

Distribution and functional traits of small mammals across the Mediterranean area: landscape composition and structure definitively matter

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ABSTRACT

Mediterranean landscapes constitute a biodiversity hotspot where species distribution and composition have been shaped by a long history of traditional land use. In this work, we investigated the effects of landscape patterns on community composition and the functional, morphological, and ecological traits of 21 small mammal species in the Mediterranean region. We extracted species abundance and trait data from 86 georeferenced Common Barn-owl pellet sites collected in Central Italy, covering 33,000 km², and stored in the OpenMICE database. Additionally, we measured 12 landscape metrics on land cover maps produced at intervals coeval with pellet collection dates. We explored the variation in species composition against landscape pattern metrics using canonical correspondence analysis (CCA). Moreover, we analysed the relationships among small mammals' occurrence, their life history traits, and landscape pattern metrics using the fourth-corner model approach. Our results highlighted the key role of landscape composition and configuration in shaping small mammal species composition and their functional traits. Species and trait composition varied along two main landscape gradients, with a simplification of species assemblage towards increasing human pressure (i.e., artificial surfaces and agricultural areas) and decreasing cover of seminatural areas. The observed variability of species assemblages and functional traits across Mediterranean landscape gradients highlights the need to preserve diverse ecosystems and land cover types to maintain small mammal biodiversity and related ecosystem functioning.

1. Introduction

Human activities have modelled the world landscape since ancient times, affecting species distribution patterns and diversity. In Europe, natural landscapes have historically been altered through selective deforestation to gain space for grazing, agriculture activities, and timber extraction. These activities contributed to creating so-called “cultural landscapes” (*sensu* Antrop, 2005), which are characterised by complex mosaics of open areas and woodland patches (Frate and Carranza, 2013; Rosati et al., 2010) and usually host high levels of biodiversity (Amici et al., 2015; Assandri et al., 2018). During the last half-century, agricultural lands and traditional agricultural practices in mountain areas have been progressively abandoned, whereas intensive agricultural

activities have increased in the lowlands (Falcucci et al., 2007). While human pressure intensification drove to a drastic simplification of landscape mosaics, especially in plains and valleys (Carranza et al., 2007; Rocchini et al., 2006), the abandonment of mountain areas was followed by a partial regrowth of natural vegetation and recovery of wildlife diversity and abundance (Pereira and Navarro, 2015; Ricotta et al., 2000). For instance, Pereira and Navarro (2015) registered a substantial expansion of top predators (e.g., large carnivores, forest birds, some birds of prey) on European abandoned mountains, which in turn regulate prey population dynamics (e.g., small mammals). The relationship between landscape dynamics (e.g., land use intensification or abandonment) and biodiversity highlights the importance of planning tailored landscape management actions to achieve specific conservation

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goals (e.g., to preserve species and habitats of conservation concern for the EU Habitats Directive 1992/43/EEC or the Convention on Biological Diversity).

Small mammals are characterised by short life cycles and relatively narrow home ranges. Therefore, they are very sensitive to landscape characteristics and can be considered a valuable indicator of the relationship between land use and biodiversity (Love et al., 2000). Small mammals support several ecosystem processes (Barrett and Peles, 1999) and contribute to many important ecological mechanisms, such as seed and spore dispersal (Martin, 2003; Xiao et al., 2006), pollination (Melidonis and Peter, 2015), soil nutrient cycling (Fischer et al., 2018; Hayward and Phillipson, 1979), and energy flux regulation (Hurst et al., 2014; Pearce and Venier, 2005). Furthermore, the abundance and diversity of small mammals are considered good indicators of sustainable or unsustainable forest management (Mortelliti et al., 2009; Paniccia et al., 2018b). The importance of forests as reservoirs of animal diversity is the most relevant criterion driving sustainable forest management, as has already been assessed in the Mediterranean region (Di Febbraro et al., 2015). Well-structured and stratified forests could offer a variety of microhabitats, providing good levels of wildlife biodiversity (Gutierrez Garzon et al., 2021; Varma et al., 2000).

Functional traits represent morpho-physio-phenological characteristics that affect the fitness of individuals of a given species in a definite environmental context (e.g., growth, reproduction, and survival; Violle et al. 2007). Despite the importance of functional traits in providing early responses to climate and land use changes, as well as in linking species diversity to ecosystem functioning (Blaum et al., 2011; Munguía et al., 2016), their use has been widely neglected in most of the studies on small mammal communities. Consequently, a trait-based approach has been largely overlooked in national conservation strategies (Bertolino et al., 2015). Integrating the analysis of species functional traits into the classical description of taxonomic diversity can improve our understanding of both ecosystem functioning (Blaum et al., 2011; Cadotte et al., 2011; Vandewalle et al., 2010) and the interactions between species assemblages and landscape patterns (Newbold et al., 2020).

Previous studies have examined the relationship between the distribution of small mammal species and landscape composition in areas dominated by forests (Cianciaruso et al., 2018; Mortelliti et al., 2009), deserts (Alvarez Guevara and Ball, 2018; Sharp Bowman et al., 2017), and agroecosystems (Benedek and Sirbu, 2018; Fischer et al., 2018; Hurst et al., 2014). Other studies have analysed small mammal community composition in different landscape types, showing that heterogeneous landscapes host a high diversity of small mammals in both urban (Crocì et al., 2008) and agricultural contexts (Reynolds et al., 2018). However, additional research is needed to better understand the relationships between species and landscape at a regional scale, accounting for both taxonomic diversity and functional groups. Specifically, since small mammal communities exploit landscape resources in spatially heterogeneous ways, the analysis of functional traits can help to identify and prioritise the most effective management strategies for a group of mammals often neglected in conservation plans.

In this context, the present work aimed to analyse the relationships among small mammal assemblages, their functional traits, and landscape patterns across several ecosystems at a regional scale in the Mediterranean.

Specifically, we hypothesised that: i) taxonomic and functional trait composition varies according to landscape composition (e.g., land cover type abundance) and configuration (e.g., aggregation or isolation of land cover patches) in small mammal communities; ii) species assemblages in human-dominated landscapes tend to be species-poor and simplified in functional strategies; and iii) heterogeneous landscapes host a high diversity of small mammal species and functional traits.

