



SMALL MAMMALS IN A CHANGING LANDSCAPE: MONITORING COMMUNITIES FROM LOCAL TO LARGE SCALE

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Chiara Paniccia

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Candidate: Chiara Paniccia

Registration number: 155904

Tutor: Prof.ssa Anna Loy

Co-tutor: Prof. Marco Marchetti

Coordinator: Prof.ssa Gabriella Stefania Scippa

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To my lovely Granma, Maria

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Chiara Paniccia

Tutor:

Prof.ssa Anna Loy

Università del Molise
Dipartimento di Bioscienze e Territorio,
Contrada Fonte Lappone, 86090 Pesche, IS, Italia

Co-tutor:

Prof. Marco Marchetti

Università del Molise
Dipartimento di Bioscienze e Territorio,
Contrada Fonte Lappone, 86090 Pesche, IS, Italia

Reviewers:

Prof. Giovanni Amori

CNR - Istituto di Ricerca sugli Ecosistemi Terrestri (IRET)
Dipartimento di Biologia e Biotecnologie "C. Darwin",
Viale dell'Università 32, 00185 Roma, RM, Italia

Prof.ssa Francesca Cagnacci

Fondazione Edmund Mach
Dipartimento di Biodiversità ed Ecologia Molecolare,
Centro Ricerca e Innovazione,
Via Mach 1, 38010 San Michele all'Adige, TN, Italia

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Summary

Small mammals are an extremely diverse non-taxonomic group, which provide many ecosystem services and play important ecological roles. Rodents and insectivores are generally characterized by small body size, high litter size, high prolificity, arboreal or fossorial habits. Some of them possess a specialized diet, a trait linked to climate and land-use changes vulnerability. Despite these characteristics make small mammal communities' make good candidates as ecological indicators, few studies have explored this aspect, i.e. environmental factors affecting species composition and abundance, especially in Mediterranean ecosystems.

My Ph.D. project was aimed at collecting and archiving a large data set on small mammal occurrences in south-central Italy, and investigating how they are affected by human activities at different spatial scales, from local (i.e. stand scale - forest management) to broad scale (i.e. landscape scale-land-cover/land-use change), and thus how this diverse group could be used as ecological indicator of human driven environmental changes.

The specific aims of my Ph.D. project were:

- i) Developing of an open-access georeferenced database of small mammal occurrences, abundance, and functional traits based on owl-pellet data;
- ii) Analyzing the influence of micro-habitat characteristics and sustainable forest management practices on arboreal rodents to evaluate how these species could act as bio-indicator of alternative forest management practices. This project has a focus on a Molise region' forested areas;
- iii) Investigating the relationships between small mammal communities and landscape heterogeneity at large geographic scale in three south-central Italian regions (Lazio, Abruzzo, and Molise).

During my research project, I implemented and designed the first standardized and accessible georeferenced database of small mammal communities based on owl pellets covering the years 1972 to 2017, including nearly 2000 records for 190 sites of south-central Italy. The relational OpenMICE database has made more widely available a remarkable amount of small mammal data to the scientific community that usually are accessible only to a restricted audience. OpenMICE will likely help in gaining a better understanding of ecological

processes occurring in human-impacted landscapes. It also filled part of the knowledge gap on small mammals' occurrence in the study area to guide future sampling and conservation efforts. The results of my project may serve to prioritize conservation areas for small mammals and to design adaptive management of EU habitats and species.

At a fine-scale, I investigated niche similarity of two forest dormice (*Muscardinus avellanarius* and *Glis glis*) in a mixed deciduous forest of Molise, and how accounting for imperfect detection can improve the statistical significance and interpretability of niche overlap estimates based on occurrence data. I combined two different modelling approaches: 'Occupancy models' and 'General Linear Mixed Models'. Arboreal rodents were surveyed in a forest of south-central Italy, and relative abundances were compared to a set of forest structural factors and habitat requirements. The key output was the definition of species-specific habitat relationships that refined information on arboreal rodent species and their distribution, and their response to forest structure and practices. In such a perspective, our findings offered a methodological framework to assess the degree of forests naturalness and to explore effects of alternative forest management systems, highlighting the importance of sustainable use of forest products in maintaining crucial biodiversity resources. In a forest management context, our quantification of niche overlap provided useful information to assess the effects of different management practices on the occurrence of these arboreal species.

At a broad-scale, the research project was focused on the effect of landscape composition and structure (i.e. measured by landscape metrics) on small mammal communities. This study will provide insights on the small mammal complex responses to habitat change from the community-level of view and represents a baseline to future predictions of possible trends under future scenarios. Finally, results may potentially provide a powerful method in support of management and planning options for land-use change mitigation and adaptation.

Key words: *Landscape changes; Central Apennines; Community Ecology; Biodiversity indices; Bioindicators*

Riassunto

I piccoli mammiferi sono un gruppo non tassonomico estremamente diversificato che fornisce numerosi servizi ecosistemici e svolge una serie di importanti ruoli ecologici. Roditori ed insettivori sono generalmente caratterizzati da piccole dimensioni corporee, abitudini fossorie o arboricole e dalla dieta spesso altamente specializzata. Queste caratteristiche rendono alcune specie appartenenti a questo gruppo sensibili ai cambiamenti climatici e alle trasformazioni ambientali, quali le alterazioni di copertura ed uso di suolo. Malgrado i piccoli mammiferi vengano considerati dei buoni indicatori ecologici, ad oggi, sono pochi gli studi che hanno esplorato questo loro ruolo applicativo negli ecosistemi mediterranei.

Il mio studio si è focalizzato sulla raccolta di un ampio set di dati di piccoli mammiferi nelle regioni dell'Italia centro-meridionale, sulla comprensione di come specie e comunità di piccoli mammiferi vengano influenzate dalle attività umane a diverse scale spaziali, partendo dalla scala locale (gestione forestale) a quella più ampia (land-use /land-cover) ed infine, come, queste specie possano essere utilizzate per monitorare cause e processi dei cambiamenti ambientali indotti dall'uomo.

In dettaglio il mio progetto ha seguito i seguenti obiettivi:

- i) Raccolta e archiviazione di presenze, abbondanze e tratti ecologico-funzionali di piccoli mammiferi tramite dati provenienti da borre di rapaci notturni;
- ii) Analisi dell'influenza delle caratteristiche di microhabitat e delle pratiche di gestione forestale su due specie di roditori arboricoli nelle foreste del Bacino della Vandra (centro Italia);
- iii) Studio delle relazioni tra la diversità dei piccoli mammiferi ed eterogeneità di paesaggio su larga scala geografica. In particolare, è stata indagata l'influenza della configurazione spaziale del paesaggio su tali comunità.

Nello specifico, il mio progetto di dottorato ha permesso di archiviare un ampio data set di presenze, abbondanze e tratti ecologico-funzionali per 23 specie di piccoli mammiferi coprendo un range temporale di 45 anni (1972 al 2017). Sono stati georeferenziati circa 50.000 individui in 190 siti dell'Italia centro-meridionale (Lazio, Abruzzo, Molise). La creazione del database relazionale openMICE ha colmato parte del gap conoscitivo per l'area mediterranea: ha permesso di sviluppare un database storico di informazioni potenzialmente

utile alla comunità scientifica; ha reso fruibili ad un ampio pubblico numerosi dati di solito accessibili solo a specialisti; ha reso disponibili dati ecologici utili per future ricerche interessate a quantificare la perdita di biodiversità.

A scala fine il mio studio ha sottolineato come l'uso dei modelli di “*occupancy*” possa migliorare la significatività statistica e l'interpretabilità della nicchia ecologica e del “*niche overlap*” (sovrapposizione della nicchia ecologica). Tale approccio ha permesso di discriminare strategie ecologiche alternative tra le due specie studiate. Il ghio ha esibito una relazione significativa con le foreste ad alto fusto, mentre il moscardino ha mostrato preferenze per una varietà di tipi forestali. Queste differenze potrebbero essere dovute principalmente alle diverse abitudini alimentari e al grado di specializzazione delle due specie. In un contesto di gestione forestale, un'accurata quantificazione della sovrapposizione di nicchia permette di progettare pratiche mirate ad un uso sostenibile delle foreste che permetta di mantenere un'elevata diversità animale al loro interno.

Poiché alcuni taxa sono più sensibili al cambiamento dell'habitat rispetto ad altri, un approccio multi-tassonomico potrebbe essere utile per valutare la risposta della biodiversità e per pianificare strategie di conservazione in paesaggi modificati dall'uomo. Il mio studio ha consentito di identificare e quantificare, come e se le comunità di piccoli mammiferi sono influenzate dalla composizione del paesaggio o dalla sua configurazione e se queste caratteristiche possono essere collegate al declino della ricchezza o dell'abbondanza specifica dei piccoli mammiferi stessi.

I risultati del mio progetto, costituiscono una base di partenza per focalizzare aree prioritarie di conservazione per i piccoli mammiferi, guidare i futuri sforzi di campionamento e conservazione e sono un valido strumento per la gestione adattativa di specie e habitat nell'area Mediterranea.

Parole chiave: *Modificazioni del paesaggio; Ecologia di comunità; Indici di diversità biologica; Italia centro meridionale; Bioindicatori*

Foreword

This thesis reports advances and findings of 36-months Ph.D. research project at the Department of Biosciences and Territory – DiBT, University of Molise, Italy.

The thesis has been supervised by Professor Anna Loy, but also Professor Marco Marchetti, University of Molise, and Professor Duccio Rocchini of Center Agriculture Food Environment, University of Trento, has functioned as an external supervisor though not officially affiliated with the project.

The research activities were based at the Environmetrics Lab and Zoology Lab at the University of Molise, though the research project involved national and international collaborations which allowed me to visit and work in various institutions abroad. Specifically, I spent six months in the laboratory of Applied Ecology, at the Fondazione Edmund Mach (Italy) and six months in the Remote Sensing and Biodiversity Research, Department of Remote Sensing at the University of Wurzburg (Germany).

The thesis consists of five chapters. First, a synopsis giving the background, overview, objectives, main findings of the thesis, and future perspectives. The central chapters consist of three research manuscript that are published, or in preparation for publication in ISI journals.

The common framework of my research project and articles is the use of different model techniques to quantify if small mammal communities have changed throughout time and space. The last chapter includes discussion, advances, and results for my research. While being a Ph.D. student, I have also acted as co-supervisor on one master thesis, as well as assistant to teaching the course ‘Zoology’ (SSD-BIO05) and ‘Ecology’ (SSD-BIO07). Hence, my works have been presented at two International conferences on Rodent Biology and Management and at various Italian conferences.

More specifically:

Chapter I provides the background of the project, with a particular reference to Conservation Biology, Community Ecology, Biology and Taxonomy of Rodentia and Euliphotypla. The necessity for studying small mammal communities is presented, as well as the opportunity that different scale approaches provide toward the implementation of cooperative conservation strategies for small mammals. The gap in scientific knowledge that justified the rationale of this research and its objectives were described in detail.

Chapter II provides the results of a two-year project run in collaboration with experts of small mammal ecology and database management from various research institution (Fondazione Edmund Mach, and University of Trento).

The outcomes of the work were published in ‘Ecology’ (Paniccia C, Di Febbraro M, Delucchi L, et al (2018) OpenMICE: an open spatial and temporal data set of small mammals in south-central Italy based on owl pellet data. Ecology. doi: 10.1002/ecy.2506).

Chapter III includes the results of testing the use of occupancy and niche overlap to study arboreal rodent species at a local scale. The outcomes of the work were published in ‘iForest - Biogeosciences and Forestry’ (Paniccia C, Di Febbraro M, Frate L, et al (2018) Effect of imperfect detection on the estimation of niche overlap between two forest dormice. IForest 11:482–490 . doi: 10.3832/ifor2738-011).

Chapter IV provides the outcomes of the spatial-temporal modeling and community ecology analyses of species’ biological traits (such as body mass, activity pattern or reproductive parameters) to determine a community’ resilience, which results are still ongoing.

Chapter V provides a general discussion on the contribution of the Ph.D. project to the improvement of knowledge and methodologies for monitoring and studying small mammal communities through time, space and spatial scales. The relevance for wildlife management and conservation is discussed as well. Finally, future research directions are discussed.

List of conferences contributions associated with the Ph.D. Thesis

The research arguments included in this Ph.D. thesis have been presented as contributions in various international conferences in the form of poster or oral presentations.

A selection of the most relevant contributions is provided below.

List of papers

Paniccia C, Di Febbraro M, Frate L, et al (2018) Effect of imperfect detection on the estimation of niche overlap between two forest dormice. *IForest* 11:482–490 . doi: 10.3832/ifor2738-011

Paniccia C, Di Febbraro M, Delucchi L, et al (2018) OpenMICE: an open spatial and temporal data set of small mammals in south-central Italy based on owl pellet data. *Ecology*. doi: 10.1002/ecy.2506

Key research contributions

Poster communication

16th International Conference of Rodent Biology and Management & 16th Rodens et Spatium, Potsdam, Germany September 3-7, 2018

Paniccia C., Rocchini D., Frate L., Di Febbraro M., Mumme S, Loy A (2018). Small mammal richness and diversity in the changing landscape of central Italy. In Proceedings of the 6th International Conference of Rodent Biology and Management & 16th Rodens et Spatium, 3-7 September 2018, Potsdam, Germany

XI ATIT Italian Mammal Society Congress, Firenze (FI), Italy June 19-20, 2018

Paniccia C., Di Febbraro, Delucchi L., Oliveto R., Marchetti M., Loy A (2018). An Accessible Georeferenced Database of Small Mammals. *Hystrix, Italian Journal of Mammology*, 29(suppl.): 80 p.

XI Congresso Nazionale SISEF, Roma, Italia 10-13 Ottobre, 2017

Paniccia C., Di Febbraro M., Frate L., Sallustio L., Santopuoli G., Altea T., Posillico M., Marchetti M., Loy A. (2017). Can imperfect detection misrepresent niche overlap? A case study on two dormice in an Apennine deciduous montane forest. In: Proceedings of the XI SISEF National Congress “La Foresta che Cambia: Ricerca, qualità della vita e opportunità in un paese che cambia” (Fares S, Alivernini A, Ferrara C, Marchi M, Sallustio L, Chianucci F, Bucci G eds). Rome (Italy) 10-13 Oct 2017. Abstract-book, Paper #c11.22.6. [online] URL: <http://www.sisef.it/sisef/xi-congresso/>

International conference “Quo vaditis agriculture, forestry and society under Global Change?” Velké Karlovice, Czech Republic October 2-4, 2017

Vizzarri M., Antonucci S., Calderaro C., Coccozza C., Conte E., De Toni A., Di Febbraro M., Di Martino P., Evangelista A., Frate L., Fravolini G., Garfi V., Lasserre B., Lombardi F., Ottaviano M., Palombo C., Paniccia C., Perone A., Sallustio L., Santopuoli G., Tognetti R., Tonti D., Marchetti M. From cell to landscape: a multi-scale framework to study climate change effects on forest ecosystems - International conference “Quo vaditis agriculture, forestry and society under Global Change?” 2 th - 4th October 2017, Velké Karlovice (Czech Republic)

III Convegno Nazionale sui Piccoli Mammiferi, Colle Val d'Elsa (SI), Italia 8-9 Novembre, 2017

Pascarelli M., Paniccia C., Scaravelli D., Loy A. (2017). Structural diversity of small mammal communities in Molise, Italy: first evidence from a broad-scale sampling of owl pellets. In: Atti III Convegno Nazionale sui Piccoli Mammiferi “Piccoli mammiferi tra gestione e conservazione”, 8-9 Novembre 2017, Colle Val d'Elsa (SI), Italia

III Convegno Nazionale sui Piccoli Mammiferi, Colle Val d'Elsa (SI), Italia 8-9 Novembre, 2017

Monti I.E., Paniccia C., Mori E., Raimondi F., Augugliaro C. (2017). Small Mammals of Mongolia. Reports from the Scientific Expedition. In: Atti III Convegno Nazionale sui Piccoli Mammiferi “Piccoli mammiferi tra gestione e conservazione”, 8-9 Novembre 2017, Colle Val d'Elsa (SI), Italia

Giornate della Ricerca scientifica Dipartimento di Bioscienze e Territorio, Pesche (IS), Italia 1-2 Marzo, 2017

Paniccia C., Di Febbraro M., L. Frate L., Scaravelli D., Pascarelli M., Marchetti M., Loy A. 2017. Where did small mammal communities go? “MICE” database as a monitoring tool for the effects of climate and land-cover changes in central Italy. In: Atti delle giornate della ricerca scientifica Dipartimento di Bioscienze e Territorio, 1-2 Marzo 2017, Pesche (IS), Italia

15th Rodens et Spatium, International Conference on Rodent Biology, Olomouc, Czech Republic July 25-29, 2016

Paniccia C., Di Febbraro M., Altea T., Frate L., Posillico M., Sallustio L., Santopuoli G., Marchetti M., Loy A. 2016. Structural niche overlap of two forest dormouse species: effects of imperfect detection on accuracy of estimates. In Proceedings of the 15th Rodens et Spatium, 148 p. ISBN 978-80-244-4984-5.

X ATIT Italian Mammal Society Congress, Acquapendente (VT), Italy April 20-25, 2016

Paniccia C., Di Febbraro M., Altea T., Posillico M., Sallustio L., Marchetti M., Loy A. 2016. Investigating microhabitat structure and spatial niche overlap of two sympatric dormouse species. A case-study in a Central Apennine forest. *Hystrix, Italian Journal of Mammology*, 27(suppl.): 128p.

Oral communication

Conferenza dei Dottorati di ricerca “Sostenibilità e cambiamento”. Università degli Studi del Molise, (14/12/2016)

Paniccia C. Le comunità microterologiche in un paesaggio che cambia: problematiche e scenari futuri. Conferenza dei Dottorati di ricerca “Sostenibilità e cambiamento”. Università degli Studi del Molise, Via De Sanctis, 86100, Campobasso, Italia

Giornate della Ricerca Scientifica, Dipartimento di Bioscienze e Territorio (1-2 Marzo 2016)

Paniccia C., Di Febraro M., Altea T., Frate L., Bucci R., Posillico M., Sallustio L., Santopuoli G., Marchetti M., Loy A. Investigating the influence of forest management and microhabitat structure on the relative abundance of small-rodents in Central Apennines. An occupancy modelling approach. Proceedings of the days of scientific research Department of Biosciences and Territory, 1-2 March 2016, Pesche (IS), Italy

CHAPTER I

Introduction and objectives

1 Introduction

Small mammals are an extremely diverse, non-taxonomic group, that provide many ecosystem services and play a number of important ecological roles (Zachos 2018a, b). Most research on small mammal decline has focused on limited spatial and temporal scales, especially in the Mediterranean region (Szpunar et al. 2008; Rugiero et al. 2012; Moreno and Rouco 2013). To better understand the relationships between diversity loss, community changes and its causes, a broader spatial-temporal approach is needed.

My Ph.D. project aimed at collecting and archiving a large data set on small mammal occurrences in south-central Italy, and investigating how they are affected by human activities at different spatial scales, from local (i.e. stand scale - forest management) to broad scale (i.e. landscape scale-land-cover/land-use change), and how ecological organizations of this diverse group could be used as an ecological indicator.

1.1 Small mammals in ecosystems

Rodentia and Eulipotyphla are two of the most important orders of mammals, both in terms of number of species and in geographical distributions (Zachos 2018a, b), and are typically addressed as small mammals. Small mammals provide important ecosystem services and functions such as seeds dispersal (Xiao et al. 2005, 2006), spore dispersal (Martin 2003), pollination (Melidonis and Peter 2015), nutrient cycling (Hayward and Phillipson 1979; Fischer et al. 2018), etc. They include species that have adapted to human beings and followed them as they spread across the globe.

