



# Landscape and microhabitat features determine small mammal abundance in forest patches in agricultural landscapes

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## ABSTRACT

Intensification of agricultural landscapes represent a major threat for biodiversity conservation also affecting several ecosystem services. The natural and semi-natural remnants, available in the agricultural matrix, represent important sites for small mammals and rodents, which are fundamental for sustaining various ecosystem functions and trophic chains. We studied the populations of two small mammals (*Apodemus agrarius*, *A. sylvaticus*) to evaluate the effects of landscape and habitat features on species abundance along a gradient of agricultural landscape intensification. The study was performed in Friuli Venezia Giulia (north-eastern Italy) during 19 months, in 19 wood remnants. Species abundance was determined using Capture-Mark-Recapture (CMR) techniques. In the same plots, main ecological parameters of the habitat (at microhabitat and patch scale) and landscape were considered. Abundance of *A. agrarius* increased in landscapes with high extent of permanent crops (i.e., orchards and poplar plantations) and low content of undecomposed litter in the wood understory. Instead, *A. sylvaticus*, a more generalist species, showed an opposite, albeit less strong, relationship with the same variables. Both species were not affected by any landscape structural feature (e.g., patch shape, isolation). Our findings showed that microhabitat features and landscape composition rather than wood and landscape structure affect populations' abundance and species interaction. The opposite response of the two study species was probably because of their specific ecological requirements. In this light, conservation management of agricultural landscapes should consider the ecological needs of species at both landscape and habitat levels, by rebalancing composition patterns in the context of ecological intensification, and promoting a sustainable forest patch management.

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## INTRODUCTION

Land use change, intensification of agricultural practices, fragmentation of natural habitats and the consequent alteration of biological communities lead to a widespread decline in farmland biodiversity, measured across many different taxa (Batáry et al., 2020; Benton,

*Vickery & Wilson, 2003; Geiger et al., 2010; Kleijn et al., 2011*). In agricultural landscapes, a principal task for the conservation of farmland biodiversity and related ecosystem services is the understanding of the relationships between habitat features, habitat pattern and species population dynamics (*Fahrig, 2007; Le Roux et al., 2008; Tschardt et al., 2005*). The need to preserve and enhance agricultural landscape diversity *via* management of non-crop habitats (*i.e.*, field margins, woodlots, hedgerows, and perennial grasslands) to support high levels of agricultural biodiversity is largely confirmed (*Carvell et al., 2011; Dainese et al., 2015; Dainese et al., 2016; De Simone, Sigura & Boscutti, 2017*).

Small forest patches may deliver several important ecosystem services to human society, but they receive little attention compared to large forest ecosystems. In particular, small forest patches represent central elements in the long-standing conflict between the need of agriculture productions and biological conservation (*Biber et al., 2015; Benayas, Bullock & Newton, 2008*).

In a recent review, *Decocq et al. (2016)* focused on the ecosystem services delivered by small forest patches of agricultural landscape highlighting their potential to support biodiversity both *in situ* (forested patch) and in the proximity area enhancing landscape connectivity. Here, patch structural features (pH of soil, nutrient availability, light) and habitat configurations patterns (*i.e.*, forest patch size, patch isolation) were defined as drivers for internal species richness and community composition.

Rodents and other small mammals are rarely target of conservation studies since they are often considered as pest or menace to production (*Brown et al., 2007; Butet, Paillat & Delettre, 2006; Dickman 1999; Putman, 1989*), thus associated with negative impacts on human activities (*Capizzi, Bertolino & Mortelliti, 2014*). However, small mammals are pivotal for important ecosystem functions (Dickman 1999). They contribute to soil aeration (*Laundré & Reynolds, 1993*) and play an important role as consumers of weeds and insects (*Bricker, Pearson & Maron, 2010; Gliwicz & Taylor, 2002*). Small mammals are crucial for diaspore dispersal of plants (Bogdziewicz et al. 2020; *Steele, Wauters & Larsen, 2005*) and fungi (*Capizzi & Santini, 2007; Sieg, 1987*). In several ecosystems they sustain food chains, representing the main prey biomass for several predator groups, such as birds, reptiles, and mammals (*Martin, 1994; Salamolard et al., 2000; Šálek et al., 2010*) and greatly contribute to the overall complexity of foodwebs (*Butet & Leroux, 2001; Korpimäki & Norrdahl, 1991*). For instance, low prey densities have been proved to affect raptor nesting densities in agricultural landscapes (see *e.g.*, *Michel, Burel & Butet, 2006*).

The populations of some small mammal species have experienced a decline, sometimes drastic, probably because of agriculture intensification (*Macdonald et al., 2007; Palmeirim, Santos-Filho & Peres, 2020*), acting at both landscape and patch levels. In particular, the intensification of agricultural landscapes has been shown to decrease the density of rare and stenocious species in favor of generalist ones (*Burel et al., 2004; Gentili, Sigura & Bonesi, 2014; Millàn de la Peña et al., 2003*), provoking idiosyncratic responses. For example, *Silva, Hartling & Opps (2005)* and *Serafini, Priotto & Gomez (2019)* found that both structural complexity (*e.g.*, coverage and shape of forest patches) and landscape heterogeneity (*e.g.*, different land-use covers) promoted small mammal species diversity.

On the other hand, *Michel, Burel & Butet (2006)* demonstrated that, in areas where land-uses are relatively homogeneous (less landscape heterogeneity), species evenness but not species richness was negatively affected by the increasing of agricultural land-use intensification. At the patch scale, forest-floor characteristics, presence of coarse woody debris, understory vegetation, canopy composition (*Carey & Harrington, 2001*), forest age, vegetation complexity (*Pearce & Venier, 2005*), presence of deadwood (logs and rotten trunks) and litter structure (*Cox, Dickman & Cox, 2000; Kemper & Bell, 1985; Marsh & Harris, 2000; Simonetti, 1989; Szymański et al., 2020; Yahner, 1986*) can also influence small mammal occurrence. A high microhabitat complexity through high shrub diversity, high vegetation cover and low percentage of ground covered by bare-soil are known to increase overall small mammal abundance and species richness (*Gelling, Macdonald & Mathews, 2007; Silva & Prince, 2008; Szymański et al., 2020*).

Most of the previous studies evidenced strong effect of environmental drivers on small mammal. Nonetheless, comprehensive assessments at multiple ecological scales are still scarce and focus on species autecology. In this light, comparing species with different behavior (*i.e.*, generalist vs specialist) should be encouraged to get new insights into future agricultural landscape management.

In this study we investigated the effects of environmental features on small mammal abundance paying particular attention to forest specialists and habitat generalist species. We considered three different ecological scales: microhabitat, habitat (patch), and landscape. In particular, we tested the effects of landscape composition and configuration, forest structure and forest ground features on two small mammal species (*i.e.*, *Apodemus sylvaticus*, and *A. agrarius*) in remnants of wood vegetation along an intensification gradient of agricultural land use. These species were chosen as they represent typical species of lowland woodlots, very common in the study area (*Dorigo, 2018*) and can easily be captured with live-capture systems.

Specifically, we ask two questions: (1) What are the relative and independent effects of heterogeneity of landscape elements, composition and configuration on small mammals abundance in woodlots within agricultural landscapes? (2) Does the effect of these mosaic properties differ between species with different ecological needs?

We expected to find a strong interplay between landscape composition and habitat features in determining small mammals species distribution and abundance. In particular, we expected to find contrasting responses between the species considered, hypothesizing that the generalist *A. sylvaticus* could be more affected by landscape composition and configuration rather than local forest characteristics.

## MATERIALS AND METHODS

### Study area, species and sampling design

The study was conducted in the agricultural landscape of Friuli Venezia Giulia region, North-East Italy (45°56'N, 12°47'E), an extensive lowland area (from 20 to 36 m a.s.l.) of alluvial deposits (*Fontana, 2006*). In the study area, a matrix of intensively-farmed arable fields of annual crops (winter cereals, *Zea mays*, and *Glycine max*) and permanent plantation (poplars and orchards) is discontinued by small hedgerows and woodlots.

Two small mammals species were considered. *Apodemus sylvaticus* (Linnaeus 1758) is a habitat generalist and opportunist species with high dispersal ability; it can occupy all woodlots and hedgerows, moving frequently between patches (Bauchau & Le Boulengé, 1991; Fuentes-Montemayor et al., 2020). Its main diet includes seeds, fruits, green parts of plants and fungi, but the animal component can be substantial only in some periods of the year (Canova & Fasola, 1993; Hansson, 1985). *Apodemus agrarius* (Pallas 1771) is a hygrophilous species which feeds on high-caloric food of animal and plant origins (Babińska-Werka & Garbarczyk, 1981). Its diet is quite varied and includes a wide range of invertebrates and plants (Babińska-Werka, 1981), in form of seeds and green parts (Babińska-Werka, 1981). In northern Italy, the species usually occurs at low altitudes, in the edges of mesophilous woods and in forest river banks (Zulian, 1987).

Sampling sites were 19 remnant woodlots not harvested in the past three years, characterized by medium-wet soils and smaller than 8 ha in size. The patches were selected along a gradient of landscape intensification ranging from 5% to 33% of semi-natural habitats with a 500 m buffer around each patch. The buffer size was established in agreement with the mobility of the most abundant small mammal species found (Liro & Szacki, 1987). The same distance was assumed to consider sampling patches as independent from each other. Patches with less than 500 m distance from each others were considered only if they are separated by barriers (i.e., watercourses more than 5 m wide and one meter depth).

## Data collection

### Small mammal sampling

As trapping method we used Sherman traps (LFA type: cm 8 × 9 × 24. H.B. Sherman Traps©). This method of capture tends to be selective because it traps mostly small mammals weighing at least 5 grams like Murids (i.e., *Apodemus*, *Mus*, and *Rattus* in the study area) (Caceres, Nápoli & Hannibal, 2011; Umetsu, Naxara & Pardini, 2006). It, therefore, precluded the capture of smaller insectivorous mammals. Within each sampling patch, 10 Sherman traps, spaced 10 m from each other, were placed along a 100 m line-transect. The traps were baited with pieces of fresh apple and sunflower seeds (Tallmon & Mills, 1994), to ensure the survival of trapped animals and were activated for four consecutive nights. Samplings during periods with excessive rainfall were excluded to avoid an excessive mortality of animals. To improve the control of temperature, each trap was lined on the bottom with dry plant material particularly important during the cold season.

In all areas (sites), four sampling sessions were repeated from April, 2013 to October 2014. Traps were checked once a day in the morning. Animals were trapped using the CMR (Catch-Mark-Recapture) method. Each individual was marked with an ear tag (Opivi Brand®), and its species, body mass, sex and age (juvenile, sub-adult and adult age classes) were recorded. The animals were released again at the same place where they were trapped. Trapping activities were authorized by the Italian Institute for Environmental Protection and Research (ISPRA) (Aut. PG/IR Rif. Int. 26358-28967/2013) and by the Friuli Venezia Giulia region (Aut. Prot. SCPA/12.5/17552-2013).