2. Materials and methods

2.1. Study area

The study area includes a large section of Central Italy ranging from the Tyrrhenian Sea to the Adriatic coast and covering the Central Apennines (surface of 33,000 km² ca; centroid coordinates: longitude 13°16'52.4"E, latitude 42°10'21.6"N, datum WSG84; Fig. 1). Elevation ranges from sea level to 2,912 m a.s.l. at Gran Sasso Mountain. The climate encompasses Mediterranean types on the coast and temperate types in the upper mountains (Pesaresi et al., 2017).

The landscape is mainly characterised by agricultural lands (60.30%), followed by forest (29.6%) and artificial areas (9.8%; EEA, 2012). Overall, Central Italy is characterised by a mosaic of traditional and modern land uses, representing typical Mediterranean landscapes. Currently, this area is shaped by two main opposite drivers: land abandonment with a consequent natural rewilding of mountain landscapes (Frate and Carranza, 2013; Malavasi et al., 2018) and land intensification (intensive agricultural and urbanisation) in lowlands (Acosta et al., 2005; Falcucci et al., 2007).

2.2. Small mammal data collection

Small mammal occurrence data were extracted from the OpenMICE database (Paniccia et al., 2018a), an open-source repository providing georeferenced occurrences and abundances derived from owl pellets over South-Central Italy and functional traits for small mammals. Specifically, we extracted data from Common Barn-owl (*Tyto alba*) pellets collected between 1983 and 2013 (step 1 in Fig. 2), selecting only sampling sites with more than 50 prey individuals (Bond et al., 2004) to ensure a reliable representation of small mammal communities. We collected data from 86 sites, including 21 small mammal species (10 Rodentia and 11 Eulipotyphla) and 20,576 specimens (Table S1). The most common species in the dataset were *Microtus savii* and *Mus domesticus* (8,832 and 2,234 specimens, respectively), followed by *Apodemus sylvaticus*, *Crocidura suaveolens*, *Crocidura leucodon*, and *Suncus etruscus*. The least common species were the Mediterranean mole (*Talpa caeca*), the Edible dormouse (*Glis glis*), and the Eurasian water shrew (*Neomys fodiens*) (Table S1). Although widely present in the forests of Central Italy, the Red squirrel (*Sciurus vulgaris*) was excluded due to its scarce occurrence in Common Barn-owl pellets (Pezzo and Morimando, 1995).

From OpenMICE (Paniccia et al., 2018a), we extracted a set of functional, morphological, and ecological traits for all the species included in our dataset (Table S2; S3), mostly focusing on traits related to ecosystem function, species behaviour, and utilisation of environmental resources. Specifically, we considered (i) *body mass*, (ii) *social system*, (iii) *pattern of torpor*, (iv) *breeding site*, (v) *prevalent habit*, (vi) *activity patterns*, and (vii) *trophic level* (Table S2). *Body mass* (i.e., the mean mass in grams across sexes) is correlated with the specific metabolic demand (Brown et al., 2004) and is a good proxy of foraging behaviour (Huey and Pianka, 1981). In addition, this trait is related to landscape pattern parameters, such as habitat patch shape and size (Barbaro and van Halder, 2009; Keinath et al., 2017) and habitat connectivity (Michalski and Peres, 2005). For this reason, *body mass* could be considered a good indicator of habitat loss and fragmentation. The *social system* (i.e., assuming a solitary distribution or associated in groups) determines species fitness and distribution patterns (Kurvers et al., 2014) across different landscapes and environmental gradients (Flynn et al., 2009). The *pattern of torpor* (i.e., hibernation and daily torpor; Ruf and Geiser, 2015) and the *activity pattern* (i.e., diurnal, cathemeral, polyphasic, and nocturnal activity, according to Halle and Stenseth (2000) reflect the temporal utilisation of resources and suitable areas. Moreover, these traits are strongly influenced by the temporal and spatial distribution of available resources across landscapes (Flynn et al., 2009), which is particularly marked in the Mediterranean and temperate