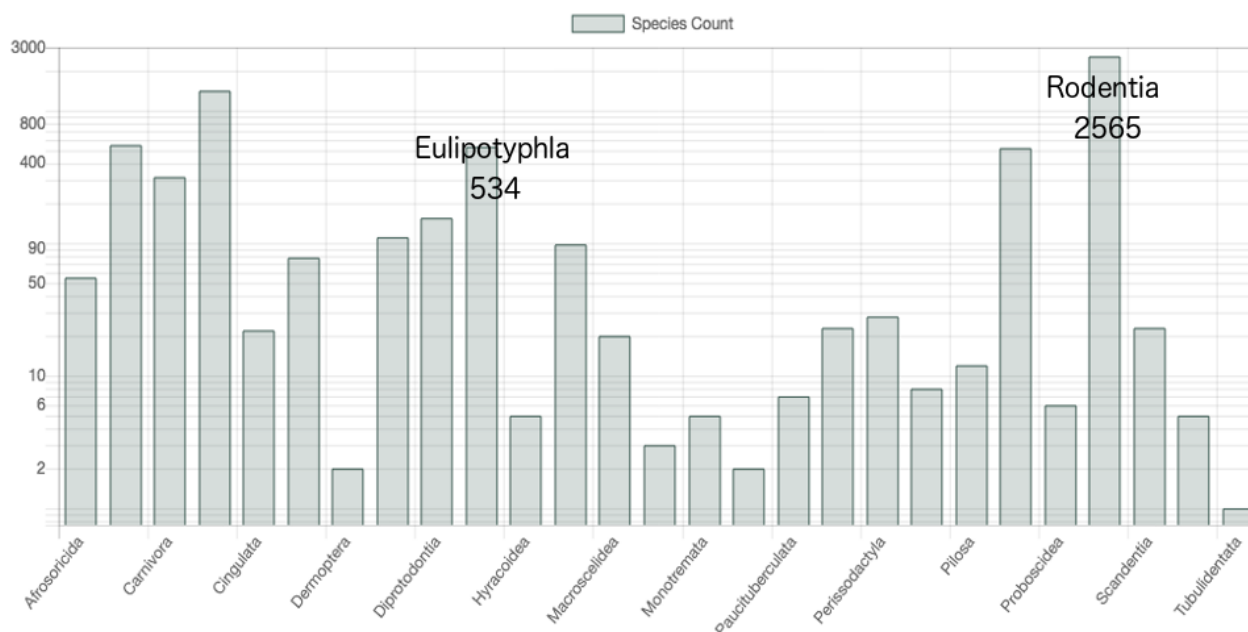


Figure 1. Histogram showing the global richness of Rodentia and Eulipotyphla in the Mammalia species diversity. Credit: Mammal Diversity Database (<https://mammaldiversity.org/>)

The order Rodentia contains about 40% of all known species of mammals, making it by far the most speciose order of mammals (Wilson, D.E., Lacher, T.E., Mittermeier 2016; Figure 1). They are the most diversified mammalian order, live in a variety of terrestrial habitats, including human-made environments, and can be found in all continents except Antarctica, throughout a wide variety of habitats from deserts to tropical rainforests and human modified landscapes such as urban areas (Wilson, D.E., Lacher, T.E., Mittermeier 2016).

This remarkable diversification and diffusion have been made possible by a vast array of morphological behavioral adaptations that allowed them not only to thrive in the world ecosystems but also to play a major role in their functioning.

Currently, 2566 species and 513 genus of Rodentia are described (ASM 2018).

The order Eulipotyphla includes 534 species and 56 genus and five families: Erinaceidae (hedgehogs and moonrats), Talpidae (moles), Solenodontidae (solenodons), Soricidae (shrews) and the extinct family Nesophontidae (Douady et al. 2002; Hutterer 2005; ASM 2018).

All the Eulipotyphla are small, ground-dwelling or subterranean mammals, and they mainly feed on invertebrates (Hutterer 2005; Zachos 2018a).

Small mammal diversity is differently distributed at global scale, especially in tropical areas (Jenkins et al. 2013; Pimm et al. 2014; Figure 2). In a global context, Italian small mammal fauna are unique and rich in endemisms (i.e. *Sorex samniticus*, *Talpa romana*, *Sciurus meridionalis*, *Dryomys aspromontis*) (Wauters et al. 2017; Amori and Castiglia 2018; Bisconti et al. 2018).

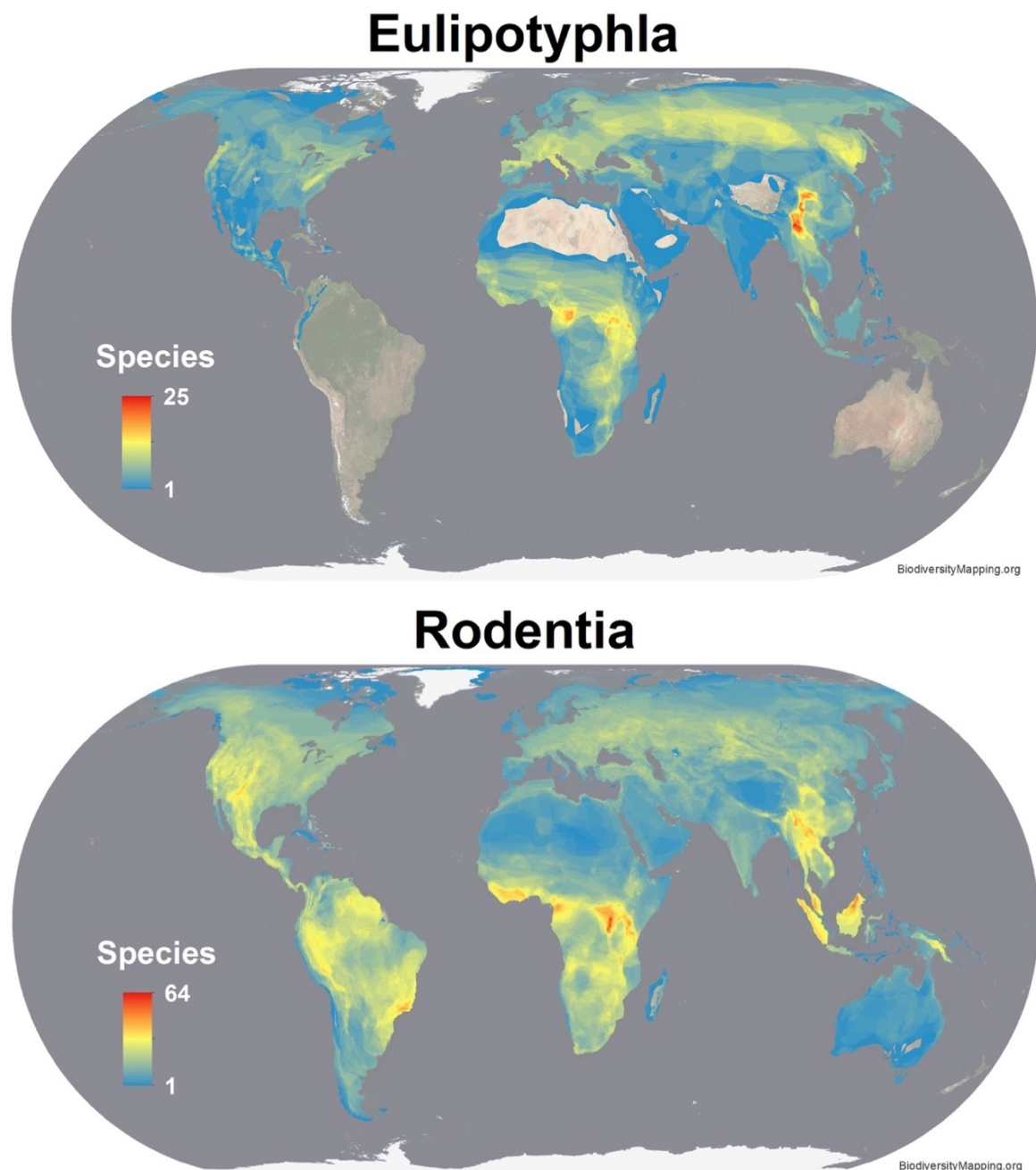


Figure 2. World maps of diversity include the total species richness for Eulipotyphla and Rodentia (Jenkins et al. 2013).

As some of the most abundant and widely distributed animals on the earth, it is not surprising that small mammals play key roles in ecosystems.

- i) Their main ecological functions are:
- ii) Vegetables consumers (rodents) or invertebrates (insectivorous);
- iii) Relatively abundant and widespread prey for many vertebrates (e.g. meso-carnivores and birds);
- iv) Active soil stirrings, aerators and fertilizers;
- v) Act as prominent seeds, fungi, and spore disperser;
- vi) As damaging for forest ecosystem and agricultural cultivation, and foodstuff.

These diverse and important roles make small mammals capable of influencing ecosystems energy fluxes and are often an important component of well-structured ecological networks (Dickman 1999; Pearce and Venier 2005; Hurst et al. 2014).

Among species groups that coexist in different landscapes, small mammals are crucial due to their contribution to well-structured food webs (Ostfeld and Keesing 2000; Salamolard et al. 2000; Butet and Leroux 2001), owing to their consumption and dispersal of plant material, seeds, and in turn, the growth and survivorship of those plants (Kollmann and Bassin 2001; Kollmann and Buschor 2003; Fischer et al. 2011). These relationships are observed in a several ways, but primarily through two processes: seed consumption and seed caching (Wilson, D.E., Lacher, T.E., Mittermeier 2016). Rodents, in particular, have also been identified as important dispersers of mycorrhizal fungi (Maser et al. 1978; Janos et al. 1995; Schickmann et al. 2012), many of which play critical roles in the ecosystems in which they exist. Several types of hypogeous fungi, such as truffles, rarely almost entirely on the dispersal of their spores by small herbivorous mammals like rodents (Wilson, D.E., Lacher, T.E., Mittermeier 2016). This process of distributing fungal spores and facilitating fungal growth in ecosystems play a crucial role in forest succession and the reestablishment of forest following significant disturbance events such as fires (McMullan-Fisher et al. 2011).

Eulipotyphla have also been identified as important consumers and controllers of invertebrates (Saarikko 1989; Gliwicz and Taylor 2002; Amori et al. 2008).

Human activities, especially the conversion and degradation of habitats, are causing global biodiversity declines. Europe has a long-standing history of human-induced landscape modification starting in the Holocene, 10,000 years ago (Antrpo 2004). This dramatic process

is certainly among the most powerful drivers of changes in wildlife distribution in the Anthropocene (Steffen et al. 2011). However, how local ecological assemblages are responding to such changes is less clear, and given their importance for many ecosystem functions and services, these processes should deserve more attention than that paid up to now by the scientific community.

Rodents and insectivores are generally characterized by large litter size, frequent litters, relatively short generation periods (Paniccia et al. 2018a; Zachos 2018a, b). Among them, rodents are typed by more ecological generalism compared to insectivores.

These characteristics, together with fossorial or arboreal habits, make rodents highly adaptable and able to cope with environmental changes, including climate (Pacifci et al. 2017). They have sufficient mobility to respond to alterations at different landscape scales (Michel et al. 2007; Rowe et al. 2015) or habitats (Pardini et al. 2005; Rodríguez and Peris 2007; Arnan et al. 2014; Marques et al. 2015). As small mammals rapidly respond to environmental change, due to their short life cycles and restricted spatial areas, such species can serve as model organisms for a better understanding of ecosystem and landscape processes (Barrett and Peles 1999) at different levels of complexity (i.e. community, population, species, etc.).

Small mammals are recognized as pests for the negative impacts they can have on certain aspects of ecosystems, also on human health and livelihood. Numerous studies have been shown negative impacts of small mammal populations on extensive annual crop, forests, and plantations, and their role in the spread of diseases (Borrecco 1976; Gratz 1988; Dickman 1999; Jacob and Tkadlec 2010).

Lastly, it should be remembered that Rodentia and Eulipotyphla are often seen as pests, yet they are actually among the most important animals on the planet. Humans, indeed, have long exploited small mammals for several purposes, including food, articles of clothing, as pets, or models organisms for laboratory studies and medical testing (Amori et al. 2008; Wilson, D.E., Lacher, T.E., Mittermeier 2016).

1.2 Small mammals as bioindicators

Small mammals are considered biological indicators of environmental risk, since they are used to monitoring metal pollutants (Ma 1989; Ieradi et al. 1998; González et al. 2008;

McLean et al. 2009; Scott et al. 2012) present in ecosystems, as well as radionuclides (Cristaldi et al. 1985, 1991, 2013; Baker et al. 1996).

Numerous research have been using small mammals species to understand the impacts of climate changes on biodiversity (Szpunar et al. 2008; Rugiero et al. 2012; Royer et al. 2016; Villar and Naya 2018); or to evaluate fragmentation and/or loss habitats in a variety of ecosystems such as forests (Capizzi et al. 2003; Mortelliti et al. 2009, 2014; Bovendorp et al. 2018), deserts (Ernest et al. 2009; Bowman et al. 2017; Guevara and Ball 2018), and agro-ecosystems (Bond et al. 2004; Hurst et al. 2014; Fischer et al. 2018; Berl et al. 2018).

1.3 Small mammal database and data management

To study and understand small mammal changes and their response to human pressure we need a great amount of data to monitoring communities and species through time and space. Despite the rapidly increasing number of data sets across many taxonomic groups, data on small mammals are still scarce and underrepresented if compared to their global species richness (Wikelski et al. 2007). Only few recent studies have focused on big-data of small mammals, that can be a useful tool to study changes from a macroecological point of view (Escribano et al. 2016; Bovendorp et al. 2017; Mendonça et al. 2018). This is likely due to the elusiveness of small mammals as well as to problematics regarding taxonomic identification. Small mammals mainly include morphologically similar, small-sized and furtive species, making direct observation and identification logistically complicated. Small mammal' morphological and physiological characteristics as well as occurrences and abundances data may be collected in a precise way using live-traps (Flowerdew et al. 2004; Chiron et al. 2018) or through indirect samplings including droppings (Pocock and Jennings 2006), tracking-plates (Glennon et al. 2002; Hacker et al. 2016), hair-traps (Chiron et al. 2018), nest-boxes (Bright et al. 1994), and remains from owl pellets (Bonvicino and Bezerra 2003). Among these methods, owl pellet remains can provide data on a wide array of species living in a restricted area (Heisler et al. 2016), while the others target only one or few species (Mortelliti and Boitani 2007; Bertolino et al. 2009). Although small mammal sampling based on owl pellets presents some degrees of spatial inaccuracy (i.e. equivalent to the hunting range of the predator), it represents a cost-effective and efficient method to sample small mammal communities across broad spatial and temporal scales (Torre et al. 2004; Heisler et al. 2016). In addition, by including data on relative abundances, this method provides quantitative data

to investigate ecological processes at broad scales (Kattge et al. 2011; Sundstrom et al. 2012; Hurst et al. 2014), as well as the response of mammal communities to local or global changes (Lovegrove 2003; Blois et al. 2010; Santini et al. 2016; Pacifici et al. 2017).

1.4 Objectives of the research project

In this context, the specific aims of my Ph.D. project were:

- 1) Collecting and storing in an open-access georeferenced database, all available and newly gathered owl-pellet data for south-central Italy;
- 2) Analyzing the influence of micro-habitat and sustainable forest management practices on arboreal rodent species and evaluating of how species could act as bio-indicator of alternative forest management practices. This project has a focus on a Molise region' forested areas;
- 3) Investigating the relationships between small mammal diversity and landscape heterogeneity on a large geographic scale. Specifically, studying the consequences of landscape spatial configuration and its changes on small mammal communities. The study covers three Italian regions (Lazio, Abruzzo, and Molise).

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CHAPTER II

Small mammal database

2.1 OpenMICE: an open spatial and temporal data set of small mammals in south-central Italy based on owl pellet data.

Paniccia C, Di Febbraro M, Delucchi L, et al (2018) OpenMICE: an open spatial and temporal data set of small mammals in south-central Italy based on owl pellet data. Ecology. doi: 10.1002/ecy.2506

Database file created by SQLite is freely available at
<https://github.com/Envixlab/OpenMICE>

Source data is accessible at
<https://esajournals.onlinelibrary.wiley.com/action/downloadSupplement?doi=10.1002%2Fecy.2506&file=ecy2506-sup-0001-DataS1.zip>

Data Papers

Ecology, 0(0), 2018, pp. 1
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OpenMICE: an open spatial and temporal data set of small mammals in south-central Italy based on owl pellet data

CHIARA PANICCIA,^{1,4} MIRKO DI FEBBRARO,¹ LUCA DELUCCHI,² ROCCO OLIVETO,³ MARCO MARCHETTI,³ AND ANNA LOY¹

¹*EnvixLab, Dipartimento Bioscienze e Territorio, Università degli Studi del Molise, Contrada Fonte Lappone, Pesche 86090 Italy*

²*Department of Biodiversity and Molecular Ecology, Research and Innovation Centre, Fondazione Edmund Mach, Via E. Mach 1, San Michele all'Adige 38010 Italy*

³*Dipartimento Bioscienze e Territorio, Università degli Studi del Molise, Contrada Fonte Lappone, Pesche 86090 Italy*

Abstract. The use of database technologies as a tool for implementing data for quantitative ecological studies and biodiversity conservation planning has recently attracted the attention of the biological community. Despite the fact that the number of biodiversity data sets is quickly rising, online databases of small mammals are still scarce, especially for Mediterranean ecosystems. We implemented the first standardized and accessible georeferenced European database of small mammal occurrences, abundances, and functional traits. Data derived from owl pellets was obtained from different sources, including original field surveys, publications, gray literature, existing databases, and museum collections. The OpenMICE database covers the years 1972 to 2017 and includes nearly 50,000 individuals from 23 species (13 Rodentia and 10 Eulipotyphla) at 190 sites in south-central Italy. Our specific goals in compiling this data set were as follows: (1) to make data that is usually accessible to a restricted audience widely available; (2) to identify the gaps in knowledge about small mammal communities and guide future sampling and conservation efforts; and (3) to gain a first insight into small mammal diversity and abundance in the study area. The potential applications of our spatial relational database are many, from individual-based to community-based models as potential indicators of environmental changes at different geographical scales. Given the long-term support for data storage, the OpenMICE database could be further expanded to include other geographical contexts and implemented with new information and traits. We would appreciate that researchers cite this paper if using all or part of the data set. We also request that researchers and teachers inform us of how they are using the data. We intend to keep it up to date as novel studies become available (see *Data Availability*).

Key words: community assemblages; community ecology; functional traits; open data; owl pellets; small mammals; species composition.

The complete data sets corresponding to abstracts published in the Data Papers section in the journal are published electronically as Supporting Information in the online version of this article at <https://onlinelibrary.wiley.com/doi/10.1002/ecy.2506/supinfo>

DATA AVAILABILITY

Associated data are available at a GitHub repository (<https://doi.org/10.5281/zenodo.1342403>) and at <http://therio.unimol.it:8080/therio/openmice/>

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⁴E-mail: c.paniccia@studenti.unimol.it

2.1.2 Metadata

OpenMICE: an open spatial and temporal data set of small mammals in south-central Italy based on owl pellet data

Chiara Paniccia^{1*}, Mirko Di Febbraro¹, Luca Delucchi², Rocco Oliveto³, Marco Marchetti³, Anna Loy¹

¹ EnvixLab, Dipartimento Bioscienze e Territorio, Università degli Studi del Molise, Contrada Fonte Lappone, I86090 Pesche, Italy

² Department of Biodiversity and Molecular Ecology, Research and Innovation Centre, Fondazione Edmund Mach, Via E. Mach 1, 38010 San Michele all'Adige, Italy

³ Dipartimento Bioscienze e Territorio, Università degli Studi del Molise, Contrada Fonte Lappone, I86090 Pesche, Italy

* Correspondence and requests for materials should be addressed to Chiara Paniccia (email: c.paniccia@unimol.studenti.it).

Tel: +39 0874404140

Fax: +39 0874404123

INTRODUCTION

From the beginning of the 21st century, the rapid development of database technologies have drawn the attention of the scientific community, and digital inventories have become an important tool for conservation biology (Bonney et al. 2009; Dickinson et al. 2010; Turner et al. 2015; Sullivan et al. 2017). Biodiversity databases have been used to identify spatially-explicit biodiversity hotspots (Werner and Buszko 2005; Fattorini 2006; Trizzino et al. 2014; Maldonado et al. 2015), to assess the risk of species extinction (Pacifici et al. 2017; Crooks et al. 2017), to study trends in species distributions (Mouquet et al. 2015; Visconti et al. 2016), as well as to quantify the risk from invasive species (e.g. Bellard et al. 2017).

Open access data and citizen-science initiatives have increased the availability of biodiversity data (Reichman et al. 2011; Costello et al. 2013). Among the most significant initiatives is the Global Biodiversity Information Facility (GBIF 2018), which provides accessible and researchable information on georeferenced occurrence records, mainly from museum collections and research institutions (GBIF 2018). The GBIF has also provided the high-quality Darwin Core standard for structuring biodiversity databases (Wieczorek et al. 2012), adopted by other citizen science-based (e.g. eBird 2018, iNaturalist 2018, Ornitho 2018) or collection-based initiatives (e.g. Dietrich et al. 2012, IDigBio 2018, Invertnet 2018). Other initiatives such as the Encyclopedia of Life (EoL 2018) or the Animal Ageing and Longevity Database (De Magalhães and Costa 2009, AnAge 2018) provide descriptive information on species or focus on the biodiversity literature (e.g. BHL 2018). Online repositories are also available for specific regions or taxonomic groups, such as the Azorean Biodiversity Portal (Borges et al. 2010), Atlantic Small-Mammal (Bovendorp et al. 2017), Atlantic Bats (Muylaert et al. 2017), the World Register of marine Cave Species (WoRCS) (Gerovasileiou et al. 2016), GlobalAnts (Parr et al. 2017; GLAD 2018) and Malagasy Animal trait Data (MADA) (Razafindratsima et al. 2018).