### **Microhabitat structure features**

Microhabitat features were measured in sub-sample areas placed along the line transects with live traps (according to [Amori et al., 2015](#)). Around each trap, the ground cover was assessed within a buffer of 5 m. In particular, the cover percentage of herbaceous layer, rocky soil, bare ground, leaf litter and coarse woody debris (considering even small deposits of material also with diameter <3 cm) were visually estimated as percentage cover ([Amori et al., 2015](#)).

Finally, litter composition was evaluated, estimating the percentage of the categories: non-decomposed litter (whole leaves); partially decomposed litter (leaves partially degraded but leaf structure still recognizable); degraded litter (leaf structure not recognizable) in the litter stratum. This was carried out by two operators simultaneously around each trap, and the results were averaged.

### **Wood structure features**

At patch scale the presence of deadwood, understory stratification, tree diameter, woody and understory species and the presence of non-native tree and shrub species were assessed.

*Deadwood* Deadwood was measured in spring 2015 following mainly the protocol of [Bianchi et al. \(2013\)](#). We measured with a caliper the diameters of all the logs (e.g., stems, branches) (if >three cm). Length of the sample and decomposition state were also recoded. We used fixed area sampling (FAS) method ([Harmon & Sexton, 1996](#)), considered more reliable than other methods, especially with high amount of necromass composed of small fragments ([Bianchi et al., 2013](#); Warren and Olsen 1964). Measures of deadwood were carried out in the central part of the forest along the transect used with traps for small mammals, around the traps 2, 5 and 8 of each transect.

Around selected traps a 5 m radius area (78.5 m<sup>2</sup>) was surveyed. We opted for a lower threshold than indicated by [Bianchi et al. \(2013\)](#), since the studied woodlots are of recent origin and deadwood is often composed of small size logs. Branches and woody fragments of diameters less than three cm were not considered in this protocol but were still evaluated as potential microhabitats (see Microhabitat, above). Each log (e.g., stems, branches) of diameter >three cm was measured (length, major radius, minor radius) and referred to one of the three categories of the following scale: (i) standing deadwood, newly formed deadwood, with logs standing ([Marsh & Harris, 2000](#)); (ii) ground deadwood, deadwood on the ground; (iii) rotten deadwood, deadwood with spongy woody tissue and soaked with water.

The deadwood volume was calculated using the following Eq. (1):

$$V = \frac{\pi \cdot h}{3} \cdot [R^2 + r^2 + (R \cdot r)] \quad (1)$$

where V is the volume, h is the height/length, R is the major radius, r is the minor radius ([Harmon & Sexton, 1996](#)). The total values of the deadwood, for each stage, were then averaged between the three FAS considered for each sampling station.

*Understory shrub density* We measured the renewal capacity and the vertical stratification of the understory layer of the studied woods. In particular, we identified, along the transect

used with the traps for the small mammals samplings (around the trap 2, 5 and 8 of each transect), circular areas of 2 m radii (6.28 m<sup>2</sup>). Within each area, all woody plants with diameter of less than 7.5 cm have been recorded, indicating the species, and measuring the stem diameter at ground level.

*Trees density and diameter* In the center of the transect (trap 5), we placed a 10x10 m plot, inside of which we noted the number of woody plants with more than 7.5 cm in diameter. For each plant we reported the species and the diameter at breast height (D.B.H). All data were finally pooled as the average diameter of each plot, considering their standard deviation as a proxy of plot variability.

*Presence of alien species* We verified the presence of non-native arboreal plants within the 10 × 10 m plots (see above: *Trees density and diameter*) as well as the presence and the number of non-native shrubby plants inside the 2 m radii plots (see above: *Understory shrub density*).

### **Landscape structure features**

Land use was mapped in two concentric buffers, respectively of 500 m (0.785 km<sup>2</sup>) and 250 m (0.196 km<sup>2</sup>) radii, around the 19 surveyed remnant woodlots. Land use types were mapped using aerial images of the study area (year 2014) in a Geographic Information System (GIS) open source environment (QGIS). Mapped land use classes were (1) arable lands, *i.e.*, annual crops; (2) permanent crops, *i.e.*, orchards, vineyards and poplars; (3) set aside, *i.e.*, fallow lands, uncultivated areas with herbs and shrub cover; (4) woods, *i.e.*, hedgerows and woodlots; (5) settlements, *i.e.*, urban areas, industrial areas and isolated buildings. Rivers and roads were not considered as polygons but measured as linear elements (length).

Landscape pattern was analyzed by means of landscape metrics considering features at both patch and landscape scales (composition and configuration). For this purpose, selected variables (*McGarigal & Marks, 1995*): woodlot surface area; woodlot perimeter; woodlot Perimeter-Area Ratio ( $k = p/a$ ); Patch Shape Index ( $PSI = \frac{Perimeter}{\sqrt{2 \cdot \pi \cdot Area}}$ ); Mean proximity index for all patches in the landscape (MPI); mean proximity index for patches comprising the wood class (MPI\_Wood); Mean nearest-neighbor distance for patches comprising the wood class (MNN); Interspersion and juxtaposition index for patches comprising the wood class (IJI); Total number of wood patches in the landscape (NumP); Mean patch size for patches comprising the wood class (MPS); Total edge for patches comprising the wood class (TE); Percent of landscape occupied by each patch type in the landscape (PLAND); Modified Simpson's diversity index based on *Pielou (1975)* modification of Simpson's diversity index (MSIDI). Landscape structure analyses were performed using the Fragstat software (*McGarigal, Cushman & Ene, 2012*).

### **Data analyses**

Low re-capture probability, and thus unreliable estimates of abundance, did not allowed us to use estimates of abundance taken from capture-recapture models, therefore an abundance index was used. Population abundance was calculated by the relative abundance

index (RAI), used as a proxy measure of population density (*Cagnin et al., 1998; Klaa, Mill & Incoll, 2005; Ouin et al., 2000*) according to the formula Eq. (2).

$$RAI = \frac{Ns}{ns} \cdot ts \cdot 100 \quad (2)$$

where  $s$  is the sampling site,  $N$  is the number of individuals of each species,  $n$  is the number of nights that a trap is open for, and  $t$  is the number of active traps.

For each site, 40 environmental variables were measured, grouped in microhabitat structure (8), wood structure (13), landscape composition (6) and landscape configuration (13). All analyses were performed using R statistical software (*R Core Team, 2021*).

All the variables were initially analyzed and selected to cope (multi-) collinearity and to obtain more parsimonious models (*Faraway, 2005*). Variable collinearity was assessed through Principal Component Analysis (PCA) and Pearson correlation (Pearson's  $r < 0.6$ ), using the 'car' package (*Fox & Weisberg, 2011*). After this selection, 19 variables were kept as environmental predictors, divided in four groups: (i) microhabitat structure, *i.e.*, litter cover percentage, coarse woody debris percentage, bare ground percentage, and undecomposed litter percentage; (ii) wood structure, *i.e.*, tree species number, tree DBH, tree density, shrub density, number of shrub species, total deadwood, and rotten deadwood; (iii) landscape composition, *i.e.*, percentage of arable land, woods, permanent crops, settlements, and set aside; (iv) landscape configuration, *i.e.*, area/perimeter ratio, PSI, and MPI\_Wood.

Multi-model inference (MMI) within an information theoretic framework was used to evaluate the influence of environmental variables on the abundance of *Apodemus agrarius* and *A. sylvaticus*, at the different scale (*Burnham & Anderson, 2002*). This technique compares the fit of all possible models (including the null model) obtained by the combination of the variables with the "dredge" function in the MuMIn package (Bartoń, 2015) of the R software. We used Akaike's information criterion (AIC) (*Akaike, 1973*) to choose the best fitting model. AIC measures the relative quality of a model dealing with the trade-off between the complexity of the model and the goodness of fit. The best fit is indicated by the lowest AIC value (AIC MIN). In a set of models each model ( $i$ ) can be ranked using its difference in AIC score to the best-fitting model ( $\Delta AIC_i = AIC_i - AIC_{MIN}$ ). A model in the set can be considered plausible if its  $\Delta AIC$  is below 2 (*Burnham & Anderson, 2002*). We also derived the Akaike's model weight ( $w_i$ ) which is the probability that the model ( $i$ ) is the best-fitting model if data were collected again under identical circumstances (*Burnham & Anderson, 2002*). We also calculated the relative importance of the variables using Akaike's model weight.

Linear mixed-effects models (LMMs) were used to estimate model parameters as model residuals approximated a normal distribution. Models included population abundance as response variable and species, environmental variables, and their interactions as fixed effects. The transect ID was included as random effect. Because of the low number of real replicates, the four groups of variables linked with the three scale levels (microhabitat, habitat, landscape composition + configuration) were modeled separately. An overall model was performed using only the variables which had a significant averaged coefficient ( $p < 0.05$ ) and a high Relative Variable Importance (RVI) value ( $RVI > 0.7$ ). LMMs were

conducted for each response variable separately using both a linear model with and without including a quadratic term to account for a possible non-linear relationship. The multi-model inference based on AIC was executed with the ‘MuMIn’ package (Bartorí, 2016). The LMMs were applied using the “nlme” package (Pinheiro et al., 2017). Model goodness-of-fit was further tested using diagnostic plots of residuals and goodness indices (Faraway, 2005; Zuur et al., 2009).

## RESULTS

In all sampling sessions 868 captures were recorded, of which 36.5% were recaptured individuals. The total capture effort was 3024 trap-nights, with a capture index ( $I_c = N \times 100 \text{ catch} / \text{trap-nights}$ ) of 28.7. Among the catches, 55.3% was represented by *A. agrarius*, 40.1% of *A. sylvaticus*, 4.1% by *Rattus norvegicus* and the remaining 0.5% by *R. rattus*, *Microtus arvalis* and *Crocidura suaveolens*.

*Apodemus sylvaticus* was caught in all sampling sites while *A. agrarius* occurred in 16 sites and, together, these species represented about 95% of the individuals caught. Both rodent species were caught in all sampling sessions. For all the investigated scales the null models showed a low weight (weight <0.001) and were not considerable as plausible (delta AIC >12).

### Microhabitat structure

For microhabitat structure, the multi-model inference showed that eight models were supported (Table 1). The models included the percentage of deadwood, ground cover of bare soil, percentage of undecomposed litter, species, and their interaction. The most important variable was the percentage of undecomposed litter and its interaction with species ( $RVI > 0.70$ ;  $p = 0.05$ ). Albeit not significant, presence of deadwood and ground cover of bare soil were also important ( $RVI = 0.71$  and  $0.68$ , respectively), whereas their interactions with species were negligible. In general, small mammals abundance decreased as undecomposed litter increased. Models explained between 27 and 29% of the total variation in small mammal abundance.

### Wood structure

For the group of variables describing the wood structure, the multi-model inference showed that there were seven plausible models, which included tree density, DBH, tree species richness, shrub richness, small mammal species and their interactions (Table 2). Among these variables, tree density, number of tree species (and its interaction), number of shrub species (and its interaction) showed a high relative importance ( $RVI > 0.7$ ), albeit none of them was significant. The models explained between 20 and 28% of the total variation in small mammal abundance.

