

ARTICLE

Agroecosystems

Landscape composition and orchard management effects on bat assemblages and bat foraging activity in apple crops

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Abstract

Bats are acknowledged as suppliers of essential ecosystem services such as insect pest control in agroecosystems. Little is known, however, on how bat assemblages respond to the gradients imposed by anthropogenic landscapes and farming practices and how these environmental effects translate into changes in bat foraging. In this study, we use cider apple crop in northern Spain as a model to address the filtering effects of landscape composition and orchard management on, simultaneously, quantitative and qualitative characteristics of bat local assemblages and their foraging activity. For that, we carried out acoustic monitoring of bats and sampled pest moth abundance across a wider range of apple orchards covering different landscape contexts and local management conditions. We found that bat assemblages markedly varied across orchards, according mostly to landscape composition gradients but with contrasting landscape effects on different assemblage characteristics. Namely, higher levels of rural urbanization and lower cover of seminatural woody habitats around orchards promoted bat total activity and the number of bat species/species complexes. However, this also altered bat assemblage composition, increasing dominance by the most abundant species, and decreased bat functional diversity. Additionally, a greater cover of apple tree canopy within the orchards decreased bat total activity. Landscape gradients led into predictable variations of bat foraging activity, suggesting a potential persistence of pest control services even in landscapes with limited seminatural habitat cover. The present study highlights the differential responses of bat assemblages to apple crop landscape and orchard-scale conditions, hindering the establishment of straightforward management guidelines. Further analysis on the relationship between bat assemblage characteristics and pest control is necessary to understand how ecosystem services can be promoted through management in the apple agroecosystem.

KEYWORDS

agroecosystems, bat activity, *Cydia pomonella*, functional diversity, pest control, *Pipistrellus pipistrellus*

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INTRODUCTION

Bats are major consumers of arthropods, having a relevant role in the control of pest insects in agricultural and forest plantations (Kunz et al., 2011). Specifically, bats are known to actively prey on at least 760 insect species considered crop pests worldwide (Tuneu-Corral et al., 2023) and such predation is assumed to lead to pest biocontrol through top-down effects (Maas et al., 2016). In fact, increases in bat activity have been frequently associated with decreases in pest abundance (e.g., Puig-Montserrat et al., 2015), reduction in plant damage (e.g., Bouarakia et al., 2023; Rodríguez-San Pedro et al., 2020), and improvement of crop yields (e.g., Maas Liu et al., 2013; Rodríguez-San Pedro et al., 2020). However, despite the assumed roles of bats in agroecosystems, little is known on how the provision of pest control depends on the features of bat assemblages (but see Augusto et al., 2024; Tortosa et al., 2023). To answer this question, it is previously required to understand how bat assemblages respond to the environmental gradients imposed by agricultural land use, both at the farm scale, derived from management actions (use of pesticides, tree pruning, etc.) and at the landscape scale, driven by agricultural expansion and land use (deforestation, cropland homogenization, etc.) (Tuneu-Corral et al., 2023).

Different studies in agroecosystems have evidenced the filtering effect of anthropogenic gradients on the size of bat assemblages, represented by quantitative features such as total activity or the number of species. For example, the loss of seminatural habitats like forests and shrublands, in parallel with the landscape homogenization derived from the expansion of croplands and urbanized areas, leads to declines of bat activity and species number in agroecosystems (Ramírez-Mejía et al., 2020; Rodríguez-San Pedro et al., 2019; Tortosa et al., 2023). Similar decaying effects have been observed in local bat assemblages confronted by intensive management and crop structural simplification within farms (Kelly et al., 2016; Olimpi & Philpott, 2018; Puig-Montserrat et al., 2021). Moreover, qualitative features of bat assemblages, describing the composition of species or the variety of functional groups, also depend on landscape and farm characteristics. For example, forest loss in agricultural areas and farm management intensity may differentially affect bat species, leading to changes in bat composition (e.g., Heim et al., 2015; Treitler et al., 2016) and in the occurrence of different functional groups (e.g., López-Baucells et al., 2022; Weier et al., 2021). Despite these findings, it is required to know better how the different quantitative and qualitative features of bat assemblages comparatively respond

to the same scenarios of landscape change and farm management (Presley & Willig, 2022; but see López-Baucells et al., 2022). Additionally, and beyond the characteristics of bat assemblages, it is crucial to understand whether the environmental filters associated with agricultural land use ultimately affect bat foraging activity in croplands (Tuneu-Corral et al., 2023). For this, a consideration of resource tracking potential by bats, for example through its relationship with the abundance of those pests that represent principal prey (e.g., Baroja et al., 2021; Tortosa et al., 2023), is necessary.

In this study, we address bat assemblage features and bat foraging activity in apple orchards, a major fruit crop type throughout the world (FAOSTAT, 2024) where active pest predation by bats has been reported (e.g., Ancillotto et al., 2024). We focus on the cider apple crops of the Asturias region in northern Spain, a system in which orchards are variable in terms of management regimes and, especially, landscape contexts within the region. In this sense, previous studies evidence that the low intensification of apple crops and the surrounding landscapes favor animal diversity within and around orchards, including both apple pest insects and natural enemies (García et al., 2018; Martínez-Sastre et al., 2020, 2021). Specifically, we seek here to answer the following questions: (1) How variable are bat assemblages in apple orchards in terms of activity, size, composition, and functional diversity? (2) How important are the filtering effects of landscape composition and orchard management on the different bat assemblage features? (3) If they occur, do the modulating effects of landscape and orchard features translate into impacts on bat foraging activity?

MATERIALS AND METHODS

Study system

We studied the agroecosystem of cider apple crop in Asturias (NW Spain), a region where cider is a highly valuable traditional product with a Protected Designation of Origin status. Asturian cider apple may be considered as a low-intensity and low-input crop system. Apple plantations are typically small (1 ha), frequently bordered by natural hedgerows and embedded in a highly variegated landscape (García et al., 2018). Plantations are mono-cropped, with trees grown on semi-dwarfing rootstock in a density of ca. 500 trees/ha, and a permanent seminatural herbaceous cover under trees. The local cultivars grown are tolerant to the main apple diseases, so fungicides are rarely applied in the

region. Moreover, given the general high cultural tolerance of growers to pests, in part because aesthetic damage is of no importance for cider apples, the use of insecticides is usually limited to narrow spectrum insecticides against the key pest, the codling moth (*Cydia pomonella* L.), and/or aphids, but many orchards do not even use pesticides.

The study was conducted in 2022 in 20 cider apple orchards distributed over a 600-km² study area in Asturias (Figure 1A). Orchards were located from 10 to 385 m above sea level, and their size varied from 0.5 to 20.6 ha. Minimum distance between orchards was 1.2 km. Within each orchard, we established a bat sampling point at its center, at least 25-m far from orchard borders.

