("active minutes", further referred as "activity") for each species/species group (Froidevaux et al., 2017; Kalcounis et al., 1999). In addition to the general activity, foraging activity was quantified by calculating the feeding buzz rate as the number of minutes with feeding buzzes per number of active minutes following Eq. (1):

$$Feeding\ buzz\ rate_i = \frac{n_{feeding\ buzzes_i}}{n_{active\ minutes_i} + 1} \tag{1}$$

Similarly, the social call rate was quantified as the number of minutes with social calls per number of active minutes following Eq. (2):

$$Social\ call\ rate_i = \frac{n_{social\ calls_i}}{n_{active\ minutes_i} + 1} \tag{2}$$

with $n_{feeding\ buzzes_i}$ (1) the number of minutes with feeding buzzes, $n_{social\ calls_i}$ (2) the number of minutes with social calls in each plot i, and $n_{active\ minutes_i}$ the total number of active minutes recorded in each plot across the three sampling dates.

2.4. Statistical analysis

In a first step, in order to analyze the effect of habitat type on bat activity, we fitted linear mixed-effect models with habitat type as explanatory variable (equation: lmer (Activity ~ Habitat + (1|Site)), R package lme4, Bates et al., 2015). Due to the nested design of the study, "Site" was used as a random factor. Post hoc tests were used to determine the pairwise differences of the total activity, social call rate and feeding buzz rate between habitats (R package *emmeans*, function *emmeans*, Lenth, 2022). In a second step, we fitted linear mixed-effect models to analyze the effect of tree type (broadleaved or conifer) and tree age on bat activity, again with "Site" as a random factor (equation: lmer (Activity ~ log10(Age) + Tree type + (1|Site)). All models were tested against their respective null model to ensure that ΔAIC was > 2.

For all statistical tests, P-values < 0.05 were considered as significant. P-values, means and standard errors of the mean (SE) are given in text and tables. All statistical analyses were conducted in R version 4.2.2 (R Core Team, 2022).

3. Results

In total, 10 species and species groups (hereafter call types) were recorded (Table 1). The most common call types were *Pipistrellus*

pipistrellus (present on 83 % of all plots), *Pipistrellus nathusii/P. kuhlii* (78 %) and *Myotis* (77 %). Almost all call types were recorded in all habitats (Table 1).

Over all sites and across all species, 7890 active minutes were recorded, including 629 minutes with feeding buzzes and 749 minutes with social calls. Together, the *Pipistrellus* species represented 78 % of the total activity recorded (Table 1). Bat activity was highest in silvopastoral plots and differed significantly from forests, cropland, pastures and marginally significantly from silvoarable and orchard plots (Fig. 2, Table 1 and Supporting Table A2). Bat total activity was four times higher in silvopastoral plots relative to cropland, more than two times higher than in silvoarable plots, orchards and pastures and 1.5-times higher than in forests. *Pipistrellus nathusii/P. kuhlii* was the dominant sonotype in silvopastures, accounting for nearly half of total bat activity. Their activity was more than three times higher in silvopastures than in pastures and silvoarable systems, more than two times higher than in forests and more than six times higher than in orchards and cropland (Table 1). Similarly, *Rhinolophus ferrumequinum*, *Pipistrellus pipistrellus* and the species groups *Myotis, Pipistrellus pygnaeus/Miniopterus schreibersii* had their highest activity in silvopastoral systems compared to the other habitats, though differences were not significant. Nyctaloid activity was more balanced between habitat types. As an exception, *Tadarida teniotis* showed a higher activity in pastures compared to the other habitats (Table 1).

The feeding buzz rate was higher in silvopastures compared to pastures, but the difference was not significant (Fig. 3**a, **Table 1**,** Supporting Table A3). The social call rate was significantly higher in silvopastoral systems and forests relative to pastures (Fig. 3b, Table 1 and Supporting Table A3).

Bat activity depended on tree type and was on average ten times higher in plots with broad-leaved trees (Spain, France-Lamartine, Italy, Germany, France-Restinclières, Switzerland and England) compared with coniferous trees (Portugal, France-Restinclières) (Fig. 4). In addition, bat activity increased with tree age. The steepest increase in activity was found up to a tree age of around 50 years. A further increase in tree age led to a gradual saturation in activity (Fig. 5).

