Grassland Management Affects Vegetation Structure, Bats and Their Beetle Prey

Max Anderson [1] ![ORCID], **Lisa Norton** [2] **and Fiona Mathews** [1,*]

1   School of Life Sciences, University of Sussex, Falmer, Brighton BN1 9QG, UK; max.anderson@sussex.ac.uk
2   UK Centre of Ecology and Hydrology, Lancaster Environment Centre, Bailrigg, Lancaster LA1 4AP, UK; lrn@ceh.ac.uk
*   Correspondence: f.mathews@sussex.ac.uk

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Abstract: Agricultural grasslands provide vital habitats for many species. Yet despite representing a significant proportion of European land use, they are disproportionately understudied compared to arable systems. Increases in productivity and intensification have led to changes in management practices, which are likely to affect grassland habitats and the ecological communities that they support. This study simultaneously monitored three trophic levels to assess the impacts of permanent versus temporary pasture (leys) on vegetation composition, carabid and dung beetle abundance, and the activity of beetle-feeding bats. Leys had lower abundances of soil-inhabiting dung beetles, which may be explained by the more recent exposure to tilling compared with permanent pasture. Beetle-feeding bat activity was also greater in leys, with positive relationships between *E. serotinus* activity and *Onthophagus* abundance across both pasture types. However, the lack of any positive relationships between beetle-feeding bat activity and *Aphodius*, a well-known prey genus, suggests that other key prey orders (Lepidoptera) may be of more influence on bat activity. As well as the management of pasture, differences in cattle management between pasture types can have a significant impact on vegetation and soil structure, which influence invertebrate communities and potentially dictate habitat suitability for bats.

1. Introduction

Agricultural grasslands are one of the dominant land-use types in Europe, and they are vitally important habitats for many species. In 2016, the total area of land use dedicated to permanent grasslands in Europe (EU 28) amounted to 34% of the total agricultural area, or 14% of total land area [1]. In the UK, land used for livestock grazing represents 60% of total agricultural area (54% permanent pasture, 6% temporary pasture), which equates to 47% of the total land area [2]. There have been important changes in grassland management over recent decades in order to improve productivity, including the use increased use of inorganic fertilizers and herbicides [3]. Intensification and changes to agricultural practices pose a significant threat to a wide range of taxa [4–7].

Permanent and temporary grasslands (hereafter referred to as 'leys') are very different habitats in terms of their management, with the latter being more similar to arable land than to permanent pasture, especially early in their establishment. Once established, permanent pasture usually has much less intervention than leys. While both tend to receive fertiliser applications (either organic or inorganic), the latter is also subject to tilling and re-seeding with varying combinations of botanical forage species at regular intervals ranging from 3 to 5 years. These processes can have a significant impact on soil structure and function, affecting, for example, soil chemistry and invertebrate fauna [8–10].

Furthermore, cattle that graze leys are typically managed in a rotation system, spending less than a month and often less than a week grazing, before being moved onto another paddock or field. This contrasts with herds grazing permanent pasture, which are often set stocked, grazing the field for over a month, and sometimes for the entire grazing season.

Despite starkly contrasting management regimes for pastoral ecosystems, grassland management has been the subject of much less research than has arable farmland management. This is at least partly because arable systems include greater inputs of agricultural chemicals—the subject of much current research—and there are also key indicator species strongly associated with arable systems (e.g., birds [11,12] and carabid beetles [13]). Yet, land-use choices and management strategies employed in livestock farming can have a significant impact on ecosystem services, and can directly influence productivity and economic viability [14,15].

As well as being important for livestock production, agricultural grasslands provide important habitats for a wide range of taxa including plants, invertebrates, birds and mammals. Many of these species also provide valuable ecosystem services. For example, bats provide ecosystem services including pest suppression in both arable and pastoral systems [16,17], and their declines are linked to agricultural intensification and increasing urbanisation [18,19]. Approximately one-third of bat species globally and one-quarter of those in Europe are considered threatened or data deficient by IUCN [20]. *E. serotinus* is currently highlighted as being of conservation concern in the UK [21]. Several bat species, including *Rhinolophus ferrumequinum*, *Nyctalus noctula*, and *Eptesicus serotinus*, are heavily reliant on cattle-grazed pasture.

Carabid beetles and dung beetles, which are commonly found in cattle-grazed pasture, are important dietary components for *R. ferrumequinum*, *N. noctula* and *E. serotinus* [22]. They also perform vital ecosystem services and are highly sensitive to changes in agricultural practices [7]. Carabid beetles contribute towards pest control by feeding on molluscs [23–25] and consuming non-crop seeds [26]. Dung beetles improve soil aeration and quality [27], recycle dung [28], suppress parasites [29], and improve the nutritional value of pasture, associated with recycling of nutrients from dung burial [30].

To establish the impacts of grassland management and composition on abundance of beetles and bat activity, comparisons between five paired permanent pastures and leys were carried out. The study aimed to (1) assess the difference in grassland composition, beetle abundances and bat activity between permanent pasture and leys; (2) determine the influence of grassland composition on the abundances of carabid beetles, *Aphodius* and *Onthophagus* dung beetles, and assess whether beetle abundance predicts the activity level of beetle-feeding bat species; and (3) assess whether relationships between grassland composition, beetle abundance, and beetle-feeding bat activity differ between grassland types.

2. Materials and Methods

Farms in the south-west of the United Kingdom containing both permanent pasture and leys were identified through their engagement with the Devon Greater Horseshoe Bat project or through their affiliation with the Pasture-Fed Livestock Association (PFLA), a farmer organisation which certifies farmers who feed only grass and forage to livestock. Carabid beetles, dung beetles and bat activity were sampled at paired study sites (permanent pasture vs. leys) for a period of seven contiguous days (Table S1). Permanent grassland, or permanent pasture, as defined by the UK's Rural Payments Agency is "land used to grow grasses or other herbaceous forage for five or more consecutive years" (Rural Payments Agency, Reading, UK, 2019). Leys are classified as any grassland under five years old, including that within an arable rotation.

At the time of sampling, cattle were not grazing the fields, but all fields had been grazed within the past 2 months, with the time since most recent grazing being very similar within paired fields (mean difference across pairs = 2 days, S.D. = 3.1). Fields within a pair were no more than 1 km apart (median distance between pairs = 348 m, S.D. = 257), avoiding any substantial variation

in geography or weather. In addition, none of the study farms applied parasiticides to their cattle, the application of which has been shown to result in reduced biomass, species richness and functional efficiency of dung beetles [31,32]. Ethical approval was granted for this research by the Animal Welfare and Ethical Review Body (Reference: ARG/16/06).

2.1. Farming Data

A short questionnaire was sent to each of the farm owners to ascertain details of land and livestock management, including the application of parasiticides, grazing schedule and the history of each field under study.