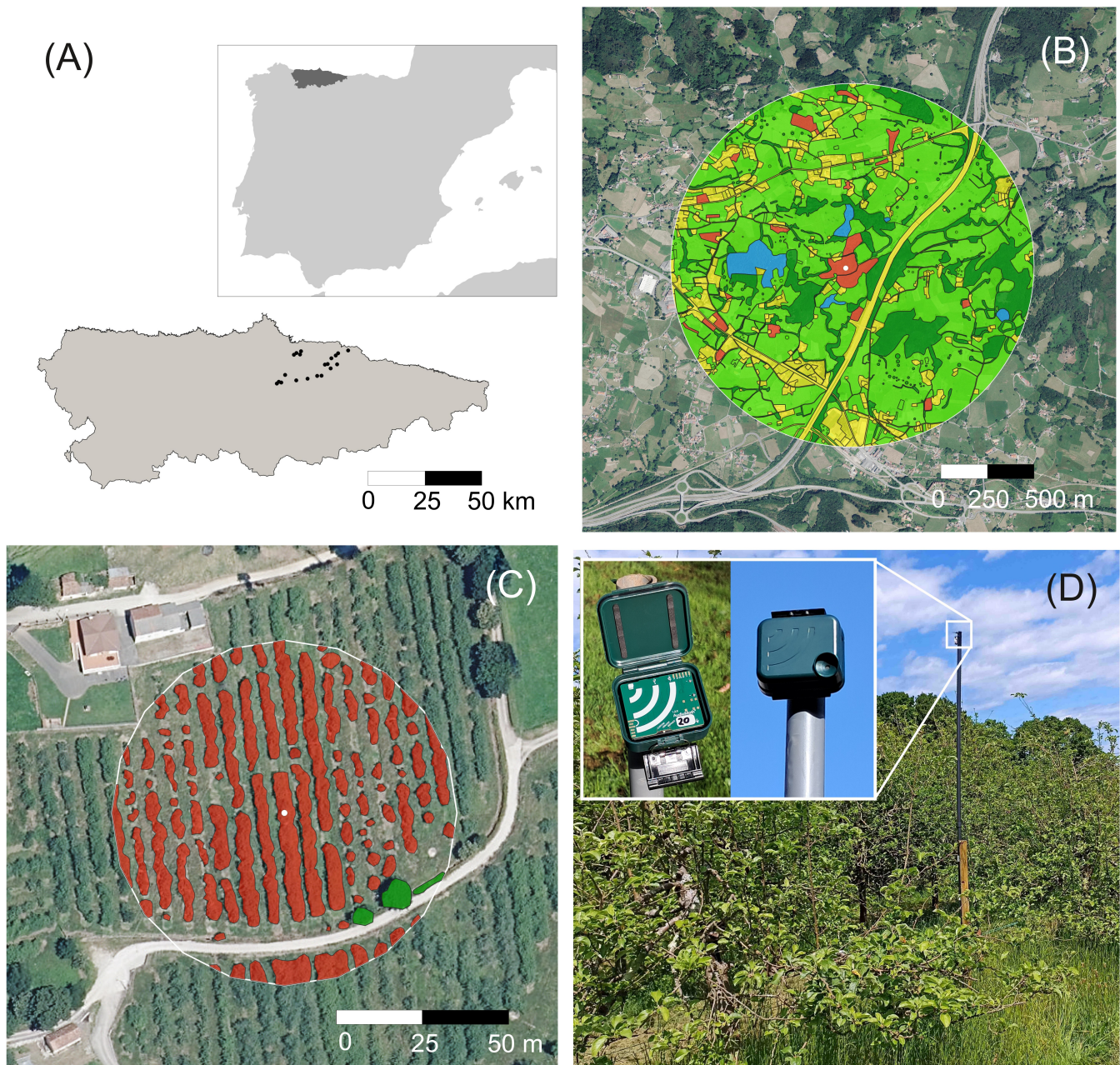


FIGURE 1 Schematic representation of study sites and spatial design, depicting (A) the region of study (Asturias province, in dark gray, within the Iberian Peninsula) and the study sites (black points in the map of Asturias), (B) an example of land cover types in the 1000-m radius plot around one orchard (fruit orchards in red; seminatural woody habitats in dark green; pastures in pale green; Urbanized ground in yellow; eucalyptus plantations in blue; orthophoto by <https://pnoa.ign.es/>), (C) apple tree canopy (in red) in a 50-m radius plot around the bat sampling point (white dot; orthophoto by <https://pnoa.ign.es/>), and (D) an ultrasonic detector (AudioMoth) mounted on a pole that rises above the apple tree canopies (photo credits: Marcos Miñarro).

Landscape composition and orchard features

Landscape composition was quantified by means of a GIS (QGIS 3.28) based on July 2021, 1:5000-scale orthophotographs. We delimited a circular plot of 1000-m radius (R1000 plot, hereafter), centered on the bat sampling point of each orchard, within which we distinguished, by carefully digitizing landscape patches, 15 types of land cover that were classified in six general categories: (1) seminatural woody habitats (including forest, heathland, hedgerows, and isolated trees); (2) timber tree plantations (eucalyptus); (3) fruit plantations (apple, kiwi, and blueberry); (4) pastures (pastures), (5) urbanized land (roads, industrial small buildings, houses, and gardens around houses); and (6) other habitats (annual crops, bodies of water). We estimated the availability of each land cover type around each orchard from the percentage of cover in each R1000 plot (Figure 1B). The landscape surrounding the orchards varied among sites but was dominated by pastures (percentage of cover average 42.8, min–max 16.7–60.2), followed by seminatural woody habitats (23.4, 10.4–41.8), urbanized land (14.5, 2.3–36.6), eucalyptus plantations (8.4, 0.0–59.8), fruit plantations (8.4, 1.9–14.6), and other cover types (2.5, 0.3–18.2) (Appendix S1: Figure S1).

In the studied region, main landscape trends emerge as interrelated variations of different land cover types, rather than as major changes in single cover types (e.g., Martínez-Sastre et al., 2020). Thus, for an accurate representation of the landscape compositional gradients around orchards, we used a principal components analysis (PCA, performed with R package *stats*; R Core Team, 2023) applied to the values of the six general land cover categories in R1000 plots. Three first principal components accounted for 82.9% of the variation in the landscape data: PC1 (41.9% of variance explained) described a gradient extending from landscapes dominated by eucalyptus plantations to pasture-dominated landscapes; PC2 (24.6%) represented a gradient from rural urbanized landscapes to landscapes dominated by seminatural woody habitat; and PC3 (16.4%) represented a gradient of increased proportions of other habitat types and fruit plantations (mainly apple) around the orchards (Appendix S1: Table S1).

As additional landscape compositional features we also estimated: (1) the cover of apple plantations in a 125-m radius area from the sampling point (R125 plot, hereafter), as a measure of small-scale availability of this land cover category and (2) a Shannon diversity index considering the proportions of the 15 specific land cover types around each orchard, as a proxy of landscape heterogeneity (e.g., Laforge et al., 2021).

We considered the cover by apple tree canopy in orchards as a local, small-scale feature with the potential to affect bat assemblages, as it not only represents the canopy volume but also the space between tree rows in which bats could fly (Kalda et al., 2015). Apple tree canopy cover was estimated from a GIS digitized layer of the apple canopy projection in a 50-m radius area from the bat sampling point (Figure 1C).

Bat activity and foraging

We recorded bat activity in the 20 orchards from spring to autumn 2022 on four different nights (mid-May, mid-July, early September, and early October). We used acoustic monitoring through ultrasonic detectors (AudioMoth, Open Acoustic Devices; Hill et al., 2019) mounted on 3.5-m poles at the bat sampling point of each orchard so that they were above apple tree canopies (Figure 1D). Sampling was conducted during good weather conditions (no precipitation; minimum temperature at night $>12^{\circ}\text{C}$; wind speed <3 m/s). We programmed the detectors to automatically record during one full night (in consecutive 5-min wav-sound files), from 30 min before sunset until 30 min after sunrise.