In the past decades, research in mammalian ecology has been requiring more and more accurate spatial data, relying on rapidly increasing data sets collected by remote-sensing platforms, animal-borne sensors using GPS/ARGOS and other bio-logging technologies (Urbano et al. 2010; Urbano and Cagnacci 2014), genetics (Borisenko et al. 2008), or camera-traps (e.g. Lima et al. 2017). Despite the rapidly increasing number of data sets

across many taxonomic groups, data on small mammals are still scarce and underrepresented if compared to their global species richness (Wikelski et al. 2007). This is likely due to the elusiveness of small mammals as well as to problematics regarding taxonomic identification. Small mammals mainly include morphologically similar, small-sized and furtive species, making direct observation and identification logistically complicated. Small mammal occurrences may be collected in a precise way using live-traps (Flowerdew et al. 2004; Chiron et al. 2018). However, live trapping is highly demanding in terms of costs and efficacy to detect all small mammal species living in an area, and can be performed only by specialist. In contrast, indirect samplings can be managed by non-specialists, can be run at lower costs, and allow to cover wide geographic areas. Indirect samplings include droppings (Pocock and Jennings 2006), tracking-plates (Glennon et al. 2002; Hacker et al. 2016), hair-traps (Chiron et al. 2018), nest-boxes (Bright et al. 1994), and remains from owl pellets (Bonvicino and Bezerra 2003). Among these methods, owl pellet remains can provide data on a wide array of species living in a restricted area (Heisler et al. 2016), while the others target only one or few species (Mortelliti and Boitani 2007; Bertolino et al. 2009). Although small mammal sampling based on owl pellets presents some degrees of spatial inaccuracy (i.e. equivalent to the hunting range of the predator), it represents a cost-effective and efficient method to sample small mammal communities across broad spatial and temporal scales (Torre et al. 2004; Heisler et al. 2016). Also, by including data on relative abundances, this method provides quantitative data to the study of the ecological processes at broad scales (Kattge et al. 2011; Sundstrom et al. 2012; Hurst et al. 2014), and of the responses of communities to local or global changes (Lovegrove 2003; Blois et al. 2010; Santini et al. 2016; Pacifici et al. 2017).

Long-term online data sets on small mammals are available for the Neotropical region (e.g. Bovendorp et al. 2017, Mendonça et al. 2018), while they are rare for Europe, especially for the Mediterranean ecosystems (e.g. Escribano et al. 2016) which, in fact, are considered among the 25 most important hotspots of terrestrial biodiversity (Myers et al. 2000).

We implemented the first standardized and accessible georeferenced database of small mammal occurrence, abundance, and functional traits in south-central Italy (Figure 1), including records from 1972 to 2017. The database was implemented by exploring all the available sources of spatial data as well as by carrying out field surveys to cover the data-

deficient areas. By collecting a large amount of published and unpublished data about individual species throughout a network of collaborators and field surveys, we were able to provide information on species abundance at each site. In addition, we included functional traits data, such as trophic level, activity pattern, social and mating system, and life-history traits (Table 3). Functional traits represent an essential source of information to investigate relevant questions in ecology, such as the effect of habitat loss/degradation on species abundance (Kosydar et al. 2014), species vulnerability to climate change (Pacifici et al. 2017), alien species invasiveness (Capellini et al. 2015), or the role of functional diversity in maintaining ecosystem functioning (Luck et al. 2012).

On this regard many databases on small mammals (Bovendorp et al. 2017; Mendonça et al. 2018) include only abundance data. By combining abundance and functional traits data, our database represents a significant advance and a meaningful addendum to Italian mammal research. Overall, our data set incorporates 42 new, unpublished and 148 published small mammal sites covering more than 33,000 km² in south-central Italy (Figure 1). The data set combines 52,650 specimens belonging to 23 small mammal species, out of 45 occurring in Italy (Amori et al. 2008). Data was derived from 44 research studies, including original field surveys run for this study, covering a time span of 45 years (1972-2017).

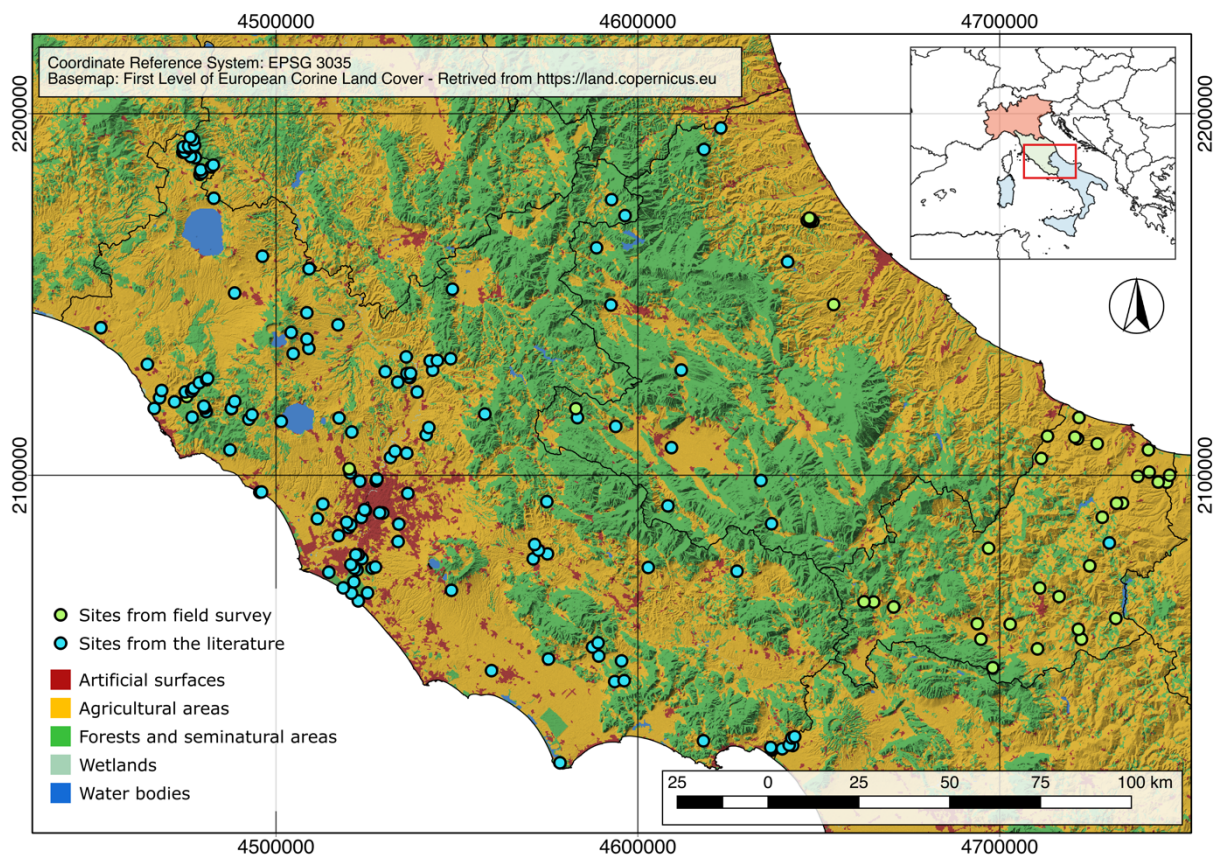


Figure 1. Distribution of the 190 owl pellet sites analyzed in the study. Light green: new sites surveyed in this study; light blue: sites obtained from the literature. At the top right corner, the colors identify: Northern Italy (light red), central Italy (light green), and southern Italy (light blue).

METADATA

CLASS I. DATA SET DESCRIPTORS

A. Data set identity: Five files: references, sites information, data, species information, predators information

Title: OpenMICE database: an open spatial and temporal data set of small mammals in south-central Italy based on owl pellet data.

OpenMICE is the first georeferenced database of the Micromammal communities of south-Central Italy, and it includes georeferenced sampling site localities and abundance, and functional trait data for species preyed upon by five owl species (*Athene noctua*, *Asio otus*, *Bubo bubo*, *Tyto alba*, and *Strix aluco*).

B. Data set and identification code:

- (1) OpenMICE_references.csv;
- (2) OpenMICE_sites_information.csv;
- (3) OpenMICE_data.csv;
- (4) OpenMICE_species_information.csv;
- (5) OpenMICE_predators_information.csv

C. Data set description:

1. Originators:

1. Chiara Paniccia, EnvixLab, Dipartimento Bioscienze e Territorio, Università degli Studi del Molise, Contrada Fonte Lappone, I86090 Pesche, Italy
2. Anna Loy, EnvixLab, Dipartimento Bioscienze e Territorio, Università degli Studi del Molise, Contrada Fonte Lappone, I86090 Pesche, Italy

Queries regarding the data sets should be sent to Chiara Paniccia (c.paniccia@studenti.unimol.it).

2. Abstract:

The use of database technologies as a tool for implementing data for quantitative ecological studies and biodiversity conservation planning has recently attracted the attention of the biological community. Despite the fact that the number of biodiversity data sets is quickly rising, online databases of small mammals are still scarce, especially for the Mediterranean ecosystems. We implemented the first standardized and accessible georeferenced European database of small mammal occurrences, abundances, and functional traits. Data derived from owl pellets was obtained from different sources, including original field surveys, publications, gray literature, existing databases and museum collections.

The OpenMICE database covers the years 1972 to 2017 and includes nearly 50,000 individuals from 23 species (13 Rodentia and 10 Eulipotyphla) at 190 sites of south-central Italy. Our specific goals in compiling this data set were as follows: (1) to make data that is usually accessible to a restricted audience widely available; (2) to identify the gaps in knowledge about small mammal communities and guide future sampling and conservation efforts; and (3) to gain a first insight into small mammal diversity and abundance in the study area.

The potential applications of our spatial relational database are many, from individual-based to community-based models as potential indicators of environmental changes at different geographical scales.

Given the long-term support for data storage, the OpenMICE database could be further expanded to include other geographical contexts, and implemented with new information and traits.

D. Keywords: *community assemblages; community ecology; open data; owl pellets; small mammals; species composition; functional traits.*

E. Description:

Data from owl pellets has been proven to provide a useful picture of the small mammals communities at a large geographic scale (Bertolino et al. 2001; Varuzza et al. 2001; Gormley et al. 2011; Meek et al. 2012; Cecere et al. 2013; Amori et al. 2015; Lemos et al. 2015). We present the OpenMICE database of small mammals occurring in owl pellet remains in south-central Italy that includes (i) information on species occurrence and abundance, (ii) a list of functional traits, (iii) spatial distribution of species richness and guilds across the study area, and (iv) temporal trends in the relative abundances of taxa.

We collected and stored 52,650 specimens from 190 owl pellet sites (Figure 1). The database covers 23 species, out of 26 which are known to occur in the study area (Amori et al. 2008), and 45 years (1972-2017). Each species is characterized by 27 functional traits extracted on relevant databases, review papers, and monographs (see Table 3 and OpenMICE_species_information.csv). We gathered the following traits: trophic level, prevalent habit, activity pattern, guild, habitat preference, social system, communal nesting, breeding site, mating system, pattern of torpor, invertebrates controller, seed disperser, spore disperser, pollinator, soil aerator, damage to forestry, damage to agriculture, body mass, female sexual maturity, litter size, litters per year, longevity, gestation time, typical body temperature, basal metabolic rate, generation length and a list of predators (for details, see Table 3).

The collected records belong to order Rodentia ($n = 41,401$, 79.05%), and Eulipotyphla ($n = 10,971$, 20.95%). Occurrence data for both orders shows strong temporal variability throughout the sampling period (Figure 2).

Figure 3 shows the abundance of each species: *Microtus savii* and *Apodemus sp.* were the most common taxa (15,843 and 13,377 specimens, respectively) followed by *Apodemus sylvaticus*, *Crocidura suaveolens*, *Crocidura leucodon*, and *Mus domesticus* (ranging between 3,509 and 4,399 specimens). The rarest species were the Mediterranean Mole, *Talpa caeca*, the Edible Dormouse, *Glis glis*, and the Eurasian Red Squirrel, *Sciurus vulgaris* (between 3 and 9 total specimens). *Muscardinus avellanarius*, which is included in Appendix IV of European Habitats Directive 1992/43/EEC, was the most common species of Gliridae (1,310 specimens at 98 sites).

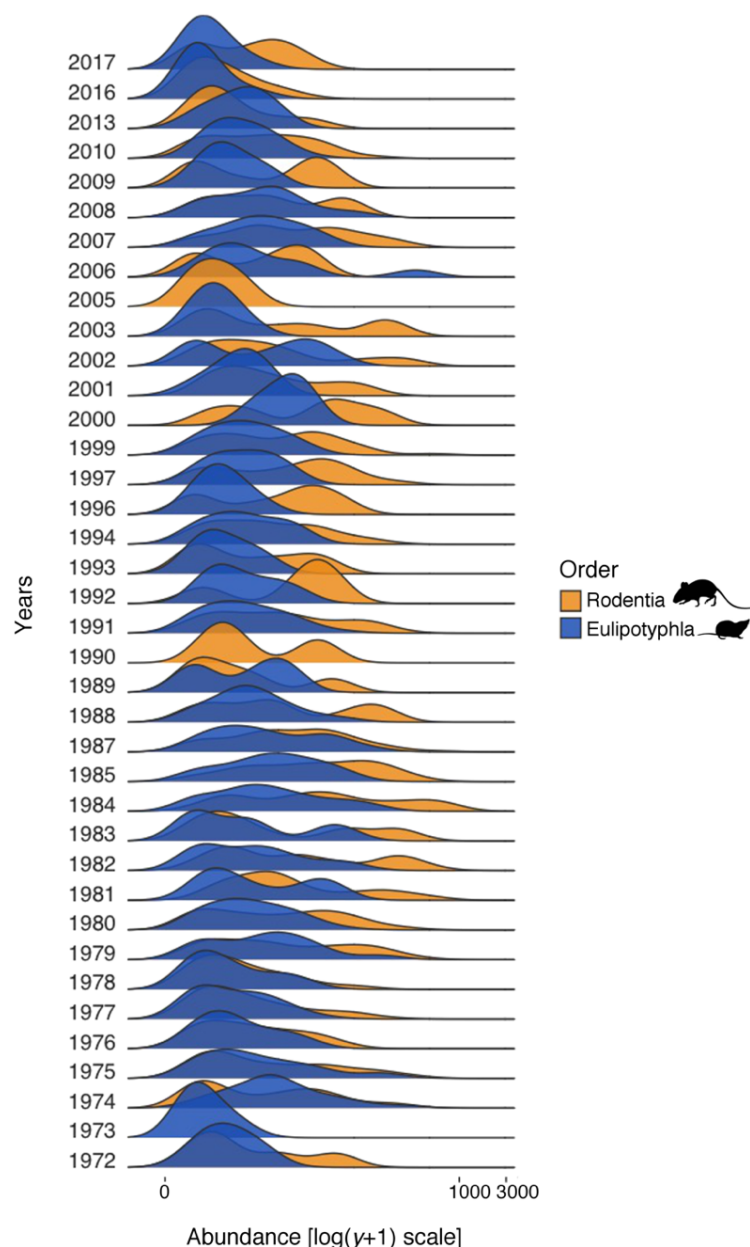


Figure 2. Density plots show order rating, and abundance data for each year of sampling. For each panel, kernel density estimates were calculated using the same bandwidth. All abundances are \log_{10} plus one transformed.

Among the species of conservation concern (Table 1), we found four species listed as Data Deficient in the Italian Red List (Rondinini et al. 2013): *Talpa caeca* ($n = 3$), *Sorex antinorii* ($n = 136$), *Neomys fodiens* ($n = 19$), *Neomys milleri* ($n = 19$) and two species listed as Near Threatened: *Arvicola italicus* ($n = 101$) and *Eliomys quercinus* ($n = 16$). Herbivores ($n = 17,184$) were the most commonly represented prey followed by omnivores ($n = 10,432$) and carnivores (i.e. insectivores; $n = 9,055$) (see Figure 4B).

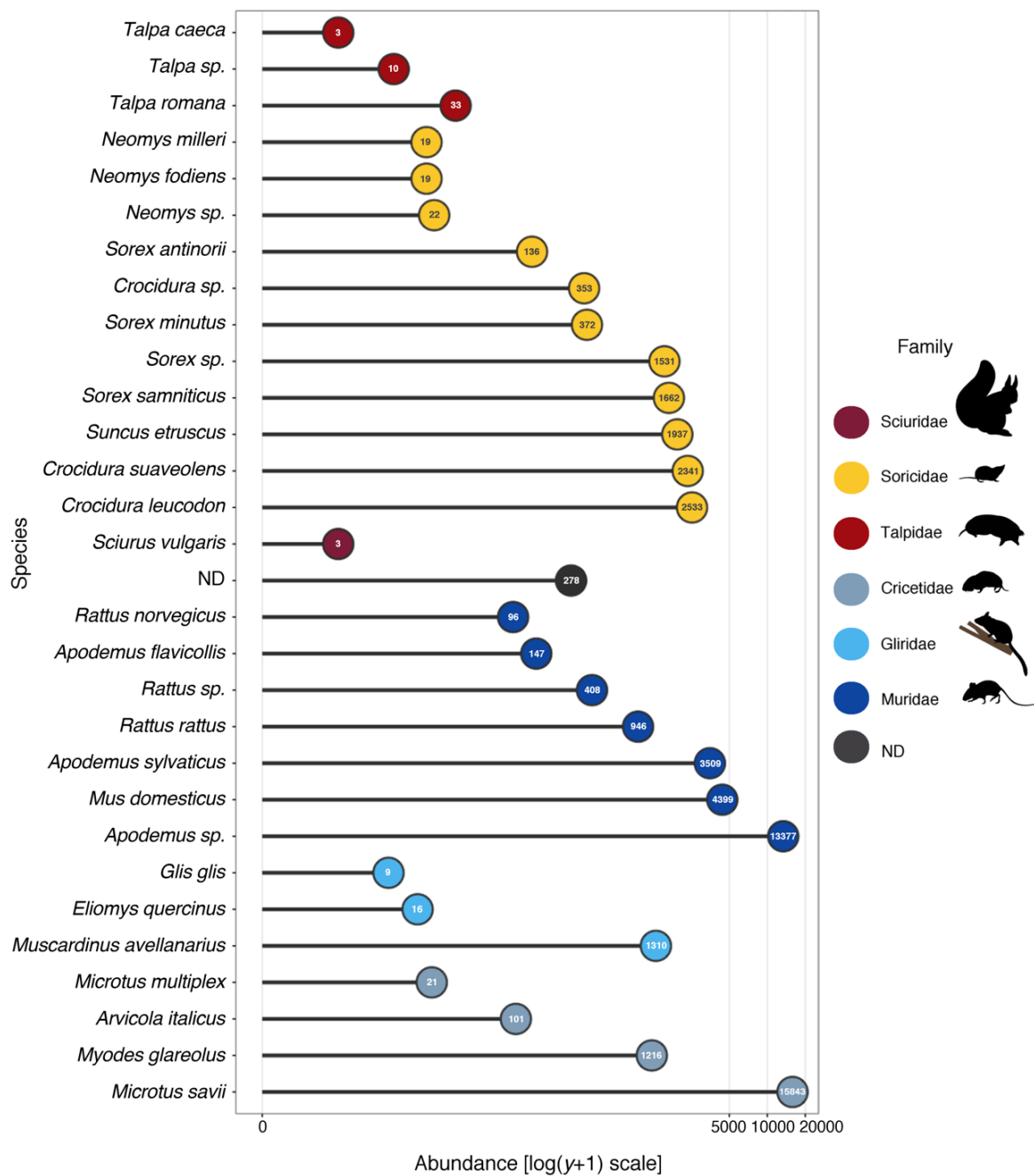


Figure 3. Number of individuals per taxa. The actual number of specimens collected are shown within the points; ND = not identified. All abundances are log10 plus one transformed.