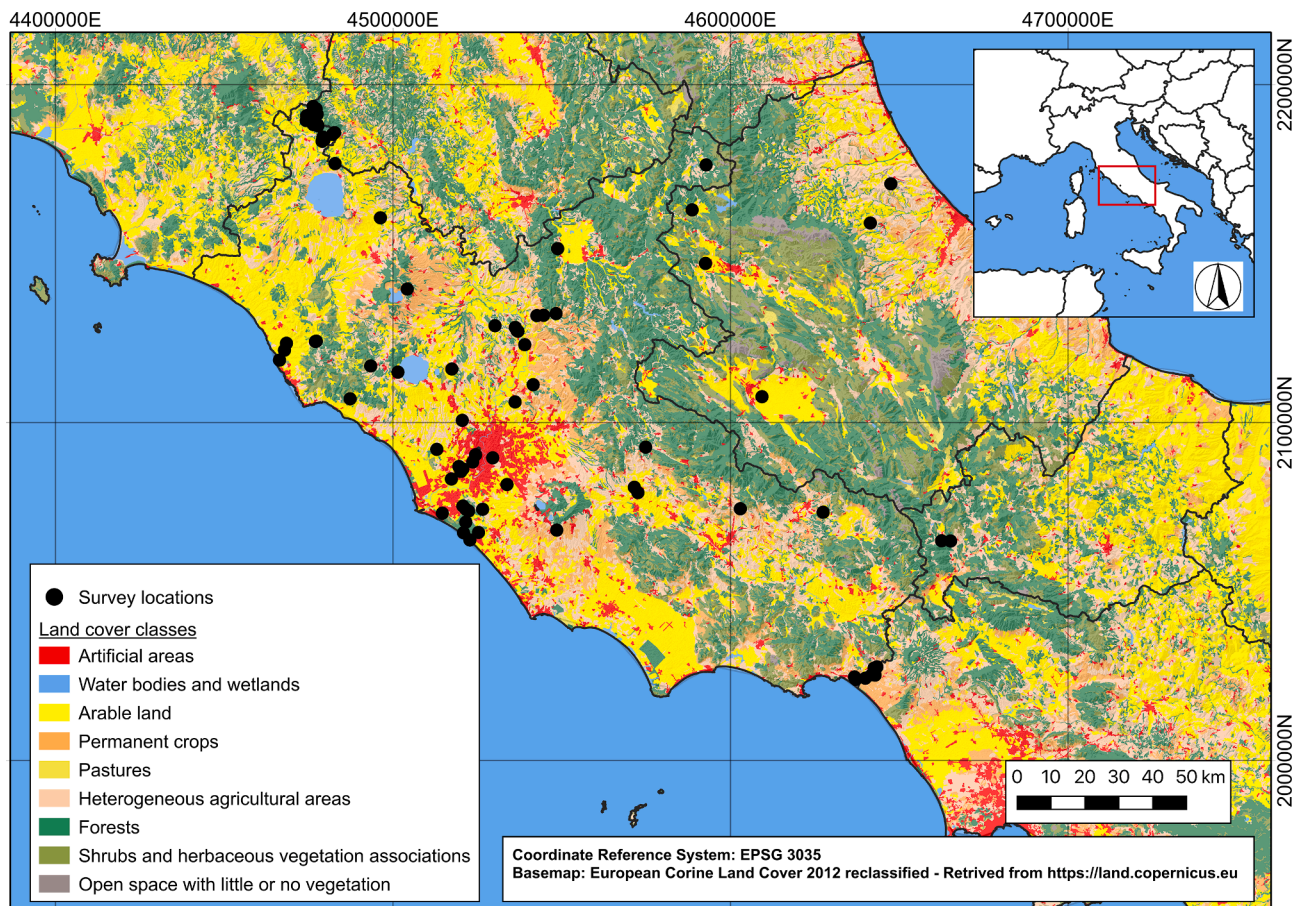


Fig. 1. Study area showing the location of nesting or roosting sites of the Common Barn-owl (*Tyto alba*) used in the analyses.

biomes. The *breeding site* (e.g., arboreal and underground) and *prevalent habit* (above ground, arboreal, fossorial, semi-aquatic) refer to species space utilisation according to abiotic (e.g., soil depth, hardness, organic content, and water; Charbonnel et al., 2016) and biotic components (e.g., vegetation structure; Sozio et al., 2016). *Trophic level* (i.e., carnivore, herbivore, or omnivore) reflects the type and amount of resources consumed and released by species, thus providing insights into ecosystem energy fluxes (Gravel et al., 2016).

2.3. Land cover data

We obtained land cover data coeval to the pellet collection dates from the European CORINE (CLC), a set of maps reporting a spatial resolution of 100 m and a minimum mapping unit of 25 ha (Copernicus 2019; <https://land.copernicus.eu/pan-european/corine-land-cover>). To ensure the temporal correspondence between pellet data and CLC maps, pellet data was grouped into ten-year intervals corresponding to the CLC map editions (pellet data 1983–1994 for 1990 CLC map; pellet data 1996–2002 for 2000 CLC map; pellet data 2006–2013 for 2012 CLC map; Table S4). According to the habitat requirements of each species assessed under the standardised procedure by Baisero et al. (2020) and Rondinini et al. (2011), we reclassified the original CLC map into nine land cover categories (Table 1).

2.4. Landscape pattern metrics

Landscape metrics were calculated within a circular 1000 m radius buffer around each pellet site, corresponding to the mean hunting territory size of the Common Barn-owl in the analysed area (see Paniccia et al., 2018a). Landscape pattern metrics were selected to capture the

relationship among small mammal species distribution and landscape composition and configuration based on their successful use in past studies (see Table S5 for a detailed description and references). For class-level metrics (*sensu* McGarigal et al., 2002), we measured the following: percentage of landscape (PLAND, i.e., landscape percent covered by each land cover type), area-weighted mean patch size (AREA_AM, e.g., probability that two randomly chosen pixels of the same class are not situated in the same patch), and clumpiness (CLUMPY, e.g., the deviation from a random distribution of pixels within the landscape; Wang et al., 2014; for index details refer to Table S6). At a landscape level, we calculated the following metrics of landscape diversity: patch richness density (PRD, number of patches/100 ha), SHEI (Shannon's evenness index, a higher value means more evenness, which is indicative of higher heterogeneity), interspersed and juxtaposition index (IJI, i.e., the extent to which pixel classes are interspersed, a higher value indicates more heterogeneity), and contrast-weighted edge density (CWED, the contrast on patch edges, which is usually high for forest/artificial edges; for details refer to Table S7).

Prior to statistical analyses, we standardised all continuous pattern metrics per site to approach normality and to reduce the influence of extreme values and different units of measurements using the function $[(x - \text{mean}(x)) / \text{sd}(x)]$ following the protocol of Zuur et al. (2010). In addition, we accounted for metric collinearity, retaining only the metrics that reported a variance inflation factor (VIF) < 3 (Guisan et al., 2017; Zuur et al., 2010). The final set of 12 landscape pattern metrics included patch richness density (PRD), interspersed and juxtaposition index (IJI), contrast-weighted edge density (CWED), clumpiness (CLUMPY for 5 classes; Table 2), and percentage of landscape (PLAND for 4 classes; Table 2). Maps were handled under QGIS 2.18 (QGIS Development Team, 2016), while landscape metrics were calculated