All wav-sound files were screened using consecutively Kaleidoscope (v. 5.4.8 Wildlife Acoustics) and SonoBat (v. 4.2.2 International, SonoBat, Arcata, CA, USA) software to select those with bat calls (positive files). All positive files were screened and assigned to bats at the finest possible taxonomical level. To ensure consistency of classification, identifications were made by a single person with expertise in the local chiropteran fauna, who could thus refine identification by considering the species probability of occurrence in the study area. A total of 72.9% of bat calls were identified to the species level, while ambiguous calls were assigned to species complexes (*Pipistrellus kuhlii*/*Pipistrellus natushi*; *Eptesicus serotinus*/*Nyctalus leisleri*; *Plecotus auritus*/*Plecotus austriacus*; and *Myotis* spp., which included *Myotis alcathoe*/*Myotis crypticus*/*Myotis daubentonii*/*Myotis emarginatus*/*Myotis escalerai*/*Myotis mystacinus*, but not *Myotis myotis*, which was identified separately). That is, we were able to distinguish 12 phonotypes assigned to eight unique species and four species complexes, all representing different taxonomic entities (as species complexes never overlap among them, or with unique species, in species composition). Although the differentiation in species and species complexes from phonotypes may underestimate actual species richness, this method is considered suitable to characterize bat assemblages in terms of total and relative activity (e.g., Tuneu-Corral et al., 2020), number of bat taxa (e.g., Charbonnier

et al., 2016; Cruz et al., 2016; Heim et al., 2015), composition (e.g., Charbonnier et al., 2016; Heim et al., 2015; Treitler et al., 2016), and functional diversity (e.g., Chakravarty et al., 2021). In fact, acoustic monitoring is frequently the only viable method to study local bat assemblages at the small scale of habitats (such as apple orchards here) where species-comprehensive, mist-netting sampling is hindered due to the absence of specific microhabitats concentrating bats (such as ponds or water courses, e.g., Augusto et al., 2024).

Bat activity is typically based on the number of bat calls detected by the ultrasonic detector (e.g., Baroja et al., 2021; Charbonnier et al., 2021). Call duration, nevertheless, may also contain information about site quality in terms of foraging potential. For example, call durations for bats exhibiting foraging behavior would be longer as they are expected to have a more sinuous flight path and slower velocity, compared with bats involved in commuting behavior between roosts and foraging areas (Kerbiriou et al., 2019). For this reason, we calculated bat activity as the total time of bat calls recorded for each orchard and night (see also Stahlschmidt & Brühl, 2012). This parameter was estimated for each bat species/species complex and for all bats pooled, and it represents a quantitative measure of bat presence across orchards and nights.

Insectivorous bats increase their sound pulse rate when attempting to hunt a prey, producing an easily identifiable feeding-buzz call sequence (Charbonnier et al., 2021; Kolkert, Andrew, et al., 2020). We estimated the number of these feeding buzzes attributed to each bat species/species complex per orchard and night. This functional parameter can be considered as a proxy of prey consumption magnitude and, therefore, pest control potential (Charbonnier et al., 2021).

Bat traits

For our functional diversity analysis, we focused on a set of functional traits of bats assumed to affect both foraging behavior and the response to environmental variability: body mass, wing load index (WLI), call band width, call peak frequency (CPF), pattern of seasonal activity, and home range (HR) size (Froidevaux et al., 2023; Liu et al., 2023). All these traits were obtained for the studied species from the database EuroBaTrait_v1.0 (Froidevaux et al., 2023). Body mass is proportional to the energy requirements and, thus, the magnitude of resource consumption, as well as to the ability to cope with prey of different sizes (Divoll et al., 2022; Liu et al., 2023). WLI relates positively with the capacity to use open spaces but also to maneuver through dense foliage

(Luck et al., 2012). CPF and call band width relate to the ability to detect and distinguish prey in different environments, with high-frequency and broadband calls not traveling far in open spaces but providing high object resolution (Jones, 1999). The pattern of seasonal activity (lower values indicating a substantially skewed distribution toward spring, and higher values toward autumn) may affect the temporal match with pests and their concomitant tracking (Baroja et al., 2021). Finally, HR size relates to the area over which a species forages, as well as to its susceptibility to decline due to habitat loss (Luck et al., 2012). We constructed a species/species complex \times trait matrix, considering, in the case of species complexes, trait average values across the species of each complex (Appendix S1: Table S2).

Moth monitoring

Moths are a major food resource for bats in agroecosystems (Tuneu-Corral et al., 2023), and moth abundance tracking across time and space is frequently observed (Baroja et al., 2021). In the orchards under study, the codling moth (*C. pomonella*), a known global apple pest (Beers et al., 2003), reaches very high numbers and causes apple damages frequently exceeding 40% of tree crop (Martínez-Sastre et al., 2021). We thus monitored the abundance of adult codling moth in each orchard by means of a delta trap with a sticky card baited with sexual pheromone, hung on tree branches at 1.5 m above the ground and at a 10-m distance from the ultrasonic detector. Traps remained active from 3 of May to 3 of October to cover the flight period of codling moth, with the pheromone bait being replaced on 13 of June and 26 of July. Traps were checked every 2 weeks, and sticky cards were removed to count trapped individuals and then replaced. Four of the fortnightly moth counts corresponded to dates with bat acoustic monitoring, thus enabling thus to estimate a value of codling moth abundance (i.e., the number of adult individuals caught the last 2 weeks) to be assigned to each bat survey per orchard.

Data analyses

Bat assemblage composition

To evaluate the variability in the composition of bat assemblages, we used nonmetric multidimensional scaling ordination (NMDS; Quinn & Keough, 2002), based on a matrix of relative activity per species/species complex, orchard, and night. Using Bray–Curtis distance measures for dissimilarity, we built a two-dimensional (NMDS1 and

NMDS2) compositional space to plot the position of bat species/species complexes. NMDS1 and NMDS2 scores of each bat assemblage (orchard \times night combination) were considered as proxies of local composition. NMDS was performed with R package *vegan* (Oksanen et al., 2022).

Functional diversity

We used the variability in bat traits to measure the potential differences between bat species/species complexes with respect to their functional contribution and their response to environmental gradients. We measured functional diversity in terms of trait-based distances among bat species/species complexes, that is, the magnitude of the differences to the average trait value in each bat assemblage. For this, we first combined all measured bat traits to build a multidimensional trait space, based on Euclidean distances, using principal coordinates analysis (PCoA; Villéger et al., 2008), in which all bat species/species complexes were projected. Then, we calculated values of functional dispersion (FDis) for each bat assemblage (i.e., each orchard \times night combination). This index reflects the average distance of the species/species complexes present locally to the centroid of the multidimensional trait space of the assemblage (Laliberté & Legendre, 2010; Villéger et al., 2008). Activity-weighted FDis values and PCoA axes were estimated with the R package *FD* (Laliberté et al., 2014).

To account for the potential effects on the estimation of functional diversity of the differences in the number of species/species complexes and the total activity across orchards and nights, we calculated standardized effect sizes (SES) for FDis values using null models. For this purpose, we compared observed values of bat assemblages (i.e., those estimated through weighting by activity matrices) to 1000 sets of randomized assemblages generated using “quasiswap count” on the activity matrices (Miklós & Podani, 2004; Oksanen et al., 2022). This permutation algorithm randomizes local activity values by keeping both dimensions of activity matrix constant (marginal totals of species/species complexes and orchard \times night combinations). To calculate SES FDis, we subtracted the mean of the randomized values from the observed local values and divided this result by the SD of the random values.