2.2. Carabid Beetles

The method for surveying ground beetles closely replicated that applied by Fuller et al. [5] (Figure 1). Within each field, 18 pitfall traps were set. Nine of these were deployed linearly along the field boundary, 2 m away from the boundary with a 15 m spacing between traps. Nine additional traps were placed in three rows of three at 2, 8 and 32 m, each row in line with the three central traps along the field boundary. Pitfall traps were 0.5 L, round plastic tubs (56 mm depth) set into the ground so that the lip of the trap was level with the ground. Vegetation in the immediate vicinity of the trap was removed to avoid trap contamination, and, where necessary, the surrounding soil was moulded to ensure direct connectivity from the ground to the pitfall trap. The traps contained a 2 cm depth of neat engine coolant to preserve any invertebrates. Upon collection, carabid beetles were grouped by pitfall trap number and preserved in 70% ethanol (*v/v*).
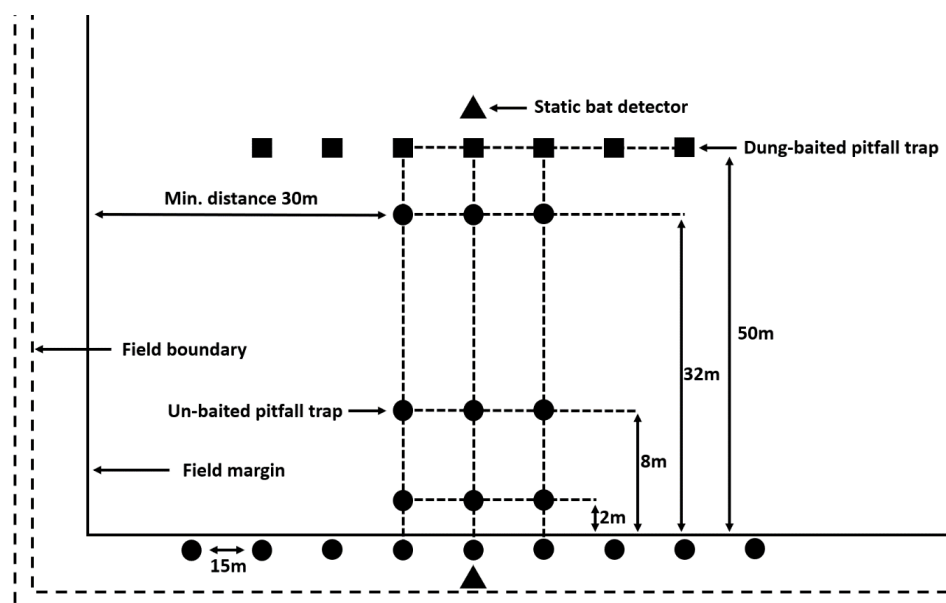

Figure 1. Diagram of equipment layout as adapted from the pitfall trap sampling method [5].

2.3. Dung Beetles

In line with the carabid beetle pitfall traps and at 50 m away from the field boundary, 7 dung-baited pitfall traps were deployed, spaced at 15 m intervals. The traps (2.4 L; 180 mm × 180 mm × 98 mm) were set in the same way as for carabid beetles. The traps were baited with fresh dung, collected from cattle on the farm being sampled, manually processed to remove invertebrates and homogenised. Processed dung (500 mL) was placed on top of each pitfall trap, supported on a 25 mm wire mesh panel (190 mm × 190 mm) to minimise by-catch of larger organisms, and covered with tissue paper to prevent spillage into the trap. The dung beetles from each trap were preserved in 70% ethanol (*v/v*).

2.4. Bat Activity

Bat acoustic data were collected using Song Meter SM2 and SM2+ full-spectrum static bat recorders, fitted with SMX-U1 ultrasonic microphones that were sensitivity-tested prior to deployment (Wildlife Acoustics, Maynard, MA, USA). Details of the detector configuration are provided in the supplementary material (Table S2). Two static bat detectors were deployed in each field, at 1 and 50 m from a linear feature with one microphone per detector. Microphones were attached to a bamboo cane at a height of 1.8–2 m from the ground and at an angle of 90° to the cane, facing each other. Recordings were collected for 7 nights, beginning at 30 min before sunset and continuing until 30 min after sunrise. Across all sampling periods, the mean minimum daily temperature was >7 °C (S.D. = 2.1) and the mean daily temperature was >10 °C (S.D. = 1.6). The average nightly rainfall was <8 mm (S.D. = 3.3) and the mean wind speed was <6 m/s (S.D. = 1.4).

2.5. Vegetation Sampling

A survey of the plant species present in each field was undertaken prior to the start of the bat activity and invertebrate sampling period, using the standard X-plot method from the national Countryside Survey [33]. A 200 m² plot (14.14 m × 14.14 m) was marked out, and the presence and percentage cover (rounded to nearest 5%) of all plant species occurring in the two smallest quadrats were recorded. In subsequent quadrats, only the percentage cover of species which had not occurred previously were recorded (Figure 2). The height of vegetation was measured to the nearest cm at five locations within the plot; at all four corners; and at the centre.
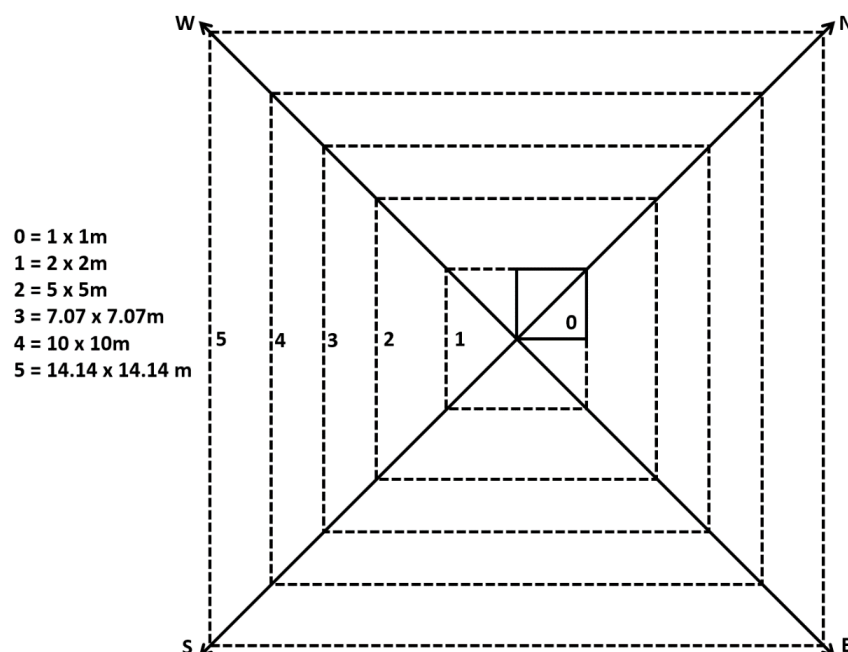

Figure 2. X-plot design for vegetation sampling [33].