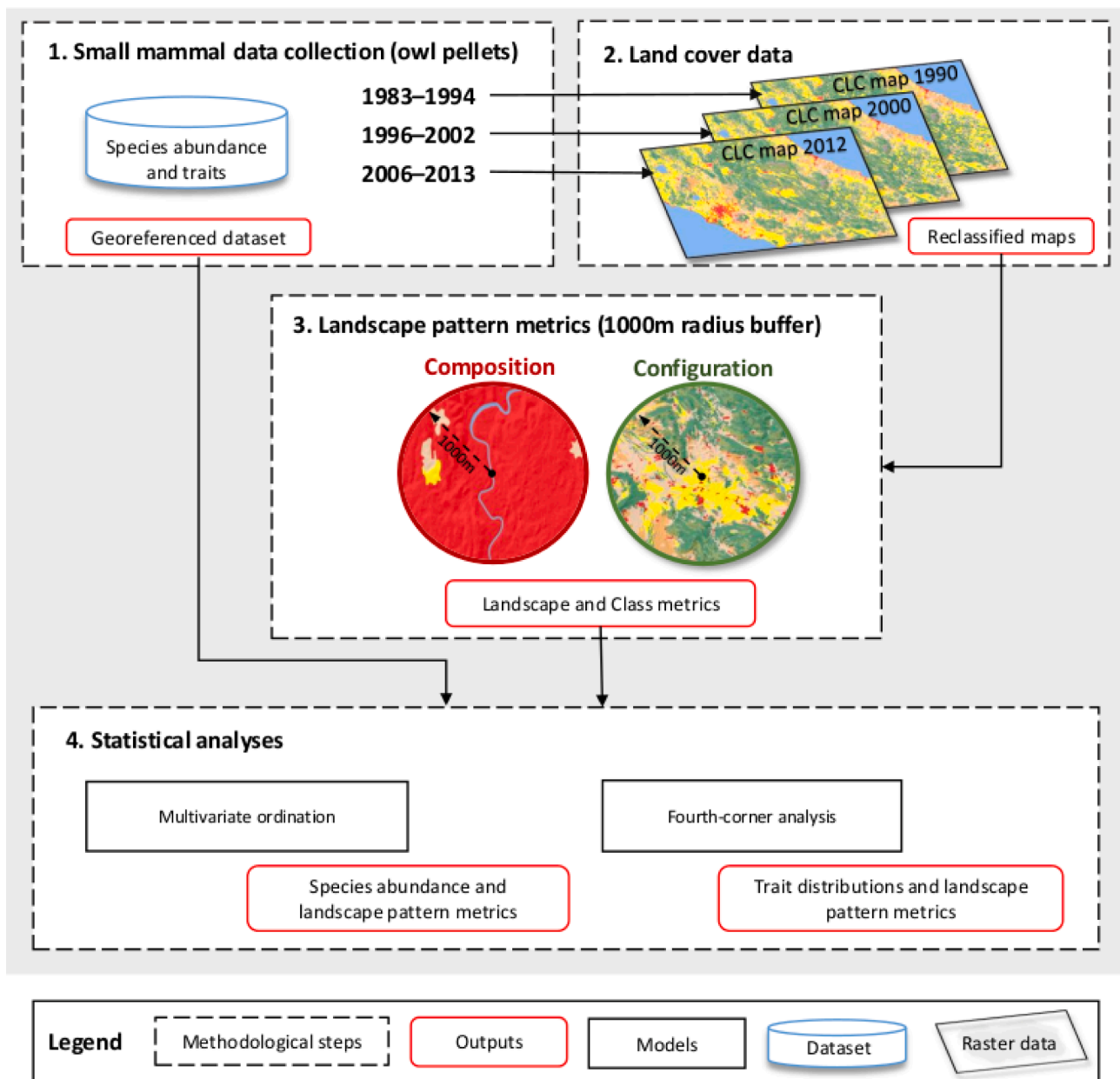


Fig. 2. Flowchart of the procedure used to evaluate the relationship among taxonomic and functional compositions of small mammal assemblages and landscape pattern metrics.

using FRAGSTATS (McGarigal et al., 2002).

2.5. Statistical analyses

a) Multivariate ordination

To explore the relationship between small mammal species distribution and landscape pattern, the final dataset, including 21 species and 12 spatial metrics, was analysed using a canonical correspondence analysis (CCA; Legendre and Legendre, 2012). To select the most parsimonious landscape pattern variables to train the CCA, we performed a forward selection procedure, as implemented in the function ‘ordstep’ of the ‘vegan’ package (Oksanen et al., 2020). This procedure allows us to sub-select pattern metrics based on their *p* values computed through a Monte Carlo permutation test, and on the Akaike information criterion (AIC; Borcard et al. 2011).

b) Fourth-corner analysis

To investigate the relationship among small mammal traits, species

abundance, and landscape pattern metrics, we adopted a model-based approach to the fourth-corner analysis (Brown et al., 2014). The fourth-corner model combines traits, environmental variables, and species abundance into the same predictive models by relying on three input matrices: i) environmental variables per site (i.e., landscape pattern metrics in our case), ii) species abundance per site, and iii) functional traits per species, to derive a “fourth” matrix of functional traits by landscape variables (Legendre and Legendre, 2012). Since we fit the generalised linear model (GLM) to abundance data, we considered a negative binomial distribution of errors. In addition, we used the LASSO penalty approach to remove all trait–covariate interactions that may reduce the model’s goodness-of-fit (Brown et al., 2014; Wang et al., 2012). Finally, to test the statistical significance of the relationship between landscape pattern metrics and traits, we computed a Monte Carlo randomisation test with 999 permutations (Wang et al., 2012). The statistical analyses were performed using the ‘traitglm’ function in the R package ‘mvabund’ (Wang et al., 2012). This method relies on an

Table 1

Reclassification scheme of CORINE Land Cover classes (CLC) following the approach proposed by [Baisero et al. \(2020\)](#) and [Rondinini et al. \(2011\)](#). Levels 1 and 2 refer to the conventional hierarchical classification in Europe.

CLC level 1	CLC level 2	Reclassified classes
1. Artificial surface	1.1 Urban fabric 1.2 Industrial, commercial and transport units 1.3 Mine, dump and construction sites 1.4 Artificial, non-agricultural vegetated areas	1. Artificial areas
2. Agricultural areas	2.1. Arable land 2.2. Permanent crops 2.3. Pastures 2.4. Heterogeneous agricultural areas	2.1. Arable land 2.2. Permanent crops 2.3. Pastures 2.4. Heterogeneous agricultural areas
3. Forest and semi-natural areas	3.1. Forests 3.2. Shrubs and herbaceous vegetation associations 3.3. Open spaces with little or no vegetation	3.1. Forests 3.2. Shrubs and herbaceous vegetation associations 3.3. Open spaces with little or no vegetation
4. Wetlands	4.1 Inland wetlands 4.2 Maritime wetlands	4. Water bodies and wetlands
5. Water bodies	5.1 Inland waters 5.2 Marine waters	

Source: <https://land.copernicus.eu/pan-european/corine-land-cover>

extension of a GLM, fitting a single multi-response model to all species across all sites simultaneously.

3. Results

3.1. Canonical correspondence analysis

The CCA ordination reported a significant relationship between species distribution and landscape pattern metrics ($F = 4.923, p = 0.001$; [Fig. 3](#); [Table S8](#)), indicating a constrained explained variance value of approximately 31%. The most parsimonious model derived by the forward variable selection includes contrast-weighted edge density (CWED), patch richness density (PRD), percentage cover of artificial areas (PLAND 1), arable land (PLAND 21), heterogeneous agricultural areas (PLAND 24), and clumpiness of artificial (CLUMPY 1) and forest patches (CLUMPY 31). The first three axes accounted for 27% of the constrained variance ([Fig. S3](#)), with the first axis explaining 15.45% ($F = 17.362, p = 0.001$), the second 8.33% ($F = 9.368, p = 0.001$), and the third 2.90% ($F = 3.270, p = 0.071$; [Table S8](#)).