Effects of landscape composition and orchard features on bat assemblages and foraging activity

Our first analytical goal was to assess the effects of landscape composition and orchard features on the different

characteristics of bat assemblages. For this, we used generalized linear mixed models (GLMMs) considering as response variables in separate models, the values of bat activity, number of bat species/species complexes, NMDS1, NMDS2, and SES FDis per orchard \times night combination. We considered a negative binomial (log link) family distribution for bat activity and a Gaussian (identity link) one for the remaining variables. For each response variable, we considered a model that incorporated the first two landscape PCA vectors (PC1 and PC2), landscape heterogeneity, apple plantation cover at R125, and within-orchard apple tree canopy cover as fixed predictors. No significant correlation existed between these predictors (all Pearson correlation coefficients between paired predictors were $r < |0.40|$, $p > 0.082$, $N = 20$), and all predictors were standardized prior to analysis. The third landscape PCA vector (PC3) was excluded from the models because it was highly correlated with landscape heterogeneity ($r = 0.721$; $p < 0.001$) and apple plantation cover at R125 ($r = 0.632$; $p = 0.003$). To control for the potential nonindependence effects of the repeated sampling of bat assemblages across orchards and nights in different months, orchard identity, and month were included as intercept random factors. All models were fitted using the R package *lme4* (Bates et al., 2015), and model adequacy was checked by visual diagnosis (residuals vs. fitted values plot, and quantile-quantile plot). Model R^2 GLMM(m) values (marginal R^2 , that is, the variance explained by the fixed effects only; Nakagawa & Schielzeth, 2013) were obtained with the R package *MuMIn* (Barton, 2022).

Our second analytical goal was to understand whether bat foraging activity in orchards was affected by the abundance of codling moth, while considering the effects of landscape composition and orchard features as environmental filters of bat foraging activity. For this, we used a GLMM considering, as a response variable, the number of bat feeding buzzes (negative binomial, log link) and, as fixed, non-correlated predictors, the first two landscape PCA vectors (PC1 and PC2), landscape heterogeneity, apple plantation cover at R125, within-orchard apple tree canopy cover, and codling moth abundance. The model also included an interaction term between apple tree canopy cover and codling moth abundance, given that the prey-tracking ability of bats can be affected by tree canopy structure (e.g., Froidevaux et al., 2021). The model also included orchard identity and month as intercept random factors. Data from October were excluded from this resource tracking analysis, as they represented a period in which *C. pomonella* was naturally unavailable as a prey for bats (no moth was captured in any orchard in October counts; Appendix S1: Figure S2).

Due to the potential risk of over-parametrization in the model of bat foraging activity (with a higher number of parameters but a lower number of analytical replicates), we followed in this case a model selection and averaging procedure (R package MuMIn; Barton, 2022). Specifically, we applied an information-theoretic approach using the corrected Akaike information criterion (AIC_c) for small sample size to select the most parsimonious among the 80 candidate models emerging from all possible combinations of predictors, including the null model (Burnham & Anderson, 2002). Then, we conducted a model-averaging procedure with all equivalent best models (i.e., those with difference in AIC_c between models [ΔAIC_c] < 2), interpreting the significance of explanatory variables from their average estimate values and the overlap with zero of their CIs (2.5% and 97.5%) (Grueber et al., 2011; Nakagawa & Cuthill, 2007).

RESULTS

Bat assemblages in apple orchards

We recorded 42,732.5 s of total bat activity, although local activity values per orchard and night were highly heterogeneous (Figure 2A). When pooling activity records per orchard, one orchard accumulated 21.4% of total activity but six contributed less than 2% each (Appendix S1: Figure S3A). Activity also varied temporally (Appendix S1: Figure S3B), increasing from May (27.0% of total activity) to July (39.6%) and sharply decreasing in September (17.6%) and October (15.9%).

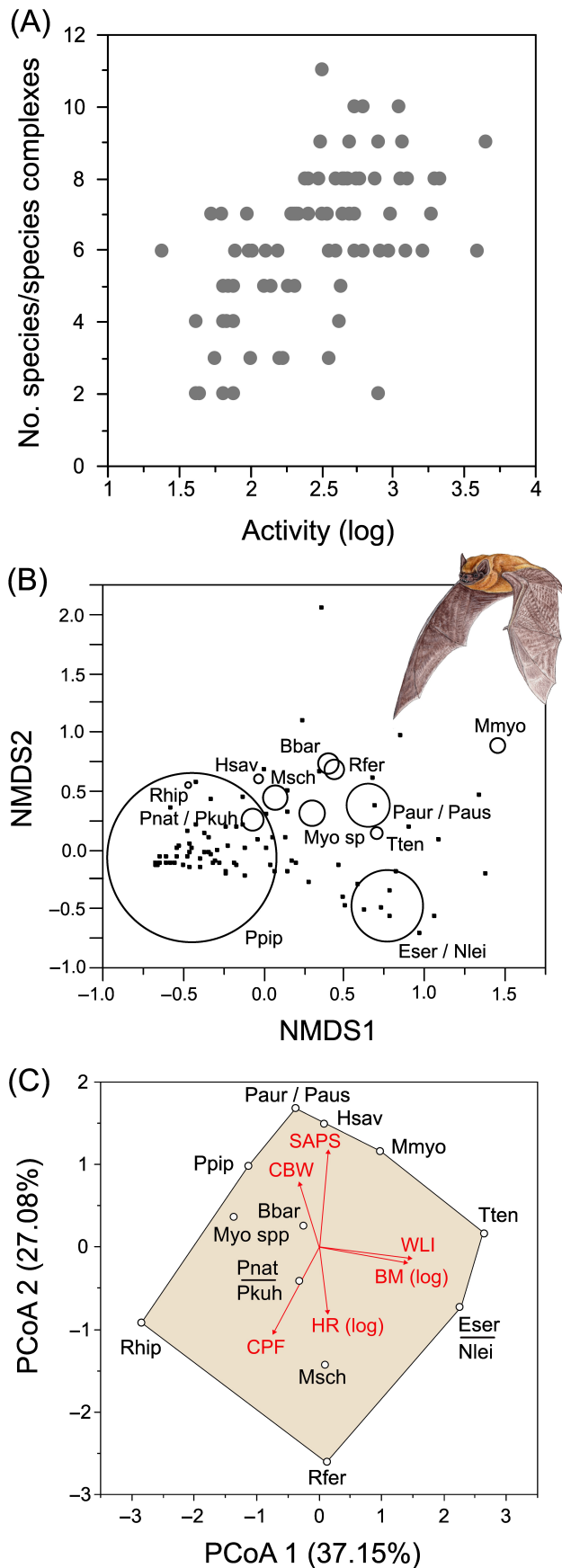
Bat activity was attributed to 12 different phenotypes, corresponding to 8 species and 4 species complexes (Table 1). The number of species/species complexes ranged from 2 to 11 (Figure 2A), with an average value of 6.31 species/species complexes per orchard and night (± 0.23 SE, $N = 80$). A higher number of species/species complexes was detected in those orchards and nights accumulating more activity ($r = 0.542$, $p < 0.001$, $N = 80$; Figure 2A). *Pipistrellus pipistrellus* was the dominant species in the global assemblage, accounting for 66.7% of the recordings, followed by the complex *E. serotinus/N. leisleri* (18.5%). The individual contribution of the rest of species/species complexes was below 4% (Table 1). *P. pipistrellus* and the complex *E. serotinus/N. leisleri* were widespread across orchards and nights (percentages of occurrence of 98.7% and 89.9%, respectively; Table 1). *P. pipistrellus* was the dominant species in all but three orchards (29.2% to 90.0% of bat activity per orchard; Appendix S1: Figure S3A) and in all months (56.3% to 85.2% of bat activity per month; Appendix S1: Figure S3B).