Table 1

Bat activity ± standard error of bat species/species groups recorded in silvoarable and silvopastoral plots, forests, orchards, cropland and pastures; letters show significant pairwise differences between habitats derived from post hoc test.

Species/Habitat	Silvoarable (n = 7)	Silvopastoral (n = 13)	Forest (n = 16)	Orchard (n = 9)	Cropland (n = 7)	Pasture (n = 13)	Total activity per species	Mean activity per species
Barbastella barbastellus	0 ± 0	0.23 ± 0.17	0.06 ± 0.06	0 ± 0	0 ± 0	0.23 ± 0.17	7	0.11 ± 0.05
Hypsugo savii	0.29 ± 0.29	0.92 ± 0.37	1.06 ± 0.60	0.89 ± 0.77	1 ± 0.43	1.92 ± 1.36	71	1.09 ± 0.33
Pipistrellus pygmaeus/ Miniopterus schreibersii	11.71 ± 10.73	42.77 ± 26.39	25.5 ± 8.64	8 ± 7.26	7.29 ± 5.98	5.69 ± 2.58	1243	19.12 ± 6.01
Myotis spp.	3 ± 1.51	14.62 ± 4.91	8.56 ± 3.65	2.11 ± 1.39	4.43 ± 2.66	5.62 ± 1.37	471	7.25 ± 1.47
Nyctaloid	4.86 ± 2.53	27.69 ± 17.06	8.75 ± 3.34	27.33 ± 11.21	5.57 ± 2.51	20.77 ± 7.30	1089	16.25 ± 4.15
Pipistrellus nathusii/P. kuhlii	14.57 ± 7.77 ab	**84.69 ± 28.11 a**	**35.56 ± 13.31 b**	6.44 ± 3.04 ab	13.29 ± 7.59 ab	**28.08 ± 10.86 b**	2288	35.20 ± 7.53
Pipistrellus pipistrellus	29.29 ± 7.69	44.54 ± 17.22	51.88 ± 13.77	33.56 ± 14.17	20.29 ± 3.92	15.31 ± 5.63	2257	34.72 ± 5.53
***Plecotus* spp.**	1.14 ± 0.63	1.46 ± 0.91	1.44 ± 0.48	0.22 ± 0.15	1.71 ± 0.89	2.92 ± 1.55	102	1.57 ± 0.40
Rhinolophus ferrumequinum	0 ± 0	0.77 ± 0.54	0.5 ± 0.18	0 ± 0	0.14 ± 0.14	0.15 ± 0.11	21	0.32 ± 0.12
Tadarida teniotis	0.43 ± 0.43 ab	2.54 ± 1.40 ab	**1.31 ± 0.49 b**	0.78 ± 0.55 ab	0.86 ± 0.70 ab	**20.85 ± 12.19 a**	341	5.25 ± 20.75
Total activity[a]	**65.29 ± 27.49 b**	**220.23 ± 52.23 a**	**134.62 ± 22.45 b**	79.33 ± 24.79 ab	**54.57 ± 18.89 b**	**101.54 ± 23.3 b**	-	-
Feeding buzzes	6.29 ± 2.29 ab	**23.46 ± 6.86 a**	11.5 ± 3.24 ab	**4 ± 1.57 b**	**4 ± 1.93 b**	**2.46 ± 0.83 b**	629	9.68 ± 1.86
Feeding buzzes rate	0.08 ± 0.03 ab	**0.15 ± 0.07 a**	0.07 ± 0.01 ab	0.03 ± 0.01 ab	0.06 ± 0.03 ab	**0.02 ± 0.01 b**	-	0.07 ± 0.02
Social calls	2 ± 1.31 ab	**32.23 ± 12.35 a**	16.19 ± 5.22 ab	3.33 ± 2.49 ab	1.71 ± 1.25 ab	**0.92 ± 0.38 b**	746	11.48 ± 3.11
Social calls rate	0.01 ± 0.01 ab	**0.11 ± 0.03 a**	**0.11 ± 0.03 a**	0.02 ± 0.01ab	0.03 ± 0.02ab	**0.01 ± 0.00 b**	-	0.06 ± 0.01