The first CCA axis ([Fig. 3](#)) was mainly correlated with the percentage cover of heterogeneous agricultural areas (PLAND 24, biplot score = -0.70), arable land (PLAND 21, biplot score = -0.38), and clumpiness of artificial surfaces (CLUMPY 1, biplot score = -0.69) and forests (CLUMPY 31, biplot score = 0.57). The second CCA axis was mainly correlated with patch richness density (PRD, biplot score = 0.57), percentage cover of artificial areas (PLAND 1, biplot score = -0.15), and contrast-weighted edge density (CWED, biplot score = 0.43).

Most of the analysed species showed a specific assembly pattern along the ordination axes ([Table S9](#)). Along the first CCA axis, it is possible to observe two main groups of species: the first (on the left of the biplot towards positive y-axis scores), including *A. sylvaticus*, *A. italicus*, *Rattus rattus*, and *T. romana*, which was mainly associated with heterogeneous agricultural lands (PLAND 24) and the second (on the right side, towards positive y-axis scores), including *G. glis*, *Myodes glareolus*, *M. avellanarius*, *N. milleri*, *S. minutus*, *S. samniticus*, and *T. caeca*, which was linked to high forest clumpiness values (CLUMPY 31) and heterogeneous landscapes with highly natural elements (CWED). Along the second CCA axis, it is also possible to observe two species assemblages: the first one (placed in the lower sector of the ordination space, towards with negative y-axis scores), including

Table 2

Spatial pattern metrics were retained for the analysis after the variance inflation factor (VIF) calculation, along with their brief description and level of analysis (*sensu* [McGarigal et al., 2002](#)). Only variables with $VIF < 3$ are reported. For a detailed description of each metric, refer to [Table S6](#).

Pattern metrics	VIF	Description	Level
Patch richness density (PRD)	1.78	The standardised number of classes per unit area. Allows comparison among landscapes of different extents	landscape
Contrast-weighted edge density (CWED)	1.88	The length (m) of each class/class edge type multiplied by the corresponding contrast weight, divided by the total landscape area (m^2)	
Interspersion and juxtaposition index (IJI)	2.60	Relationship among the length (m) of each class/class edge type and the sum of all the class/class landscape edges expressed in percentage	
PLAND 1	1.73	The percentage of the CLC class “artificial areas” in the landscape	class
PLAND 21	1.93	The percentage of the CLC class “arable land” in the landscape	
PLAND 22	1.26	The percentage of the CLC class “permanent crops” in the landscape	
PLAND 24	2.22	The percentage of the CLC class “heterogeneous agricultural areas” in the landscape	
CLUMPY 1	1.58	Level of adjacency between pixels of the CLC class “artificial areas” indicating its aggregation or discontinuity in the landscape	
CLUMPY 21	2.00	Level of adjacency between pixels of the CLC class “arable land” indicating its aggregation or discontinuity in the landscape	
CLUMPY 23	1.36	Level of adjacency between pixels of the CLC class “pastures” indicating its aggregation or fragmentation in the landscape	
CLUMPY 24	2.07	Level of adjacency between pixels of the CLC class “heterogeneous agricultural areas”. Indicates the clumped or fragmented distribution of the class in the landscape	
CLUMPY 31	1.71	Level of adjacency between pixels of the CLC class “forests” indicating its aggregation or fragmentation in the landscape	

R. norvegicus and *M. domesticus*, which are linked with high percentages of artificial areas, and the second one (in the upper sector of the biplot, towards positive scores), including *Eliomys quercinus*, *C. leucodon*, and *A. flavicollis*, which are mainly related to highly heterogeneous and fragmented landscapes. *R. norvegicus* shows a strong correlation with urban areas compared to other synanthropic species, such as *R. rattus* and *M. domesticus* ([Fig. 3](#)). A small group of species (e.g., the insectivores *C. suaveolens*, *S. etruscus*, *S. antinorii*, and the cricetine rodent *M. savii*) did not show a clear trend, suggesting that their abundance pattern does not depend on the landscape factors considered in this study.

3.2. Fourth-corner model

The fourth-corner analysis depicted an overall significant relationship (deviance = 379.4; $p = 0.001$) between species traits and landscape pattern metrics. Some traits, such as body mass, the pattern of torpor, prevalent habit, activity pattern, and trophic level, showed the strongest association with heterogeneous agricultural areas (PLAND 24), arable land (PLAND 21), and artificial areas (PLAND 1), as well as with the presence of clumped forests (CLUMPY 31). Other traits, such as breeding sites and social systems, presented an overall weak relationship with landscape features. Lastly, some trait categories (e.g., arboreal breeding