2.6. Data Processing

Beetles from all dung-baited and un-baited pitfall traps were identified, to species where possible and to genus otherwise, with the aid of a binocular dissecting microscope and by reference to field guides [34–36]. For the purpose of analysis, beetles from dung-baited pitfall traps were aggregated into three genera—*Aphodius*, *Onthophagus* and *Geotrupes*—and abundances of beetles were calculated per trap.

Bat acoustic data were analysed using Kaleidoscope software version 3.1.1 (Wildlife Acoustics Inc., Maynard, MA, USA, 2015). Automatic classifiers for European bats were used, and calls identified

as common and soprano pipistrelles were accepted after being manually checked for the presence of horseshoe bat calls within the same file. All other species were identified manually, with reference to the call parameters described by Russ [37]. All species in the genus *Myotis* were considered together because of the difficulty of identifying species with certainty using acoustic data alone. Using Russ [37], serotine, noctule and Leisler's calls were identified to species where possible and were classified as 'nyctaloid' otherwise. Each audio file was used as a proxy for a single bat pass.

2.7. Statistical Analyses

Statistical analyses were performed using R version 3.5.3 (R Core Team, Vienna, Austria) [38]. The relationships between beetle abundances and vegetation structure, and between bat activity and beetle abundances were assessed using generalised linear mixed models with negative binomial error structures, built using the 'lme4' package [39]. For the relationships between beetle abundance and vegetation structure, sward height, plant species richness, percentage cover of grasses and field management type (ley = 0; permanent pasture = 1) were specified as fixed effects, with field number and farm number specified as random effects to account for the possible autocorrelation of replicates within fields and within farms. Separate models were created for the following dependent variables: carabid beetle abundance, total dung beetle abundance, *Aphodius* dung beetle abundance, *Onthophagus* dung beetle abundance, *Nebria brevicollis* abundance, *Aphodius rufipes* abundance and *Onthophagus coenobita* abundance. Finally, whether the availability of beetles influenced bat activity was tested by using generalised linear mixed models with negative binomial error structures, built using the 'lme4' package [39]. Carabid abundance, *Aphodius* abundance, *Onthophagus* abundance, field management type (ley = 0; permanent pasture = 1) were specified as fixed effects with field number, farm number and detector location (centre = 0, margin = 1) specified as random effects. Separate models were created for the following dependent variables: total beetle-feeding bat activity, *Rhinolophus ferrumequinum* activity, *Eptesicus serotinus* activity and *Nyctalus noctula* activity.

To test whether relationships between predictors and outcome measures varied according to the field categories being studied (permanent pasture vs. leys), interactions between field management type and the other predictors were included. Interaction terms were checked by comparing successive models using analysis of variances (ANOVA). Where interaction terms were significant ($p < 0.05$), further analyses were conducted on each field management type separately. Model selection was undertaken by using stepwise removal of the least significant predictor variables, comparing successive models using ANOVA, checking the model AIC values and looking for over-dispersion. If there were no significant differences revealed from the ANOVA, the model AIC values were similar and the over-dispersion ratios were both reasonably close to 1, then the most parsimonious model, i.e., the model with fewer variables was selected. Residual plots were also produced to check for model fit and checks for collinearity of predictors undertaken by generating VIF values. Finally, to account for multiple comparisons, and reduce the likelihood of encountering type 1 errors, *p*-values were adjusted by applying the Benjamini–Hochberg method [40].

3. Results

3.1. Vegetation Structure

There were no significant differences in the percentage grass cover ($p = 0.269$), plant species richness ($p = 0.265$) or sward height ($p = 0.438$) between permanent pasture and leys (Figure 3). Variability in sward height in leys (Figure 3a) and plant species richness in permanent pasture (Figure 3c) were high.

3.2. Beetles

A total of 790 carabid beetles belonging to 26 species (Table S3) and 2466 dung beetles belonging to 16 species were collected from the five paired farms (Table S4). A median of 23 and 22 dung

beetles per trap (Figure 4a), and 4 and 3 carabid beetles per trap (Figure 4b) were recorded in leys and permanent pasture, respectively. *Nebria brevicollis* was the most abundant species of carabid recorded across all sites, representing over 42% of all carabid beetles (Figure 4d). For dung beetles, the most abundant species were *Aphodius rufipes* and *Onthophagus coenobita,* representing over 67% of all dung beetles recorded across all sites (Figure 4c,e).