The NMDS analysis (stress = 0.14; linear fit $R^2 = 0.941$) evidenced nonrandom variability in the composition of bat assemblages across orchards and nights (Figure 2B). NMDS dimensions 1 and 2 represented a compositional space in which bat assemblages mostly transitioned from being strongly dominated by *P. pipistrellus* (in numerous orchard and night combinations) to having a high proportion of *E. serotinus/N. leisleri*. The compositional changes represented by the NMDS1 dimension were independent of changes in the number of species/species complexes ($r = 0.115$, $p = 0.310$).

The PCoA applied to bat traits led to a functional space whose two first dimensions accounted for 64.23% of trait variability across bat taxa (Figure 2C). PCoA1 represented a positive gradient of body size and the correlated WLI, whereas PCoA2 represented a negative gradient of HR size and CPF correlated with a positive gradient of seasonal activity and call band width. The PCoA1 and PCoA2 scores delimited a wide functional space for the bat assemblage, where the different species/species complexes occupied distant positions with a loosely clustered distribution that indicated gradual changes in trait variability (Figure 2C; Appendix S1: Table S2). Values of FDis varied considerably across orchards and nights (1.81 ± 0.04 [mean \pm SE], min–max: 0.38–2.41). The number of bat species/species complexes was significantly correlated with FDis ($r = 0.345$, $p = 0.002$, $N = 80$) but not with their SES (SES FDis, $r = 0.205$, $p = 0.068$, $N = 80$). FDis and SES FDis were correlated with NMDS1 ($r > 0.57$, $p \leq 0.001$, $N = 80$, in both cases).

Effects of landscape composition and orchard features on bat assemblages

GLMM analyses evidenced that bat assemblages were influenced by landscape composition and/or orchard features in multiple ways (Table 2). Bat activity was positively affected by PC1 (gradient from eucalyptus plantations to pastures; Figure 3A) but negatively affected by PC2 (gradient from rural urbanized areas to seminatural woody habitats; Figure 3B) and by the cover by apple tree canopy within orchards (Figure 3C; Table 2). The number of species/species complexes significantly decreased in orchards with a higher proportion of seminatural woody habitats in their surrounding landscape (PC2; Figure 3D), and also in orchards immediately surrounded by other apple plantations (Figure 3E; Table 2). Conversely, this response variable increased in orchards located in more heterogeneous landscapes (Figure 3F; Table 2). The gradient from rural urbanized areas to seminatural woody habitats (PC2) also affected bat assemblage composition, with a positive effect on



NMDS 1 (Figure 3G; Table 2; no effect was found on NMDS2; Appendix S1: Table S3). Similarly, landscapes rich in seminatural woody habitats favored bat functional diversity (SES FDis) in apple orchards (Figure 3H; Table 2).

Effects of codling moth abundance, landscape composition, and orchard features on bat foraging activity

Ultrasonic sampling led to the detection of 1700 bat feeding buzzes across orchards and nights, 96.1% of which belonged to *P. pipistrellus* (Table 1). The number of feeding buzzes was higher in July (36.5%), September (28.6%), and May (28.0%) but decreased notably in October (6.9%). Across orchards and nights, the number of feeding buzzes was positively correlated with bat activity ($r = 0.860$; $p < 0.001$). Pheromone traps captured a total of 14,250 codling moths, ranging from 333 to 1294 moths per orchard. Captures showed a temporal pattern, with peaks in May and August, corresponding to the emergence of two generations of *C. pomonella* (Appendix S1: Figure S2).

The GLMM that evaluated the effects of codling moth abundance, landscape composition, and orchard features on the number of feeding buzzes accounted for half of the variability of this response variable (marginal $R^2 = 0.51$, conditional $R^2 = 0.60$; Table 3). The complete model including all predictors evidenced significant effects of landscape composition variables, but not of the abundance of codling moth or its interaction with

FIGURE 2 (A) Values of activity (in seconds) and the number of species/species complexes for bat assemblages of different orchard \times night combinations in Asturian apple orchards. (B) Results of nonmetric multidimensional scaling analysis (NMDS), in which different bat assemblages in orchard \times night combinations (dots) and bat species/species complexes (circles with size proportional to bat activity) are positioned according to scores from NMDS dimensions 1 and 2 (*Pipistrellus pipistrellus* is shown; artwork by Daniel García). (C) Bat trait space based on body mass (BM, log), wing load index (WLI), call band width (CBW), call peak frequency (CPF), pattern of seasonal activity (SAPS) and home range (HR, log) size. Red arrows indicate the effect of each trait in the gradients represented by principal coordinates analysis (PCoA) dimensions 1 and 2 (variance accounted by each dimension is shown between parentheses). White circles represent bat species/species complexes positioned according to scores from PCoA dimensions 1 and 2. Abbreviations of species/species complex names are used for identification in B and C (e.g., Ppip: *P. pipistrellus*); see all complete names in Table 1).

TABLE 1 Time of activity and number of feeding buzzes recorded for each bat species/species complex, with percentage per species/species complex, and occurrence as percentage of samples (orchard × night) in which each species/species complex was recorded.

Bat species/species complex	Activity			Feeding buzzes		
	Time (s)	Percentage	Occurrence (%)	N	Percentage	Occurrence (%)
<i>Barbastella barbastellus</i>	428.5	1.0	41.8	5	0.3	5.1
<i>Eptesicus serotinus/Nyctalus leisleri</i>	7915.5	18.5	89.9	43	2.5	10.1
<i>Hypsugo savii</i>	118.5	0.3	17.7			
<i>Miniopterus schreibersii</i>	901.5	2.1	75.9	2	0.1	2.5
<i>Myotis myotis</i>	267	0.6	24.1			
<i>Myotis</i> spp.	1071.5	2.5	68.4	3	0.2	3.8
<i>Pipistrellus nathusii/Pipistrellus kuhlii</i>	1376	3.2	49.4	12	0.7	2.5
<i>Pipistrellus pipistrellus</i>	28,487.5	66.7	98.7	1634	96.1	69.6
<i>Plecotus auritus/Paustriacus austriacus</i>	1219	2.9	79.7			
<i>Rhinolophus ferrumequinum</i>	545.5	1.3	51.9			
<i>Rhinolophus hipposideros</i>	73.5	0.2	13.9			
<i>Tadarida teniotis</i>	328.5	0.8	19.0	1	0.1	1.3
Totals	42,732.5		100	1700		70.9

orchard features (Table 3). Specifically, bat foraging activity was positively affected by PC1 (Figure 4A) and landscape heterogeneity (Figure 4B) but negatively by PC2 (Figure 4C). The model selection procedure identified the two most parsimonious models as including these three predictors together with the cover of apple tree canopy within orchards (Appendix S1: Table S4). Model-averaging confirmed the significant effects of PC1, PC2, and landscape heterogeneity on the number of feeding buzzes (Appendix S1: Figure S4).

DISCUSSION

In the present work, we studied bat assemblages of cider apple orchards in NW Spain through quantitative and qualitative community features and bat foraging activity. Covering a large set of orchards over a regional extent, our study shows that the various assemblage features were differentially modulated by the same environmental gradients, this mostly being imposed by landscape composition. For example, bat assemblages in orchards surrounded by landscapes with a higher degree of rural urbanization and lower cover of seminatural woody habitats accumulated more total activity and more species/species complexes but suffered from dominance biases and functional diversity losses. In addition, our results detected that landscape gradients translate into predictable variations of bat foraging activity, suggesting the potential persistence of pest control bat services derived from different ecological mechanisms across different types of landscape.