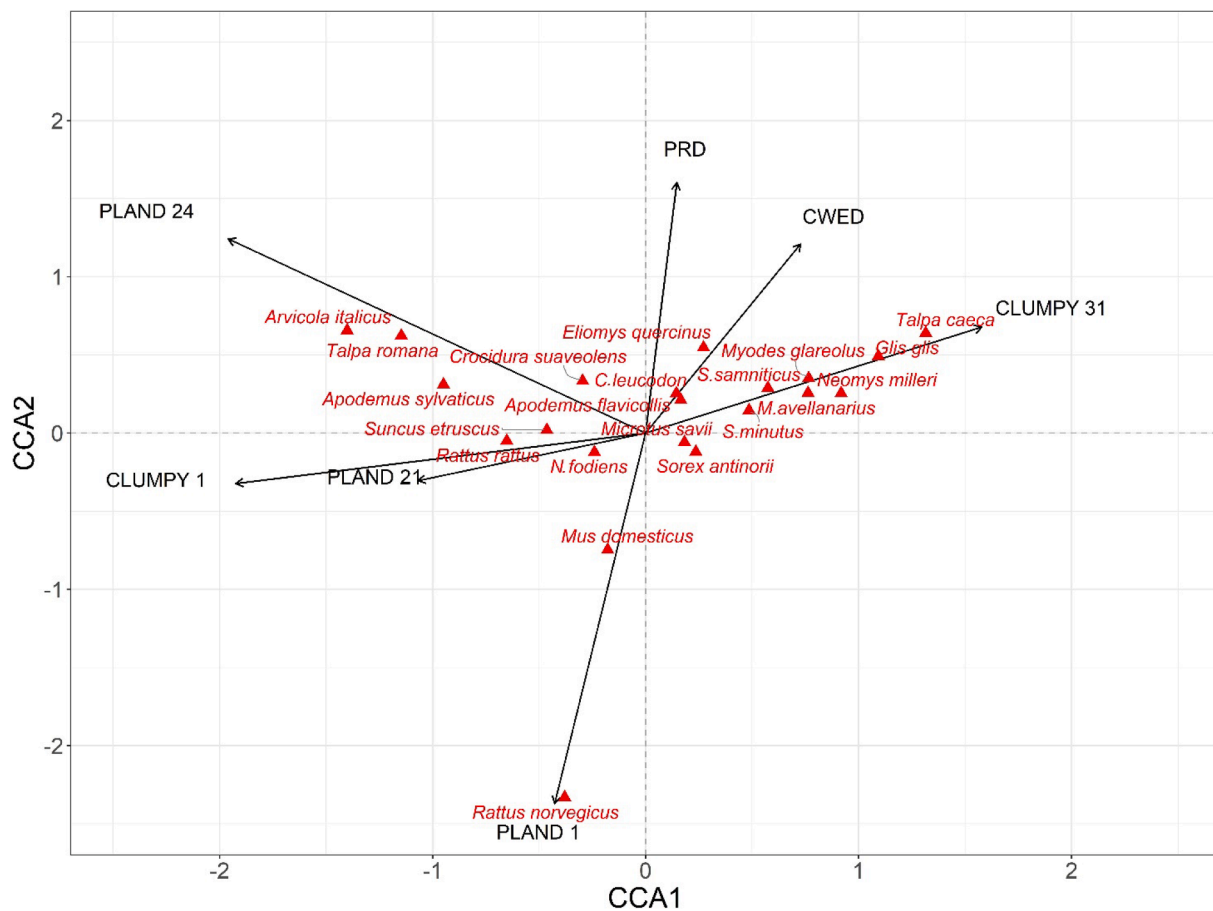


Fig. 3. Canonical correspondence analysis (CCA) biplot with landscape pattern metrics as explanatory variables. Vectors indicate the relationship (i.e., direction and magnitude) between small mammals' distribution (in red) and landscape pattern metrics (in black). CWED: contrast-weighted edge density; PRD: patch richness density; PLAND 1: % artificial areas; PLAND 21: % arable land; PLAND 24: % heterogeneous agricultural areas; CLUMPY 1: extent of clumped artificial areas; CLUMPY 31: extent of clumped forests (for pattern metrics description, refer to Table 2 and Table S6).

site, above ground habit) did not show any significant relationship with the considered pattern metrics (Fig. 4).

The visual inspection of the fourth-corner interaction diagram shows higher body mass values in agricultural (PLAND 24) and urbanised landscapes (PLAND 1). Daily torpor prevailed in agricultural areas (PLAND 24 and PLAND 21) but was scarcely dominant in clumped forested areas (CLUMPY 31) and highly heterogeneous landscapes with highly natural elements (CWED). As the prevalent habit is concerned, the only semi-aquatic species, *A. italicus*, showed a clear preference for heterogeneous agricultural areas (PLAND 24) and non-fragmented landscapes (negative relationship with CWED), whereas arboreal species, such as *M. avellanarius*, were associated with a variety of semi-natural landscapes (PRD). Regarding species activity patterns, nocturnal species preferred artificial surfaces (PLAND 1), while polyphasic species were mainly linked with forests (CLUMPY 31), highly heterogeneous landscapes (CWED), and arable land (PLAND 21), showing a negative correlation to heterogeneous agricultural areas (PLAND 24). Similarly, trophic levels were strongly related to land cover characteristics, where herbivores were associated with forests (CLUMPY 31) and omnivores with dense artificial areas (CLUMPY 1 and PLAND 1).

Overall, forested areas (CLUMPY 31) showed the strongest associations with species traits and were mostly preferred by small, polyphasic, solitary, or herbivore species, such as shrews (*Sorex* sp.) and *M. glareolus*, and avoided by large or semi-aquatic species, such as *R. rattus* and *A. italicus*. The latter, instead, preferred heterogeneous agricultural areas (PLAND 24). Nocturnal and omnivore species, such as *R. norvegicus* and *M. domesticus*, were strongly associated with artificial areas (PLAND 1 and CLUMPY 1, respectively), which are in turn avoided by arboreal

species, including *M. avellanarius* and *G. glis*. Omnivore and nocturnal species preferred urban areas (PLAND 1) and avoided highly clumped patches of forests (CLUMPY 31), which are in turn preferred by herbivore and polyphasic species.

4. Discussion

Our results highlighted the key role of landscape composition and configuration in shaping small mammal species assemblages and functional trait distributions. Specifically, our research revealed that species composition and trait distribution vary along two main landscape gradients: the first one ranging from seminatural landscapes, mainly forests, to heterogeneous agricultural lands in which human economic activities are carried out, and the second one from anthropogenic landscapes, mainly artificial surfaces, to highly heterogeneous landscapes (i.e., where natural and agricultural patches are intermixed).

CCA ordination showed a clear segregation of species groups in relation to pattern metrics. Our results evidenced a high number of species associated with forested areas and few species associated with agricultural areas and anthropogenic landscapes. Concerning functional traits, the fourth-corner analysis highlighted that some traits (e.g., trophic level — omnivore, herbivore) varied according to a landscape gradient ranging from agricultural areas with sparse vegetation to forests, whereas others (e.g., body mass, activity pattern — nocturnality) varied according to an anthropogenic gradient (from sparse to dense urban areas).

The first landscape gradient in the CCA ordination ranges from forests and heterogeneous and complex landscapes to heterogeneous