[a] number of active minutes; feeding buzzes and social calls excluded

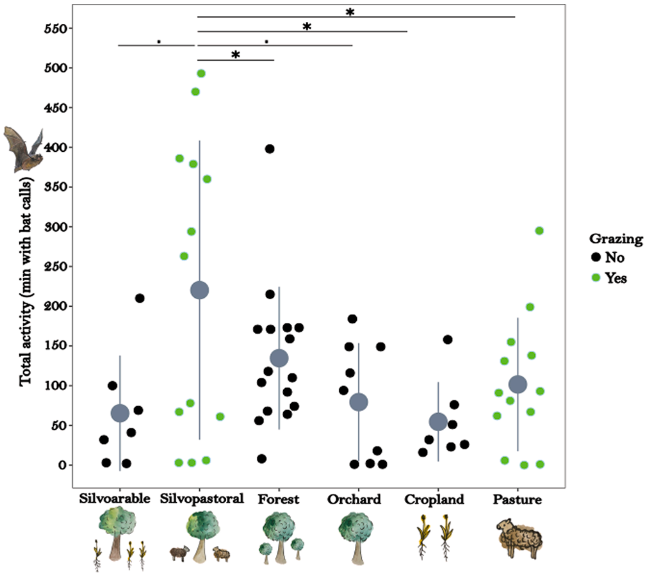

Fig. 2. Bat total activity (number of active minutes) in agroforestry (silvoarable n = 7, silvopastoral n = 13), forest (n = 16), orchards (n = 9) and open agriculture (cropland n = 7, pasture n = 13). Significance levels: **.** P < 0.1, *P < 0.05. Grey dots indicate mean values. See Table 1 for the detailed results of activity (± SE) in each habitat. See Supporting Table A3 for the results of the mixed-effect models and post hoc tests used to determine the pairwise differences between habitats.

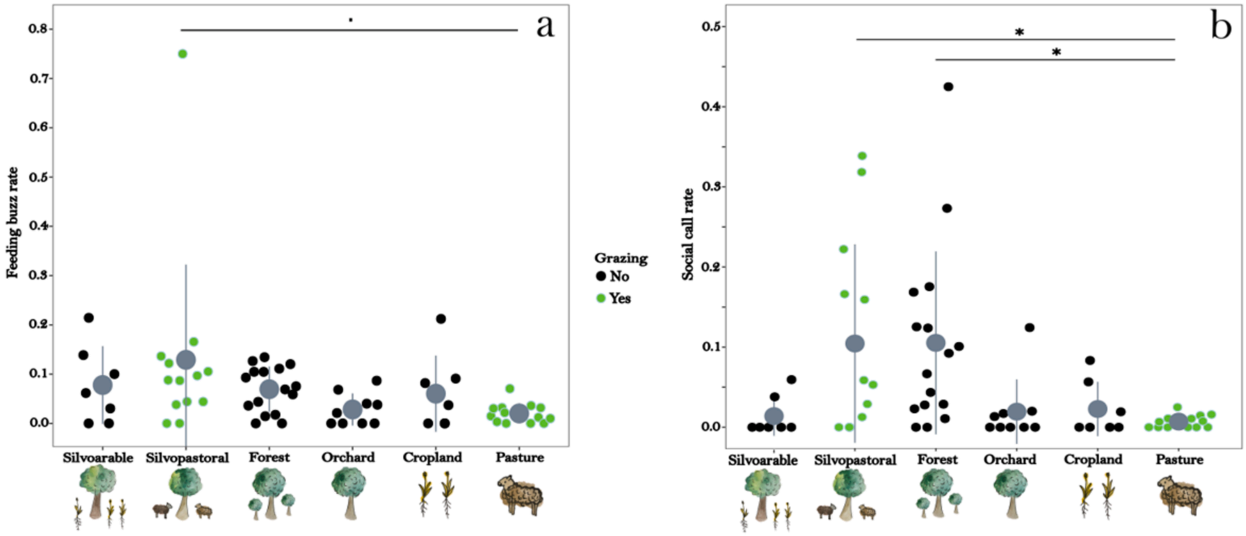

Fig. 3. Feeding buzz rate (a) and social call rate (b) in agroforestry (silvoarable n = 7, silvopastoral n = 13), forest (n = 16), orchards (n = 9) and open agriculture (cropland n = 7, pasture n = 13). Significance levels: **.** P < 0.1, *P < 0.05. Grey dots indicate mean values. See Table 1 for the detailed results of activity (± SE) in each habitat. See Supporting Table A4 for the results of the mixed-effect models and post hoc tests used to determine the pairwise differences between habitats.