Sampling in permanent pasture yielded 64% more carabid beetles compared to leys. However, this difference was not significant (Figure S1) and there was no interaction between botanical measures and management type for total carabid abundance, or for the abundance of *N. brevicollis* alone. There were 22% more dung beetles collected in permanent pasture and there were interactions between pasture management type and species richness ($p < 0.001$), percentage grass cover ($p < 0.001$) and sward height ($p < 0.001$). *Aphodius* beetles were 79% more abundant in leys, and the effect of management type depended on plant species richness ($p = 0.036$) and percentage grass cover ($p < 0.001$), but not on sward height. The abundance of *Onthophagus* beetles was 88% higher in permanent pasture compared to leys, and there was a significant interaction between management type and sward height ($p = 0.018$), but not on percentage grass cover or plant species richness. There were also significant interactions between field management type and plant species richness ($p = 0.014$), and sward height ($p = 0.008$) for the abundance of *O. coenobita*. However, there were no interactions between botanical measures and management type for *A. rufipes* abundance.
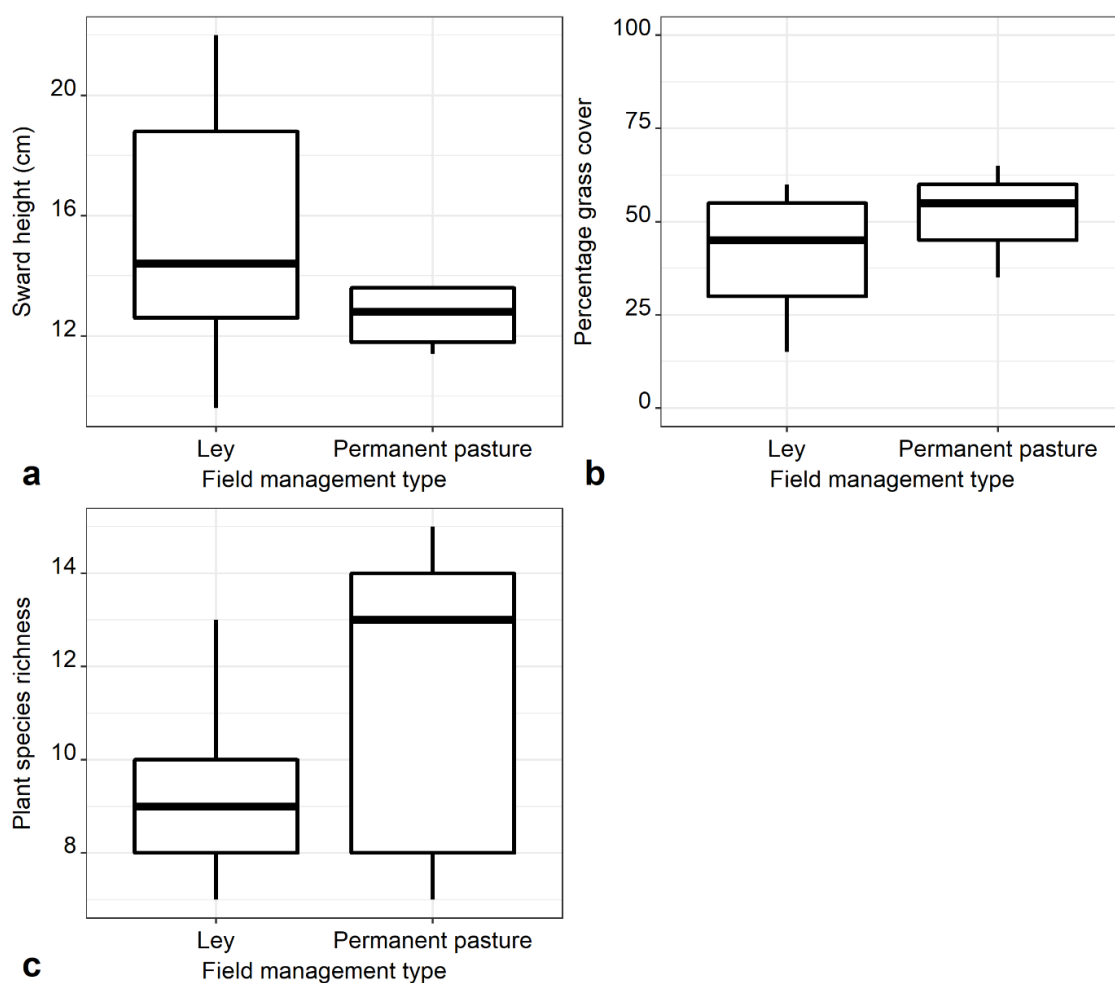

Figure 3. Box plots showing (**a**) sward height, (**b**) percentage grass cover, and (**c**) plant species richness between permanent pasture and leys.
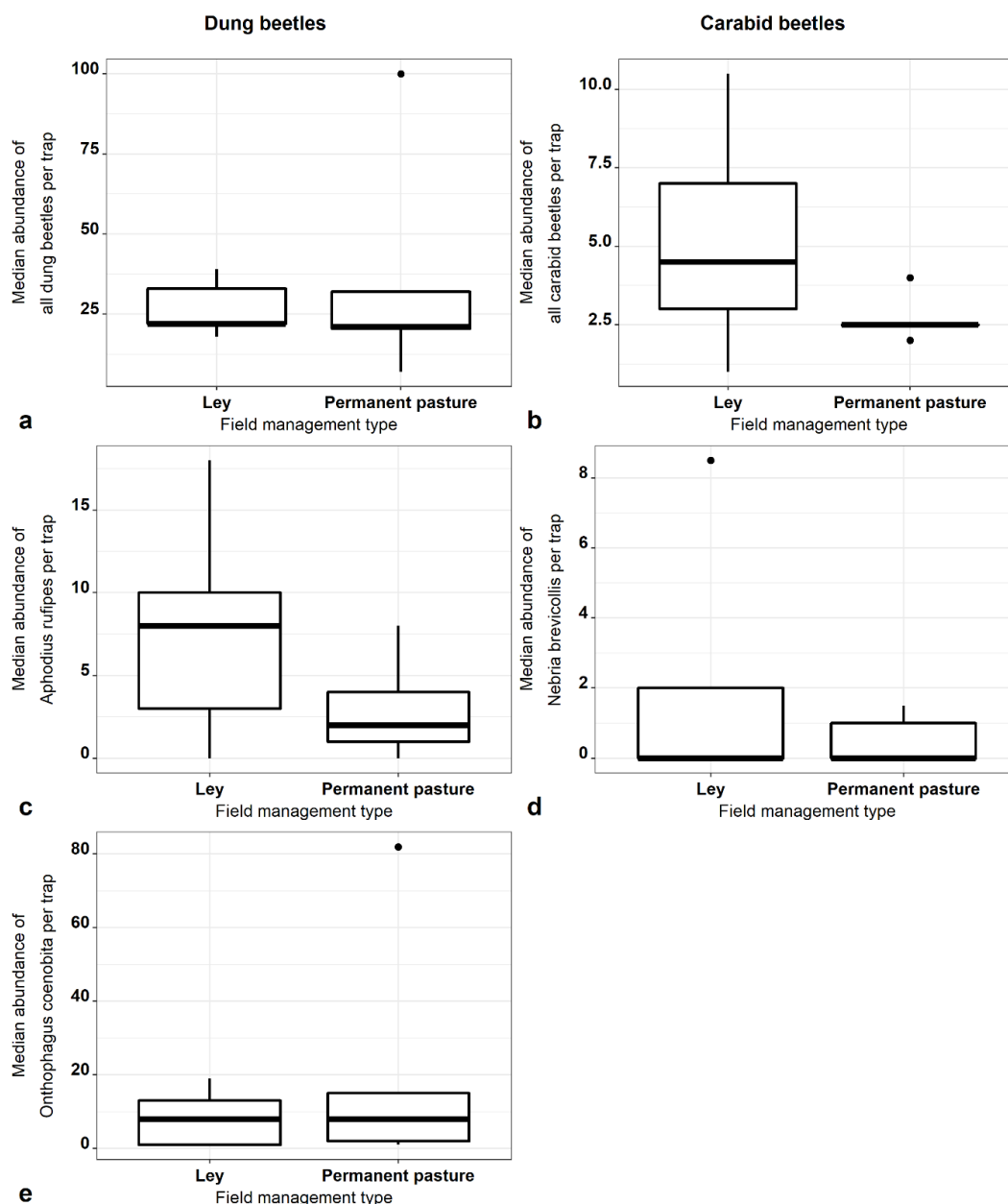
Figure 4. Box plots showing median abundance per trap for (**a**) all dung beetles, (**b**) all carabid beetles, (**c**) *Aphodius rufipes*, (**d**) *Nebreia brevicollis*, and (**e**) *Onthophagus coenobita*, between leys and permanent pasture.