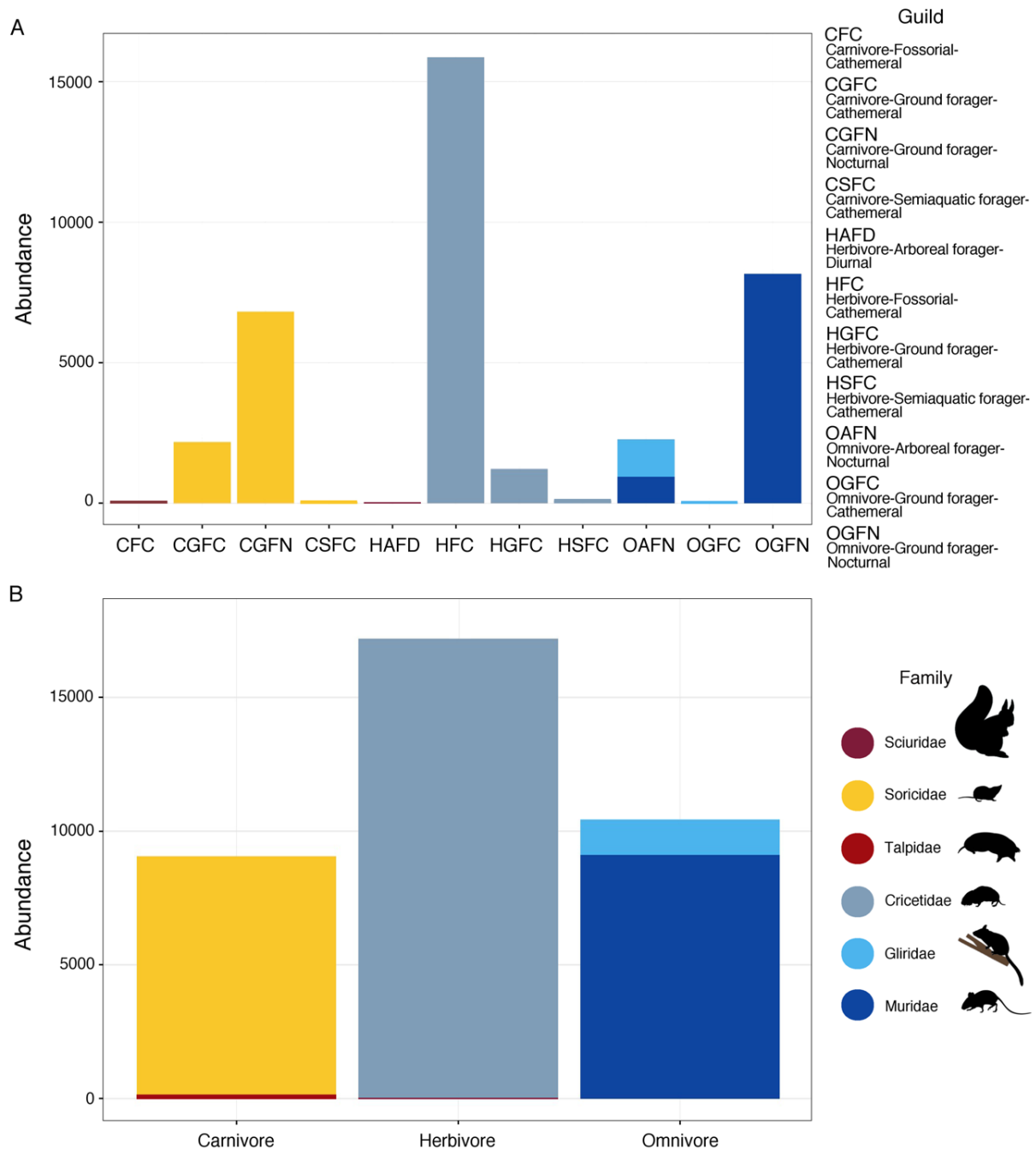


Figure 4. Number of individuals per guild (A) and trophic level (B). Abundance refers the total number of specimens for each family.

Species and guild richness were mapped by overlaying occurrence data with a 10 x 10 km square grid cell and summing the number of species occurring within each cell. Specifically, the median number of species per cell was 7 ($SD = \pm 0.69$), ranging from 1 to 18 species (Figure 5A), while the median number of guilds per cell was 5 ($SD = \pm 0.66$), ranging from 1 to 10 guilds (Figure 5B).

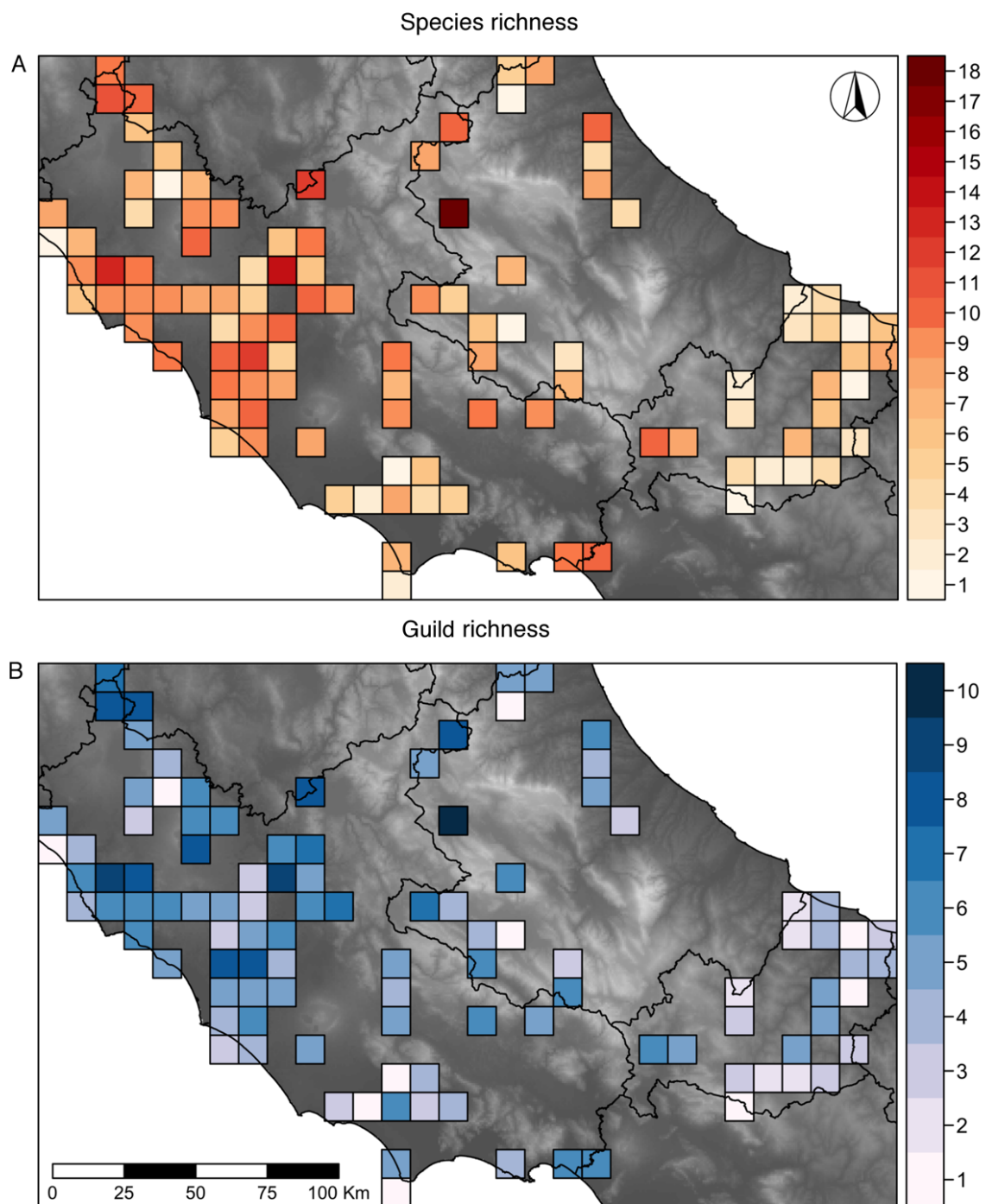


Figure 5. Distribution of small mammal diversity within each 10 km x 10 km cell. A) Species richness: number of species; B) Guild richness: number of guilds (guilds are shown in Table 3).

CLASS II. RESEARCH ORIGIN DESCRIPTORS

A. Overall project description

1. Identity:

A compilation of species-level occurrence, abundance, and functional traits information on small mammals from south-central Italy derived from owl pellet remains at 190 sites.

2. Period of study:

Field surveys were run between 2015 and 2017. Dates of source publications range from 1972 to 2017.

3. Objectives:

During the last century, both the abundance and range of species have substantially declined due to habitat loss, fragmentation and deterioration (Walther et al. 2002; Carpenter et al. 2010; Maiorano et al. 2011; Foley et al. 2012; Kosydar et al. 2014; Pacifici et al. 2017).

The effects of human activities on biodiversity can be measured by analyzing spatial and time-series data from ecological communities, assemblages or populations to relate changes in biodiversity to changes in human activity (Magurran et al. 2010; Vačkář et al. 2012; Turner et al. 2015).

However, long-term data suitable for such modeling techniques has limited coverage both geographically and taxonomically and often only record the presence or absence of species (Dornelas et al. 2012).

In this context, even the smallest data sets can contribute key knowledge to inform large-scale problem solving, as this data is frequently produced by hands-on work at scales not under-taken by others (Hampton et al. 2013).

Our data set represents a first attempt to obtain an inventory of small mammal communities that includes occurrence, abundance, and functional trait data, which will have potential applications in macro-ecological studies, conservation strategies and community ecology

research (Homburg et al. 2014; Kosydar et al. 2014; Sullivan et al. 2017).

Our specific goals in compiling this data set were as follows: (1) summarize information about small mammal inventories derived from owl pellets in south-central Italy with a focus on species richness, abundance, and functional traits; (2) make data that is usually restricted to specialized research groups available to a large audience; and (3) fill gaps in knowledge of small mammals in south-central Italy to guide future sampling and conservation efforts.

4. Abstract: Same as above.

5. Source (s) of funding:

CP is supported by a three years PhD fellowship at the University of Molise (Italy).

B. “Specific subproject” description

1. Site description:

The OpenMICE database covers a study area of ca. 33,000 km² in south-central Italy (Figure 1), which is characterized by a wide range of climate conditions from oceanic to Mediterranean and is associated with high landscape diversity from the Tyrrhenian and Adriatic coastal zones to the Apennine chain (Marchetti et al. 2017).

2. Experimental or sampling design

Data collection:

We first performed data gathering that included an exhaustive literature review of data on pellets obtained from five owl species occurring in Italy (i.e. *Athene noctua*, *Asio otus*, *Bubo bubo*, *Tyto alba*, and *Strix aluco*).

Between 2015 and 2017, we performed approximately 200 field surveys to fill spatial data gaps and discovered 42 new sampling sites (see Figure 1). Owl pellets were searched for and collected at both the nesting and roosting sites of Common Barn-Owls (*Tyto alba*), Eurasian Eagle-Owls (*Bubo bubo*), Little Owls (*Athene noctua*), Northern Long-eared Owls (*Asio otus*), and Tawny Owls (*Strix aluco*). Pellets were transferred to the laboratory,

treated with camphor to remove arthropods, and soaked in warm water, and the remains were dissected by separating the bones from the fur and feathers (Yalden and Morris 2003). Species identification was mainly based on head parts following a standard methodology with particular reference to tooth root patterns (Nappi 2001; Yalden and Morris 2003). When key characters were missing (e.g. teeth), specimens were identified to the level of genus. The number of individuals of each species was ascertained by counting skulls and left and right lower jawbones (Contoli 1986; Nappi 2001). Skulls and mandibles were sealed in zip plastic bags and labelled with an identification number, taxonomic information, coordinates of the sampling site, and sampling date. All samples were stored in the Zoological Collection of the Department of Biosciences and Territory at the University of Molise, Italy.

3. Research methods:

The following Internet search engines were used to find peer-reviewed articles on owl pellet analyses in the study area: Google Scholar (<http://www.scholar.google.com>), Scopus (<https://www.scopus.com>), ISI Web of Science (<https://www.ebofknowledge.com>) and ResearchGate (<https://www.researchgate.net>). The following keywords were combined to search for articles: *owl**, *diet**, *bird of prey**, *prey**, *regurgitated pellets**, *small mammal**, *Barn Owl**, *Asio otus**, *Bubo bubo**, *Athene noctua**, *Strix aluco**, *Tyto alba**, *Prey abundance**, *pellet**, *Small mammal community**, *Italy**, *central Italy**. In addition, we analyzed all alternative sources of data including unpublished material such as BA, MSc and PhD dissertation theses, expert field reports, museum collections, occasional samplings and data mined from gray literature. This last source included technical reports, protected areas and Natura 2000 management plans, monographs, zoological reports and un-published databases such as SISTRO (Contoli et al. 1985). Finally, we interviewed scientists and organizations known to have conducted owl pellet surveys in the study area. Small mammal data (occurrence and abundance) was obtained from a list of 44 studies (included in the file OpenMICE_references.csv) and on our own unpublished data. The bibliographic information and details for each sampling site were stored in an Excel file. The coordinates of each site were recorded as latitude and longitude (WGS84 datum), and when not provided by the authors, the geographic coordinates of sampling localities were derived from maps or schemes available from the published sources.

The geographic coordinates of each site were obtained using a Geographic Information System (GIS) for each site center or point location using the software QGIS (QGIS Development Team 2016). All information on sampling sites (i.e. latitude, longitude, elevation, verbatim locality, municipality, province and region) and the spatial inaccuracies (sources or degrees of uncertainty in georeferenced locality) were included in a specific section of OpenMICE (OpenMICE_sites_information.csv; Table 2).

We standardized all records according to the DarwinCore Terms (Wieczorek et al. 2012). It should be emphasized that the term “event_date” corresponds to the date on which the pellets were collected and not the date that the prey was captured, which is unknown.

We provided the abundance values at the sampling site for each small mammal species. Abundances were directly extracted from the original articles or original data sets as described in the Research methods section.

Additionally, we recorded 27 functional and ecological traits for each small mammal species that were derived from the literature such as relevant databases, review papers, and monographs (see OpenMICE_references.csv; Table 3).

Data was gathered for the following traits: life-history traits (i.e. activity pattern, social system, mating system, pattern of torpor, body mass, litter size, litters per year, longevity, typical body temperature, basal metabolic rate, female sexual maturity, gestation time, generation length), ecological traits (i.e. trophic level, habitat preference, prevalent habit, breeding site, communal nesting, guild), functional role in ecosystem (i.e. invertebrates controller, seed disperser, spore disperser, pollinator, soil aerator), ecosystem impact (damage to forestry and to agriculture), and a list of predators (for details, see Table 3).

All information was stored in a relational SQLite database (Halder 2015).

We worked with a local database such as SpatiaLite (SpatiaLite 2018), a user-friendly software, that restricts data entry to a single person and may limit the possibility of errors or redundancies. This also allows the database to be archived in a single file and for data to be easily shared with other collaborators.

The OpenMICE database was designed following normalization rules to minimize redundancy and dependency, and to isolate data. This means that design changes (e.g. additions and modifications of a field) can be made in just one table and then propagated throughout the database (Codd 1971). Thus, data is addressed by value rather than position, and larger tables are divided into smaller ones with defined relationships among them. Data

standardization derives from the constraints of the fixed architecture of the database. The database is designed around a circular (and fixed) relation with five central tables, i.e. “species_information”, “sites_information”, “predators_information”, “references”, and “data”. The organization of the database and the SQLite format are freely available for download at <http://therio.unimol.it:8080/therio/openmice/> and at a GitHub repository (<https://doi.org/10.5281/zenodo.1342403>).

Taxonomy and systematics:

The taxonomic scheme and the nomenclature reported in the original sources were homogenized and updated according to recent taxonomic revisions following Amori et al. (2008), Wilson and Reeder (2005), Mammal Diversity Database (2018), and the Catalogue of Life (2018).

C. Data Limitations and Potential Enhancements:

Users of these data should be aware that the small mammal occurrence data is derived from owl pellet remains, so the data correspond to the owl resting or nesting site. Therefore, the spatial accuracy of an occurrence datum is equivalent to the hunting range of the predator (Contoli 1975; Lovari et al. 1976). This limitation is especially relevant for spatial distribution modeling and habitat preference analysis.

Prey selection by owls can be affected by various factors: latitude, habitat (de la Peña et al. 2003; Bond et al. 2004), season (Romanowski and Zmihorski 2008), foraging preferences (Bertolino et al. 2001; Embar et al. 2014), prey abundance and size (Comay and Dayan 2018). Common Barn-Owls and Little Owls prefer to hunt in open habitat, avoiding large forests areas (Zerunian et al. 1982), Tawny Owls, and Northern *Long-eared Owls* hunt in woodlands or at their margin (Bertolino et al. 2001; Cecere et al. 2013), while Eurasian Eagle-Owls in open habitats or at the edge of woodlands (Sergio et al. 2007). Although certain owls show feeding preferences, the Common Barn-owl is a non-selective predator which hunts any available prey in the area (Capizzi and Luiselli 1995), and is considered as the best tool to collect small-mammal communities data (Alasdair Love et al. 2000; Heisler et al. 2016). The Eurasian Eagle-Owl is considered as a food and habitat generalist (Sergio et al. 2007), while the Tawny Owl is a generalist predator. The Northern *Long-*

eared Owl is considered a food specialist, its diet being mostly composed by rodents (Capizzi et al. 1998; Bertolino et al. 2001). The Tawny Owl preys more on invertebrates or forest small mammals (Galeotti et al. 1991; Galeotti 1994). Last, the Little Owl diet includes a broad spectrum of prey, especially insects (Zerunian et al. 1982; Gotta and Pigozzi 1997).

The prey size spectra could be a source of bias on real abundance data. Comay and Dayan (2018) found a strong relationship between predator body size and prey size. Capizzi and Luiselli (1998) and Alivizatos et al. (2005) explored different diet of owls and reported that the larger owl species take significantly heavier prey than the smaller ones.

Additionally, although the majority of small mammal species that occur in south-central Italy are represented in our database, some species are rare or totally lacking due to their elusiveness (e.g. *Talpidae*) or diurnal habits (e.g. *Sciuridae*), and sampling abundances are, as already mentioned, biased toward preferred owl preys.

More specifically, OpenMICE does not include three species that occur in the study area: the European Snow Vole (*Chionomys nivalis* Martin, 1842), the Western European Hedgehog (*Erinaceus europaeus* Linnaeus, 1758), and the Calabria Pine Vole (*Microtus brachycercus* von Lehmann, 1961). The European Snow Vole has rarely been found into *Strix aluco* (Nappi et al. 2007) and *Asio otus* pellets (Gerdol et al. 1982). Also, in the Apennines the species is a glacial relict (Amori et al. 2008), living in restricted open areas above 1,000 m (Nappi 2002), while owls that forager in open areas are distributed under 1200 m asl (Brichetti and Fracasso 2006).

The Western European Hedgehog may weigh up to 1 kg and it has been normally reported in the diet of *Bubo bubo* (Marchesi et al. 2002; Sergio et al. 2007) though, hedgehogs have rarely been tracked into the pellets of *Asio otus* (Comay and Dayan 2018).

The Calabria Pine Vole is endemic to the Calabrian Peninsula (Wilson and Reeder 2005), though genetic data also indicates its occurrence in Abruzzo and Molise regions (Castiglia et al. 2008; Bezerra et al. 2016). However, it is not yet possible to distinguish this species from *Microtus savii* on skull measurements and molar teeth morphology (Amori et al. 2008; Bezerra et al. 2016). Based on these considerations, it could not be excluded that some *Microtus savii* samples could belong to *Microtus brachycercus*.

Another consistent limitation of the OpenMICE data set is the uneven sampling across space and time due to our opportunistic sampling design, which was based on available studies and owl pellet sites.

Some limitation is also apparent at the taxonomic level, as species identification is sometime limited to the genus (Nappi 2001). We specifically used genera to identify similar species such as *Apodemus sp.* (*A. flavicollis/A. sylvaticus*) or *Neomys sp.* (*N. fodiens/N. milleri*) from limited data such as skull fragments or damaged teeth morphology (Amori et al. 2008).

Despite these impediments and limitations, OpenMICE represents the best available data set on the small mammals occurring in Italy. The outcomes from this data set can detect gaps to improve the sampling of terrestrial mammals and facilitate the understanding of community composition and potential trophic cascades (Szpunar et al. 2008; Rugiero et al. 2012; Milana et al. 2016, 2018; Roulin 2016).

Future studies based on this database will contribute to improved knowledge on how global changes (e.g., climate, land use) may act to rearrange species distributions and community assemblages, providing relevant information to develop adaptive strategies for preserving small mammal biodiversity.

The OpenMICE data set could be easily implemented with data from other geographic contexts, and with occurrence, and abundance data from other sampling approaches with higher spatial accuracy, such as road-killed animals, live and hair trapping, nest box occupancy studies, and, more rarely, camera trapping.

CLASS III. DATA SET STATUS AND ACCESSIBILITY

A. Status

Latest update: July 2018

Latest archive date: July 2018

Metadata status: Last updated July 2018, version submitted

Data verification:

Chiara Paniccia collected original data in the field, identified part of specimens, searched and read studies for inclusion on this data set, checked data, converted all latitudes and longitudes to Geographic Coordinate System WGS84, checked site locations by using Google Earth, corrected transcription errors, and updated the taxonomic information (see the Research methods section for further details). Chiara Paniccia and Mirko Di Febbraro analyzed the data set and produced the figures. Anna Loy reviewed the taxonomy and conceived the work with Chiara Paniccia and Rocco Oliveto. Chiara Paniccia, Mirko Di Febbraro, and Anna Loy wrote and revised the manuscript. Marco Marchetti provided fundings to CP for her fieldwork and contributed overview advices for functional traits. Luca Delucchi and Chiara Paniccia designed the structure and produce the SQLite version of the database. Rocco Oliveto provided access to <http://therio.unimol.it:8080/therio/openmice/>.

The data set may be limited by select cases of missing data and uncertainty in the literature, and will definitely benefit from further quality control and curation. We aim to facilitate this process by sharing our current data and any future updates and/or revisions at <http://therio.unimol.it:8080/therio/openmice/> and at a GitHub repository (<https://doi.org/10.5281/zenodo.1342403>).