4. Discussion

In line with our hypotheses, our results clearly underline the high value of silvopastoral agroforestry systems for bats. The presence of woody elements combined with livestock had a positive effect on bat activity. Bat activity was higher in silvopastoral systems than in all other habitats, both habitats with trees (silvoarable systems, forests, orchards) and without (cropland and pastures). In addition, feeding and social activity were higher in silvopastures compared with pastures. Broad-leaved trees were associated with a higher bat activity compared with coniferous trees and activity increased with increasing tree age. This suggests that across the studied European agroclimatic zones, silvopastoral systems with mature broad-leaved trees are of outstanding value for the foraging and socializing of bats. However, in our study, coniferous tree stands tended to be younger than broadleaved trees, as well as silvoarable systems being

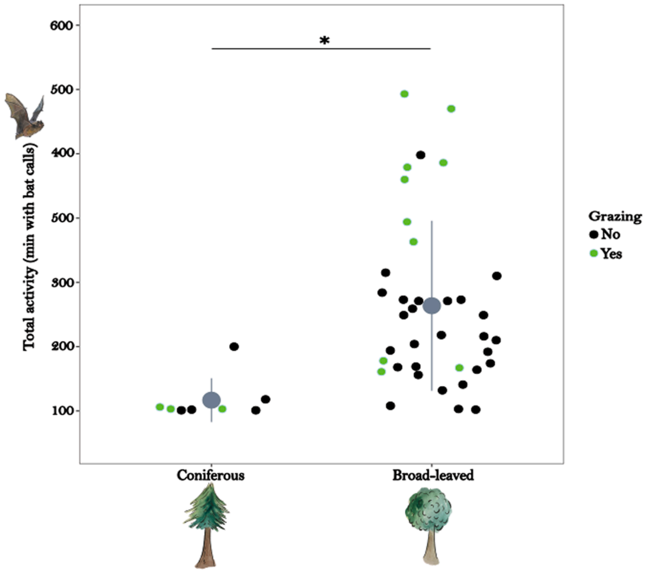

Fig. 4. Comparison of bat total activity (number of active minutes) between plots with coniferous trees (silvoarable n = 1, silvopastoral n = 3, orchards n = 4) and plots with broad-leaved trees (silvoarable n = 6, silvopastoral n = 10, forest n = 16, orchards n = 6). Significance levels: *P < 0.05. Grey dots indicate mean values.

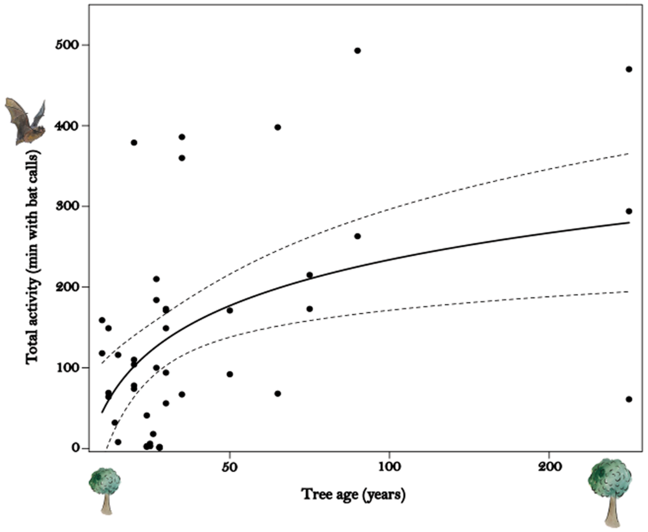

Fig. 5. Effect of tree age on bat total activity (number of active minutes) in agroforestry plots (silvoarable n = 7, silvopastoral n = 13), forests n = 16 and orchards n = 9. Predicted response (black line) and associated 95 % confidence intervals (dashed lines).