Bat assemblages in apple orchards

We present here a community of bats that inhabit apple orchards, supporting at least 16 species (Table 1; this value considers two species for each species complex, e.g., *P. auritus/P. austriacus*, including the *Myotis* spp. group, of which at least *M. crypticus* and *M. escalerai* were present, as demonstrated by mist-netting sampling in the study area). This value may be considered moderate to high when compared with other European agroecosystems (e.g., Ancillotto et al., 2023; Puig-Montserrat et al., 2021; Tortosa et al., 2023). It must be acknowledged that acoustic monitoring, as used here, restricted our ability to assess the actual number of species per orchard and night, as the detection of a single species complex may correspond to several species, and thus, censuses may underestimate the richness of species in some orchards and nights. Here, we assume that biases in the estimation of richness are uniform across the studied environmental gradients and depend exclusively on the number and the identity of the species complex involved (Chakravarty et al., 2021). In fact, complementary analyses evidenced that the potential underestimation would almost exclusively affect bat assemblages already containing a high number of species/species complexes, but not species-poor assemblages where the occurrence of species complexes is rare (Appendix S1: Figure S5).

The variation in the number of species/species complexes across orchards and nights encompassed the changes in total bat activity. Assuming activity as a surrogate of total abundance (e.g., Tortosa et al., 2023), this relationship suggests a potential mechanistic role of

TABLE 2 Results of generalized linear mixed models evaluating the effects of landscape composition (PC1, PC2), landscape heterogeneity, the cover of apple plantations in a 125-m radius plot and the cover of apple tree canopy on bat activity, number of species/species complexes, bat composition (nonmetric multidimensional scaling ordination [NMDS] dimension 1), and bat functional diversity (standardized effect sizes functional dispersion [SES FDis]).

Dependent variable and factors in models	Estimate	SE/SD	z/t	p	R^2
Bat activity (negative binomial, log)					0.339 (0.530)
PC1	0.438	0.152	2.89	0.004	
PC2	-0.458	0.133	-3.45	0.001	
Landscape heterogeneity	0.197	0.142	1.39	0.165	
Apple cover R125	-0.045	0.144	-0.31	0.756	
Apple canopy cover	-0.330	0.145	-2.27	0.023	
Orchard (random factor)	0.188	0.433			
Month (random factor)	0.047	0.217			
No. species/species complexes (Gaussian, identity)					0.307 (0.365)
PC1	0.193	0.253	0.76	0.459	
PC2	-0.907	0.225	-4.04	0.001	
Landscape heterogeneity	0.576	0.233	2.48	0.027	
Apple cover R125	-0.563	0.237	-2.38	0.032	
Apple canopy cover	-0.507	0.244	-2.08	0.057	
Orchard (random factor)	0.236	0.486			
Month (random factor)	0.030	0.174			
Composition NMDS1 (Gaussian, identity)					0.156 (0.298)
PC1	-0.093	0.078	-1.19	0.254	
PC2	0.161	0.069	2.32	0.036	
Landscape heterogeneity	0.055	0.072	0.77	0.456	
Apple cover R125	-0.094	0.073	-1.29	0.217	
Apple canopy cover	-0.056	0.075	-0.75	0.469	
Orchard (random factor)	0.038	0.195			
Month (random factor)	0.005	0.072			
Functional diversity SES FDis (Gaussian, identity)					0.112 (0.331)
PC1	-0.128	0.283	-0.45	0.657	
PC2	0.537	0.251	2.14	0.049	
Landscape heterogeneity	0.131	0.260	0.50	0.623	
Apple cover R125	-0.322	0.264	-1.22	0.243	
Apple canopy cover	0.082	0.273	0.30	0.770	
Orchard (random factor)	0.632	0.795			
Month (random factor)	0.111	0.333			

Note: Significant ($p < 0.05$) factors appear in boldface. Details of the family of distribution and link function used (in parentheses), values of marginal and conditional (in parentheses) R^2 , values of z (for negative binomial distributions) and t (for Gaussian) statistics, as well as variance (SD) estimates for orchard identity and month, considered as random factors, are also shown.

abundance as an assembly rule of bat local communities, since environments that enable higher abundance would concomitantly foster viable populations of more species (Seoane et al., 2017). The rise in bat activity across orchards and nights entailed, in any case, an increased dominance of *P. pipistrellus* in the local assemblages

(correlation between total bat activity and the proportion of that activity accounted for by *P. pipistrellus*, $r = 0.26$, $p = 0.016$, $N = 80$). Similar patterns of dominance by *Pipistrellus* species have been found in bat assemblages of other European agroecosystems (Ancillotto et al., 2023; Puig-Montserrat et al., 2021; Tortosa et al., 2023).