Across both management types, lower plant species richness and lower sward heights both predicted higher abundances of all carabid beetles, and lower sward heights also predicted higher abundances of *N. brevicollis* alone (Figure 5). Additionally, an increase in percentage grass cover predicted an increase in the abundance of *A. rufipes* (Figure 6). For all dung beetles combined, an increase in all three botanical measures predicted higher abundance within leys. In permanent pasture, the opposite relationship was found for all dung beetles, with higher grass cover, plant species abundance and sward height predicting lower beetle abundances. This result was also found specifically for the abundance of *Onthophagus* species (Figure 7), whilst *Aphodius* abundance (Figure 7) was lower under increased grass cover only. A decrease in percentage grass cover and plant species richness predicted an increase in *O. coenobita* abundance in leys, and a decrease in sward height predicted an increase in *O. coenobita* abundance in permanent pasture (Figure 6).
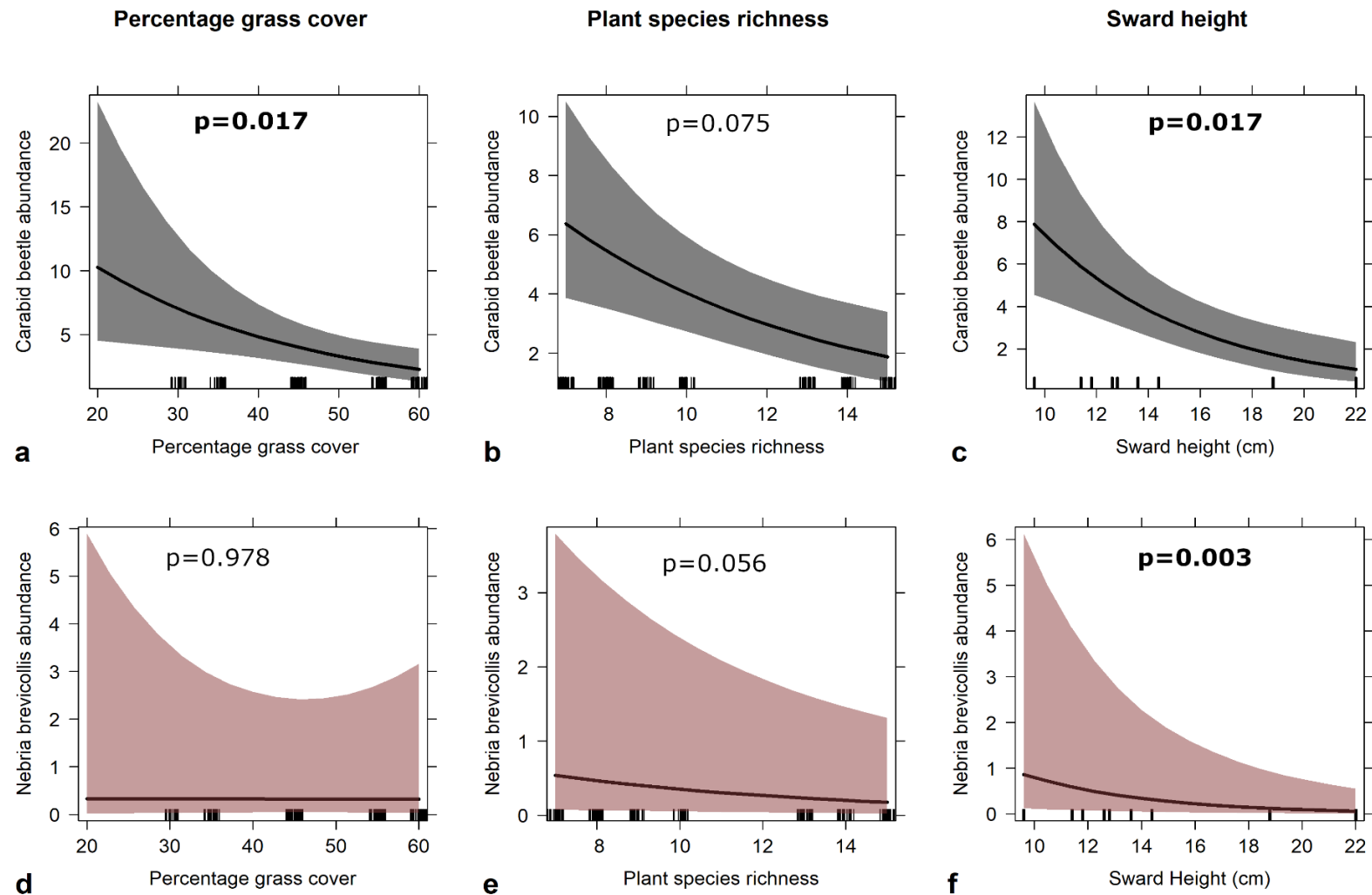
Figure 5. Model predictions (with 95% confidence intervals in colour and *p*-values) for relationships between beetle abundance and vegetation characteristics for (**a**–**c**) all carabid beetles, and (**d**–**f**) *Nebria brevicollis*.
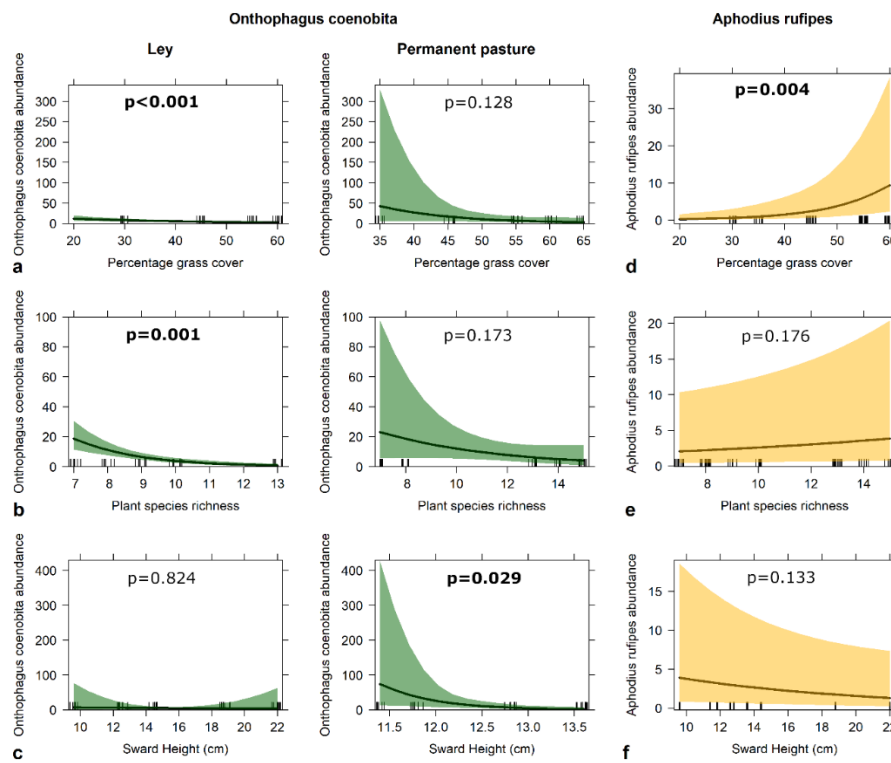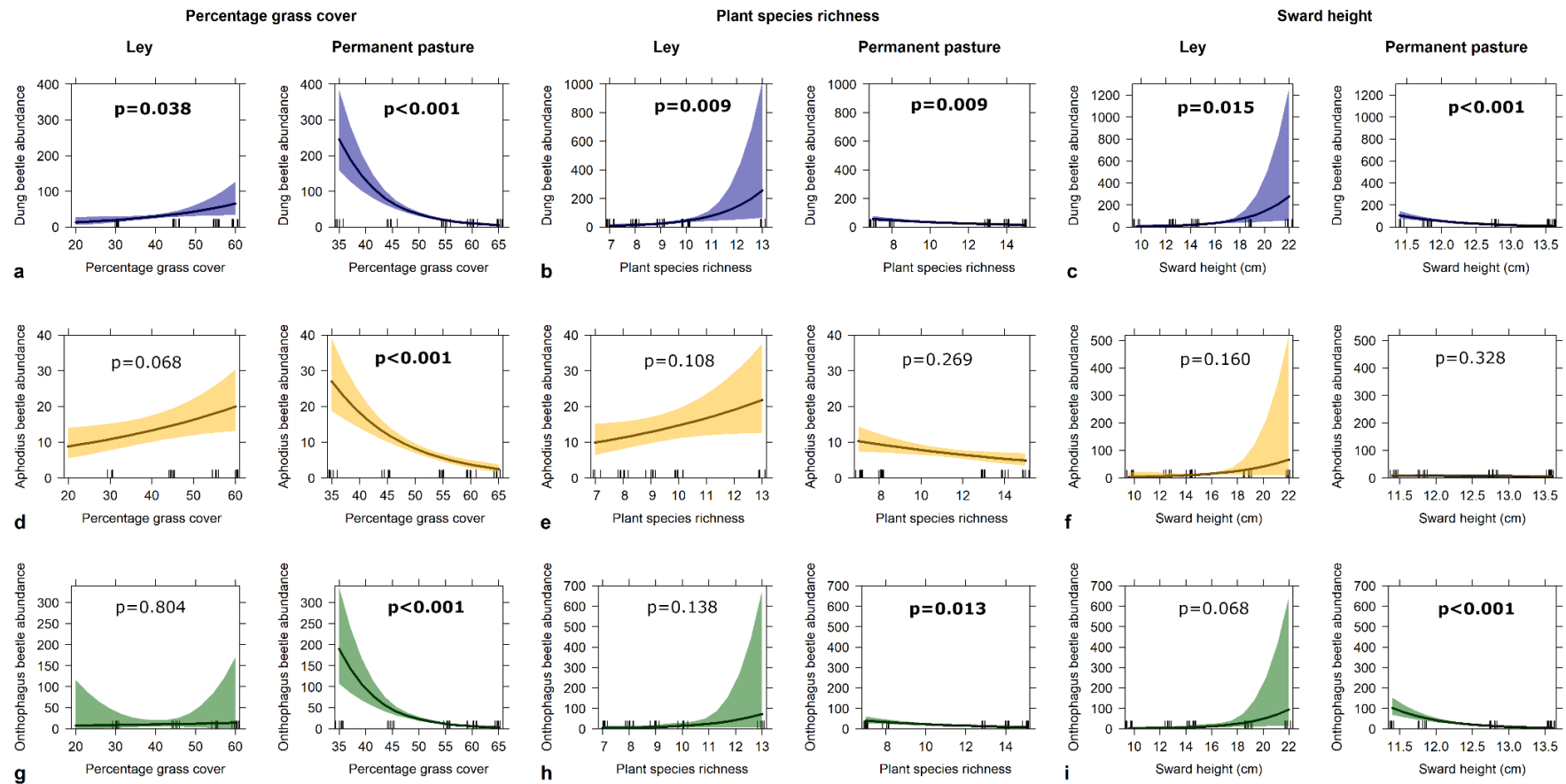
Figure 6. Model predictions (with 95% confidence intervals in colour and *p*-values) for the relationships between the abundance of (**a**–**c**) *Onthophagus coenobita*, and (**d**–**f**) *Aphodius rufipes*, and vegetation characteristics in permanent pasture and leys.