### Landscape configuration

The analysis was conducted for both 500 m and 250 m.

Using landscape configuration variables in 250 m buffers, three models were supported (Table 3), which included the following variables: area/perimeter ratio, PSI, species. The



**Table 1** List of plausible models performed with multi-model inference for microhabitat structure. The estimates are reported: the intercept (Int), the variables considered in each model (ddW = mean percentage of surface around the traps occupied by deadwood; grn = mean percentage of surface around the traps occupied by bare soil; spcs = species; und = mean percentage of undecomposed litter in the litter stratum),  $R^2$ , AIC,  $\Delta AIC$  and model weight (wi). Relative Variable Importances values and significance are shown in bold.

(Int)	ddW	grn	spcs	und	ddW:spcs	grn:spcs	spcs:und	$R^2$	AIC	delta	weight
126.7	-0.25	0.03	+	-1.30	+	+	+	0.29	344.6	0	0.11
127.5	-0.26		+	-1.31	+		+	0.29	344.9	0.31	0.10
127.4	-0.26	0.00	+	-1.31	+		+	0.29	345.4	0.87	0.07
120		0.13	+	-1.25		+	+	0.28	345.6	1.04	0.07
122.4			+	-1.27			+	0.27	345.6	1.05	0.07
111.3	0.33	0.26	+	-1.17		+	+	0.28	345.9	1.38	0.06
116.1	0.33		+	-1.23			+	0.28	346.2	1.59	0.05
124.8		-0.13	+	-1.30			+	0.27	346.4	1.8	0.05
	<b>0.71</b>	<b>0.68</b>	<b>1</b>	<b>0.86</b>	<b>0.46</b>	<b>0.44</b>	<b>0.72</b>				

**Table 2** List of plausible models performed with multi-model inference at wood structure scale. The estimates are reported: the intercept (Int), the variables considered in each model (Tree\_dns = tree density; Mean\_dmt = mean trunk diameter; Tree\_spcs = number of tree species; Shr\_spcs = number of shrub species; spcs = species),  $R^2$ , AIC,  $\Delta AIC$  model weigh AIC and model weight (wi). Relative Variable Importances values and significance are shown in bold.

(Int)	Tree_dns	Mean_dmt	Tree_spcs	Shr_spcs	spcs	Tree_dns:spcs	Mean_dmt:spcs	Tree_spcs:spcs	Shr_spcs:spcs	$R^2$	AIC	delta	weight
95.33	0.57	-1.01	-6.66	-1.89	+	+	+	+	+	0.28	333.7	0	0.23
75.24	0.94		-6.98	-2.90	+	+		+	+	0.22	334.1	0.36	0.19
94.61	0.60	-1.01	-6.66	-1.85	+		+	+	+	0.28	334.8	1.1	0.13
84.17	0.77	-0.45	-6.8	-2.45	+	+		+	+	0.24	334.8	1.11	0.13
106.4		-1.06	-6.74	-2.56	+		+	+	+	0.26	334.9	1.21	0.12
78.33	0.77		-7.01	-3.13	+			+	+	0.22	335.2	1.46	0.11
92.39			-7.15	-4.14	+			+	+	0.20	335.6	1.83	0.10
	<b>0.75</b>	<b>0.66</b>	<b>0.99</b>	<b>0.95</b>	<b>1</b>	<b>0.48</b>	<b>0.42</b>	<b>0.9</b>	<b>0.83</b>				

**Table 3** List of plausible models performed with multi-model inference for landscape configuration in 250 m buffer. The estimates are reported: the intercept (Int), the variables considered in each model (Are\_prm = area/perimeter ratio of wood patches, PSI = patch shape index),  $R^2$ , AIC,  $\Delta AIC$  and model weight (wi). Relative Variable Importances values and significance are shown in bold.

(Int)	Are_prm	PSI	spcs	Are_prm:spcs	PSI:spcs	$R^2$	AIC	delta	weight
38,7		3,52	+		+	0,06	342,9	0	0,45
26,01	0,43	5,17	+		+	0,1	343,7	0,83	0,3
32,87	0,2	4,28	+		+	0,11	344,1	1,19	0,25
	<b>0,55</b>	<b>0,99</b>	<b>1</b>	<b>0,25</b>	<b>0,91</b>				

most important, albeit not statistically significant, was Patch Shape Index and its interaction with species ( $RVI > 0.91$ ). Models explained between 6 and 11% of the total variation in small mammals abundance.

Considering the same descriptors within 500 m buffers, seven plausible models were obtained, including the variables: area/perimeter ratio, PSI, MSI, species and their interactions with the variables (Table 4). Also in this case, no variable showed a high

**Table 4** List of plausible models performed with multi-model inference for landscape configuration in 500 m buffer. The estimates are reported: the intercept (Int), the variables considered in each model (Are\_prm = area/perimeter ratio of wood patches, PSI = patch shape index, MSI\_500 = Modified Simpson's Diversity Index in 500 m buffer),  $R^2$ , AIC,  $\Delta AIC$  and model weight (wi). Relative Variable Importances values and significance are shown in bold.

(Int)	Are_prm	MSI_500	PSI	spcs	Are_prm:spcs	MSI_500:spcs	PSI:spcs	$R^2$	AIC	delta	weight
38,7			3,52	+			+	0,06	342,9	0	0,19
-18,15		0,57	6,78	+		+	+	0,2	343,3	0,41	0,15
26,01	0,43		5,17	+			+	0,09	343,7	0,83	0,12
-15,68	-0,15	0,59	6,31	+	+	+	+	0,26	343,9	1,04	0,11
32,87	0,2		4,28	+	+		+	0,11	344,1	1,19	0,1
-23,34	0,31	0,53	7,75	+		+	+	0,22	344,7	1,84	0,07
15,32		0,23	4,86	+			+	0,11	344,8	1,88	0,07
	<b>0,54</b>	<b>0,55</b>	<b>0,99</b>	<b>1</b>	<b>0,27</b>	<b>0,39</b>	<b>0,91</b>				

**Table 5** List of plausible models performed with multi-model inference for landscape composition in 250 m buffer. he estimates are reported: the intercept (Int), the variables considered in each model (crp\_250 = percentage of surface area occupied by crops; prm\_250 = percentage of surface area occupied by permanent crops; stt\_250 = percentage of surface area occupied by settlements),  $R^2$ , AIC,  $\Delta AIC$  and model weight (wi). Relative Variable Importances values and significance are shown in bold.

(Int)	crp_250	prm_250	stt_250	spcs	crp_250:spcs	prm_250:spcs	stt_250:spcs	$R^2$	AIC	delta	weight
32.16		0.96	-0.46	+		+		0.36	345.3	0	0.29
27.81		1.01		+		+		0.30	345.3	0.06	0.28
34.72		0.92	-0.73	+		+	+	0.37	345.6	0.38	0.24
90.76	-0.77		-1.4	+	+		+	0.38	346	0.75	0.20
	<b>0.44</b>	<b>0.8 *</b>	<b>0.72</b>	<b>1</b>	<b>0.28</b>	<b>0.71 *</b>	<b>0.43</b>				

RVI value ( $>0.7$ ), with the exception of the PSI (and its interaction with the species). The most important, albeit not statistically significant, was PSI and its interaction with species ( $RVI > 0.91$ ). Models explained between 6 and 26% of the total variation in small mammals abundance.

### Landscape composition

The analysis was conducted for both 500 m and 250 m radius buffers.

Using landscape composition variables in 250 m buffers, four models were supported (Table 5). These models included crop percentage, permanent crop percentage, and settlement percentage. The most important variable was the percentage of permanent crops and its interaction with species ( $RVI > 0.70$ ;  $p = 0.05$ ). Settlement percentage was also important among models ( $RVI = 0.72$ ), but not statistically significant.

Considering landscape composition variables within 500 m buffers, three models were supported (Table 6). These models included crop percentage, permanent crop percentage, and settlement percentage. The most important variable was the percentage of permanent crops and its interaction with species ( $RVI > 0.89$ ;  $p = 0.05$ ).

### Overall model

The multi-model inference applied to the selected variables from each environment structural level (overall model) showed one supported model both in 250 m and 500 m

**Table 6** List of plausible models performed with multi-model inference for landscape composition in 500 m buffer. The estimates are reported: the intercept (Int), the variables considered in each model (crp\_500 = percentage of surface area occupied by crops; prm\_500 percentage of surface area occupied by permanent crops; stt\_500 = percentage of surface area occupied by settlements),  $R^2$ , AIC,  $\Delta AIC$  and model weight (wi). Relative Variable Importances values and significance are shown in bold.

(Int)	crp_500	prm_500	stt_500	spcs	crp_500:spcs	prm_500:spcs	stt_500:spc	$R^2$	AIC	delta	weight
24,08		1,25		+		+		0,31	343,9	0	0,25
29,18		1,14	-0,38	+		+		0,35	344,8	0,95	0,15
0,96	0,34	1,49		+		+		0,34	345,1	1,26	0,13
	<b>0,47</b>	<b>0,94*</b>	<b>0,51</b>	<b>1</b>	<b>0,21</b>	<b>0,89*</b>	<b>0,21</b>				

**Table 7** List of plausible models performed with multi-model inference in 250 m buffer. The estimates are reported: the intercept (Int), the variables considered in each model (prm\_250 = percentage of surface area occupied by permanent crops; spcs = species; und = undecomposed litter percentage),  $R^2$ , AIC,  $\Delta AIC$  and model weight (wi). Relative Variable Importances values and significance are shown in bold.

(Int)	prm_250	spcs	und	prm_250:spcs	spcs:und	$R^2$	AIC	delta	weight
20,68	0,1873	+	-0,267	+	+	0,56	214,8	0	0,748
	<b>0,73***</b>	<b>0,91.</b>	<b>0,81***</b>	<b>0,7***</b>	<b>0,75***</b>				

**Table 8** List of plausible models performed with multi-model inference in 500 m buffer. The estimates are reported: the intercept (Int), the variables considered in each model (prm\_500 = percentage of surface area occupied by permanent crops; spcs = species; und = undecomposed litter percentage),  $R^2$ , AIC,  $\Delta AIC$  and model weight (wi). Relative Variable Importances values and significance are shown in bold.