B. Accessibility

1. Storage location and medium:

Associated data are available at a GitHub repository (<https://doi.org/10.5281/zenodo.1342403>) and at <http://therio.unimol.it:8080/therio/openmice/>

Contact person:

Chiara Paniccia

EnvixLab, Dipartimento Bioscienze e Territorio, Università degli Studi del Molise,
Contrada Fonte Lappone, I86090 Pesche, Italy

Email: c.paniccia@unimol.studenti.it

2. Copyright restrictions:

None.

Proprietary restrictions

We would appreciate that researchers cite this paper if using all or part of the data set.
We also request that researchers and teachers inform us of how they are using the data.
We intend to keep it up to date as novel studies become available (server link above).

Costs: None

CLASS IV. DATA STRUCTURAL DESCRIPTORS

A. Data set file

1. Identity:

- (1) OpenMICE_references.csv
- (2) OpenMICE_sites_information.csv
- (3) OpenMICE_data.csv
- (4) OpenMICE_species_information.csv
- (5) OpenMICE_predators_information.csv

2. Size:

- (1) 159 records (included header) and 5 fields. Total file size is 33 KB
- (2) 195 records (included header) and 13 fields. Total file size is 29 KB
- (3) 2000 records (included header) and 13 fields. Total file size is 279 KB
- (4) 31 records (included header) and 68 fields. Total file size is 29 KB
- (5) 6 records (included header) and 14 fields. Total file size is 4 KB

Format and storage mode: available as comma-separated values (*.csv)

Other information

Header: Headers describe contents of columns. Detailed descriptions of column headers and contents are shown in Tables 2, 3, 4.

Alphanumeric attributes: Mixed

Data anomalies: If no information is available for a given record the field is empty.

Special characters/fields: None

B. Variable information

- 1) Table 2. Tables information.
- 2) Table 3. Species information.
- 3) Table 4. References information.

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TABLES

Table 1. List of small mammal species included in OpenMICE with their conservation status according to the IUCN – Italian Red List (Rondinini et al. 2013).

Scientific name	Accepted name usage	IUCN National Assessment
<i>Apodemus flavicollis</i>	Yellow-necked Field Mouse	LC
<i>Apodemus sylvaticus</i>	Long-tailed Field Mouse	LC
<i>Arvicola italicus</i>	European Water Vole	NT
<i>Crocidura leucodon</i>	Bicolored Shrew	LC
<i>Crocidura suaveolens</i>	Lesser Shrew	LC
<i>Eliomys quercinus</i>	Garden Dormouse	NT
<i>Glis glis</i>	Edible Dormouse	LC
<i>Microtus multiplex</i>	Alpine Pine Vole	LC
<i>Microtus savii</i>	Savi's Pine Vole	LC
<i>Mus domesticus</i>	House Mouse	NA
<i>Muscardinus avellanarius</i>	Common Dormouse	LC
<i>Myodes glareolus</i>	Bank Vole	LC
<i>Neomys fodiens</i>	Eurasian Water Shrew	DD
<i>Neomys milleri</i>	Southern Water Shrew	DD
<i>Rattus norvegicus</i>	Brown Rat	NA
<i>Rattus rattus</i>	House Rat	NA
<i>Sciurus vulgaris</i>	Eurasian Red Squirrel	LC
<i>Sorex antinorii</i>	Valais Shrew	DD
<i>Sorex minutus</i>	Eurasian Pygmy Shrew	LC
<i>Sorex samniticus</i>	Apennine Shrew	LC
<i>Suncus etruscus</i>	Pygmy White-toothed Shrew	LC
<i>Talpa caeca</i>	Mediterranean Mole	DD
<i>Talpa romana</i>	Roman Mole	LC

Table 2. Description of variables included in the tables. DATA – file OpenMICE_data.csv; SITES INFORMATION – file OpenMICE_sites_information.csv; PREDATORS INFORMATION – file OpenMICE_predators_information.csv.

Table name	Field label	Variable definition	Levels	Format
DATA	id	Unique code identifying each entry	1-1999	integer
	inserted_by	A list (concatenated and separated) of names of people responsible for inserting data in the OpenMICE database	1-2	text
	species_information_id	Unique code identifying each species or genus included in the OpenMICE database	1-30	
	event_date	The verbatim original representation of the date information. The date refers to the event when owl pellets were collected		text
	sites_information_id	Unique code identifying each site and related information	1-194	integer
	predators_information_id	Unique code identifying each predator species (owl)	1-5	text
	identified_by	A list (concatenated and separated) of names of people, groups, or organizations who identified the Taxon	1-40	text

DATA	references_id	Unique code identifying each reference for record attribution	1-45	integer
	dataset_name	An identifier for the collection or data set from which the record was derived	1-4	text
	institution	An identifier for the institution having custody the related voucher specimens (collection or museum)	1-5	text
	rights_holder	A person or organization owning or managing rights over the resource	1-48	text
	recorded_by	A list (concatenated and separated) of names of people, groups, or organizations responsible for recording or collecting owl pellets	1-53	text
	individual_count	The number of specimens found in owl pellets at each survey. Species abundance data were extracted directly from the species lists published in primary research articles or collected from field surveys		text

SITES INFORMATION	id	Unique code identifying each site information	1-194	integer
	occurrence_code	Unique code identifying each coordinate, event date and geographical region	1-194	text
	latitude	Latitude in decimal degrees: EPSG 4326		numeric
	longitude	Longitude in decimal degrees: EPSG 4326		numeric
	locality	The specific description of the place. This term may contain information modified from the original to correct perceived errors or standardize the description		text
	verbatim_locality	The original textual description of the place		text
	municipality	The name of a single urban or administrative division. Site name as given by original authors or as defined by us where there was no unique name given to the site		text
	province	The name of the Italian administrative division in which the location occurs		text
	region	The full, unabbreviated name of the Italian administrative region in which the location occurs		text

	georeferenced_by	A list (concatenated and separated) of names of people, groups, or organizations who georeferenced (spatial representation) the location	1-4	text
	georeferenced_sources	A list (concatenated and separated) of maps, gazetteers, or other resources used to georeferenced the location	1-11	text
	coordinate_precision	Georeferencing accuracy of site. Categories are: Low (general description of the topography, physical features of an area), Medium (toponym), High (GPS coordinates)	1-3	text
	elevation_in_meters	The original description of the elevation (meters) of the location		numeric
PREDATORS INFORMATION	id	Unique code identifying each entry	1-5	integer
	class	Class in which the given species is included	1	text
	order	Order in which the given species is included	1	text
	family	Family in which the given species is included	1-2	text
	genus	Genus in which the given species is included	1-5	text
	species	The epithet of the species	1-5	text
	scientific_name	The species binomial name	1-5	text

PREDATORS INFORMATION	common_name	Species English common name	1-5	text
	iucn_national_status	The current conservation status, following the IUCN Italian Red List Rondinini et al. (2013). Categories are: Extinct (EX), Extinct in the wild (EW), Endangered (EN), Regionally Extinct (RE), Critically endangered (CR), Vulnerable (VU), Near Threatened (NT), Least Concern (LC), Data Deficient (DD), Not applicable (NA)		text
	scientific_name_authorship	The authorship information for the scientific name		text
	hunting_territory_(mean_m)	Mean radius for hunting territory (expressed in meters). Data were extracted from the literature		numeric
	hunting_territory_(min_m)	Minimum radius for hunting territory (expressed in meters). Data were extracted from the literature		numeric
	hunting_territory_(max_m)	Maximum radius for hunting territory (expressed in meters). Data were extracted from the literature		numeric
	references_id	Unique code identifying each bibliographic reference for record attribution		integer

Table 3. Species information: Summary of variables information and functional traits data available for each small mammal species – file

OpenMICE_species_information.csv. If no information is available for a given record the field is empty.

Table name	Field label	Variable definition	Format
SPECIES INFORMATION	id	Unique code identifying each entry	integer
	class	Class in which the given species is included.	text
	order	Order in which the given species is included	text
	family	Family in which the given species is included	text
	genus	Genus in which the given species is included	text
	species	Specific epithet of the given species	text
	scientific_name	Binomial name of the given species	text
	accepted_name_usage	Full taxon name, with authorship and date information of the currently valid zoological taxon	text
	common_name	Species English common name	text
	iucn_national_status	The current conservation status, following the IUCN Italian Red List Rondinini et al. (2013). Categories are: Extinct (EX), Extinct in the wild (EW), Endangered (EN), Regionally Extinct (RE), Critically endangered (CR), Vulnerable (VU), Near Threatened (NT), Least Concern (LC), Data Deficient (DD), Not applicable (NA)	text
	habitat_directive	Number of Annex in which the species is listed under the Habitats Directive (1992/43/EEC)	text

SPECIES INFORMATION	trophic_level	The trophic level which the given species belongs. Categories are: Carnivore (predominantly eating animals), Herbivore (predominantly eating plant material), Omnivore (feeding on both animals and plants)	text
	prevalent_habit	The prevalent habit of a species. Categories are: Above ground, Arboreal, Fossorial, or Semi-aquatic	text
	activity_pattern	Daily activity cycle of the species. Categories are: Diurnal (obligate diurnal), Nocturnal (obligate nocturnal), Cathemeral (irregularly active at any time of night or day) or Cathemeral-Polyphasic (cathemeral pattern with several short-term activity cycles per 24h), according to Halle and Stenseth (2012)	text
	guild	Ecological guild of the species, described by combining trophic level, foraging habit and the activity pattern. Categories are: Carnivore – Fossorial – Cathemeral, Carnivore – Ground forager – Cathemeral, Carnivore – Ground forager – Nocturnal, Carnivore – Semi-aquatic forager – Cathemeral, Herbivore – Arboreal forager – Diurnal, Herbivore – Fossorial – Cathemeral, Herbivore – Ground forager – Cathemeral, Herbivore – Semi-aquatic forager – Cathemeral, Omnivore – Arboreal forager – Nocturnal, Omnivore – Ground forager – Cathemeral, and Omnivore – Ground forager – Nocturnal	text
	habitat_preference	Preferred habitat of the species. Categories are: Agricultural areas, Artificial surfaces, Forest and semi natural areas, Water body	text

SPECIES INFORMATION	social_system	Degree to which individuals tend to associate in social groups and form cooperative societies. Categories are: Solitary or Group-living	text
	communal_nesting	Whether individuals of the species share nest with conspecifics during winter time or breeding season. Presence of communal nesting (1); Absence of communal nesting (0)	integer
	breeding_site	Location used as breeding site by the species. Categories are: Arboreal or Underground	text
	mating_system	The prevalent mating strategy of the species. Categories are: Monogamy or Polygamy	text
	pattern_of_torpor	Patterns of torpor of the species. Categories are: Daily torpor or Hibernator, according to Ruf and Geiser (2015)	text
	invertebrates_controller	Whether individuals of the given species mainly feed on invertebrates or are considered as controller of invertebrate populations (1) or not (0)	integer
	seed_disperser	Whether individuals of the given species eat or stores seeds, contributing to their dispersal (1) or not (0)	integer
	spore_disperser	Whether individuals of the given species eat fungi, contributing to their dispersal (1) or not (0)	integer
	pollinator	Whether individuals of the given species feed on flowers (1) or not (0)	integer
	soil_aerator	Whether individuals of the given species create burrows or stirs up the soil (1) or not (0)	integer
	damage_to_forestry	Whether the given species is considered noxious for forest plants (1) or not (0)	integer

SPECIES INFORMATION	damage_to_agriculture	Whether the given species is considered noxious for cultivated plant or a pest for stored foodstuff in European agricultural systems (1) or not (0)	integer
	body_mass	Mean mass (grams), which refers to the mean mass of individuals (age unspecified) of the species	decimal
	litter_size_mean	Litter size, considered as the mean number of offspring born per litter per female	decimal
	litters_per_year	The mean number of litters per female per year	decimal
	female_sexual_maturity_(d)	Age at first conception (days)	integer
	maximum_longevity	Maximum adult age measured in captivity or in wild populations (years)	decimal
	gestation_time_(d)	Gestation time (days)	decimal
	typical_body_temperature_(C°)	Mean body temperature expressed in C° (age unspecified)	decimal
	basal_metabolic_rate_(mlO₂/h)	Basal metabolic rate (mL O ₂ /h) of adult individual(s) (or age unspecified)	decimal
	generation_length_(d)	Generation length (days), which refers to the average age of parents of the current cohort, defined following Pacifici et al. (2013)	decimal
	predators	A list (concatenated) of predators known to feed upon the species	text
	references_id	Unique code identifying each reference for traits attribution	integer

Table 4. References information: Description of the fields related with reference information of each study. When this information came from unpublished source collected by our research groups, we cited it as unpublished data – file OpenMICE_references.csv

Table name	Field	Description	Levels	Example
REFERENCES	id	Unique code identifying each entry	1-158	1
	reference	Extended information of the reference		Aloise, G., M. Pelosi, and M. Ronca. 1990. I popolamenti di micromammiferi della riserva naturale “Monte Rufeno” (Lazio): dati da borre di Barbagianni (<i>Tyto alba</i>). <i>Hystrix</i> 2:23–34.
	publication_year	Year of publication		1990
	original_language	Original language of the document	English	Italian
			Italian	
			French	
	type_of_publication	Type of publication	Article	Article
			Book	
			Conference proceedings	
			Data paper	
			Report	
			Thesis	
			Unpublished	
			Web site	

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CHAPTER III

Small mammals in Apennine deciduous montane forest: studying ecological niches for a sustainable forest management

3.1 Effect of imperfect detection on the estimation of niche overlap between two forest dormice.

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Effect of imperfect detection on the estimation of niche overlap between two forest dormice

Chiara Paniccia⁽¹⁾,
Mirko Di Febbraro⁽¹⁾,
Ludovico Frate⁽¹⁾,
Lorenzo Sallustio⁽²⁻³⁾,
Giovanni Santopuoli⁽²⁾,
Tiziana Altea⁽⁴⁾,
Mario Posillico⁽⁵⁻⁶⁾,
Marco Marchetti⁽²⁾,
Anna Loy⁽¹⁾

Quantification of niche overlap represents an important topic in several aspects of ecology and conservation biology, although it could be potentially affected by imperfect detection, *i.e.*, failure to detect a species at occupied sites. We investigate the effect of imperfect detection on niche overlap quantification in two arboreal rodents, the edible dormouse (*Glis glis*) and the hazel dormouse (*Muscardinus avellanarius*). For both species, we used Generalized Linear Mixed Models (GLMM) to estimate the occurrence probability and Occupancy Models (OM) to calculate occurrence and detection probabilities. By comparing these predictions through niche equivalency and similarity tests, we first hypothesised that methods correcting for imperfect detection (OM) provide a more reliable estimate of niche overlap than traditional presence/absence methods (GLMM). Furthermore, we hypothesised that GLMM mainly estimate species detectability rather than actual occurrence, and that a low number of sampling replicates provokes an underestimation of species niche by GLMM. Our results highlighted that GLMM-based niche overlap yielded significant outcomes only for the equivalency test, while OM-based niche overlap reported significant outcomes for both niche equivalency and similarity tests. Moreover, GLMM occurrence probabilities and OM detectabilities were not statistically different. Lastly, GLMM predictions based on single sampling replicates were statistically different from the average occurrence probability predicted by GLMM over all replicates. We emphasized how accounting for imperfect detection can improve the statistical significance and interpretability of niche overlap estimates based on occurrence data. Under a habitat management perspective, an accurate quantification of niche overlap may provide useful information to assess the effects of different management practices on species occurrence.

Keywords: Occupancy Models, Generalized Linear Mixed Models, Forest Management, Niche Overlap

Introduction

The niche is a central concept in ecology and evolution that dates back at least to Grinnell (1917). The fundamental ecological niche as conceptualized by Hutchinson (1957) is the space bounded by an *n*-dimen-

sional hypervolume, consisting of a range of abiotic and biotic variables, wherein a species is able to persist indefinitely in the absence of competition.

Concerns on how global change will influence niche dynamics in evolutionary and

community contexts, highlight the growing need for robust methods to quantify niche differences between or within taxa (Broennimann et al. 2012). During the last decade, statistical approaches have been developed allowing to compare species niches in a gridded environmental space (Warren et al. 2008, Broennimann et al. 2012). As a consequence, the estimation of niche overlap has become an important tool for investigating ecological requirements of invasive species (Gregory & MacDonald 2009), relative abundance distributions (McGill et al. 2007), species coexistence (Gregory & MacDonald 2009), evolutionary diversification (Araya et al. 2011) and conservation strategies (Russo et al. 2015). However, specific factors were shown to affect estimates of niche overlap. For instance, recent studies highlighted how niche overlap quantification may yield misleading results depending on the grain size (Kirchheimer et al. 2016) and the geographical scale (Russo et al. 2015) used to perform the analysis. Among other factors, imperfect detection, *i.e.*, failure to detect a species at occupied sites was shown to affect niche estimation itself. For instance,

✉ (1) Envix-Lab, Dipartimento di Bioscienze e Territorio, Università degli Studi del Molise, c.da Fonte Lappone, I-86090 Pesche, IS (Italy); (2) Centro di Ricerca per le Aree Interne e gli Appennini (Aria), Dipartimento di Bioscienze e Territorio, Università degli Studi del Molise, c.da Fonte Lappone, I-86090 Pesche, IS (Italy); (3) CREA Research Centre for Forestry and Wood, v.le Santa Margherita 80, I-52100 Arezzo (Italy); (4) Coordinamento Territoriale Carabinieri per l'Ambiente, Parco Nazionale "Abruzzo-Lazio-Molise", Pescasseroli, AQ (Italy); (5) Reparto Carabinieri Biodiversità Castel di Sangro, Centro Ricerche Ambienti Montani, Via Sangro, 45-67031. Castel di Sangro, AQ (Italy); (6) Consiglio Nazionale delle Ricerche, Istituto di Biologia Agroambientale e Forestale, v. Salaria km 29.300, I-00015 Montelibretti, RM (Italy)

@ Mirko Di Febbraro (mirkodifebbraro@gmail.com)

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predictions of species distribution through species distribution modelling (SDM), which are based on quantifying realized niche by means of the spatial (geographic) distribution of species across a study area (Raes 2012), may be underestimated if not accounting for imperfect detection (Rota et al. 2011, Lahoz-Monfort et al. 2014). In light of this evidence, investigating which bias could be introduced when quantifying overlap of two niches that are already affected by imperfect detection, represents an intriguing research topic.

Niche estimation and modelling typically relies on presence/absence or presence/background data (Lahoz-Monfort et al. 2014). However, these data could be biased by the fact that species (both animals and plants – Chen et al. 2013) often remain undetected, making imperfect detection a serious issue in species surveys (Lahoz-Monfort et al. 2014, Guillera-Aroita 2017), and a major source of bias in wildlife distribution studies (MacKenzie et al. 2002). Unless a suitably large sampling effort is invested at surveyed locations, imperfect detection will result in the recording of false absences in presence/absence data, potentially leading to biased conclusions and incorrect conservation actions (MacKenzie et al. 2002, Green et al. 2011). Many studies demonstrated that detectability varies among species, over time, and among habitats, and there may be serious consequences when this variability is ignored (Guillera-Aroita 2017). The occurrence of a species could be easy to prove, but species absence and non-detection can be often confounded, especially in case of species with low detectability (MacKenzie et al. 2002, MacKenzie & Royle 2005).

A popular approach was proposed to overcome this problem by explicitly accounting for imperfect detection when quantifying species distribution (MacKen-

zie & Royle 2005, Bailey et al. 2014). Hence, the so-called “occupancy models” are based on the detection history at sites and the proportion of sites where the species is detected, jointly modelling the processes describing where the species occurs and its detection at occupied sites (MacKenzie et al. 2002). In recent years, several studies highlighted the importance of explicitly accounting for imperfect detection when modelling species distribution (Rota et al. 2011, Lahoz-Monfort et al. 2014), though its effect on the quantification of niche overlap among species have been surprisingly overlooked. We aimed at filling this gap by evaluating the effect of imperfect detection on the quantification of niche overlap between two sympatric forest rodents. Specifically, we aimed at testing the following hypotheses:

- H1: the probability of occurrence corrected for imperfect detection provides a more reliable estimate of niche overlap than predictions from traditional presence/absence methods;
- H2: predictions of occurrence probability derived from traditional presence/absence methods reflects the species detectability rather than its actual occurrence pattern;
- H3: a low number of sampling replicates in traditional presence/absence methods causes an underestimation of species niche.

The three hypotheses respectively focused on niche overlap between species (H1), between modelling methods (H2) and among sampling replicates (H3). We targeted the analyses to two arboreal rodents: the edible dormouse (*Glis glis*) and the hazel dormouse (*Muscardinus avellanarius*), occurring sympatrically in a Central Apennines deciduous forest.