Figure 7. Model predictions (with 95% confidence intervals in colour and *p*-values) for the relationships between invertebrate abundance and vegetation characteristics in permanent pasture and leys for (**a**–**c**) all dung beetles, (**d**–**f**) *Aphodius* beetles, and (**g**–**i**) *Onthophagus* beetles.

3.3. Bats

Beetle-consuming bat species accounted for 4.4% of all 6812 bat passes recorded across the five paired fields. Within this group, *Nyctalus noctula* had the highest proportion of activity (42%), followed by *Eptesicus serotinus* (32.9%) and *Rhinolohphus ferrumequinum* (25.1%) (Table S5). There were a median of 9 and 2 beetle-feeding bat passes recorded across the sampling period in leys and permanent pasture, respectively (Figure 8d).
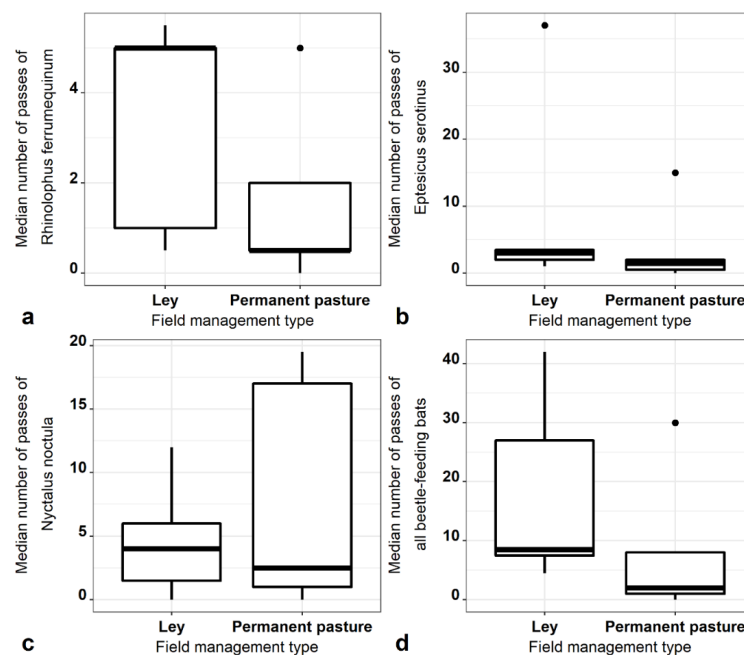
Figure 8. Box plots showing median number of passes recorded per field over the 7 night sampling period for (**a**) *Rhinolophus ferrumequinum*, (**b**) *Eptesicus serotinus*, (**c**) *Nyctalus noctula*, and (**d**) all beetle-feeding bat species combined, between permanent pasture and leys. Free-standing dots (●) on box plots represent outlying data points.