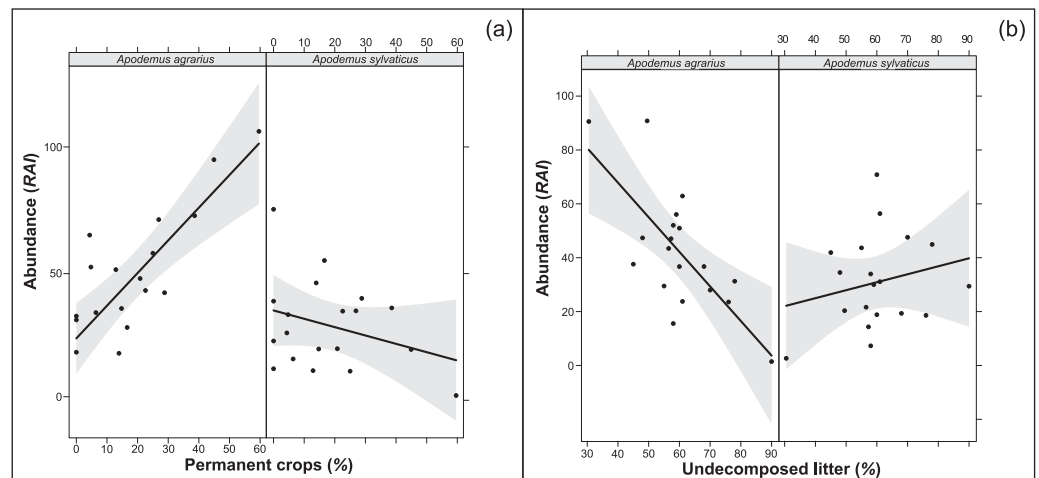
(Int)	prm_500	spcs	und	prm_500:spcs	spcs:und	$R^2$	AIC	delta	weight
101,5	1,267	+	-1,295	+	+	0,51	336,9	0	0,904
	<b>0,99***</b>	<b>1</b>	<b>0,97**</b>	<b>0,98**</b>	<b>0,91*</b>				

buffers (Tables 7, 8). The models confirmed the importance of the extension of permanent crops and the undecomposed litter layer, highlighting a significant interaction of the study species with the variables ( $p < 0.001$ ;  $RVI > 0.7$ ). In particular, where the landscape had a higher percentage of permanent crops, the abundance of *A. agrarius* increased, whereas the abundance of *A. sylvaticus* decreased (Fig. 1A). Instead, an increase of undecomposed litter favors *A. sylvaticus*, decreasing the abundance of *A. agrarius* (Fig. 1B). The models including variables within the 250 and 500 m buffers explained respectively 56 and 51% of the total variation in small mammals abundance.

## DISCUSSION

Our findings shed new light on the interplay between different ecological scales in determining small mammals abundance and distribution. We found species with different ecological niches to differ significantly in landscape and habitat features, suggesting the occurrence of alternative strategies for species coexisting in fragmented forest patches in agricultural landscapes.

Considering the contribution of each variable group and their selection, we found both landscape composition and microhabitat features to significantly affect species abundance, with contrasting species responses. On the contrary, wood structure did not directly influence the abundance of the two studied species, not confirming previous studies



**Figure 1** Relationships between population abundance, species and their interactions with environmental variables (A: permanent crops; B: undecomposed litter). Relationships between population abundance, species and their interactions with environmental variables, calculated with the best fitting model chosen within Multi-model inference. (A) Permanent crops. (B) Undecomposed litter. Permanent crops = proportion of area covered by permanent crops (poplars, orchards) in buffer area of 250 m around the sampling plot; undecomposed litter = mean percentage of undecomposed litter in the litter stratum. Confidence intervals (95%) are also shown.

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evidencing significant relationships between abundance of small mammal forest species and forest tree density (Capizzi & Santini, 2007) and size (Capizzi, Battistini & Amori, 2003). Albeit not significant, our results also highlighted positive relationships between small mammal abundance and tree density, as well as number of tree species and number of shrub species, that could be interpreted as direct relationship with the complexity of the ecological niche. Several studies reported a strong relationship between deadwood abundance and the presence of small mammals. In fact, deadwood represents a source of potential shelters and hosts large invertebrate communities which are potential sources of food (Amori et al., 2015; Bellocq & Smith, 1997; Bowman et al., 2000; Harmon et al., 1986; Kemper & Bell, 1985; McCay, 2000; Miller & Getz, 1977; Szymański et al., 2020; Tallmon & Mills, 1994; Yahner, 1986). Several studies also indicate that the decay stage may be important in habitat selection of small mammals (Bowman et al., 2000; McCay, 2000). Availability of understory cover is also a key condition for small mammals (Barry, Botje & Grantham, 1984; Bellocq & Smith, 1997; Carey & Harrington, 2001; Cox, Dickman & Cox, 2000; Marsh & Harris, 2000; Simonetti, 1989). Probably its importance is connected with food availability and the related possibility to reduce either the areas of predation (Bellocq & Smith, 1997; Miller & Getz, 1977; Simonetti, 1989) or the competition, by expanding the available space (Montgomery, 1980). Regarding microhabitat structure, the bare soil cover, presence of deadwood and litter structure are known to affect small mammal populations (Amori et al., 2015; Cox, Dickman & Cox, 2000; Denny et al., 2021; Kemper & Bell, 1985; Marsh & Harris, 2000; Simonetti, 1989; Yahner, 1986). Our results confirmed these findings, but highlighted the pivotal role of the litter decomposition stage. Litter

decomposition rate is driven by environmental conditions, chemical composition of soil and intensity of soil organism activity (Aerts, 1997; Harmon *et al.*, 1986).

The speed and degree of degradation of leaves depends mainly on the species of tree (He *et al.*, 2019; Mathews & Kowalczewski, 1969; Nykvist, 1962) and other environmental variables such as temperature and humidity. In addition, the presence of large invertebrates such as earthworm, millipedes and other taxa is also relevant, enhancing the degradation of organic matter (Bocock, 1964; Mathews & Kowalczewski, 1969; Tresch *et al.*, 2019). The dynamics of the soil degradation process is connected to invertebrate biodiversity: well developed temperate woodland soils can host up to a hundred species of animals (Anderson, 1975; Tresch *et al.*, 2019). Moreover, leaf litter quality affects numerous trophic levels such as insects, other invertebrates (Koivula *et al.*, 1999; Sabo, Soykan & Keller, 2005) and small mammals (Canova & Fasola, 1991; Hansson, 1978; Kaminski *et al.*, 2007). Litter cover affects the use of habitat by black rats (Cox, Dickman & Cox, 2000), which spend most of the time foraging on the ground, probably obtaining food from the litter (Cox, Dickman & Cox, 2000).

A dense litter cover would produce suitable mesic conditions in soil and litter ensuring appropriate microenvironments for litter-dwelling arthropods used as food (Yahner, 1986). Wood mice catch and find invertebrate prey, which are an important source of food, under litter cover (Piper, Lewis & Compton, 2014). The microclimate conditions of the litter can influence movements of small mammals, whom sounds are more difficult to hear in moist than in dry litter, influencing predation (Vickery & Bider, 1981). Predation risk is considered one of the most important factors determining selection of microhabitat in small mammals (Bellocq & Smith, 1997; Fragoso, Santos-Reis & Rosalino, 2020; Simonetti, 1989).

Despite this evidence, we found a different interaction of the two considered species with the environment conditions. In fact, abundance of *A. agrarius* was inversely related with the percentage of undecomposed litter, while the opposite trend was observed in *A. sylvaticus*.

Probably *A. agrarius* is more dependent on litter quality because it generally avoids xeric conditions, as reported by Yahner (1986) for other species in relation to the moisture of the habitat. This species is known to prefer habitats with dense soil cover and it usually moves through the litter stratum because of its fossorial behaviour (Kuncová & Frynta, 2009), probably to escape predators (Orlandi & Paolucci, 2004).

On the contrary, *A. sylvaticus* occurs in both woody and in open habitats (Heroldová *et al.*, 2007) avoiding cut crops or cut set aside (Tattersall *et al.*, 2001) and bare soil (Tew, Todd & Macdonald, 2000), showing this species is poorly influenced by the structure of litter, in disagreement with what is reported in other studies (e.g., Balestrieri *et al.*, 2017).

Moreover, *A. sylvaticus* is apparently not affected by wood characteristics probably because this ubiquitous species prefers the diversity of the complex mosaic created by agricultural landscape rather than the continuous forest habitat (Geuse, Bauchau & Boulengé, 1985; Kozakiewicz *et al.*, 1999).

It is well known that composition of landscape can influence the population dynamics of small mammals (Fischer & Schröder, 2014; Silva, Hartling & Opps, 2005). Our results

confirmed this evidence pointing out the positive role of some non-natural habitats (*i.e.*, permanent crops) in agreement with what was found in other studies ([Fitzgibbon, 1997](#); [Macdonald et al., 2007](#); [Tattersall et al., 1999](#); [Vieira et al., 2009](#)). Even though some studies showed small mammal abundances to be related with landscape structure ([Fischer, Thies & Tscharrntke, 2011](#); [Kozakiewicz et al., 1999](#); [Macdonald et al., 2007](#); [Van Apeldoorn et al., 1992](#); [Vieira et al., 2009](#)), in our study, no significant relationship emerged considering landscape configuration. We observed a positive relationship between the abundance of *A. agrarius* and the presence of permanent crops, despite the percentage of natural woods was relatively low in the studied area (ca. 8% on average). This result suggests that permanent woody crops, such as poplars and orchards, may be important habitats for the study species, especially if placed in the surroundings of woodlots, offering canopy cover and in some cases a dense leaf litter. On the contrary, we did not observe such strong relation for *A. sylvaticus*, which seems less influenced by the presence of permanent crops in the landscape but with a negative relationship. It seems that *A. sylvaticus* in Mediterranean areas uses mostly nests positioned far away from orchards, probably to avoid predation ([Rosalino et al., 2011](#)), although other studies show that the species is quite common in poplar plantations ([Balestrieri et al., 2017](#)) and orchards ([Dickman & Doncaster, 1987](#)).

The differences found for the two species could be linked to their ecological requirements.

Our results suggest that *A. agrarius*, a species connected to the presence of wood mosaic, uses permanent plantations in highly modified landscapes probably as surrogate of forest habitats. The abundance of this species was negatively related with the amount of arable land so that it becomes absent in very simplified landscapes ([Fischer, Thies & Tscharrntke, 2011](#)). Then, permanent crops could become an important secondary habitat for this rodent in intensive agricultural landscapes.

*A. sylvaticus*, instead, has a broad ecological niche and can exploit many different habitats ([Halle, 1993](#); [Michel, Burel & Butet, 2006](#)), such as fallow lands ([Heroldová et al., 2007](#); [Macdonald et al., 2007](#)) and crops (see for instance [Tattersall et al., 2001](#)). This species has high dispersal abilities ([Marsh & Harris, 2000](#)) and is supposed to have higher abilities to navigate in crops ([Sozio, Mortelliti & Boitani, 2013](#)).

In cultivated landscapes, *A. sylvaticus* moves from hedgerows to crop fields according to seasons ([Ouin et al., 2000](#)). At the time of the crop, wood mice massively overrun the fields and remain there until the time of ploughing ([Heroldová et al., 2007](#)); during winter more mice are found in field edges than in the center of fields, and when the crop are cut down they prefer hedgerows, woodland edges ([Macdonald et al., 2000](#); [Tattersall et al., 2001](#)), woods and fallow lands ([Tew & Macdonald, 1993](#)). This allowed them, to avoid predation, which can bring high rates of mortality ([Tew & Macdonald, 1993](#)). The wood mouse is therefore well represented in intensified sites because it certainly benefits from landscape heterogeneity as it can find and exploit many resources ([Michel, Burel & Butet, 2006](#)). As observed by [Bellows, Pagels & Mitchell \(2001\)](#) for other rodent species, the lack of relations between the species and microhabitat characteristic is probably because of its ability to exploit a variety of sources.