younger when compared to silvopastoral systems (Supporting Table A1). Consequently, the separation of the effects of tree type and tree age would require additional study of a larger set of agroforestry systems with more balanced age between conifers and broad-leaved trees, both in silvoarable and silvopastoral systems. The observed differences between habitat types are probably caused by differences in habitat structure and prey availability, which are in turn driven by the presence, age and type of trees, and by the cropping or grazing regime.

4.1. Effects of trees

The presence of trees has a strong influence on bats because woody structures represent important shelter and foraging habitats for them. Bat activity has thus been shown to increase near single trees (Fischer et al., 2010), tree lines and hedges (Boughey et al., 2011; Froidevaux et al., 2019; Wickramasinghe et al., 2003). Linear woody landscape features serve as flight paths for bats, for example between their roosts and feeding habitats (Heim et al., 2015; Verboom and Huitema, 1997). Finch et al. (2020) and Treitler et al.

(2016) showed that bat activity was higher near linear woody features than in the middle of agricultural fields. In addition to increasing foraging efficiency by concentrating insect prey, linear vegetation elements facilitate the navigation of echolocating bats and offer them protection from wind and from predators relying on vision (Verboom and Spoelstra, 1999; Downs and Racey, 2006; Froidevaux et al., 2019). Considering this, bats in silvopastoral systems may leave their roosts earlier than in treeless areas, which would enable them to forage for a longer time and consume more prey (Russo et al., 2007). The higher rates of feeding buzzes in silvopastoral systems relative to pastures further underlines the high value of silvopastoral systems as foraging habitat. During our recording season, bats use social calls to communicate with other individuals, for example as territorial or hunting area occupancy calls (Arthur and Lemaire, 2015) or to indicate the location of the roost. Hence, the high rates of social calls in silvopastoral systems and forest underline their importance as foraging habitat. The high social call rates in silvopasture and forest may indicate additional functions for roosting, especially when compared to e.g. open pastures that had high bat activity but distinctly fewer social calls.

Our results show that, irrespective of habitat type, bat activity is highly influenced by tree age and tree species composition (Downs and Racey, 2006; Russo et al., 2016), which are both known to correlate with roosting opportunities. The steep increase in bat activity we measured up to a tree age of around 50 years suggests that the woody habitats with the highest ecological value for bats are those with mature trees. As trees age they develop more cavities and other roosting sites, not only for bats but also for their prey (Boye and Dietz, 2005; Russo et al., 2016). Traditional silvopastoral agroforestry systems have long been known to supoort high biodiversity (e.g. Herzog, 1998, Moreno et al., 2016; Torralba et al., 2016) and Russo et al. (2005) already showed their importance for the bat species *Rhinolophus mehelyi* in the Dehesas region of Spain. Furthermore, older trees with their larger crowns may also provide more effective shelter from wind and predators (Downs and Racey, 2006). The higher bat activity measured in plots with broad-leaved trees compared with coniferous trees is in line with previous studies (Entwistle et al., 1996; Walsh and Harris, 1996; Boye and Dietz, 2005; 2006) but in contrast with the study of Węgiel et al. (2023)) who found no differences in bat activity between coniferous, deciduous and mixed tree stands. The often reduced attractiveness of coniferous tree stands for bats may be explained by a lower insect prey availability (Lepidoptera: Entwistle et al., 1996) as well as a lower availability of suitable roosting cavities for bats relative to broadleaved tree stands (Boye and Dietz, 2005; Russo et al., 2016). The differences in bat activity we measured between coniferous and deciduous tree plantations could also have been influenced, beyond the tree species, by other characteristics as spatial structure, clutter condition, management or habitat fertility (Węgiel et al., 2023). In our study, coniferous tree stands had slow growing trees (particularly in Portugal) due to the arid climate prevailing in the Mediterranean, which probably contributed to a low habitat quality of those trees for bats.