The total activity of all beetle-feeding bats was higher in leys than in permanent pasture, though it comprised a greater proportion of total bat activity in permanent pasture. The activity of *R. ferrumequinum* and *E. serotinus* were also higher in leys, with *N. noctula* being more active in permanent pasture (Figure S2).

For all beetle-feeding bats combined and *N. noctula*, relationships between activity and beetle abundances did not depend on pasture management type, and there were no significant relationships between invertebrate abundances and activity. For the activity of *E. serotinus,* there was a significant interaction between *Onthophagus* abundance and pasture management type ($p < 0.001$). Within leys, the most parsimonious model indicated an inverse relationship between *E. serotinus* activity and carabid abundance, and a positive relationship between *E. serotinus* activity and *Onthophagus* abundance (Figure 9). There was no significant relationship with *Aphodius* abundance. For permanent pasture, the most parsimonious model indicated that a higher abundance of *Onthophagus* predicted a greater amount of *E. serotinus* activity, with no significant relationships with carabid or *Aphodius* abundance (Figure 9).

Similarly, for the activity of *R. ferrumequinum,* there was a significant interaction between *Onthophagus* abundance and pasture management type ($p = 0.008$). In leys, the most parsimonious model indicated an inverse relationship with both *Onthophagus* and *Aphodius* abundance (Figure 9). There was no relationship with carabid abundance. For permanent pasture, there were no significant relationships between *R. ferrumequinum* activity and abundances of all beetle groups (Figure 9)
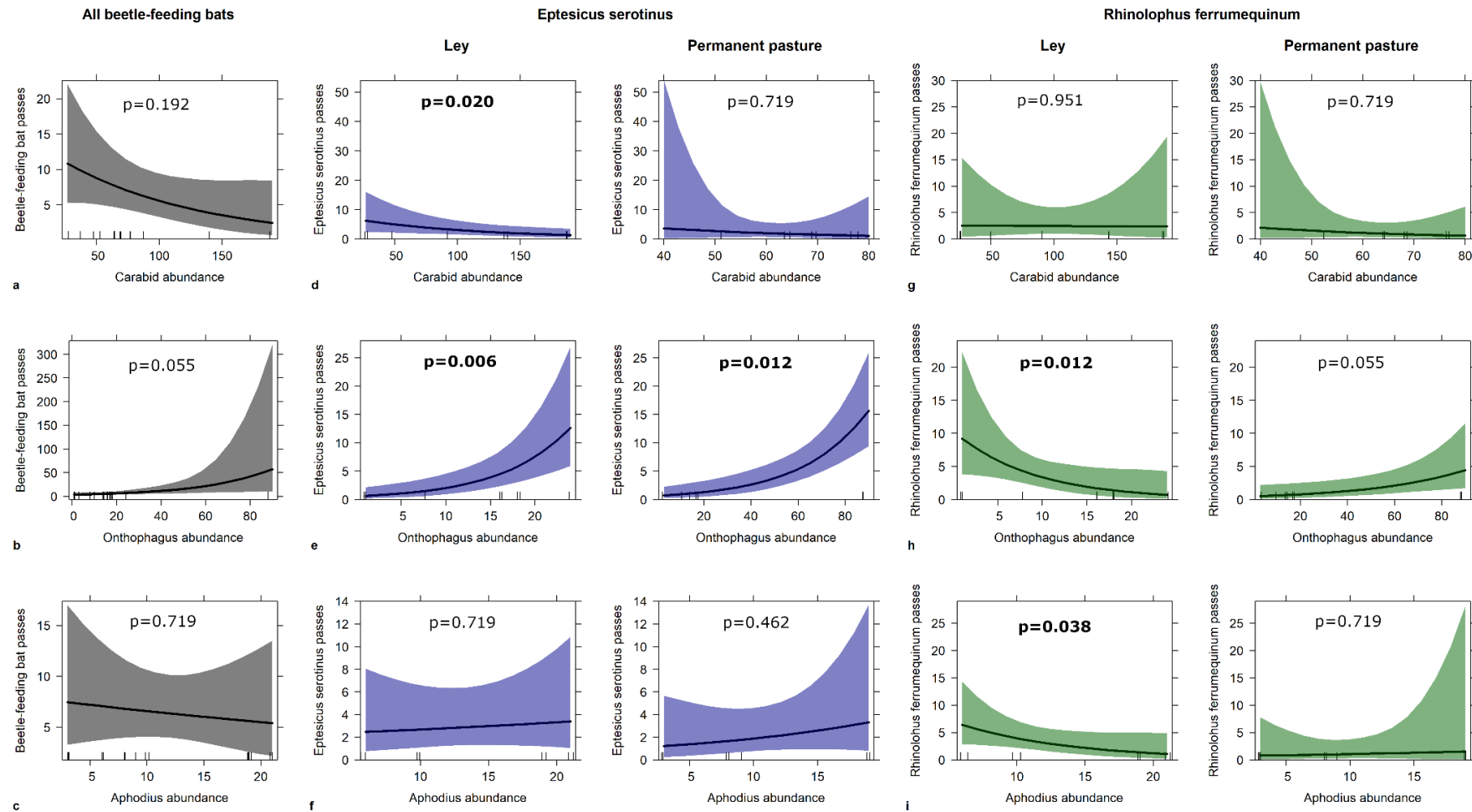
Figure 9. Model predictions (with 95% confidence intervals in colour and *p*-values) for the relationships between invertebrate abundance and activity of (**a**–**c**) all beetle-feeding bat species over both field management types, (**d**–**f**) *Eptesicus serotinus* in leys and permanent pasture, and (**g**–**i**) *Rhinolophus ferrumequinum* in leys and permanent pasture, over the entire 7 night sampling period.

4. Discussion

The ecology of productive agricultural grasslands is significantly understudied compared to arable systems. This study addressed the impacts of differing grassland management practices on the plant assemblages, the abundance of beetles and, simultaneously, on the activity of some of their predators. Results from this study revealed no significant differences in the plant species richness, sward height or percentage grass cover between permanent pasture and leys, although sward height was more variable and on average higher in leys then in permanent pasture. A limited sample size and high variability within management types (as indicated for sward height in leys, but also for species richness in permanent pasture) may have influenced the lack of significant differences in vegetation parameters and the potential for attributing differences observed in abundance of beetles to management practices.