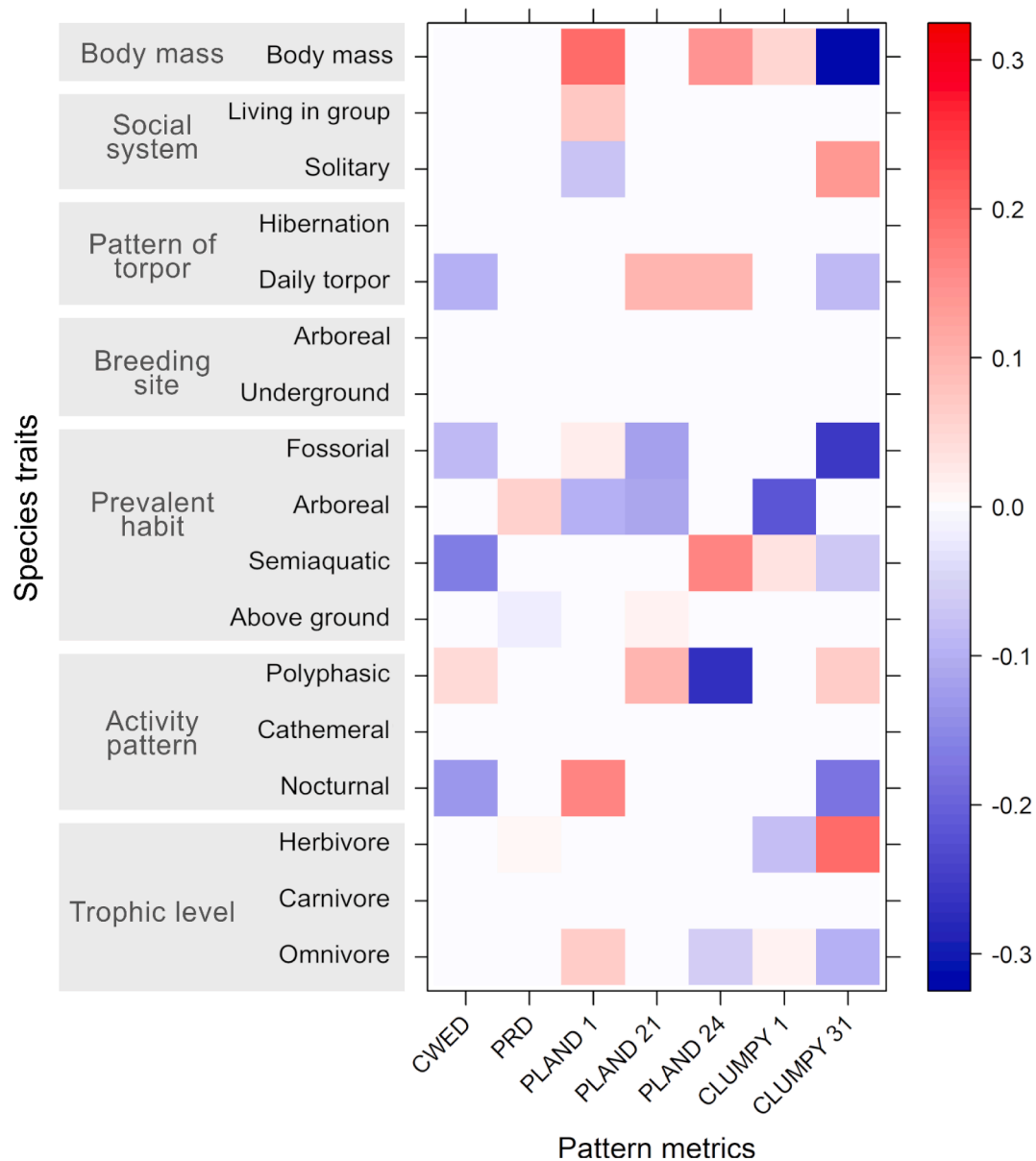


Fig. 4. Fourth-corner interaction coefficients showing the relationship between small mammal traits and landscape pattern metrics. Relationships were indicated in red (positive) and blue (negative), with colour intensity representing the strength of the association. CWED: contrast-weighted edge density; PRD: patch richness density; PLAND 1: % artificial areas; PLAND 21: % arable land; PLAND 24: % heterogeneous agricultural areas; CLUMPY 1: extent of clumped artificial areas; CLUMPY 31: extent of clumped forests (for pattern metrics description, refer to Table 2 and Table S6).

agricultural lands (Fig. 3). The most upper right sector of this gradient corresponding to forests is associated with two rodent species (e.g., *G. glis* and *M. glareolus*) and several insectivores (e.g., *N. milleri*, *S. minutus*, *S. samniticus*, and *T. caeca*). These species assemblage are characterised by highly heterogeneous functional traits, including different trophic levels, habits, and activity patterns. The coexistence of so many functional and ecological traits is most likely related to the complex vertical structure of forests, which assures a wide spectrum of trophic and spatial niches (e.g., roots, leaves, seeds, and fruits; Hansson 1979). Moreover, in forested areas, several small mammal species are nocturnal or polyphasic, two strategies likely adopted to reduce diurnal predator pressure (e.g., snakes, and birds; Halle 2006). In addition to clumped forests, a seminatural gradient is secondarily denoted by highly heterogeneous and complex landscapes characterised by *E. quercinus*, *A. flavicollis*, and *C. leucodon*. While *E. quercinus* prefers heterogeneous woodlands with a developed shrub layer able to assure food and shelter, *A. flavicollis* occurs preferentially in natural-agricultural margins (Marsh

and Harris, 2000), typically prevailing in landscapes where different patch types coexist. Aggregated forest patches on highly heterogeneous landscapes seem to promote a high variability of small mammal species and functional traits. Complex landscapes with natural elements embedded into seminatural ones should provide shelter from predators, spatial and trophic resources, and ensure good levels of habitat connectivity, thus promoting a rich small mammal diversity (Fischer and Schröder, 2014; Serafini et al., 2019).

On the left side of the seminatural landscape gradient, corresponding to permanent and annual crops intermixed with seminatural vegetation, we observed a second group of species, including *R. rattus*, *A. sylvaticus*, *A. italicus*, and *T. romana* (Fig. 3). These are generalist species occurring in almost all habitat types within agroecosystems and are particularly effective in exploiting resources and spatial niches provided by complex landscapes rich in ecotones (Amori et al., 2008; Loy et al., 2017; Tattersall et al., 2001). Species living in heterogeneous agricultural areas were also large-sized and characterised by daily torpor habits (i.e.,

not hibernating). Potential advantages of a larger size include improvements in the capacity to cope with unpredictable food shortages, the ability to exploit patchily distributed resources (Santini et al., 2019), and predation deterrence (Zollner, 2000). Daily torpor allows breeding in late winter, before the onset of major habitat disturbances due to agricultural practices (e.g., mowing, grazing, pesticide spraying, and harvesting), thus maintaining species reproductive success and persistence (Nowack et al., 2017). The preference of semi-aquatic species, such as *A. italicus* and *N. fodiens*, for agricultural lands might be related to the presence of irrigation channels often occurring in European agricultural systems (Bartolini et al., 2007). These results suggest the potential role of irrigated arable lands in preserving habitat quality and connectivity for semi-aquatic mammals (Carranza et al., 2012). In this regard a large body size in semi-aquatic mammals is advantageous both to reduce aquatic predator pressure (mainly fish; Wolff and Guthrie, 1985) and to improve a better thermoregulation capacity (Smith and Lyons, 2011).