Although both species are strictly forest dependent, they exhibited different eco-

logical preferences with regard to forest characteristics (Capizzi et al. 2002, Panchetti et al. 2007) therefore representing ideal candidate species for a niche comparison study. The two species were surveyed with a sampling design addressed to provide both occurrence and detection probabilities (MacKenzie et al. 2002). Fine scale environmental covariates were then measured at each sampled plot and related to both occurrence and detectability.

Materials and methods

Study area

The study area is located in Central Apennines (Molise, Italy; 41° 43' N, 14° 06' E – Fig. 1), with an elevation ranging from 650 to 1300 m a.s.l.

The area covers approximately 18 km² and it is mainly dominated by European beech (*Fagus sylvatica* L.) and Turkey oak (*Quercus cerris* L.) forests (Vizzarri et al. 2015), with different ownership, forest structures (i.e., coppices and high forests) and management objectives (i.e., timber harvesting, biodiversity conservation, hydrogeological protection etc.). The climate is classified as “temperate”, with a mean annual precipitation of 1100 mm and a mean annual temperature of 8.6 °C (Blasi et al. 2005).

According to Amori et al. (2008), the study area hosts 25 small mammal species, including 14 rodents (order Rodentia, families Cricetidae, Gliridae, Muridae and Sciuridae) and 11 insectivores (order Eulipotyphla, families Erinaceidae, Soricidae and Talpidae), most of which (ca. 58%) are listed in the Appendix III of the Bern Convention, in the Annex IV of 357/97/EC Habitats Directive or are protected by the Italian law 157/1992.

Dormice occurrence sampling

A total of 83 sampling plots were randomly located in the study area with a minimum distance of 200 m (mean nearest neighbour distance = 316 ± 111 m), in order to guarantee the independence of data based on the average home range size of the target species (Bright & Morris 1991, Bright & Morris 1992, Mortelliti et al. 2009). A nest box and a hair-tube were installed at each site (see Appendix 1 in Supplementary material). Sampling plots were checked for species presence/absence at 15 days intervals during the pre-hibernation period from the end of August until mid-October 2013 (Panchetti et al. 2007, Amori et al. 2008) for a total of four sampling replicates. Specifically, nest boxes were considered occupied either when individuals, nests, food remains or droppings were detected inside the box (Bright et al. 1994). Species presence at hair-tubes was determined by analysing hair samples found inside the tubes (for further details on the hair identification protocol, see Appendix 1 in Supplementary material).

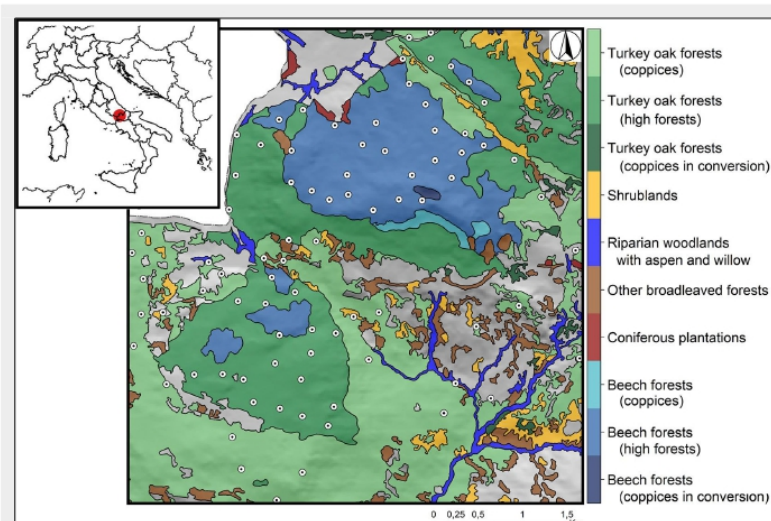


Fig. 1 - Map of the study area with sampling plots location.

*Estimation of niche overlap between two forest dormice**Forest parameters estimation and selection*

A set of 12 dendrometric and typological-structural forest parameters were measured at each sampling plot following the Italian National Forest Inventory protocol (Gasparini & Tabacchi 2011 – see also Appendix 2). In particular, dendrometric attributes were measured for all the living trees with a Diameter at Breast Height (DBH) ≥ 7.5 cm, considering circular plots of 13 m radius. Forest attributes related to deadwood were also quantified within the same circular plots (Lombardi et al. 2008). Typological-structural parameters including forest category, forest management and stand age were attributed according to the regional forest type and age maps (Vizzarri et al. 2015, Frate et al. 2016). Numerical covariates were standardized and sub-selected to avoid multicollinearity, considering a Variance Inflation Factor lower or equal to 10 (Zuur et al. 2010). This procedure led to a final set of seven forest predictors that were included in the subsequent analyses (Tab. 1).

Modelling framework

The modelling framework proceeds through three steps: (1) investigate the statistical relationships between species presence/absence and forest covariates through Generalized Linear Mixed Models (GLMM) and Occupancy Models (OM); (2) calculate the niche overlap between the two target species starting from the values of occurrence probability predicted by both modelling approaches; (3) quantify, for both species, the degree of niche similarity between GLMM and occupancy predictions, and by GLMM and detectability predictions, respectively.

Generalized linear mixed models

To investigate the statistical relationship between species occurrence and forest variables, we applied GLMM (McCullagh & Nelder 1989) implemented in the “lme4” package (Bates et al. 2015) of R statistical language ver. 3.4.0 (R Development Core Team 2018). GLMM proved useful when re-

peated measurements are made on the same statistical units (i.e., longitudinal studies), therefore violating the independence of sampling units (Zuur et al. 2013, Johnson et al. 2015). The presence/absence data detected at each site during the four sampling replicates were used as response variable. We started from a full model including, as fixed effect terms, all the seven forest covariates (allowing both linear and quadratic relationships for the continuous ones), along with an interaction term with forest management (Tab. 1). Besides, we considered the sampling replicate as random effect. Specifically, we allowed the model to change its intercept according to the sampling replicate to take into account non-independence of data between different sampling of the same sites. We then applied a variable selection procedure allowing to compare models with all the possible combinations of the starting covariates and random effect terms. The “dredge” function in the R package “MuMIn” (Barton 2018) was used for model selection, ranking the candidate models according to their AICc (Burnham & Anderson 2002). To account for uncertainty in model selection, we used a model averaging approach (i.e., we averaged all models within two $\Delta AICc$ of the top model – Burnham et al. 2011, Nakagawa & Freckleton 2011). The goodness-of-fit of the models was assessed by calculating the conditional and marginal coefficients of determination for GLMM (R_{GLMM}^2 – Nakagawa et al. 2013).

Conditional R_{GLMM}^2 is interpreted as the variance explained by both fixed and random factors (i.e., the entire model), whereas marginal R_{GLMM}^2 refers to variance explained by the fixed factors (i.e., excluding the random effect – Nakagawa et al. 2013).

Occupancy models

This statistical approach consists of two hierarchically coupled sub-models, one governing the true state of sites (presence/absence) and the other governing the observations (detection/non-detection – Mac-

Kenzie et al. 2002). OM can correct for imperfect detection due to false absences (i.e., failure to detect a species that is present at the site – MacKenzie et al. 2002), which represents a major source of bias in wildlife distribution studies (MacKenzie et al. 2002, Mackenzie & Royle 2005). We applied a single-season, single-species model (MacKenzie et al. 2002) to compute the probability of occurrence (occupancy, ψ) and the probability of detecting the species (detectability, p), using the R package “unmarked” (Fiske & Chandler 2011). In this case, we used the detection history of each species per site, i.e., the sequence of presences/absences over the complete survey period (four replicates), as response variable in the model. Similarly to GLMM, we started from a full model including all the seven forest covariates (allowing both linear and quadratic relationships for the continuous ones), along with an interaction term with forest management. Following Mortelliti et al. (2015), we split the variable selection procedure in two steps: (1) the detection probability was modelled as a function of different combinations of forest predictors, keeping the occupancy as constant and retaining the best subset of variables in the subsequent step; (2) the selection procedure was repeated simultaneously including both occupancy and detectability, while including, for the latter, only the variables combinations selected in step 1. As for GLMM, we averaged all models within $\Delta AICc \leq 2$ from the top model. The goodness-of-fit of each model was measured using the Nagelkerke’s pseudo- R^2 (Nagelkerke 1991). Predicted values of occurrence probability (from GLMM), ψ and p (from OM) were projected over the study area by spatializing the predictors selected in the top-ranked models (i.e., models within $\Delta AICc \leq 2$). Further details on the spatialization procedure are provided in Appendix 3 (Supplementary material).

Niche overlap

For both species, we ran the niche overlap analyses considering the following pa-

Tab. 1 - Explanatory variables used for GLMM and OM.

Forest parameter	Type	Levels	Description
Forest category (F_cat)	Categorical	Beech forest Turkey oak forest	Category of forest defined by its composition
Forest management (F_man)	Categorical	Coppice with standard Coppice in conversion to high forest Mature high forest	Prevalent silvicultural system adopted
Tree species richness (SR)	Continuous	-	Number of tree species (n)
Tree density (T_density)	Continuous	-	Mean number of trees per hectare (n ha ⁻¹)
Mean of the trees' heights (Mean_height)	Continuous	-	Average height of trees (m)
σ^2 Height (Stdev_height)	Continuous	-	Standard deviation of trees heights (m)
Stand basal area (Basal_area)	Continuous	-	The cross-sectional area of the tree stems measured at breast height (m ² ha ⁻¹)

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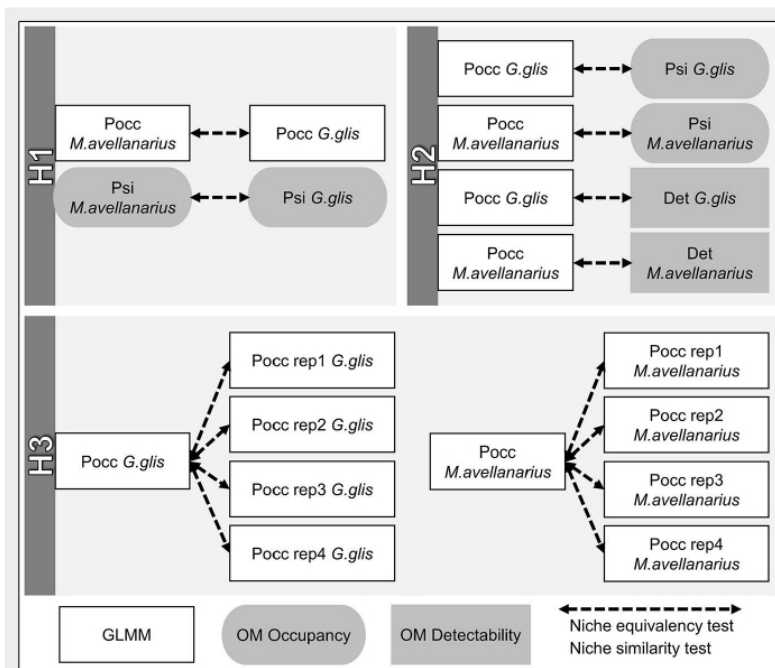


Fig. 2 - Flowchart of the niche overlap analysis implemented to test the three study hypotheses. White rectangles with black borders refer to occurrence probability values predicted by GLMM, grey rectangles with rounded borders indicate occupancy values predicted by OM and grey rectangles with squared borders indicate detectability values predicted by OM. Dashed arrows refer to niche equivalency and similarity tests used to compare the predictions.

rameters: P_{occ} (average values of occurrence probability predicted by GLMM along all of the four replicates), $P_{occ_rep_i}$ (occurrence probability predicted by GLMM for the i -th sampling replicate); Psi (occurrence probability predicted by OM), Det (detection probability predicted by OM). The flowchart of the methodological sequence followed to implement niche overlap analyses is depicted in Fig. 2.

To test H1, we performed the following niche overlap tests: P_{occ_Gglis} vs. $P_{occ_Mavellanarius}$ and Psi_Gglis vs. $Psi_Mavellanarius$. Then, we compared P_{occ} vs. Psi and P_{occ} vs. Det for both species to test H2. Lastly, we tested H3 by calculating P_{occ} vs. $P_{occ_rep_i}$ for both species and the four sampling replicates, separately. All the niche overlap tests are shown in Fig. 2.

Analysis of niche overlap between the two species was carried out using the analytical framework proposed by Broennimann et al. (2012) and recently adopted in different studies (Russo et al. 2015). Within this framework, the environmental space is defined by the axis of occurrence probabilities predicted by GLMM and OM for the two species. The output of such models comprises a single vector of predicted occurrence probabilities derived from complex combinations of functions of original environmental variables; the niche overlap is analysed along this gradient of predictions (Broennimann et al. 2012). Niche

overlap was computed in terms of Schoener's D (Schoener 1970), a metric that ranges from 0 (no overlap) to 1 (complete overlap).

We performed niche equivalency and similarity tests sensu Warren et al. (2008). The first test evaluates if the two species are identical (null hypothesis) in their niche space by using their exact locations and not including the surrounding space. The second also accounts for the differences in the surrounding environmental conditions and assess if the two species are more different than expected by chance. In particular, similarity between niches was tested in both directions, i.e., the amount of species 1 niche included in species 2 niche, and vice versa, following Broennimann et al. (2012). All the procedures were performed using the R package "ecospat" (Broennimann et al. 2017).

Results

Throughout the duration of the study, we reported 31 detections of *G. glis* at 27 of 83 sampling plots and 31 detections of *M. avellanarius* at 16 of 83 sampling plots (further details are provided in Tab. S1, Supplementary material). In GLMM, model selection procedure identified 15 top-ranked models for *G. glis* and three for *M. avellanarius* out of 3136 candidate models. Both species showed high values of conditional R_{GLMM}^2 (*G. glis*: mean = 0.523, SD =

0.065; *M. avellanarius*: mean = 0.640, SD = 0.006). Conditional R_{GLMM}^2 were always higher than marginal ones, indicating that the inclusion of the random effect systematically improved the models goodness-of-fit (Tab. S2). Occurrence of *G. glis* was predominantly explained by stand basal area (15 models) through a direct relationship. In addition, eight out of 15 top-ranked models predicted higher occurrence probabilities at increasing tree density values and in Turkey oak stands (Tab. S2, Fig. 3b). For *M. avellanarius*, mean tree height and interaction between tree density and forest management were the most important variables, resulting inversely related with species occurrence in all the top-ranked models. In addition, standard deviation of tree height and forest category were retained in more than a half of the top-ranked models, predicting higher occurrence probabilities in forests with high variability in tree heights and beech stands (Tab. S2, Fig. 3c).

In OM, the final model set included eight top-ranked models for *G. glis* and two for *M. avellanarius* out of 3136 candidate models. Goodness-of-fit statistics for the top-ranked models reported a mean pseudo- R^2 equal to 0.370 (SD = 0.033) for *G. glis* and to 0.549 (SD = 0.030) for *M. avellanarius* (Tab. S3 in Supplementary material). For *G. glis*, both occupancy and detectability were directly related with stand basal area in all the top-ranked models. Six out of eight models also included forest management, predicting higher occupancy values in high forests and coppices in conversion rather than in coppices. Besides, mean tree height was retained in four models, always showing a direct relationship with the occurrence probability (ψ – Tab. S3, Fig. 3e). For *M. avellanarius*, occupancy was predominantly explained by standard deviation of tree heights, showing an inverse relationship in both top-ranked models. In addition, tree density and forest category were retained in half of the top-ranked models, predicting higher occupancy values in dense forests and beech stands (Tab. S3, Fig. 3f). Finally, *M. avellanarius* detectability was mainly explained by mean and standard deviation of tree height and tree density (Tab. S3 in Supplementary material). Maps of predicted detectability for the two species show overall higher values of p for *M. avellanarius* (mean = 0.192, SD = 0.041) than for *G. glis* (mean = 0.154, SD = 0.004; Fig. 4). For both species, GLMM predicted lower values of occurrence probability (*G. glis*: mean = 0.104, SD = 0.083; *M. avellanarius*: mean = 0.114, SD = 0.201) than probability values corrected by detectability under OM (ψ , *G. glis*: mean = 0.599, SD = 0.163; *M. avellanarius*: mean = 0.504, SD = 0.337 – Fig. S1).

As for niche overlap tests, GLMM's P_{occ_Gglis} vs. $P_{occ_Mavellanarius}$ (Schoener's D = 0.41 – Fig. 3a) showed significant outcomes only for the equivalency test. On the other hand, niche overlap computed on OM's Psi_Gglis vs. $Psi_Mavellanarius$

Estimation of niche overlap between two forest dormice

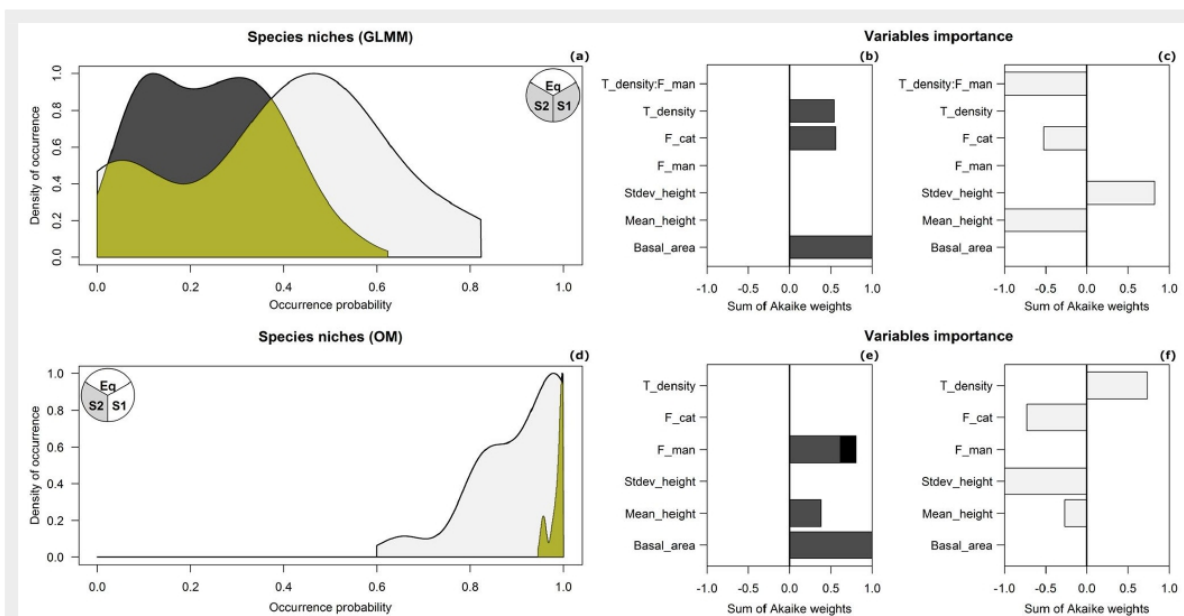


Fig. 3 - Models' outcomes. The two rows show results for GLMM and OM, respectively. First column depicts niches of edible (dark grey) and hazel (light grey) dormice calculated from GLMM (a) and OM (d) predictions. Yellow areas refer to niche overlap. Circles (a, d) show the significant outcomes (white) of the equivalency and similarity tests. Bar plots on the right display variables importance for the two species calculated by GLMM (b, c) and OM (e, f), as the cumulative sum of Akaike weights over the top-ranked models. Only variables being selected in at least a half of the top-ranked models were included. For forest management (F_man) two of the three levels are shown: high forests (dark grey) and coppices in transition (black). For forest category (F_cat) the level referring to "Turkey oak" category was displayed.

(Schoener's $D = 0.26$ – Fig. 3d) yielded significant outcomes for both niche equivalency and similarity (i.e., niche 1 vs. niche 2 – Fig. 3a, Fig. 3d, Tab. 2).

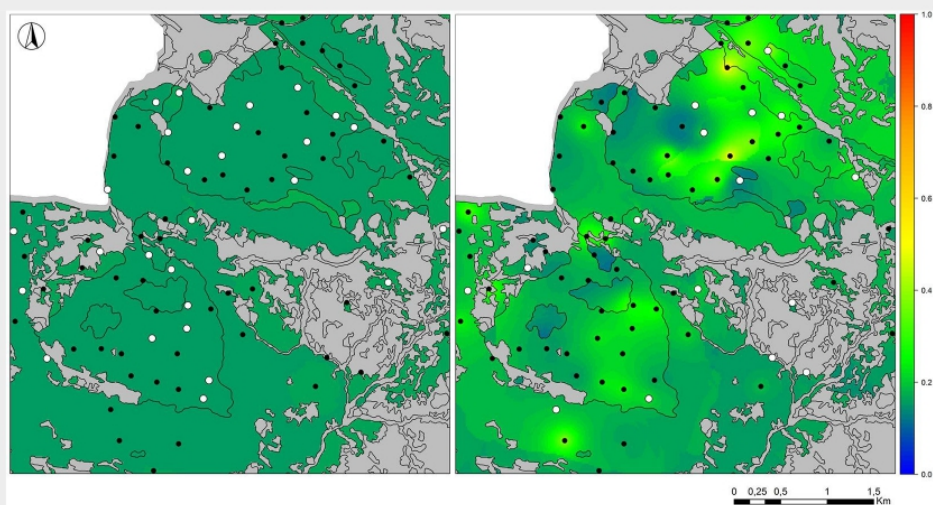
For both species, overlap values calculated between GLMM predictions and OM detectabilities (i.e., P_{occ} vs. Det) were higher than those calculated between GLMM predictions and OM occupancy (i.e., P_{occ} vs. Psi). Specifically, Schoener's D calculated for P_{occ_Gglis} vs. Det_Gglis were higher than for P_{occ_Gglis} vs. Psi_Gglis , with

both tests resulting significant for the equivalency hypothesis (Warren et al. 2008 – Tab. 2). We found a similar pattern for $P_{occ_Mavellanarius}$ vs. $Det_Mavellanarius$, showing higher values of Schoener's D than $P_{occ_Mavellanarius}$ vs. $Psi_Mavellanarius$. In addition, $P_{occ_Mavellanarius}$ vs. $Det_Mavellanarius$ failed to reject the null hypothesis of the equivalency test, i.e., the two niches were identical (Warren et al. 2008 – Tab. 2).