The total abundance of all dung beetles was relatively similar between management types, with 22% more being captured in permanent pasture. The impact of management type on abundance depended on vegetation measures, with higher levels of species richness, percentage grass cover and vegetation height predicting an a greater in abundance in leys, and a lower abundance in permanent pasture. The abundance of *Aphodius* dung beetles was higher in leys compared to permanent pasture. These results may be owing to differences in cattle management between field types or the fact that leys involve regular ploughing. Leys tend to be grazed in a rotation system, which will result in greater heterogeneity of vegetation structure, whereas in permanent pasture, vegetation structure will be more homogenous and over the course of the management cycle, will become shorter due to the consistent grazing pressure.

Livestock grazing systems operate as vital habitats for dung beetles, which provide ecosystem services. These services include recycling dung back into the ground and improving soil quality and structure [27,28], which can help to sustain and even improve the economic value of agricultural land. Dung beetles in the UK can be categorised into two functional groups—paracoprids, or 'tunnellers'—such as *Onthophagus* spp. which tunnel under pats and bury dung in brood chambers so their eggs and larvae can develop, and endocoprids, or 'dwellers', which include a majority of *Aphodius* spp. which typically lay eggs, feed and develop inside the dung pat [41]. This study found that the total abundance of paracoprid dung beetles was higher in permanent pasture compared to leys. This is corroborated by a substantial evidence base demonstrating the negative impacts of ploughing and other practices which impact soil structure have on paracoprid dung beetles and other soil-dwelling invertebrates [42–45].

Results from this study also showed that despite there being over 60% more carabid beetles recorded in leys, there was no significant difference in abundance between management types. This may, in part, reflect small sample sizes, but previous work focusing on the impacts of ploughing and other processes involving soil disturbance on carabid beetle communities have also yielded mixed results [46]. While some publications report higher carabid beetle abundances in reduced or no-till systems [47], there are others which show that the opposite is true [48] or that there are no differences [49,50]. The lack of any consistent and well-substantiated relationships between ploughing and species abundance and diversity indicates that there may be alternative factors influencing the observations.

Higher levels of structural heterogeneity within vegetation facilitates greater insect diversity and abundance [51–53]. A higher level of sward height and percentage grass cover predicted lower carabid abundances, and there was no significant relationship with plant species richness. Other studies have similarly found that vegetation structure and heterogeneity play a more important role than plant species richness in dictating the activity-abundance of carabid beetles in agricultural habitats [54]. Future research should ensure that a range of measures are taken to account for potential sources of heterogeneity in vegetation structure and composition, given how important it is in impacting invertebrate abundance and diversity. There would also be great merit in researching the landscape and field-scale distributions of dung beetles, carabid beetles and other invertebrate prey in different pasture types. The distribution of invertebrates can have significant implications for the conservation of bats and other insectivores, and for the delivery of ecosystem services by invertebrates.

Insectivorous bats play a crucial role in agricultural landscapes by controlling pest species. The larvae of some noctuid moth species are pests in grasslands, acting as defoliators or attacking the roots of grasses [55]. *Eptesicus serotinus*, *Nyctalus noctula* and *Rhinolophus ferrumequinum* are all dependent on moths and beetles for a significant part of their diet. However, because of the seasonal fluctuations in invertebrate abundances, there is notable variation in dietary composition throughout the year [56]. The activity of *Pipistrellus* spp. was greater in leys compared to permanent pasture, representing 90% of activity across both field management types (Table S5). The paired fields in this study were in relatively close proximity (median distance between pairs = 348 m, S.D. = 257) to minimise any substantial variation in landscape composition. However, the differences observed in the activity of *Pipistrellus* spp. may be attributed to a number of other factors including differences in the structure or composition of hedgerows and other local features which are used for commuting, foraging and roosting [57–59].

This study found that total beetle-feeding bat activity was greater in leys compared with permanent pasture, and showed no significant relationships with beetle abundances. Similarly, the activity of *R. ferrumequinum* was also higher in leys. The impact of pasture type on *R. ferrumequinum* activity depended on *Onthophagus* abundance, with significant negative relationships with *Onthophagus* and *Aphodius* in leys. Dung beetles are a particularly important dietary component for juvenile *R. ferrumequinum* [56]. However, over the course of the summer season, Lepidoptera typically form a higher volume of the diet [22,60]. It is important to highlight that the occurrence or abundance of invertebrate prey does not necessarily indicate that they are available or accessible to bats. Nonetheless, the availability of other, unmeasured, invertebrate groups may have a greater influence on the activity of *R. ferrumequinum*. The activity of *Nyctalus noctula* was not significantly different between pasture types and yielded no significant relationships with beetle abundances, possibly because of the high altitude at which these bats fly and hence the difficulty of relating activity to local factors at ground level. Further examination of how field and livestock management practices impact the distribution of bats within fields would be of great value in future studies.

Results showed that *E. serotinus* activity was similar between pasture types, and an increase in *Onthophagus* abundance predicted an increase in *E. serotinus* activity in both pasture types. The diet of *E. serotinus* is most typically dominated by Coleoptera, followed by Lepidoptera and Diptera [22,61–63]. One study of *E. serotinus* in Belgium identified that *Aphodius* dung beetles comprised 19% of the diet, second only in abundance to *Melolontha* spp., with notable seasonal variation [64]. There is no previous evidence to suggest that *Onthophagus* beetles are prey items for *E. serotinus*, but they are known to feed opportunistically [63]. Despite finding no significant relationships between *Aphodius* abundance and *E. serotinus* activity in this study, it may again be the case that Lepidoptera and other invertebrate prey groups are playing a more significant role in dictating the observed activity.

5. Conclusions

This study applies a unique approach to determining differences between the impacts of permanent pasture and leys through investigations at multiple trophic levels. Overall, activity of all beetle-feeding bats was higher in leys compared to permanent pasture. The activity of *E. serotinus* was positively related to *Onthophagus* abundance in both pasture types. Relationships between *R. ferrumequinum* activity and *Aphodius* and *Onthophagus* abundance in leys were negative, despite *Aphodius* being a well-known prey item. The availability of other prey species e.g., Lepidoptera may have a strong influence on the activity of *R. ferrumequinum* and *E. serotinus*. Leys had greater abundances of carabid beetles and endocoprid dung beetles (*Aphodius*). Creating or maintaining heterogeneity in vegetation structure can increase the abundance and diversity of invertebrate species, whilst also having positive impacts for bats. Conversely, there were lower abundances of paracoprid dung beetles (*Onthophagus*) in leys compared to permanent pasture. These results suggest that management of leys should aim to reduce the negative impacts of soil disturbance events (e.g., tillage) on soil-inhabiting invertebrates, which provide crucial ecosystem services.

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