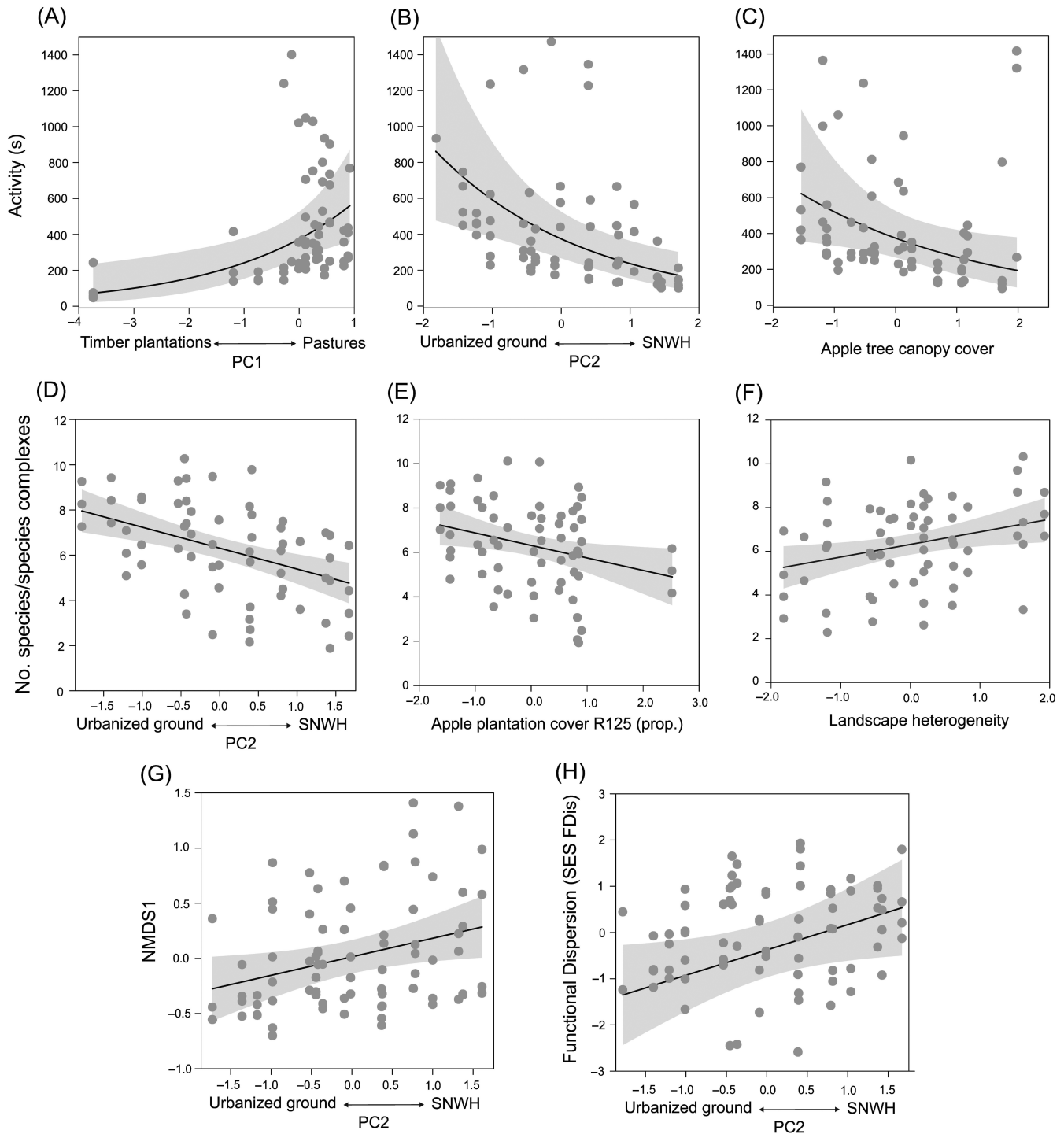


FIGURE 3 Effects of different landscape composition parameters or orchard features predicted by generalized linear mixed models on (A–C) bat total activity, (D–F) number of bat species/species complexes, (G) bat assemblage composition (nonmetric multidimensional scaling analysis [NMDS] 1), and (H) functional diversity (standardized effect sizes functional dispersion [SES FDis]). PC1 represents a gradient from eucalyptus plantations to pastures, and PC2 one from urbanized ground to seminatural woody habitat (SNWH). Confidence bounds and fitted values of partial effects predicted by the model, as well as standardized values of all predictors, are shown.

Bat composition markedly varied across orchards and nights, moving along a gradient from *P. pipistrellus* highly dominated assemblages to more even assemblages accounting for a higher proportion of *E. serotinus*/

N. leisleri activity. There was, therefore, a compositional turnover across the spatiotemporal landscape of apple orchards (see, for other temperate agroecosystems; Heim et al., 2015; Treitler et al., 2016).

TABLE 3 Results of the generalized linear mixed model evaluating the effects of landscape structure (PC1, PC2), landscape heterogeneity, the cover of apple plantations in a 125-m radius plot, the cover of apple tree canopy, the abundance of the codling moth and the interaction of the last two variables on the number of feeding buzzes (negative binomial distribution, log).

Predictor	Estimate	SE/SD	z	p
Intercept	2.221	0.345	6.44	<0.001
PC1	1.100	0.445	2.47	0.013
PC2	-0.789	0.279	-2.83	0.005
Landscape heterogeneity	0.715	0.337	2.12	0.034
Apple cover R125	0.234	0.339	0.69	0.490
Apple canopy cover	-0.284	0.308	-0.92	0.356
Codling moth abundance	0.047	0.237	0.20	0.844
Apple canopy cover × codling moth	-0.249	0.245	-1.02	0.309
Orchard (random factor)	0.471	0.686		
Month (random factor)	0.000	0.000		

Note: Significant ($p < 0.05$) factors appear in boldface. Variance (SD) estimates for orchard identity and month considered as random factors, are also shown.

Bat assemblages in apple orchards were highly heterogeneous in functional terms. Indeed, the trait gradients studied here suggest functional differences even among phylogenetically related taxa. For example, *Rhinolophus ferrumequinum* body mass is four times that of *Rhinolophus hipposideros*, and this contrast probably entailed foraging differences (Dietz & Kiefer, 2017; Flanders & Jones, 2009). The wide functional space studied here represented a set of species/species complexes with low to moderate similarity among them. This suggests a high potential of functional complementarity between species/species complexes, which probably increases the potential of bat assemblages to provide pest control (Cadotte, 2017; Gagic et al., 2015). Moreover, our estimation of FDis evidenced large differences across bat assemblages, with higher functional diversity in those with more species/species complexes and with compositions richer in *E. serotinus*/*N. leisleri* but poorer in *P. pipistrellus*. Further dietary analysis across bat species would enable to answer whether the present assemblage differences lead to increased levels of pest control in apple orchards (Hughes et al., 2021).

Effects of landscape composition and orchard features on bat assemblages

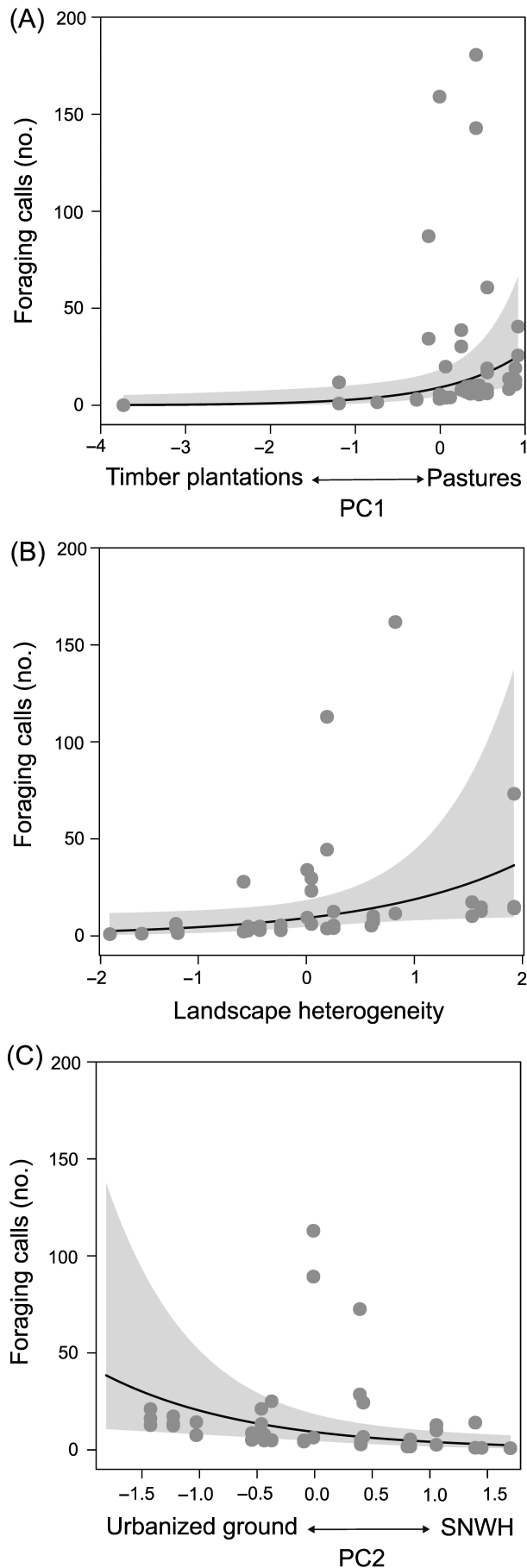
Our results suggest that bat assemblages were filtered by several environmental features that operate at the

different spatial scales of the apple orchards and their surrounding landscape, as suggested for other agroecosystems (e.g., Olimpi & Philpott, 2018; Rodríguez-San Pedro et al., 2019; Tortosa et al., 2023). Nevertheless, these environmental filters differentially affected the distinct characteristics of bat assemblages.