Finally, $G. glis$ GLMM predictions by the

first three sampling replicates ($P_{occ_Gglis_rep_1-3}$) scarcely overlapped with the average predicted probability of occurrence (P_{occ_Gglis}), also showing significant niche equivalency (i.e., not equivalent niches) and similarity tests (niche 2 vs. niche 1). $M. avellanarius$ yielded a similar pattern, showing GLMM predictions by the first two replicates ($P_{occ_Mavellanarius_rep_1-2}$) as not equivalent to the average predicted occurrence probability ($P_{occ_Mavellanarius}$ – Tab. 2). Only GLMM predictions from repli-

Fig. 4 - Maps of predicted detection probabilities for *G. glis* (left) and *M. avellanarius* (right). Detectability values, which range from 0 (blue) to 1 (red), were projected over the study area by spatializing the predictors selected in the top-ranked models (see also Appendix 3 in Supplementary material). White (black) dots indicate presence (absence) sites.



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Tab. 2 - Results of niche overlap tests. (Schoener's D): niche overlap index; (Similarity1): similarity between the first species vs. the second; (Similarity2): similarity between the second species vs. the first; (*): $p < 0.05$; (ns): not significant.

Hypothesis	Test	Schoener's D	Equivalency	Similarity 1	Similarity 2
H1	P_{occ_Gglis} vs. $P_{occ_Mavellanarius}$	0.41	*	ns	ns
	Psi_Gglis vs. $Psi_Mavellanarius$	0.26	*	*	ns
H2	P_{occ_Gglis} vs. Psi_Gglis	0.00	*	ns	ns
	P_{occ_Gglis} vs. Det_Gglis	0.47	*	ns	ns
	$P_{occ_Mavellanarius}$ vs. $Psi_Mavellanarius$	0.32	*	ns	ns
	$P_{occ_Mavellanarius}$ vs. $Det_Mavellanarius$	0.71	ns	*	ns
	P_{occ_Gglis} vs. $P_{occ_Gglis_rep_1}$	0.08	*	ns	*
H3	P_{occ_Gglis} vs. $P_{occ_Gglis_rep_2}$	0.07	*	ns	*
	P_{occ_Gglis} vs. $P_{occ_Gglis_rep_3}$	0.15	*	ns	*
	P_{occ_Gglis} vs. $P_{occ_Gglis_rep_4}$	0.52	ns	ns	ns
	$P_{occ_Mavellanarius}$ vs. $P_{occ_Mavellanarius_rep_1}$	0.02	*	ns	ns
	$P_{occ_Mavellanarius}$ vs. $P_{occ_Mavellanarius_rep_2}$	0.00	*	ns	ns
	$P_{occ_Mavellanarius}$ vs. $P_{occ_Mavellanarius_rep_3}$	0.08	ns	*	*
	$P_{occ_Mavellanarius}$ vs. $P_{occ_Mavellanarius_rep_4}$	0.33	ns	*	*

cates 3 and 4 for *M. avellanarius*, and 4 for *G. glis*, resulted identical to the average predicted occurrence probability (P_{occ} – Tab. 2).

Discussion

Our results showed how niche overlap estimation corrected for imperfect detection was statistically more robust than classical models. This outcome is likely due to the fact that occurrence probabilities uncorrected for imperfect detection reflected the species detectability rather than its actual occurrence pattern. Being affected by this bias, occurrence probability values estimated by traditional presence/absence methods also led to a substantial niche underestimation, especially when relying on a low number of sampling replicates.

Correcting for imperfect detection increases significance in niche overlap tests

Niche overlap tests based on GLMM predictions showed significant outcomes only for the equivalency test. On the other hand, niche overlap computed on OM yielded significant outcomes for both niche equivalency and similarity. In particular, OM's niche similarity tests were significant only in one direction (from *G. glis* niche to *M. avellanarius*), indicating niche of *G. glis* to be completely included within that of *M. avellanarius*, but not vice versa. Such an asymmetric pattern suggests the edible dormouse and the hazel dormouse to be characterized by a narrow and a large niche respectively, with the first acting as habitat specialist and the latter as generalist, in accordance with several literature evidences. As a matter of fact, the edible dor-

mouse is known to prefer forest stands with a continuous canopy cover (Capizzi et al. 2002, Juškaitis & Siozinyte 2008), whereas the hazel dormouse is found in a variety of habitats, from deciduous woodland, to coppices, and other wooded areas with a dense understory layer dominated by shrubs (Sozio et al. 2016).

Such differences in forest habitat requirements between the two dormice species are strongly supported by OM predictions, whereas GLMM outcomes appeared less coherent with existing knowledge about the ecology of the studied species. Specifically, occupancy of *G. glis* was directly related with increasing stand basal area and mean tree height, with higher occupancy values in high forests and coppices in conversion. This evidence supports the findings that edible dormouse is an arboreal species which lives on the canopy of mature broadleaved (Cornils et al. 2017) or mature mixed woodlands (Capizzi et al. 2003). For *M. avellanarius*, occupancy was predominantly explained by low standard deviations of tree height, high tree densities and beech stands. These outcomes suggest *M. avellanarius* to prefer a wide variety of forests with different stand characteristics (Capizzi et al. 2002, Panchetti et al. 2007, Sozio et al. 2016), which in the study area include even-aged, highly dense stands (typical of the coppice management system) as well as beech forests predominantly managed as high forests (Frate et al. 2016). These differences in the ecological strategies of the two dormice is coherent with their feeding habits. While the edible dormouse is known to feed mainly on beechnuts and adapted to yearly fluctuations in seed production (Bieber & Ruf

2009), the hazel dormouse exhibited a wide dietary spectrum including berries, a variety of nuts and even insects eggs and larvae (Amori et al. 2008). It is important to note that seed production and availability are strongly influenced by forest management systems; for instance, the regeneration in high forests is mainly achieved by sexual reproduction, thus one of the main management goal is to ensure seed production by adopting long rotation cycles. On the contrary, in the coppice system the regeneration is ensured by the resprouting capacity of certain forest species: short rotation cycles (usually less than 20 years) reduce flowering and seed production (Ciancio et al. 2006). However, coppices have a higher number of understory species compared to high forests (Scolastri et al. 2017), including many shrubs species which offer a great variety of food resource for rodents, and in particular for hazel dormouse. In such a perspective, findings of the present study offer a methodological framework to assess forests naturalness and to explore possible effects of alternative forest management systems on stand structure, i.e., towards natural evolution and the establishment of old-growth forests (i.e., for beech forests – Chiavetta et al. 2012).

Uncorrected occurrence probabilities reflect species detectability instead of its occurrence

Our analyses showed that for both species, GLMM mostly estimated the species detectability rather than their actual occurrence pattern. This outcome was particularly evident for *M. avellanarius* for which GLMM predictions were statistically undistinguishable from the species detectability, i.e., the equivalency test failed to reject the null hypothesis. The bias introduced by imperfect detection in GLMM led this modelling technique to substantially spurious estimates of the two species niches and, consequently, to a lack of significance in their overlap pattern. Lahoz-Monfort et al. (2014) showed similar evidences for presence/absence and presence-only SDMs. In fact, these modelling approaches can wrongly identify a covariate influencing species detection as a covariate driving its occurrence, thus resulting in poor inference and predictions (Lahoz-Monfort et al. 2014). This argument would explain why, for *M. avellanarius*, GLMM predictions were statistically undistinguishable from the species detectability. For this species, occupancy and detectability are influenced by similar covariates, although through relationships with opposite signs (Fig. S2 in Supplementary material). This would have made GLMM particularly unable in discriminating between the covariates driving *M. avellanarius* occupancy and those influencing its detectability. This interpretation would be further confirmed by the fact that GLMM occurrence probabilities and OM detectabilities for *M. avellanarius* are

Estimation of niche overlap between two forest dormice

explained by approximately the same predictors through relationships with the same signs (except forest category – see Fig. 3 and Fig. S2). Such outcomes point out how modelling species occurrence without correcting for imperfect detection could lead to capture only where a species is more likely to be detected, making it difficult to distinguish between predictions that reliably reflect ecological processes and those that are related to detectability effects (Lahoz-Monfort et al. 2014, Guillera-Arroita 2017). As a consequence, two species whose occurrence predictions would be affected by such kind of bias, would reveal an inconsistent and likely unreliable overlap pattern between their niches.

Few sampling replicates lead to a niche underestimation

It is noteworthy how GLMM predictions based on the first three (for *G. glis*) and the first two (for *M. avellanarius*) sampling replicates were mostly different from the average occurrence probability predicted by GLMM over all the four replicates. In particular, the statistical significance in niche equivalency tests for the first three replicates of *G. glis* indicated these niches to be non-identical to that calculated from the average occurrence probability over all the replicates. In addition, niche similarity tests for these three replicates were significant only in one direction (from $P_{occ_Gglis_rep_1-3}$ niches to $P_{occ_Gglis_one}$). This asymmetry suggested that *G. glis* niches estimated by each of these sampling replicates represent only a subpart of that calculated from the average occurrence probability over all the replicates.

We found a similar result also for *M. avellanarius*, though involving only the first two sampling replicates, likely due to the overall higher detectability of such species compared to *G. glis* (Fig. 4). Such evidences point out how imperfect detection, besides leading GLMM to estimate species detectability rather than occurrence, provokes a substantial underestimation of species niche, by introducing a high number of false absences at occupied sites. A similar outcome was also highlighted for SDMs by Lahoz-Monfort et al. (2014) and could be explained considering that a high rate of false absences likely results in an incomplete sampling of the species niche, thus affecting niche estimation and predictions.

Under this perspective, imperfect detection seems to affect niche estimation similarly to the bias introduced by the geographic truncation in sampling occurrence data. In fact, it is well documented how covering the entire species niche is crucial to assess niche overlap and change without bias (Raes 2012, Guisan et al. 2014). Specifically, an incomplete sampling of species niche may prevent capturing the full environmental variation under which a species is known to occur, often resulting in a niche underestimation (Raes 2012). Therefore, when geographic truncation

leads to environmental truncation, assessment of niche overlap should be carefully considered (Guisan et al. 2014).

In light of the environmental truncation effect exerted by imperfect detection on niche overlap estimates, an adequate number of sampling replicates is highly advisable, also taking into account that differences in species detectability among sampling replicates covering different periods of the year may be a result of seasonal effects, e.g., climate (Mackenzie & Royle 2005). For instance, the overall increase in detection probability observed from the first to the last sampling replicate, might be a consequence of an intensified activity to gather trophic resources as the cold season was approaching, leading the two dormice species to visit the sampling sites more frequently than during the first replicates (Sozio et al. 2016, Cornils et al. 2017). While our results strongly support a role by the number of sampling replicates to estimate niche overlap, we cannot exclude that alternative sampling protocols (e.g., one-per-stratum) might have yielded different outcomes from those showed here.

Conclusions

Our study emphasized how accounting for imperfect detection can improve the statistical significance and interpretability of niche overlap estimates based on occurrence data. Such approach allowed to identify alternative ecological strategies between the two forest dormice i.e., habitat generalist vs. habitat specialist. The edible dormouse exhibited a strict link with high forests, while the hazel dormouse showed to prefer a wide variety of forest types. These differences could be mainly due to the different feeding habits of the two species, which are in turn affected by the forest management system. In a forest management context, an accurate quantification of niche overlap provides useful information to assess the effects of different management practices on the occurrence of these arboreal species. For instance, a management strategy oriented at promoting high forests would likely favor both the specialist edible dormouse and the generalist hazel dormouse, as the two species share a significant portion of their niches corresponding to forests with these characteristics. On the other hand, practices enhancing forest stands with different characteristics would primarily have a positive effect on the occurrence of *M. avellanarius* and not necessarily on *G. glis*.

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Authors' contribution

CP and MDF have equally contributed to this paper.

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- Supplementary Material**
- Appendix 1** - Details on the hair identification protocol.
- Appendix 2** - Description of the 12 explanatory variables measured and estimated at each sampling plot.
- Appendix 3** - Details on the spatialization procedure.
- Tab. S1** - Summary of presence (1) and absence (0) of two arboreal rodent species (*G. glis* and *M. avellanarius*) in the 83 sampling sites.
- Tab. S2** - Top-ranked GLMMs derived from the model selection procedure. W indicates the Akaike weight of each model.
- Tab. S3** - Top-ranked OMs derived from the model selection procedure.
- Fig. S1** - First (second) row depicts maps of predicted occurrence probabilities for *G. glis* (left) and *M. avellanarius* (right) by GLMM (OM).
- Fig. S2** - Detectability variables importance for edible (dark grey) and hazel (light grey) dormice, as the cumulative sum of Akaike weights over the top-ranked models.
- Link:** Paniccia_2738@supp001.pdf

3.1.2 Supplementary material

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Supplementary Material

Appendix 1 - Details on the hair identification protocol.

A total of 83 dormouse wooden nest-boxes (210×120×160) mm with an entrance hole of 30 mm) were installed in August 2013. Nest boxes were constructed using pressure-treated plywood; these were mounted at 1,5 meters, facing the tree trunks, trying to prevent the occupation by bird species from occupying them (Morris et al. 1990, Sarà et al. 2005).

Hair-tubes made from PVC flexible tubes (250-300 mm length; 75 mm diameter) were installed and attached to horizontal tree branches with metal wire and baited following the sampling protocol described in Mortelliti & Boitani (2007) and Amori et al. (2011).

Hazelnuts (*Corylus avellana*, L.) were glued into the inner part of the tube. Hairs were identified to species using reference collection and atlas (Teerink 1991, De Marinis & Agnelli 1993, Lombardi & Ragni 2012). As a preliminary step, guard hairs were first cleaned with 70% alcohol and then were dry on paper towels. The configuration of medulla was investigated through a microscope (10x), then hair was pressed in celluloid sheet (thickness 1 mm) to get imprints of cuticle pattern by applying acetone. Imprints were analysed through a binocular microscope (40x) and further examined based on cuticle and scale patterns using identification keys. Nest types, pellets and gnawed hazelnuts were identified with the aid of field guides (Olsen 2013).

Different types of nests of the two rodents are showed in the image below:

(a-b) *Glis glis*;

(c-d) *Muscardinus avellanarius*.



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Appendix 2 - Description of the 12 explanatory variables measured and estimated at each sampling plot.

Forest category (F_cat): The forest category is a combination of the geographical/ecological distribution of the type, tree species composition. Its name usually reflects the most abundant tree species of the stand. In our study, this information was provided by the forest types map of the Molise region (Vizzarri et al. 2015) and then verified *in situ* during the field surveys.

Forest management (F_man): the silvicultural system adopted to achieve specific stand structural and management objectives, based on the biological requirements of the trees. The silvicultural treatments integrates specific harvesting, regeneration, and stand tending methods to maintain forests healthy and vigorous, and to achieve a predictable yield from the stand over time. In our study, this information was provided by the forest types map of the Molise region (Vizzarri et al. 2015) and then verified *in situ* during the field surveys. The main forest management systems in the study area are: coppice (usually with standards), coppice in conversion to high forests, and high forest.

Age: the age of trees within the forest stands. It is determined by counting the tree's rings of the trees belonging to the most frequent class of diameter at the breast height (DBH). The increment borer was used to collect tree's cores during the field survey and then analysed in laboratory using dendrochronological techniques.

Tree density (T_density): mean number of trees per hectare ($\text{pt} \cdot \text{ha}^{-1}$). A quantitative measure of tree stocking expressed in terms of number of trees per unit area. Human interventions affect the tree density of both living trees and stand dead trees. T_density was estimated using the data collected per each sampling plot during the field surveys.

Mean of the heights (Mean_height): the arithmetic mean of the heights of all the living trees (in m) with DBH higher than 7.5 cm within the sampling plots.

σ^2 Height (Stdev_height): the standard deviation of the heights of all the living trees (in m) with DBH higher than 7.5 cm within the sampling plots.

Stand basal area (Basal_area): Basal area of a forest stand is the sum of the basal areas of all the living trees (in $\text{m}^2 \cdot \text{ha}^{-1}$). The basal area (g) is the cross-sectional area of a tree trunk at breast height, then calculated as follows:

$$g = \frac{\pi}{4} \cdot d^2$$

where d is the DBH.

Mean DBH: the DBH of the tree with the mean basal area within the sampling plot (cm). At first we calculated the mean basal area (\bar{g}) of the stand trees as follows:

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$$\bar{g} = \frac{G}{n}$$

where G is the basal area of the stand ($\text{m}^2 \text{ha}^{-1}$) and n is the number of the stand trees ($\text{pt} \cdot \text{ha}^{-1}$). Then the mean DBH is calculated using the equation:

$$\text{mean DBH} = \sqrt{\bar{g} \cdot \frac{4}{\pi}}$$

σ -DBH: the standard deviation of the DBH of all the living trees measured within the sampling plot (cm).

CWD: the volume of coarse woody debris measured within the sampling plot (dead trees, snag, and stumps), including lying deadwood (downed trees and logs) ($\text{m}^3 \cdot \text{ha}^{-1}$). For standing dead trees the DBH threshold value was 10 cm, while for the lying deadwood only the lying longer than 1 m and ≥ 10 cm in diameter at cutting point were measured. Volume (V_{CWD}) was then calculated as follows:

$$V_{CWD} = \frac{\pi}{4} \cdot d^2 \cdot l$$

where d is the diameter of the CWD while l is the length. The volume of each CWD were then summed up within the sampling plot and reported to the ha.

Volume (V): the volume of all the living trees within each sampling plot having a DBH greater than 7.5 cm as estimated by using the equations proposed by the Italian National Forest Inventory and referred to a 1 ha area (Gasparini & Tabacchi 2011).

Tree species richness (SR): the number of tree species occurring within each sampling plot. The value is based on the ground observations.

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Appendix 3 - Details on the spatialization procedure.

Numerical predictors selected in the top-ranked models, *i.e.*, SR, T_density, Basal_area, Mean_height and Stdev_height, were spatialized over the study area by applying a regression kriging technique. Kriging is a method to interpolate the values of a dependent variable at points between field observations. Unlike classical statistics, which relies on the independence of data points, kriging assumes that observations are not independent (Hudak et al. 2002). Regression kriging represents a modification of ordinary kriging and relies on interpolating a poorly sampled variable (the primary variable) with the help of a well-sampled variable (the secondary variable; Papritz & Stein, 1999). It prescribes to use multiple regression to describe the relationship between the primary variable the secondary predictors, then applying kriging on the regression residuals (Hudak et al. 2002). In our study, each numerical predictors that was selected in the top-ranked models was interpolated over the study area including Forest category and Forest management as secondary variables in the regression kriging procedure. These secondary variables were derived from the forest types map (Vizzarri et al. 2015). We assessed the predictive accuracy of the interpolation phase by applying a 10-fold cross validation procedure and calculating the mean absolute percentage error (MAPE). MAPE values follow:

Variable	MAPE (mean + sd)
SR	5.12 ± 10.1
T_density	3.11 ± 2.91
Basal_area	5.70 ± 16.46
Mean_height	18.35 ± 10.75
Stdev_height	5.63 ± 5.63

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Tab. S1 - Summary of presence (1) and absence (0) of two arboreal rodent species (*G. glis* and *M. avellanarius*) in the 83 sampling sites; “-” indicate no data; I-II-III-IV represent the number of replicate.