An important limitation with respect to our habitat comparison is that bat calls are transmitted further in open habitats than in densely cluttered environments (Haupert et al., 2023; Sugai et al., 2020). This can lead to a declining sampling efficiency of acoustic recorders from open habitats over orchards/agroforestry to forest. This could affect our results with respect to bat activity. The reduced transmission in cluttered environments means that the true positive effects of agroforestry over open agriculture areas are likely higher than recorded in the current study, since sampling efficiency was likely reduced in agroforestry relative to open land. By contrast, the 1.5 times higher bat activity in silvopastures compared to forest may be an artefact of higher sampling efficiency in the more open silvopastures. Such limitations in the comparison of different habitat types can be overcome through the measurement of sound detection spaces (Darras et al., 2016), which would however be a major effort that was not feasible in the multiple sampling sites of the current study.

Another possible bias from our study design is the spatial proximity of forest, agroforestry and open agricultural plots. This likely means that open agricultural reference plots are closer to woody habitats than average open agricultural fields, and thus not fully representative. Since bat activity tends to decrease with distance from forest (e.g., Chavez et al. In press; Heim et al., 2015; Stahlschmidt et al., 2017), bat activity in open agriculture may be even more strongly suppressed than recorded in our study.

4.2. *Effects of agricultural management*

Our most interesting finding is probably the outstanding value of grazed agroforestry systems for bats, even when compared with forests. This may be explained by a higher food availability in silvopastoral systems due to the presence of livestock (Fuentes-Montemayor et al., 2013; Ancillotto et al., 2017, 2021). Many insects are associated with dung, including dipterans (Davies, 1957; Steelman, 1976) and beetles (Merritt and Anderson, 1977) that provide important food resources for bats (Downs and Sanderson, 2010; Ancillotto et al., 2017, 2021) but also for other taxa including birds (Wilson et al., 1999). Interestingly, Ancillotto et al. (2017) and Downs and Sanderson (2010) found that bat foraging activity was higher in the presence of cattle than in the presence of only dung, suggesting that flies (Diptera) attracted to the livestock themselves represent important additional prey for foraging bats. The higher activity recorded in silvopastoral plots was mostly the result of the presence of several *Pipistrellus* species which are aerial hawkers feeding on flying insects foraging in relatively open areas (low tree densities and sparse understory cover). Other species, including *Myotis* spp., that forage in more cluttered environments, also showed a tendency to be more active in silvopastoral plots. *Rhinolophus ferrumequinum* is another example of a species that benefits from both a cluttered environment and the presence of livestock, feeding on dung-dwelling beetles (Jones, 1990) preferably in forests and semi-open habitats. Previous studies have also shown an elevated activity of *Pipistrellus* spp. in grazed sites (Downs and Sanderson, 2010; Fuentes-Montemayor et al., 2013; Costa et al., 2019; Ancillotto et al., 2017, 2021).

Differences in agricultural management may modulate the effects of agroforestry on bats. For example, high grazing intensity can reduce insect biomass (Jerrentrup et al., 2014), potentially lowering the food availability to bats. On the other hand, short swards may facilitate foraging for ground-gleaning species such as *Myotis myotis* (e.g. Zahn et al., 2006). Pesticide use can lead to food prey shortage and/or chemical exposure of bats, particularly in field crops and orchards, and turn such sites into “ecological sinks” (Russo et al., 2024; Stahlschmidt et al., 2017). In our study, all agroforestry and respective control plots were grazed at low intensity and managed according to the standards of organic farming (EEC regulation No. 834/2007). In conventional animal husbandry, the use of anthelmintics can have particularly negative effects on the dung-associated fauna (De Souza and Guimarães, 2022). Organic grazing systems were thus shown to sustain higher insect abundance and diversity, which in turn can exert a positive effect on bat activity (Wickramasinghe et al., 2003, 2004; Ancillotto et al., 2023).