The landscape trend accounting for the highest variability in the studied region, that is, the gradient between eucalyptus plantations and pasture-dominated areas, affected positively bat activity. This effect may well be related to the reluctance of many European bat species to occupy dense stands of exotic timber (e.g., Cruz et al., 2016; Kirkpatrick et al., 2017), but probably also to the favoring effects of cattle pastures for bats (Downs & Sanderson, 2010; Russo et al., 2018).

The gradient of increasing rural urbanization in farmland, which expanded at the expense of seminatural woody habitats, favored bat activity, in a trend that contrasts with other studies on bats in agroecosystems (e.g., Ramírez-Mejía et al., 2020; Rodríguez-San Pedro et al., 2019). As suggested above, the overwhelming dominance of *P. pipistrellus* seems to underpin such activity pattern (see additional analyses in Appendix S1: Table S5, Figure S6), an unexpected fact, given that other studies suggest this species to be favored by forest habitat availability (e.g., Boughey et al., 2011; Russo & Jones, 2003). Our results also evidence a similar positive effect of increased urbanization on the number of species/species complexes. This may be related to the fact that several species may be favored by the conditions imposed by coarse-grain, rural urbanization (e.g., refuges in small and abandoned buildings and cow stables, Ancillotto et al., 2015; artificial illumination, Barré et al., 2022). Even considering the limitations imposed by acoustic monitoring for estimating the actual species richness of bat assemblages, our data support the idea that apple orchards surrounded by more urbanized land harbor larger bat communities. In this sense, additional models including as response variables the number of species (i.e., without species complexes) or the potential maximum number of species (i.e., including the total number of species covered by each species complex to the species count) led to similar effects of urbanization and seminatural forest cover (Appendix S1: Table S6).

Conversely to bat activity and the number of species/species complexes, the increased cover of seminatural woody habitats fostered the functional diversity of bat assemblages and altered assemblage composition, increasing the dominance of *E. serotinus*/*N. leisleri* and reducing that of *P. pipistrellus*. Similar positive effects of forest availability on bat functional diversity have been found in previous studies (López-Baucells et al., 2022;



Ramírez-Mejía et al., 2020; but see Moir et al., 2020). The functional diversity decays associated with increased urbanization encompassed changes in average traits values of bat assemblages, namely, smaller body mass, wind load, and HR size of bat assemblages, but higher call peak frequencies, were associated with the loss of forests around apple orchards (Appendix S1: Table S7). These relationships suggest that the ability of the studied bats to respond to environmental variability and disturbance may also depend on these traits (that is, they represent response traits, Farneda et al., 2015).

Landscape heterogeneity also showed a positive effect on the number of species/species complexes in apple orchards (for similar results, see Tortosa et al., 2023; Tuneu-Corral et al., 2023). Considering the fine-grain resolution used here to estimate this index, a more heterogeneous landscape probably meant higher availability of bat friendly elements, such as linear hedgerows, gardens, small water courses and ponds, and abandoned small buildings, as well as shorter distances to high-quality habitat patches such as mature forests (Heim et al., 2015; Rodríguez-San Pedro et al., 2019). A positive effect of fine-grained heterogeneity may also be inferred from the negative response of the number of species/species complexes to the cover of apple plantation in the immediate surroundings of the sampling stations. In other words, orchards surrounded by, or adjacent to, other orchards would represent homogenized patches leading to smaller bat assemblages (Tortosa et al., 2023).

Compared with landscape compositional effects, our study failed to identify within-orchard management features as major filters of bat assemblages. This was partially related to the fact that only a single within-orchard feature, the gradient of apple canopy closeness (from 13.8% to 54.8% of percentage cover) was analyzed (because gradients like the organic vs. conventional contrast, pesticide use, or crop diversification are gentle in Asturian cider apple orchards). In our case, bat activity decreased in orchards with high apple canopy cover, probably because canopy closeness hampered flight maneuverability and effective foraging along tree rows (Froidevaux et al., 2021).

FIGURE 4 Effects predicted by generalized linear mixed models of (A) PC1 (gradient from eucalyptus plantations to pastures), (B) landscape heterogeneity, and (C) PC2 (gradient from urbanized ground to seminatural woody habitat [SNWH]) on the number of bat feeding buzzes detected per orchard and night. Confidence bounds and fitted values of partial effects predicted by the model, as well as standardized values of all predictors, are shown.

Effects of codling moth abundance, landscape composition and orchard features on bat foraging activity

Bat foraging activity, estimated from the number of feeding buzzes, was higher in orchards immersed in more urbanized landscapes, those surrounded by pastures, and those in more heterogeneous landscapes. Although this pattern is probably the consequence of the strong correlation between general bat activity and the number of feeding buzzes, it confirms a widespread bat insectivory in apple orchards and its response to landscape features. Both facts are relevant to developing pest control, as suggested for apple orchards elsewhere (Ancillotto et al., 2024) and for other agroecosystems (Puig-Montserrat et al., 2015; Rodríguez-San Pedro et al., 2020).

However, our study failed to show large-scale tracking of codling moth by bats (but see Baroja et al., 2021; Kolkert, Smith, et al., 2020). This lack of bat response was probably related to the high abundance and diversity of potential prey in the low-input orchards studied here. In fact, we collected between 300 and 1300 codling moths per orchard in a single pheromone trap, an amount that represents just a small proportion of the true moth population (an emergence of at least 17,500 moths/ha can be expected in the studied orchards; Martínez-Sastre et al., 2021). Thus, the apparently huge availability of potential prey for bats in these apple orchards could result in satiation leading to a lack of predatory response beyond certain prey abundance thresholds (Zwolak et al., 2022). Further analysis on bat diet by means of, for example, metabarcoding techniques, could provide more conclusive evidence on the actual relationship between bat foraging behavior and codling moth abundance (e.g., Baroja et al., 2021).

CONCLUSION

The present study highlights the complex responses of bat assemblages to landscape and farm scale conditions in apple orchards. As such, establishing management guidelines for the promotion of bats and a concomitant pest control service requires several constraints to be taken into consideration. The first is that the combination of the opposing effects of environmental gradients on the different features of bat assemblages may lead to the failure of pest control following management actions. The ultimate effects of landscape management would depend, therefore, on whether the magnitude of pest control depends more on quantitative (e.g., total activity) than on qualitative (e.g., functional diversity) assemblage

features. As it happens for most bat assemblages of different agroecosystems (but see Augusto et al., 2024), this sort of comparative information is lacking in our case, and it would require an explicit assessment of pest predation magnitude across variable bat assemblages (e.g., Peña et al., 2023, for an approach with birds).

A second constraint is that the changes in landscape composition and within-orchard management may also affect other animal groups providing pest control in apple orchards, leading to compensatory trade-offs with bats. Specifically, this is the case with insectivorous birds in apple orchards, whose abundance, functional diversity, and insectivore role are promoted by surrounding forest cover and within-orchard apple tree canopy (García et al., 2018; Peña et al., 2023). Further analysis on the trophic and spatial complementarity between bats and other natural enemies is thus mandatory to discern how best to promote pest control through landscape and orchard management in the apple agroecosystem.

AUTHOR CONTRIBUTIONS

Marcos Miñarro and Daniel García contributed equally to study design and data interpretation. Marcos Miñarro led data collection and curated the data. Daniel García performed data analysis and led manuscript writing.

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CONFLICT OF INTEREST STATEMENT


The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Miñarro & García, 2024) are available from Repositorio Institucional de la Universidad de Oviedo: https://doi.org/10.17811/ruo_datasets.75892.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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