We did not observe significant relationships between species abundance and percentage of settlements in the surroundings, within the considered buffers. This fact may be

interpreted as the low presence of urban areas, reduced in the study sites to a few scattered agglomerates of buildings (ca 8.5% in a 500 m buffer).

## CONCLUSIONS

Our findings revealed that, in the study areas, landscape composition rather than landscape configuration significantly affect small mammals species in the considered agricultural landscapes, which, along with microhabitat features and species interaction, drives species abundance.

Our results showed that composition of agricultural landscapes is not perceived by all species in the same way. Species respond to each ecological scale in relation to their own ecological requirements, spatial behaviors, mobility, and dependency on habitat (Kozakiewicz *et al.*, 1999; Serafini, Priotto & Gomez, 2019). The maintenance of wider woodlots (or hedgerows) is, hence, necessary for several aims, as: (i) protecting wildlife species with different ecological needs, (ii) maintaining/enhancing habitat continuity, and (iii) avoiding structure simplification (Dondina *et al.*, 2016). Functional connectivity among habitat patches is proven to be one of the most important factors affecting the presence of small mammals in urban areas (Fitzgibbon, Putland & Goldizen, 2007) but also matrix composition and management is fundamental since forest species can cross agricultural surroundings (Mortelliti *et al.*, 2013; Paise, Vieira & Prado, 2020). Our results showed that the presence of anthropogenic habitats in the landscape with plausible landscape connectivity functions (such as permanent plantations) can also affect small mammals.

Studies have been carried on connectivity in the agricultural matrix, but the effect of forest plantations on functional connectivity has received limited attention (Mortelliti, Westgate & Lindenmayer, 2014).

Permanent tree crops, especially those aimed at producing woody biomass, have a negative effect on biodiversity when they replace native forest vegetation (Brockerhoff *et al.*, 2008; Greene, Martin & Wigley, 2019). It is already commonly believed that their effect may have less impact than that of the agricultural matrix, since they are working as a semi-permeable barrier for organisms, representing a compromise between maintaining the economic value of an area and reducing the effect of habitat fragmentation, increasing connectivity (Norton, 1998; Brockerhoff *et al.*, 2008; Vanbeveren & Ceulemans, 2019). Landscape connectivity as well as the habitat function, could greatly increase if management rules are properly applied (Norton, 1998; Lindenmayer, Hobbs & Salt, 2003; Zitzmann, Reich & Schaarschmidt, 2021). This process may guarantee, for example, the permanence of mature plants within plantations (Hanowski, Niemi & Christian, 1997) or increase the shrub and herbaceous layers (Moser *et al.*, 2002), whose positive effect on small mammals is already known (Balestrieri *et al.*, 2017). Even the understory cover and litter can promote biodiversity, if they are not completely eliminated (Christian *et al.*, 1997; Christian *et al.*, 1998; Moser *et al.*, 2002; Vanbeveren & Ceulemans, 2019).

Our results showed that several properties of agricultural land mosaics had a strong influence on small mammal abundance, and all of them are within the reach of farmers

management. In this study, we get new insight to support the concept of ‘wildlife-friendly farming’ (Fischer *et al.* 2014), which emphasizes the ecological interactions of farmed and unfarmed coexisting areas and the improvement of natural and cultivated areas as strategy for an agricultural landscape management aimed to increasing biodiversity. This would contribute to the implementation of policy for the conservation of agricultural landscape at local and regional scales, and to farm landscape design.

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### Competing Interests

The authors declare there are no competing interests.

### Author Contributions

- Luca Dorigo conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
- Francesco Boscutti conceived and designed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
- Maurizia Sigura conceived and designed the analyzed landscape data, or reviewed drafts of the paper, and approved the final draft.

### Animal Ethics

The following information was supplied relating to ethical approvals (i.e., approving body and any reference numbers):

Trapping activities were authorized by the Italian Institute for Environmental Protection and Research (ISPRA) (Aut. PG/IR Rif. Int. 26358-28967/2013) and by the Friuli Venezia Giulia region (Aut. Prot. SCPA/12.5/17552-2013).

### Data Availability

The following information was supplied regarding data availability:

The raw data are available in the [Supplementary File](#).

### Supplemental Information

Supplemental information for this article can be found online at <http://dx.doi.org/10.7717/peerj.12306#supplemental-information>.



## REFERENCES

- Aerts R.** 1997. Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. *Oikos* **79**(3):439–449 DOI 10.2307/3546886.
- Akaike H.** 1973. Information theory and an extension of the maximum likelihood principle. In: Csáki F, Petrov BN, eds. *Proceedings of the 2nd International symposium on information theory*. Akadémiai Kiadó, Budapest, Hungary, 267–281.
- Amori G, Luiselli L, Milana G, Casula P.** 2015. Small scale factors affect population size of the wood mouse (*Apodemus sylvaticus*) in a mediterranean island (Sardinia). *Revue D'Ecologie (Terre Et Vie)* **70**(1):58–69.
- Anderson JM.** 1975. Succession, diversity and trophic relationships of some soil animals in decomposing leaf litter. *The Journal of Animal Ecology* **44**:475–495 DOI 10.2307/3607.
- Babinska-Werka J.** 1981. Food of the striped field mouse in different types of urban Green Areas. *Acta Theriologica* **26**(17):285–299 DOI 10.4098/AT.arch.81-24.
- Babińska-Werka J, Garbarczyk H.** 1981. Animal component of diet of striped field mouse under urban conditions. *Acta Theriologica* **26**:301–318 DOI 10.4098/AT.arch.81-25.
- Balestrieri A, Remonti L, Morotti L, Saino N, Prigioni C, Guidali F.** 2017. Multilevel habitat preference of *Apodemus sylvaticus* and *Clethrionomys glareolus* in an intensively cultivated agricultural landscape. *Ethology Ecology and Evolution* **29**(1):38–53 DOI 10.1080/03949370.2015.1077893.
- Barry RE, Botje MA, Grantham LB.** 1984. Vertical stratification of *Peromyscus leucopus* and *Peromyscus maniculatus* in southwestern Virginia. *Journal of Mammalogy* **65**:145–148 DOI 10.2307/1381217.
- Bartón K.** 2016. MuMIn: multi-model inference. R package version, 1.15.6. Available at <https://CRAN.R-project.org/package=MuMIn>.
- Batáry P, Báldi A, Ekroos J, Gallé R, Grass I, Tschardt T.** 2020. Biologia Futura: landscape perspectives on farmland biodiversity conservation. *Biologia Futura* **71**:9–18 DOI 10.1007/s42977-020-00015-7.
- Bauchau V, Le Boulengé E.** 1991. Population biology of woodland rodents in a patchy landscape. In: Le Berre M, Le Guelte L, eds. *Le Rongeur et l'Espace*. R. Chabaud, Paris: 275–283.
- Bellocq MI, Smith SM.** 1997. Microhabitat preferences of *Peromyscus maniculatus* (Rodentia, Cricetidae) in young pine plantations in the Canadian boreal forest. *Ecología Austral* **7**:57–64.
- Bellows S, Pagels JF, Mitchell JC.** 2001. Macrohabitat and microhabitat affinities of small mammals in a fragmented landscape on the upper Coastal Plain of Virginia. *The American Midland Naturalist* **146**(2):345–360 DOI 10.1674/0003-00312001.146%5B0345:MA
- Benayas JMR, Bullock JM, Newton AC.** 2008. Creating woodland islets to reconcile ecological restoration, conservation, and agricultural land use. *Frontiers in Ecology and the Environment* **6**(6):329–336 DOI 10.1890/070057.

- Benton TG, Vickery J, Wilson JD. 2003.** Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology and Evolution* **18**(4):182–188  
DOI [10.1016/S0169-5347\(03\)00011-9](https://doi.org/10.1016/S0169-5347(03)00011-9).
- Bianchi L, Brovelli M, Maltoni A, Calamini G. 2013.** Confronto tra metodologie di stima della necromassa legnosa in un ceduo invecchiato di leccio. *Forest@* **10**:34–42  
DOI [10.3832/efor0795-010](https://doi.org/10.3832/efor0795-010).
- Biber P, Borges JG, Moshhammer R, Barreiro S, Botequim B, Brodrechtova Y, Brukas V, Chirici G, Cordero-Debets R, Corrigan E, Eriksson LO, Favero M, Galev E, Garcia-Gonzalo J, Hengeveld G, Kavaliauskas M, Marchetti M, Marques S, Mozgeris G, Navrátil R, Nieuwenhuis M, Orazio O, Paligorov I, Pettenella D, Sedmák R, Smreček R, Stanislovaitis A, Tomé M, Trubins R, Tuček J, Vizzarri M, Wallin I, Pretzsch H, Sallnäs O. 2015.** How sensitive are ecosystem services in European forest landscapes to silvicultural treatment? *Forests* **6**(5):1666–1695 DOI [10.3390/f6051666](https://doi.org/10.3390/f6051666).
- Bocock KL. 1964.** Changes in the amounts of dry matter, nitrogen, carbon, and energy in decomposing woodland leaf litter in relation to the activities of the soil fauna. *Journal of Ecology* **52**(2):273–284 DOI [10.2307/2257595](https://doi.org/10.2307/2257595).
- Bogdziewicz M, Crone EE, Zwolak R. 2020.** Do benefits of seed dispersal and caching by scatterhoarders outweigh the costs of predation? An example with oaks and yellow-necked mice. *Journal of Ecology* **108**(3):1009–1018 DOI [10.1111/1365-2745.13307](https://doi.org/10.1111/1365-2745.13307).
- Bowman J, Sleep D, Forbes GJ, Edwards M. 2000.** The association of small mammals with coarse woody debris at log and stand scales. *Forest Ecology and Management* **129**:119–124 DOI [10.1016/S0378-1127\(99\)00152-8](https://doi.org/10.1016/S0378-1127(99)00152-8).
- Bricker M, Pearson D, Maron J. 2010.** Small-mammal seed predation limits the recruitment and abundance of two perennial grassland forbs. *Ecology* **91**(1):85–92 DOI [10.1890/08-1773.1](https://doi.org/10.1890/08-1773.1).
- Brockerhoff EG, Jactel H, Parrotta JA, Quine CP, Sayer J. 2008.** Plantation forests and biodiversity: oxymoron or opportunity? *Biodiversity and Conservation* **17**:925–951 DOI [10.1007/s10531-008-9380-x](https://doi.org/10.1007/s10531-008-9380-x).
- Brown PR, Huth NI, Banks PB, Singleton GR. 2007.** Relationship between abundance of rodents and damage to agricultural crops. *Agriculture, Ecosystems & Environment* **120**:405–415 DOI [10.1016/j.agee.2006.10.016](https://doi.org/10.1016/j.agee.2006.10.016).
- Burel F, Butet A, Delettre YR, Millàn de la Peña N. 2004.** Differential response of selected taxa to landscape context and agricultural intensification. *Landscape and Urban Planning* **67**:195–204 DOI [10.1016/S0169-2046\(03\)00039-2](https://doi.org/10.1016/S0169-2046(03)00039-2).
- Burnham KP, Anderson DR. 2002.** *Model selection and multimodel inference: a practical information-theoretic approach*. New York: Springer.
- Butet A, Leroux ABA. 2001.** Effects of agriculture development on vole dynamics and conservation of Montagu's harrier in western French wetlands. *Biological Conservation* **100**:289–295 DOI [10.1016/S0006-3207\(01\)00033-7](https://doi.org/10.1016/S0006-3207(01)00033-7).
- Butet A, Paillat G, Delettre Y. 2006.** Seasonal changes in small mammal assemblages from field boundaries in an agricultural landscape of western France. *Agriculture, Ecosystems & Environment* **113**:364–369 DOI [10.1016/j.agee.2005.10.008](https://doi.org/10.1016/j.agee.2005.10.008).