The lower bat activity in forests compared with silvopastoral systems is surprising since forests are known to represent one of the most important roosting and feeding habitats for bats (Mickleburgh et al., 2002; Fuentes-Montemayor et al., 2013; Heim et al., 2015; Russo et al., 2016; Frick et al., 2019). An explanation could be that apart from an increased prey availability, grazing with livestock helps to maintain an open understory and a lower tree density. This has been shown to benefit bats, as prey becomes more easily accessible, especially for ground-foraging bat species (Rainho et al., 2010) and aerial hawkers (e.g. *Pipistrellus* spp.) (Fuentes-Montemayor et al., 2013). Silvopastoral systems with their high structural diversity may resemble landscapes that were formerly maintained by mega-herbivores now extinct in Western Europe, such as bison and wild horses (Galetti et al., 2018). Such semi-open, savanna-like landscapes provide very different conditions from today's production forests with their closed canopies and may thus explain the high bat occurrence in silvopastoral systems. Our results are in line with those found by Obrist et al. (2011) who measured a higher bat species richness as well as a higher bat activity in managed orchards (grazed, pruned or mowed) with a less dense vegetation compared to unmanaged ones. Whilst bats benefit from the presence of livestock, the relationship may be mutualistic. Bats are known to play a crucial role in consuming hematophagous insects and can thus help prevent the transmission of pathogens to livestock (Downs and Sanderson, 2010; Ancillotto et al., 2017; Palmer et al., 2019). Bats have also been shown to regulate herbivorous and fungal pests in forests and agroecosystems (Böhm et al., 2011; Maine and Boyles, 2015; Charbonnier et al., 2021; Ancillotto et al., 2022; Maslo et al., 2022). Overall, bats support a wide range of ecosystem functions and services in agricultural areas, some of which may be economically significant (Boyles et al., 2011; Kunz et al., 2011; Maine and Boyles, 2015).

5. Conclusion

In conclusion, silvopastoral systems are highly beneficial for bat conservation. This is particularly true for systems in which old broadleaf trees are combined with livestock. Silvopastoral agroforestry met the requirements of a wide range of different bat foraging and hunting guilds including open/edge foragers and forest species. Given the current rise of interest in the benefits of agroforestry for biodiversity conservation, it is important to note that the benefits were strongest in systems with mature trees of $>$ 50 years of age. This limits the conclusions that can be drawn on bat conservation from recently established agroforestry systems, and it indicates that systems with a short rotation of the tree component may be of limited conservation value. On the other hand, it emphasizes the importance of conservation of aged agroforestry stands. The results add to the growing evidence on the benefits of agroforestry systems to support farmland biodiversity and ecosystem service delivery through insectivory. Thus, agroforestry should be more widely adopted by farmers and supported with adequate policies. The role of agroforestry systems in supporting bat conservation may only be effective if they are extensively managed, with a low pesticide input and the absence of human induced threats (e.g. wind turbines and roads) in the vicinity.

Authors' contributions

ME, MHE, FH, JHNP, WS, JS and VR contributed to the study conception and design. ME, AW, JHNP, WS and JS collected the data. ME, VR, KN, AS and AW analyzed the data. ME led the writing, and ME, MHE, FH, JHNP, WS, JS and VR contributed to the finalization the manuscript. All authors read and approved the final version of the manuscript.

Article impact statement

Agroforestry systems with old broadleaf trees positively affect bats and deserve more attention in conservation planning.

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Declaration of Competing Interest

We confirm having no conflicts of interests with them as well as no previous co-authored publications.

The work as submitted has not been published or accepted for publication, nor is being considered for publication elsewhere, either in whole or substantial part.
All authors and relevant institutions have read the submitted version of the manuscript and approve its submission.
All persons entitled to authorship have been so included.
The work is original and all necessary acknowledgements have been made.

The work conforms to the legal requirements of the country in which it was carried out, including those relating to conservation and welfare, and to the journal's policy on these matters.

Third party data sets used in this work are either publicly available for unrestricted reuse or permission for reuse has been obtained from the data owners

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Appendix A. Supporting information

Habitat characteristics and sampling dates of all studied plots (Supporting Table A1), results of post-hoc pairwise comparison showing and total bat activity differences (Supporting Table A2), feeding buzz and social call rate differences (Supporting Table A3) as well as the activity of different bat species in each sampled plot (raw data) (Supporting Table A4) are available as supporting information in the online version of the article at the publisher's website. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2024.e03369.

Data availability

Data will be made available on request.

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