For the second landscape gradient ranging from anthropogenic areas to highly heterogeneous landscapes, we observed that artificial surfaces are preferentially occupied by species with nocturnal activity habits, an omnivore diet, and large size. As stated above, anthropogenic environments are preferred by nocturnal species (Gaynor et al., 2018; Ritzel and Gallo, 2020), as a nocturnal habit reduces their exposure to diurnal human activities. As widely established in the literature, the synanthropic Norway rat (*R. norvegicus*) preferentially occurs in cities (e.g., Feng and Himsworth 2014), strongly supporting the “human dependence” hypothesis, which describes rats as “obligate pests” (Aplin et al., 2003). The potential advantages of a larger size in the Norway rat include predation deterrence and a good capacity to exploit food resources heterogeneously distributed over time (abundance and food scarcity periods) and space (patchy distribution; Santini et al. 2019). We also reported that the House mouse (*M. domesticus*) preferentially occurs in discontinuous urban areas, thus suggesting the coexistence in Central Italy of both feral and commensal (*sensu* Pocock et al., 2004) populations (Castiglia and Caporioni, 2005).

Our results finally evidenced that the presence of some species was weakly related to the considered landscape metrics, e.g., the insectivore shrews *C. suaveolens*, *S. etruscus*, and *S. antinorii*, and the cricetine rodent *M. savii*. Such inconsistencies could be partly due to a microhabitat specialisation of these species, which is particularly difficult to detect by the 25 ha minimum mapping unit of CORINE Land Cover maps (not enough for describing small elements). The coarse-grained resolution used for our large-scale analysis may have masked some relationships between communities and landscape patterns, as similarly reported for bats (Ducci et al., 2015) or habitat types (Campagnaro et al., 2017). Finally, the high number of prey associated with the wide hunting territory of the Common Barn-owl (ca. 962 m; Panicia et al., 2018a) were aggregated to a single geographic location (i.e., the pellet site), making microhabitat–species relationship at a finer scale difficult to detect.

The distribution pattern of small mammal functional traits (e.g., body mass, trophic levels, activity patterns, and prevalent habit) was mainly correlated with landscape composition (e.g., CLC classes cover) and subordinately with configuration characteristics. Consistent with previous studies on vertebrates of other regions (e.g., Arroyo-Rodríguez et al., 2016; Carrara et al., 2015), in the Mediterranean landscape, composition represents the main variable shaping small mammal distribution. As previously observed by Ritzel and Gallo (2020), disturbed or anthropogenic landscapes are preferred by large-sized and vigilant small mammals, probably due to their great perceptual ability and low susceptibility to predation (Zollner, 2000). Furthermore, the observed avoidance of artificial areas by insectivores could be explained by the well-known trivialisation of the trophic hierarchy on communities living in disturbed environments, such as cities. However, heterogeneous landscapes where seminatural and agricultural patches are intermixed host omnivores, generalists, and more tolerant species, as similarly observed by Arroyo-Rodríguez et al. (2016) and Gentili et al. (2014).

Future land change scenarios for the next decades in Central Italy (Di Pirro et al., 2021) suggest a strong conversion of plains and hilly arable land into urban areas. Meanwhile, forests and permanent crops are expanding on other wooded land and arable areas, respectively (Frate et al., 2014; Malandra et al., 2018). This conversion process can lead to a simplification of small mammal communities colonising new urbanised areas and the depletion of species, particularly successful in exploiting complex landscapes rich in ecotones and field margins. Planning actions aimed at increasing the extension of green areas and gardens inside cities and conservation measures for improving the quality of agricultural and seminatural areas (e.g., preserving natural patches mixed with open areas and structural elements) should be crucial for preserving small mammal diversity. These measures offer a conservation opportunity for common mammal species that are adapted to urban environments but also for some of the most threatened mammals (Goddard et al., 2010; Van Helden et al., 2020). Concerning the ongoing expansion of wooded areas, conservation-oriented forest management should be implemented to enhance the overall forest quality (Di Febbraro et al., 2015) and their key role in ensuring a high variety of small mammal species and the coexistence of many functional traits.

5. Conclusions

Small mammal assemblages in the Mediterranean area are significantly related to landscape composition and configuration characteristics. Species and trait distributions vary along two main landscape gradients. The first one ranges from seminatural environments, mainly forests, to heterogeneous agricultural lands, and the second one from highly heterogeneous landscapes (i.e., where natural and agricultural patches are intermixed) to anthropogenic landscapes, mainly artificial surfaces (cities and discontinuous urban areas).

The observed species assemblages and functional trait variability across Mediterranean landscape composition and configuration gradients highlight the need to preserve different ecosystems and land cover types to retain most of the small mammal biodiversity. For instance, preserving heterogeneous mosaics may support the conservation of several insectivorous and rodent species, which in turn assure ecosystem functioning and support basic ecosystem services, such as pollination, spore and seed dispersal, and soil nutrient cycling. Preserving forested areas should assure a great variety of microhabitats and, consequently, long food chains and a good number of small mammal species. Our findings suggest that conservation strategies aimed at promoting small mammal biodiversity should maintain several cover types and a wide variety of landscape configuration patterns. Conservation strategies in agricultural and anthropised areas should preserve natural patches intermixed with open areas and structural elements, supporting high taxonomic and functional diversity. The continuity and homogeneity of habitats should be assured in forested areas to host a set of forest specialists. Moreover, wetlands and irrigation channels offer an important and adequate habitat connecting landscape elements to semi-aquatic species.

The present work is based on a free and standardised database (OpenMICE), and on standard CLC maps with potential for replicability to other landscapes at different scales. This is particularly important to improve landscape monitoring tools across Europe and to prioritise the most effective management practices in Mediterranean landscapes for an often-neglected group of mammals in conservation plans. As small mammals play a variety of functional roles in the ecosystem, this approach may help to identify effective conservation strategies in Mediterranean ecosystems under different climate and land cover change scenarios.

CRedit authorship contribution statement

Chiara Panicia: Conceptualization, Data curation, Formal analysis, Visualization, Methodology, Writing – original draft, Writing – review &

editing. **Maria Laura Carranza:** Conceptualization, Investigation, Methodology, Writing – original draft, Writing – review & editing. **Ludovico Frate:** Conceptualization, Formal analysis, Methodology, Writing – review & editing. **Mirko Di Febbraro:** Methodology, Writing – review & editing. **Duccio Rocchini:** Supervision, Methodology, Writing – review & editing. **Anna Loy:** Conceptualization, Supervision, Investigation, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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