- Caceres NC, Nápoli RP, Hannibal W. 2011.** Differential trapping success for small mammals using pitfall and standard cage traps in a savannah region of southwestern Brazil. *Mammalia* 75:45–52 DOI [10.1515/mamm.2010.069](https://doi.org/10.1515/mamm.2010.069).
- Cagnin M, Moreno S, Aloise G, Garofalo G, Villafuerte R, Gaona P, Cristaldi M. 1998.** Comparative study of Spanish and Italian terrestrial small mammals coenoses from different biotopes in Mediterranean peninsular tip regions. *Journal of Biogeography* 25:1105–1113 DOI [10.1046/j.1365-2699.1998.00248.x](https://doi.org/10.1046/j.1365-2699.1998.00248.x).
- Canova L, Fasola M. 1991.** Communities of small mammals in six biotopes of northern Italy. *Acta Theriologica* 36(1–2):73–86 DOI [10.4098/AT.arch.91-4](https://doi.org/10.4098/AT.arch.91-4).
- Canova L, Fasola M. 1993.** Food habits and trophic relationships of small mammals in six habitats of the northern Po plain (Italy). *Mammalia* 57(2):189–200 DOI [10.1515/mamm.1993.57.2.189](https://doi.org/10.1515/mamm.1993.57.2.189).
- Capizzi D, Battistini M, Amori G. 2003.** Effects of habitat fragmentation and forest management on the distribution of the edible dormouse *Glis glis*. *Acta Theriologica* 48:359–371 DOI [10.1007/BF03194175](https://doi.org/10.1007/BF03194175).
- Capizzi D, Bertolino S, Mortelliti A. 2014.** Rating the rat: global patterns and research priorities in impacts and management of rodent pests. *Mammal Review* 44(2):148–162 DOI [10.1111/mam.12019](https://doi.org/10.1111/mam.12019).
- Capizzi D, Santini L. 2007.** *I Roditori italiani. Ecologia, impatto sulle attività umane e sugli ecosistemi, gestione delle popolazioni*. Roma: Antonio Delfino Editore.
- Carey AB, Harrington CA. 2001.** Small mammals in young forest: implications for management for sustainability. *Forest Ecology and Management* 154:289–309 DOI [10.1016/S0378-1127\(00\)00638-1](https://doi.org/10.1016/S0378-1127(00)00638-1).
- Carvell C, Osborne JL, Bourke AFG, Freeman SN, Pywell RF, Heard MS. 2011.** Bumble bee species' responses to a targeted conservation measure depend on landscape context and habitat quality. *Ecological Applications* 21(5):1760–1771 DOI [10.1890/10-0677.1](https://doi.org/10.1890/10-0677.1).
- Christian DP, Collins PT, Hanowski JM, Niemi GJ. 1997.** Bird and small mammal use of short-rotation hybrid poplar plantations. *The Journal of Wildlife Management* 61:171–182 DOI [10.2307/3802426](https://doi.org/10.2307/3802426).
- Christian DP, Hoffman W, Hanowski JM, Niemi GJ, Beyea J. 1998.** Bird and mammal diversity on woody biomass plantations in North America. *Biomass and Bioenergy* 14(4):395–402 DOI [10.1016/S0961-9534\(97\)10076-9](https://doi.org/10.1016/S0961-9534(97)10076-9).
- Cox MPG, Dickman CR, Cox WG. 2000.** Use of habitat by the black rat (*Rattus rattus*) at North Head, New South Wales: an observational and experimental study. *Austral Ecology* 25:375–385 DOI [10.1046/j.1442-9993.2000.01050.x](https://doi.org/10.1046/j.1442-9993.2000.01050.x).
- Dainese M, Luna DI, Sitzia T, Marini L. 2015.** Testing scale-dependent effects of seminatural habitats on farmland biodiversity. *Ecological Applications* 25:1681–1690 DOI [10.1890/14-1321.1](https://doi.org/10.1890/14-1321.1).
- Dainese M, Montecchiari S, Sitzia T, Sigura M, Marini L. 2016.** High cover of hedgerows in the landscape supports multiple ecosystem services in Mediterranean cereal fields. *Journal of Applied Ecology* 54(2):380–388 DOI [10.1111/1365-2664.12747](https://doi.org/10.1111/1365-2664.12747).

- De Simone S, Sigura M, Boscutti F. 2017.** Patterns of biodiversity and habitat sensitivity in agricultural landscapes. *Journal of Environmental Planning and Management* **60**(7):1173–1192 DOI [10.1080/09640568.2016.1205971](https://doi.org/10.1080/09640568.2016.1205971).
- Decocq G, Andrieu E, Brunet J, Chabrerie O, De Frenne P, De Smedt P, Deconchat M, Diekmann M, Ehrmann S, Giffard B, Gorriz Mifsud E, Hansen K, Hermy M, Kolb A, Lenoir J, Liira J, Moldan F, Prokofieva I, Rosenqvist L, Varela E, Valdés A, Verheyen K, Wulf M. 2016.** Ecosystem services from small forest patches in agricultural landscapes. *Current Forestry Reports* **2**(1):30–44 DOI [10.1007/s40725-016-0028-x](https://doi.org/10.1007/s40725-016-0028-x).
- Denny KN, Bilodeau KN, Dumont CA, Olson ZH. 2021.** Separating effects of spatial location and microhabitat density on perceived predation risk in small mammals. *Acta Ethologica* **24**(2):79–85 DOI [10.1007/s10211-021-00365-y](https://doi.org/10.1007/s10211-021-00365-y).
- Dickman CR. 1999.** Rodent-ecosystem relationships: a review. In: Singleton GR, Leirs H, Hinds LA, eds. *Ecologically-based management of rodent pests. Re-evaluating our approach to an old problem*. vol. 59. Canberra: Australian Centre for International Agricultural Research, 113–133.
- Dickman CR, Doncaster CP. 1987.** The ecology of small mammals in urban habitats. I. Populations in a patchy environment. *Journal of Animal Ecology* **56**(2):629–640 DOI [10.2307/5073](https://doi.org/10.2307/5073).
- Dondina O, Kataoka L, Orioli V, Bani L. 2016.** How to manage hedgerows as effective ecological corridors for mammals: a two-species approach. *Agriculture, Ecosystems & Environment* **231**:283–290 DOI [10.1016/j.agee.2016.07.005](https://doi.org/10.1016/j.agee.2016.07.005).
- Dorigo L. 2018.** Eterogeneità del paesaggio agricolo e piccoli mammiferi in agroecosistemi: un approccio multiscala. PhD Thesis, University of Udine.
- Fahrig L. 2007.** Non-optimal animal movement in human-altered landscapes. *Functional Ecology* **21**:1003–1015 DOI [10.1111/j.1365-2435.2007.01326.x](https://doi.org/10.1111/j.1365-2435.2007.01326.x).
- Faraway JJ. 2005.** *Extending the linear model with r: generalized linear, mixed effects and nonparametric regression models*. CRC Press.
- Fischer C, Schröder B. 2014.** Predicting spatial and temporal habitat use of rodents in a highly intensive agricultural area. *Agriculture, Ecosystems & Environment* **189**:145–153 DOI [10.1016/j.agee.2014.03.039](https://doi.org/10.1016/j.agee.2014.03.039).
- Fischer C, Thies C, Tschardt T. 2011.** Small mammals in agricultural landscapes: opposing responses to farming practices and landscape complexity. *Biological Conservation* **144**:1130–1136 DOI [10.1016/j.biocon.2010.12.032](https://doi.org/10.1016/j.biocon.2010.12.032).
- Fischer J, Abson DJ, Butsic V, Chappell MJ, Ekroos J, Hanspach J, Kuemmerle T, Henrik G, Smith HG, von Wehrden H. 2014.** Land sparing versus land sharing: moving forward. *Conservation Letters* **7**(3):149–157 DOI [10.1111/conl.12084](https://doi.org/10.1111/conl.12084).
- Fitzgibbon CD. 1997.** Small mammals in farm woodlands: the effects of habitat, isolation and surrounding land-use patterns. *Journal of Applied Ecology* **34**(2):530–539 DOI [10.2307/2404895](https://doi.org/10.2307/2404895).
- Fitzgibbon SI, Putland DA, Goldizen AW. 2007.** The importance of functional connectivity in the conservation of ground dwelling mammal in urban Australian landscape. *Landscape Ecology* **22**:1513–1525 DOI [10.1007/s10980-007-9139-x](https://doi.org/10.1007/s10980-007-9139-x).

- Fontana A. 2006.** *Evoluzione geomorfologica della bassa pianura friulana e sue relazioni con le dinamiche insediative antiche.* Udine: Ed. del Museo Friulano Di Storia Naturale.
- Fox J, Weisberg S. 2011.** *An R companion to applied regression.* 2nd edn. Thousand Oaks, CA, USA: SAGE Publications.
- Fragoso R, Santos-Reis M, Rosalino LM. 2020.** Drivers of wood mouse body condition in Mediterranean agroforestry landscapes. *European Journal of Wildlife Research* 66(1):1–11 DOI 10.1007/s10344-019-1356-5.
- Fuentes-Montemayor E, Ferryman M, Watts K, Macgregor NA, Hambly N, Brennan S, Coxon R, Langridge H, Park KJ. 2020.** Small mammal responses to long-term large-scale woodland creation: the influence of local and landscape-level attributes. *Ecological Applications* 30(2):e02028 DOI 10.1002/eap.2028.
- Geiger F, Bengtsson J, Berendse F, Weisser WW, Emmerson M, Morales MB, Ceryngier P, Liira J, Tsharntke T, Winqvist C, Eggers S, Bommarco R, Pärt T, Bretagnolle V, Plantegenest M, Clement LW, Dennis C, Palmer C, Oñate JJ, Guerrero I, Hawro V, Aavik T, Thies C, Flohre A, Hänke S, Fischer C, Goedhart PW, Inchausti P. 2010.** Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland. *Basic and Applied Ecology* 11(2):97–105 DOI 10.1016/j.baae.2009.12.001.
- Gelling M, Macdonald DW, Mathews F. 2007.** Are hedgerows the route to increased farmland small mammal density? Use of hedgerows in British pastoral habitats. *Landscape Ecology* 22(7):1019–1032 DOI 10.1007/s10980-007-9088-4.
- Gentili S, Sigura M, Bonesi L. 2014.** Decreased small mammals species diversity and increased population abundance along a gradient of agricultural intensification. *Hystrix* 25(1):39–44 DOI 10.4404/hystrix-25.1-9246.
- Geuse P, Bauchau V, Le Boulengé E. 1985.** Distribution and population dynamics of bank voles and wood mice in a patchy woodland habitat in central Belgium. *Acta Zoologica Fennica* 173:65–68.
- Gliwicz J, Taylor JR. 2002.** Comparing life histories of shrews and rodents. *Acta Theriologica* 47(1):185–208 DOI 10.1007/BF03192487.
- Greene R, Martin JA, Wigley TB. 2019.** 1 Short-rotation woody crops and wildlife conservation. In: Moorman CE, Grodsky SM, Rupp S, eds. *Renewable energy and wildlife conservation. Renewable energy and wildlife conservation, 13,* Baltimore, Maryland: JHU Press.
- Halle S. 1993.** Wood mice (*Apodemus sylvaticus* L.) as pioneers of recolonization in a reclaimed area. *Oecologia* 94:120–127 DOI 10.1007/BF00317312.
- Hanowski JM, Niemi GJ, Christian DC. 1997.** Influence of within-plantation heterogeneity and surrounding landscape composition on avian communities in hybrid poplar plantations. *Conservation Biology* 11(4):936–944 DOI 10.1046/j.1523-1739.1997.96173.x.
- Hansson L. 1978.** Small mammal abundance in relation to environmental variables in three Swedish forest phases. *Studia Forestalia Suecica* 147:1–40.
- Hansson L. 1985.** The food of bank voles, wood mice and yellow-necked mice. *Symposium of the Zoological Society of London* 55:141–168.

- Harmon ME, Franklin JF, Swanson FJ, Sollins P, Gregory SV, Lattin JD, Anderson NH, Cline SP, Aumen NG, Sedell JR, Lienkaemper GW, Cromack K, Cummins KW. 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research* 15:133–302 DOI 10.1016/S0065-2504(08)60121-X.
- Harmon ME, Sexton J. 1996. Guidelines for measurements of woody detritus in forest ecosystems. Publ. 20, US. Longterm Ecological Research Network Office, University of Washington, Seattle, USA.
- He W, Ma Z, Pei J, Teng M, Zeng L, Yan Z, Huang Z, Zhou Z, Wang P, Luo X, Xiao W. 2019. Effects of predominant tree species mixing on lignin and cellulose degradation during leaf litter decomposition in the Three Gorges Reservoir, China. *Forests* 10(4):360 DOI 10.3390/f10040360.
- Heroldová M, Bryja J, Zejda J, Tkadlec E. 2007. Structure and diversity of small mammal communities in agriculture landscape. *Agriculture, Ecosystems & Environment* 120:206–210 DOI 10.1016/j.agee.2006.09.007.
- Kaminski JR, Davis ML, Kelly M, Keyser PD. 2007. Disturbance effects on small-mammal species in a managed Appalachian forest. *American Midland Naturalist* 157:385–397 DOI 10.1674/0003-00312007.157[385:DEOSMS]2.0.CO;2.
- Kemper C, Bell DT. 1985. Small mammals and habitat structure in lowland rain forest of Peninsular Malaysia. *Journal of Tropical Ecology* 1(01):5–22 DOI 10.1017/S0266467400000043.
- Klaa K, Mill PJ, Incoll LD. 2005. Distribution of small mammals in a silvoarable agroforestry system in Northern England. *Agroforestry Systems* 63:101–110 DOI 10.1007/s10457-004-1110-0.
- Kleijn D, Rundlöf M, Scheper J, Smith HG, Tschardt T. 2011. Does conservation on farmland contribute to halting the biodiversity decline? *Trends in Ecology and Evolution* 26(9):474–481 DOI 10.1016/j.tree.2011.05.009.
- Koivula M, Punttila P, Haila Y, Niemela J. 1999. Leaf litter and the small-scale distribution of carabid beetles (Coleoptera, Carabidae) in the boreal forest. *Ecography* 22:424–435 DOI 10.1111/j.1600-0587.1999.tb00579.x.
- Korpimäki E, Norrdahl K. 1991. Numerical and functional responses of kestrels, short-eared owls, and long-eared owls to vole densities. *Ecology* 72:814–826 DOI 10.2307/1940584.
- Kozakiewicz M, Gortat T, Kozakiewicz A, Barkowska M. 1999. Effects of habitat fragmentation on four rodent species in a Polish farm landscape. *Landscape Ecology* 14(4):391–400 DOI 10.1023/A:1008070610187.
- Kuncová P, Frynta D. 2009. Interspecific morphometric variation in the postcranial skeleton in the genus *Apodemus*. *Belgian Journal of Zoology* 139(2):133–146.
- Laundré JW, Reynolds TD. 1993. Effects of soil structure on burrow characteristics of five small mammal species. *The Great Basin Naturalist* 53(4):358–366.
- Lindenmayer DB, Hobbs RJ, Salt D. 2003. Plantation forests and biodiversity conservation. *Australian Forestry* 66(1):62–66 DOI 10.1080/00049158.2003.10674891.

- Liro A, Szacki J. 1987.** Movements of field mice *Apodemus agrarius* (Pallas) in a suburban mosaic of habitats. *Oecologia* **74**(3):438–440 DOI [10.1007/BF00378942](https://doi.org/10.1007/BF00378942).
- Macdonald DW, Tattersall FH, Service KM, Firbank LG, Feber RE. 2007.** Mammals, agri-environment schemes and set-aside—what are the putative benefits? *Mammal Review* **37**(4):259–277 DOI [10.1046/j.1440-1770.2002.00172\\_37\\_4.x](https://doi.org/10.1046/j.1440-1770.2002.00172_37_4.x).
- Macdonald DW, Tew TE, Todd IA, Garner JP, Johnson PJ. 2000.** Arable habitat use by wood mice (*Apodemus sylvaticus*) 3. A farm-scale experiment on the effects of crop rotation. *Journal of Zoology* **250**(3):313–320 DOI [10.1111/j.1469-7998.2000.tb00775.x](https://doi.org/10.1111/j.1469-7998.2000.tb00775.x).
- Marsh ACW, Harris S. 2000.** Partitioning of woodland habitat resources by two sympatric species of *Apodemus*: lessons for the conservation of the yellow-necked mouse (*A. flavicollis*) in Britain. *Biological Conservation* **92**:275–283 DOI [10.1016/S0006-3207\(99\)00071-3](https://doi.org/10.1016/S0006-3207(99)00071-3).
- Martin SK. 1994.** Feeding ecology of American martens and fishers. In: Buskirk SW, Harestad AS, Raphael MG, Powell RA, eds. *Martens, sables, and fishers. Biology and conservation*. Ithaca and London: Comstock Publishing Association. Cornell University Press, 297–315.
- Mathews CP, Kowalczewski A. 1969.** The disappearance of leaf litter and its contribution to production in the river thames. *Journal of Ecology* **57**(2):543–552 DOI [10.2307/2258398](https://doi.org/10.2307/2258398).
- McCay TS. 2000.** Use of woody debris by cotton mice (*Peromyscus gossypinus*) in a southeastern pine forest. *Journal of Mammalogy* **81**(2):527–535 DOI [10.1644/1545-15422000.081j0527:UOWDBC;2.0.CO;2](https://doi.org/10.1644/1545-15422000.081j0527:UOWDBC;2.0.CO;2).
- McGarigal K, Cushman SA, Ene E. 2012.** FRAGSTATS v4: spatial pattern analysis program for categorical and continuous maps. Computer software program produced by the authors at the University of Massachusetts, Amherst..
- McGarigal K, Marks BJ. 1995.** Spatial pattern analysis program for quantifying landscape structure. Gen. Tech. Rep. PNW-GTR-351. US Department of Agriculture, Forest Service, Pacific Northwest Research Station.
- Michel N, Burel F, Butet A. 2006.** How does landscape use influence small mammal diversity, abundance and biomass in hedgerow networks of farming landscapes? *Acta Oecologica* **30**:11–20 DOI [10.1016/j.actao.2005.12.006](https://doi.org/10.1016/j.actao.2005.12.006).
- Miller DH, Getz LL. 1977.** Factors influencing local distribution and species diversity of forest small mammals in New England. *Canadian Journal of Zoology* **55**:806–814 DOI [10.1139/z77-105](https://doi.org/10.1139/z77-105).
- Montgomery WI. 1980.** The use of arboreal runways by the woodland rodents, *Apodemus sylvaticus* (L.), *A. flavicollis* (Melchior) and *Clethrionomys glareolus* (Schreber). *Mammal Review* **10**(4):189–195 DOI [10.1111/j.1365-2907.1980.tb00239.x](https://doi.org/10.1111/j.1365-2907.1980.tb00239.x).
- Mortelliti A, Santarelli L, Sozio G, Fagiani S, Boitani L. 2013.** Long distance field crossings by hazel dormice (*Muscardinus avellanarius*) in fragmented landscapes. *Mammalian Biology* **78**:309–312 DOI [10.1016/j.mambio.2012.09.006](https://doi.org/10.1016/j.mambio.2012.09.006).
- Mortelliti A, Westgate MJ, Lindenmayer DB. 2014.** Experimental evaluation shows limited influence of pine plantations on the connectivity of highly fragmented bird populations. *Journal of Applied Ecology* **51**(5):1179–1187 DOI [10.1111/1365-2664.12313](https://doi.org/10.1111/1365-2664.12313).

- Moser BW, Pipas MJ, Witmer GW, Engeman RM. 2002. Small mammal use of hybrid poplar plantations relative to stand age. *Northwest Science* 76(2):158–165.
- Norton DA. 1998. Indigenous biodiversity conservation and plantation forestry: options for the future. *New Zealand Forestry* 43:34–39.
- Nykvist N. 1962. Leaching and decomposition of litter. V. Experiments on Leaf Litter of *Alnus glutinosa*, *Fagus sylvatica* and *Quercus robur*. *Oikos* 13(2):232–248 DOI 10.2307/3565087.
- Orlandi A, Paolucci P. 2004. Biologia ed ecologia del topo selvatico dal dorso striato (*Apodemus agrarius*) (Mammalia, Muridae). *Ricerche Naturalistiche a Bosco Fontana - Quaderni Conservazione Habitat* 3:79–86.
- Ouin A, Paillat G, Butet A, Burel F. 2000. Spatial dynamics of Wood Mouse (*Apodemus sylvaticus*) in an agricultural landscape under intensive use in the Mont Saint Michel Bay (France). *Agriculture, Ecosystems & Environment* 78:159–165 DOI 10.1016/S0167-8809(99)00119-X.
- Paise G, Vieira EM, Prado PI. 2020. Small mammals respond to extreme habitat fragmentation in the Brazilian Atlantic Forest according to the landscape continuum model. *Mammal Research* 65(2):309–322 DOI 10.1007/s13364-019-00464-z.
- Palmeirim AF, Santos-Filho M, Peres CA. 2020. Marked decline in forest-dependent small mammals following habitat loss and fragmentation in an Amazonian deforestation frontier. *PLOS ONE* 15(3):e0230209 DOI 10.1371/journal.pone.0230209.
- Peña N Millàndela, Butet A, Delettre Y, Paillat G, Morant P, LeDu L, Burel F. 2003. Response of the small mammal community to changes in western French agricultural landscapes. *Landscape Ecology* 18:265–278 DOI 10.1023/A:1024452930326.
- Pearce J, Venier L. 2005. Small mammals as bioindicators of sustainable boreal forest management. *Forest Ecology and Management* 208(1):153–175 DOI 10.1016/j.foreco.2004.11.024.
- Pielou EC. 1975. *Ecology diversity*. New York: J. Wiley and Sons.
- Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team. 2017. nlme: Linear and nonlinear mixed effects models. R package version, 3.1-131. Available at <https://CRAN.R-project.org/package=nlme>.
- Piper RW, Lewis Z, Compton SG. 2014. Life in the leaf-litter: a novel metal detector technique to investigate the over-wintering survival of rare, case-bearing beetle larvae. *Journal of Insect Conservation* 18:1163–1169 DOI 10.1007/s10841-014-9727-4.
- Putman RJ. 1989. *Mammals as pests*. London: Chapman and Hall.
- Rosalino LM, Ferreira D, Leitao I, Santos-Reis M. 2011. Selection of nest sites by wood mice *Apodemus sylvaticus* in a Mediterranean agro-forest landscape. *Ecological Research* 26:445–452 DOI 10.1007/s11284-010-0797-9.
- Le Roux X, Barbault R, Baudry J, Burel F, Doussan I, Garnier E, Herzog F, Lavorel S, Lifran R, Roger-Estrade J, Sarthou J-P, Trommetter M. 2008. Agriculture et Biodiversité. Valoriser les Synergies. In: *Expertise scientifique collective*. France: synthèse du rapport, INRA.
- Sabo JL, Soykan CU, Keller A. 2005. Functional roles of leaf litter detritus in terrestrial food webs. In: De Ruiter P, Wolters V, Moore JC, Melville-Smith K, eds. *Dynamic*



- Food Webs. Multispecies Assemblages, Ecosystem Development, and Environmental Change. Volume 3. Theoretical Ecology Series*, London: Academic Press, 211–222.
- Salamolard M, Butet A, Leroux A, Bretagnolle V. 2000.** Responses of an avian predator to variations in prey density at a temperate latitude. *Ecology* **81**:2428–2441 DOI [10.1890/0012-96582000.081\[2428:ROAAPT\]2.0.CO;2](https://doi.org/10.1890/0012-96582000.081[2428:ROAAPT]2.0.CO;2).
- Šálek M, Kreisinger J, Sedláček F, Albrecht T. 2010.** Do prey densities determine preferences of mammalian predators for habitat edges in an agricultural landscape? *Landscape and Urban Planning* **98**(2):86–91 DOI [10.1016/j.landurbplan.2010.07.013](https://doi.org/10.1016/j.landurbplan.2010.07.013).
- Serafini VN, Priotto JW, Gomez MD. 2019.** Effects of agroecosystem landscape complexity on small mammals: a multi-species approach at different spatial scales. *Landscape Ecology* **34**(5):1117–1129 DOI [10.1007/s10980-019-00825-8](https://doi.org/10.1007/s10980-019-00825-8).
- Sieg CH. 1987.** Small Mammals: pest or Vital Components of the Ecosystem. VIII Wildlife Damage Control Workshop, 26–30 1987. Rapid City, South Dakota 88–92.
- Silva M, Hartling L, Opps SB. 2005.** Small mammals in agricultural landscapes of Prince Edward Island (Canada): effects of habitat characteristics at three different spatial scales. *Biological Conservation* **126**:556–568 DOI [10.1016/j.biocon.2005.07.007](https://doi.org/10.1016/j.biocon.2005.07.007).
- Silva M, Prince ME. 2008.** The conservation value of hedgerows for small mammals in Prince Edward Island, Canada. *The American Midland Naturalist* **159**(1):110–124 DOI [10.1674/0003-0031\(2008\)159\[110:TCVOHF\]2.0.CO;2](https://doi.org/10.1674/0003-0031(2008)159[110:TCVOHF]2.0.CO;2).
- Simonetti JA. 1989.** Microhabitat use by small mammals in central Chile. *Oikos* **56**:309–318 DOI [10.2307/3565615](https://doi.org/10.2307/3565615).
- Sozio G, Mortelliti A, Boitani L. 2013.** Mice on the move: wheat rows as a means to increase permeability in agricultural landscapes. *Biological Conservation* **165**:198–202 DOI [10.1016/j.biocon.2013.05.022](https://doi.org/10.1016/j.biocon.2013.05.022).
- Steele M, Wauters LA, Larsen KW. 2005.** Selection, predation and dispersal of seeds by tree squirrels in temperate and boreal forest: are tree squirrels keystone granivores? In: Lambert JE, Hulme PE, Vander Wall SB, eds. *Seed fate: predation, dispersal and seedling establishment*. Cambridge, MA: CABI Publishing, 205–221.
- Szymański CR, Alvarez JA, Campos CM, Tabeni S. 2020.** A first assessment of the land management effect on the ecological role of large trees as habitat refuges for desert small mammals. *Basic and Applied Ecology* **48**:136–145 DOI [10.1016/j.baae.2020.09.005](https://doi.org/10.1016/j.baae.2020.09.005).
- Tallmon D, Mills S. 1994.** Use of logs within home ranges of California red-backed voles on a remnant of forest. *Journal of Mammalogy* **75**(1):97–101 DOI [10.2307/1382240](https://doi.org/10.2307/1382240).
- Tattersall FH, Hart BJ, Manley WJ, Macdonald DW, Feber RE. 1999.** Does the method of set-aside establishment affect its use by wood mice? *Journal of Zoology* **249**:472–476 DOI [10.1111/j.1469-7998.1999.tb01218.x](https://doi.org/10.1111/j.1469-7998.1999.tb01218.x).
- Tattersall FH, Macdonald DW, Hart BJ, Manley WJ, Feber RE. 2001.** Habitat use by wood mice (*Apodemus agrarius*) in a changeable arable landscape. *Journal of Zoology* **255**:487–494 DOI [10.1017/S095283690100156X](https://doi.org/10.1017/S095283690100156X).
- Team RCore. 2021.** R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Available at <https://www.R-project.org/>.

- Tew TE, Macdonald DW. 1993.** The effects of harvest on arable wood mice *Apodemus sylvaticus*. *Biological Conservation* **65**:279–283 DOI [10.1016/0006-3207\(93\)90060-E](https://doi.org/10.1016/0006-3207(93)90060-E).
- Tew TE, Todd IA, Macdonald DW. 2000.** Arable habitat use by wood mice (*Apodemus sylvaticus*). 2. Microhabitat. *Journal of Zoology* **250**:305–311 DOI [10.1111/j.1469-7998.2000.tb00774.x](https://doi.org/10.1111/j.1469-7998.2000.tb00774.x).
- Tresch S, Frey D, Le Bayon RC, Zanetta A, Rasche F, Fliessbach A, Moretti M. 2019.** Litter decomposition driven by soil fauna, plant diversity and soil management in urban gardens. *Science of the Total Environment* **658**:1614–1629 DOI [10.1016/j.scitotenv.2018.12.235](https://doi.org/10.1016/j.scitotenv.2018.12.235).
- Tscharntke T, Klein AM, Kruess A, Steffan-Dewenter I, Thies C. 2005.** Landscape perspectives on agricultural intensification and biodiversity: ecosystem service management. *Ecology Letters* **8**:857–874 DOI [10.1111/j.1461-0248.2005.00782.x](https://doi.org/10.1111/j.1461-0248.2005.00782.x).
- Umetsu F, Naxara L, Pardini R. 2006.** Evaluating the efficiency of pitfall traps for sampling small mammals in the Neotropics. *Journal of Mammalogy* **87**(4):757–765 DOI [10.1644/05-MAMM-A-285R2.1](https://doi.org/10.1644/05-MAMM-A-285R2.1).
- Van Apeldoorn RC, Oostenbrink WT, Van Winden A, Van Der Zee FF. 1992.** Effects of habitat fragmentation on the bank vole, *Clethrionomys glareolus*, in an agricultural landscape. *Oikos* **65**(2):265–274 DOI [10.2307/3545018](https://doi.org/10.2307/3545018).
- Vanbeveren SP, Ceulemans R. 2019.** Biodiversity in short-rotation coppice. *Renewable and Sustainable Energy Reviews* **111**:34–43 DOI [10.1016/j.rser.2019.05.012](https://doi.org/10.1016/j.rser.2019.05.012).
- Vickery WL, Bider JR. 1981.** The influence of weather on rodent activity. *Journal of Mammalogy* **62**(1):140–145 DOI [10.2307/1380484](https://doi.org/10.2307/1380484).
- Vieira MV, Olifiers N, Delciellos AC, Antunes VZ, Bernardo LR, Grelle CEV, Cerqueira R. 2009.** Land use vs. fragment size and isolation as determinants of small mammal composition and richness in Atlantic Forest remnants. *Biological Conservation* **142**:1191–1200 DOI [10.1016/j.biocon.2009.02.006](https://doi.org/10.1016/j.biocon.2009.02.006).
- Warren WG, Olsen PF. 1964.** A line intersect technique for assessing logging waste. *Forest Science* **10**(3):20–26 DOI [10.1093/forestscience/10.3.267](https://doi.org/10.1093/forestscience/10.3.267).
- Yahner RH. 1986.** Microhabitat use by small mammals in even-aged forest stands. *American Midland Naturalist* **115**(1):174–180 DOI [10.2307/2425847](https://doi.org/10.2307/2425847).
- Zitzmann F, Reich M, Schaarschmidt F. 2021.** Potential of small-scale and structurally diverse short-rotation coppice as habitat for large and medium-sized mammals. *Biologia* **76**:1–12 DOI [10.1007/s11756-021-00686-0](https://doi.org/10.1007/s11756-021-00686-0).
- Zulian E. 1987.** Reperti sulla distribuzione e sulla biologia di *Apodemus agrarius* (Pallas) (Rodentia Muridae) nell'Italia nord-orientale. *Lavori Società Veneziana Scienze Naturali* **12**:133–147.
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM. 2009.** *Mixed effects models and extensions in ecology with R*. New York, NY, USA: Springer DOI [10.1111/1365-2745.13307](https://doi.org/10.1111/1365-2745.13307).