Sampling plot	<i>Glis glis</i>				<i>Muscardinus avellanarius</i>			
	I	II	III	IV	I	II	III	IV
1	0	-	-	-	-	-	-	-
2	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0
5	0	0	0	1	0	0	0	0
6	0	0	0	0	0	1	1	1
7	0	0	0	0	0	1	0	0
8	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0
10	0	0	0	0	1	1	1	1
11	0	0	0	0	0	0	0	1
12	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0
14	0	0	0	1	0	0	0	0
15	0	0	0	0	0	0	0	0
16	0	0	0	0	0	-	0	0
17	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0
21	0	0	0	1	0	1	1	1
22	1	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0
24	0	0	0	1	0	0	0	0
25	0	0	0	0	0	0	0	0
26	0	0	0	0	0	0	0	1
27	1	0	0	0	0	0	0	0
28	0	0	0	0	-	0	1	1
29	-	-	-	0	-	-	-	0
30	0	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0	0
32	0	0	-	1	0	0	-	0
33	0	-	-	-	1	1	1	1
34	-	0	0	0	-	0	0	0
35	0	0	0	0	0	0	0	0
36	0	0	0	1	0	0	0	1
37	0	0	0	0	0	0	0	0
38	0	0	0	0	0	0	0	0
39	0	0	0	0	0	0	1	1
40	0	0	0	0	0	0	0	0
41	0	0	0	0	0	0	0	0
42	0	1	0	0	0	0	0	1
43	0	0	0	1	0	0	0	0
44	0	0	0	0	0	0	0	0
45	0	0	0	0	0	0	0	0

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Sampling plot	<i>Glis glis</i>				<i>Muscardinus avellanarius</i>			
	I	II	III	IV	I	II	III	IV
46	0	0	0	0	0	0	0	0
47	0	0	1	1	1	0	0	0
48	0	0	0	0	0	0	0	0
49	0	0	0	0	1	1	1	1
50	0	1	0	1	0	0	0	0
51	0	0	0	0	0	0	0	0
52	0	0	0	0	0	0	0	0
53	0	0	0	1	0	0	0	0
54	0	0	0	1	0	0	0	0
55	0	0	0	1	0	0	0	0
56	0	0	0	1	0	0	0	0
57	0	0	0	1	0	0	0	0
58	0	0	1	0	0	0	0	0
59	0	0	0	0	0	0	0	0
60	0	0	0	0	0	0	0	0
61	0	0	0	0	0	0	0	0
62	0	0	0	1	0	0	0	0
63	0	0	0	0	0	0	0	0
64	0	0	0	1	0	0	0	0
65	0	0	0	1	0	0	0	0
66	0	0	0	0	0	0	0	0
67	0	0	0	0	0	0	0	0
68	0	0	0	-	0	0	0	0
69	0	0	1	0	0	0	0	0
70	0	0	0	0	0	0	0	0
71	0	0	0	1	0	0	0	0
72	0	0	1	0	0	0	0	0
73	0	0	0	1	0	0	0	0
74	0	0	0	1	0	0	0	0
75	0	0	0	0	0	0	0	0
76	0	0	1	1	0	0	0	0
77	0	0	0	1	0	0	0	1
78	0	0	0	0	0	0	0	0
79	0	0	0	0	0	0	0	0
80	0	0	0	0	0	0	0	0
81	0	0	0	0	0	0	0	0
82	0	0	0	0	0	1	0	0
83	1	1	0	0	0	1	0	0

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Tab. S2 - Top-ranked GLMMs derived from the model selection procedure. W indicates the Akaike weight of each model. The goodness-of-fit of the models was assessed by calculating the conditional (in parentheses) and marginal coefficients of determination for GLMM. Continuous variables in fixed effect part enter as linear and quadratic terms and “:” indicate interaction between predictors.

Species	Models (fixed effect terms)	Models (random effect terms)	AICc	ΔAICc	W	R ² c (R ² m)
<i>G. glis</i>	Pocc~Basal_area+F_cat+F_man:Mean_height	1 replicate	182.2	0	0.111	0.560 (0.439)
	Pocc~Basal_area+T_density+F_man:Basal_area	1 replicate	182.7	0.41	0.090	0.497 (0.363)
	Pocc~Basal_area+F_man:Mean_height	1 replicate	182.7	0.46	0.088	0.555 (0.439)
	Pocc~Basal_area+F_cat+ T_density+F_man:SR+F_man:F_cat	1 replicate	182.9	0.68	0.079	0.555 (0.422)
	Pocc~Basal_area+F_cat+ T_density+F_man:Mean_height	1 replicate	182.9	0.68	0.079	0.556 (0.431)
	Pocc~Basal_area+T_density	1 replicate	183.2	0.91	0.071	0.406 (0.254)
	Pocc~Basal_area+F_cat+ T_density	1 replicate	183.2	0.95	0.069	0.409 (0.251)
	Pocc~Basal_area+F_cat+F_man:F_cat	1 replicate	183.4	1.14	0.063	0.605 (0.496)
	Pocc~Basal_area+F_cat+T_density+F_man:Basal_area	1 replicate	183.5	1.26	0.059	0.506 (0.362)
	Pocc~Basal_area+F_cat+F_man:Mean_height+F_man:T_density+F_man:Stdev_height	1 replicate	183.6	1.39	0.055	0.637 (0.527)
	Pocc~Basal_area+T_density+F_man:Mean_height	1 replicate	183.7	1.44	0.054	0.544 (0.422)
	Pocc~Basal_area+F_man:T_density	1 replicate	183.9	1.69	0.048	0.504 (0.369)
	Pocc~Basal_area+T_density+F_man:Stdev_height	1 replicate	184.0	1.76	0.046	0.475 (0.335)
	Pocc~Basal_area+F_man:Stdev_height	1 replicate	184.0	1.78	0.046	0.471 (0.335)
	Pocc~Basal_area+F_man:Mean_height+F_man:Stdev_height	1 replicate	184.2	1.93	0.042	0.564 (0.443)
<i>M. avellanarius</i>	Pocc~Mean_height+Stdev_height+F_man:T_density	1 replicate	151.3	0	0.472	0.648 (0.632)
	Pocc~Mean_height+F_cat+Stdev_height+F_man:T_density	1 replicate	151.9	0.58	0.353	0.638 (0.622)
	Pocc~Mean_height+F_cat+F_man:T_density	1 replicate	153.3	1.99	0.175	0.634 (0.620)

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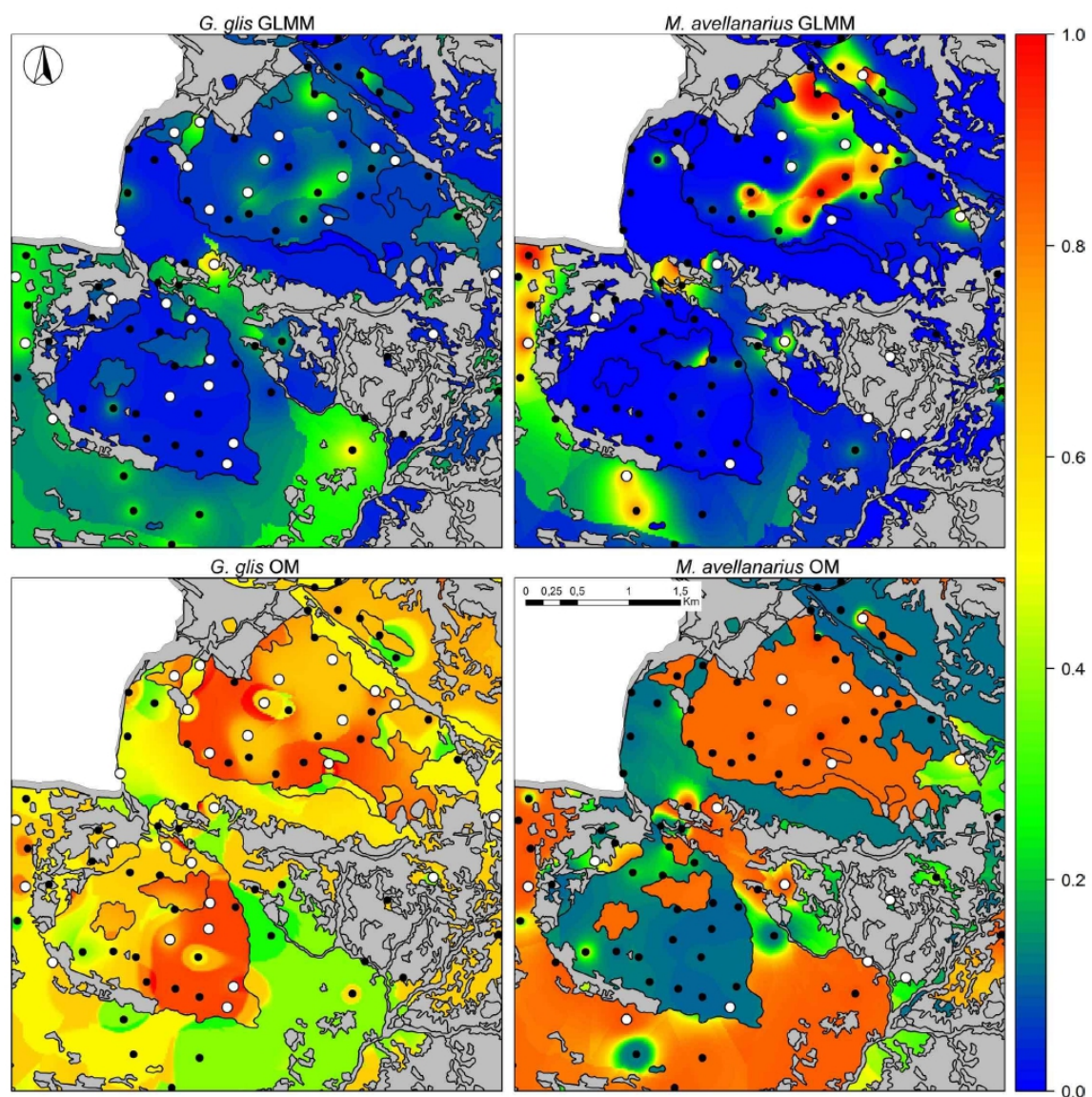
Tab. S3 - Top-ranked OM's derived from the model selection procedure. ψ = probability of occupancy, p = detection probability, W = Akaike weight of each model, pseudo- R^2 = Nagelkerke's coefficient of determination. Continuous variables enter as linear and quadratic terms, with “:” indicating interaction between predictors.

Species	Models	AICc	Δ AICc	W	pseudo- R^2
<i>G. glis</i>	$\psi \sim \text{Basal_area} + \text{T_density} + \text{F_cat} + \text{F_man} + \text{Mean_height} : \text{F_man}$ $p \sim \text{Basal_area}$	192.0	0.00	0.192	0.424
	$\psi \sim \text{Basal_area} + \text{T_density} + \text{F_man} + \text{Mean_height} : \text{F_man}$ $p \sim \text{Basal_area}$	192.1	0.07	0.185	0.403
	$\psi \sim \text{Basal_area} + \text{F_man} + \text{A.S.Rich} : \text{F_man}$ $p \sim \text{Basal_area} + \text{T_density}$	192.6	0.54	0.146	0.340
	$\psi \sim \text{Basal_area} + \text{Mean_height}$ $p \sim \text{T_density} + \text{Basal_area}$	192.9	0.91	0.121	0.334
	$\psi \sim \text{Basal_area} + \text{Mean_height} + \text{F_man} + \text{T_density} : \text{F_man}$ $p \sim \text{Basal_area}$	193.3	1.24	0.103	0.394
	$\psi \sim \text{Basal_area} + \text{F_man} + \text{A.S.Rich} : \text{F_man}$ $p \sim \text{Basal_area}$	193.4	1.42	0.094	0.351
	$\psi \sim \text{Basal_area} + \text{F_man} + \text{A.S.Rich} + \text{Mean_height}$ $p \sim \text{Basal_area}$	193.6	1.61	0.086	0.371
	$\psi \sim \text{Basal_area} + \text{F_cat} + \text{Mean_height} + \text{Stdev_height}$ $p \sim \text{Basal_area}$	194.0	1.94	0.072	0.347
<i>M. avellanarius</i>	$\psi \sim \text{Stdev_height} + \text{F_cat} + \text{T_density}$ $p \sim \text{Mean_height} + \text{Stdev_height} + \text{F_cat} + \text{T_density}$	130.3	0.00	0.726	0.570
	$\psi \sim \text{Mean_height} + \text{Stdev_height}$ $p \sim \text{Mean_height} + \text{T_density} + \text{Stdev_height}$	132.2	1.95	0.274	0.528

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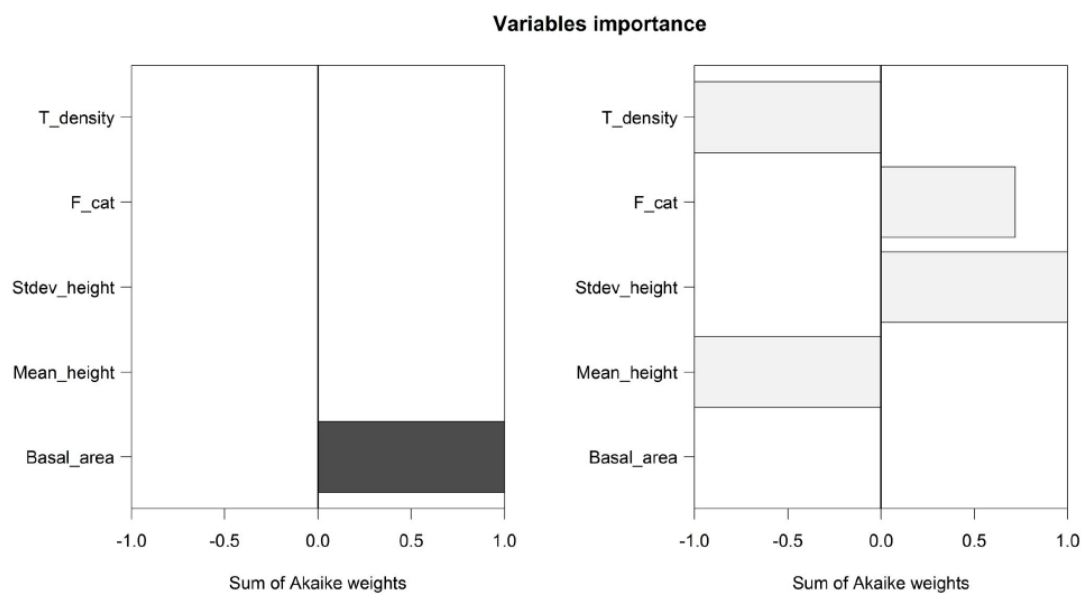
Fig. S1 - First (second) row depicts maps of predicted occurrence probabilities for *G. glis* (left) and *M. avellanarius* (right) by GLMM (OM). Occurrence probability values, which range from 0 (blue) to 1 (red), were projected over the study area by spatializing the predictors selected in the top-ranked models (see also Appendix 3).



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Fig. S2 - Detectability variables importance for edible (dark grey) and hazel (light grey) dormice, as the cumulative sum of Akaike weights over the top-ranked models.



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CHAPTER IV

Distribution of small mammal communities across Mediterranean landscapes

4.1 Distribution of small mammal communities across Mediterranean landscapes

**Chiara Paniccia*¹, Ludovico Frate¹, Mirko Di Febbraro¹, Maria Laura Carranza¹,
Marco Marchetti², Anna Loy¹**

1. EnvixLab, Department of Biosciences and Territory, University of Molise, C. da Fonte Lappone, 86090 Pesche, Italy;

2. Department of Biosciences and Territory, University of Molise, C. da Fonte Lappone, 86090 Pesche, Italy;

in prep.

* Corresponding author

email: chiara.paniccia12@gmail.com

Tel: +39 0874404140

Fax: +39 0874404123

1. Introduction

Rodentia and Eulipotyphla are two of the most important orders of mammals, both in terms of number of species and in geographical distributions (Zachos 2018a, b), and are typically addressed as small mammals. Small mammals are an extremely diverse, non-taxonomic group, that provides many ecosystem services and plays a number of important ecological roles such as seeds dispersal (Xiao et al. 2005, 2006), spore dispersal (Martin 2003), pollination (Melidonis and Peter 2015), nutrient cycling (Hayward and Phillipson 1979; Fischer et al. 2018). These diverse and important roles make small mammals capable of influencing ecosystems energy fluxes and are often an important component of well-structured ecological networks (Dickman 1999; Pearce and Venier 2005; Hurst et al. 2014). They have sufficient mobility to respond to alterations at different landscape scales (Michel et al. 2007; Rowe et al. 2015) or habitats (Pardini et al. 2005; Rodríguez and Peris 2007; Arnan et al. 2014; Marques et al. 2015). As small mammals rapidly respond to environmental change, due to their short live cycles and restricted spatial areas, such species can serve as model organisms for a better understanding of ecosystem and landscape processes (Barrett and Peles 1999) at different levels of complexity (i.e. community, population, species, etc.). Numerous research have been using small mammals species to evaluate fragmentation and/or loss habitats in a variety of ecosystems such as forests (Capizzi et al. 2003; Mortelliti et al. 2009, 2014; Bovendorp et al. 2018), deserts (Ernest et al. 2009; Bowman et al. 2017; Guevara and Ball 2018), and agro-ecosystems (Bond et al. 2004; Hurst et al. 2014; Fischer et al. 2018; Berl et al. 2018).

Global biodiversity is declining at an unprecedented rate (Sala 2000; Pereira et al. 2012) as a result of multiple environmental human-induced changes (Walther et al. 2002; Maiorano et al. 2011; Foley et al. 2012; Dirzo et al. 2014). The current landscape patterns in the world are mainly the result of centuries of land-use evolution (Kienast 1993). For instance, European mountain and hilly temperate forests currently survive in patches included into a mosaic landscape, shaped by centuries of extensive forest exploitation, agricultural practices and cattle farming (Diekmann et al. 1999; Rosati et al. 2010). More recently, spontaneous reforestation process, occurred after a '*rural exodus*' and the abandonment of traditional agricultural practices (MacDonald et al. 2000; Rudel et al. 2005; Bracchetti et al. 2012).

In this context, habitat fragmentation due to land-use changes is recognized as one of the most serious threats to wildlife populations' persistence (Carpenter et al. 2010; Hudson et al. 2014;

Crooks et al. 2017). These negative effects of land-cover changes can be detected by either direct measurements of biodiversity, such as species richness (Bartlett 1979), the abundance and distribution of populations (Andrén and Andren 1994; Hinsley et al. 1995), and the genetic diversity of populations (Diffendorfer et al. 1995; Gaines et al. 1997; Gerlach and Musolf 2000).

Animal and plants assemblages are impoverished both taxonomically and functionally, with a leading to biotic homogenization at the landscape level (Tabarelli et al. 2012).

The composition of nearby habitats in the surrounding landscape will also affect the suitability of local habitat patches. Animals that exploited multiple habitat types may depend on combinations of different habitats in the landscape to maintain viable populations (Galitsky and Lawler 2015; Arroyo-Rodríguez et al. 2016; Buelow et al. 2017). Furthermore, the possibility of organisms to disperse between habitat patches depends on the quality of habitats in the surrounding landscape (Bennett et al. 1994).

Species functional traits can be defined as any morphological, biochemical, physiological, structural, phenological or behavioral attribute of an organism that influences fitness, their responses to the environment and ecosystem processes (García-Llamas et al. 2019).

In a functional traits approach, species traits and species abundance were associated with environmental predictors. This is known as the fourth-corner problem (Legendre et al. 1997), where the aim is to combine matrices of environmental data, species abundance or presence/absence data, and trait data to create a matrix that describes the trait-environment relationship. Brown et al. (2014) proposed a modelling solution to complement the existing methods, whereby a predictive model is fitted for species abundance as a function of matrices of environmental data and species traits. The resulting matrix of environment by trait interaction coefficients can then be used to quantify the direction and strength of the associations between traits and environmental factors (Brown et al. 2014).

Albeit, this approach focus of recent efforts to bridge a gap between species distribution modelling and multivariate analyses in ecology (Warton et al. 2015a) and can improve the interpretation of mammal communities response throughout changes in time and space, most research on small mammal communities ruled out the use of functional traits. In addition, most of the study has focused on limited spatial and temporal scales, especially in the Mediterranean region (Szpunar et al. 2008; Rugiero et al. 2012; Moreno and Rouco 2013).

The objective of this paper was to assess the importance and relationship between land-cover configuration and composition on small mammal abundance, community structure and functional-traits of two taxonomic groups (Rodentia and Eulipotyphla) in a heterogeneous Mediterranean landscape. These taxa represent a major part of the mammal biodiversity and they differ widely in their resource use. We addressed this information gap with the aim to obtain a better understanding of how land-cover pattern can affect the composition of small mammal communities in south-central Italy. In the present study, we used a statistical method to: (i) identify which factors shape the structure, abundance and diversity of small mammal communities in Mediterranean landscapes; (ii) screen keystone traits related to landscape that shape the composition of the small mammal community.

2. Materials and Methods

Study area

The study area includes a wide array of Mediterranean landscapes in central Italy and covers three regions (Abruzzo, Lazio, and Molise) for total surface of 33.000 km² ca (centroid coordinates: longitude 13°16'52.4"E, latitude 42°10'21.6"N, datum WSG84). Altitudes range from sea level to 2.912 m a.s.l. (Mt. Gran Sasso, Aquila), while the climate encloses Mediterranean types on the coast to continental ones in the upper mountains (Pesaresi et al. 2017). The landscape is dominated by agricultural lands (58.0 %), followed by forest (29.6 %), artificial areas (4.9 %), and other typologies (7.2 %) (EEA 2012).

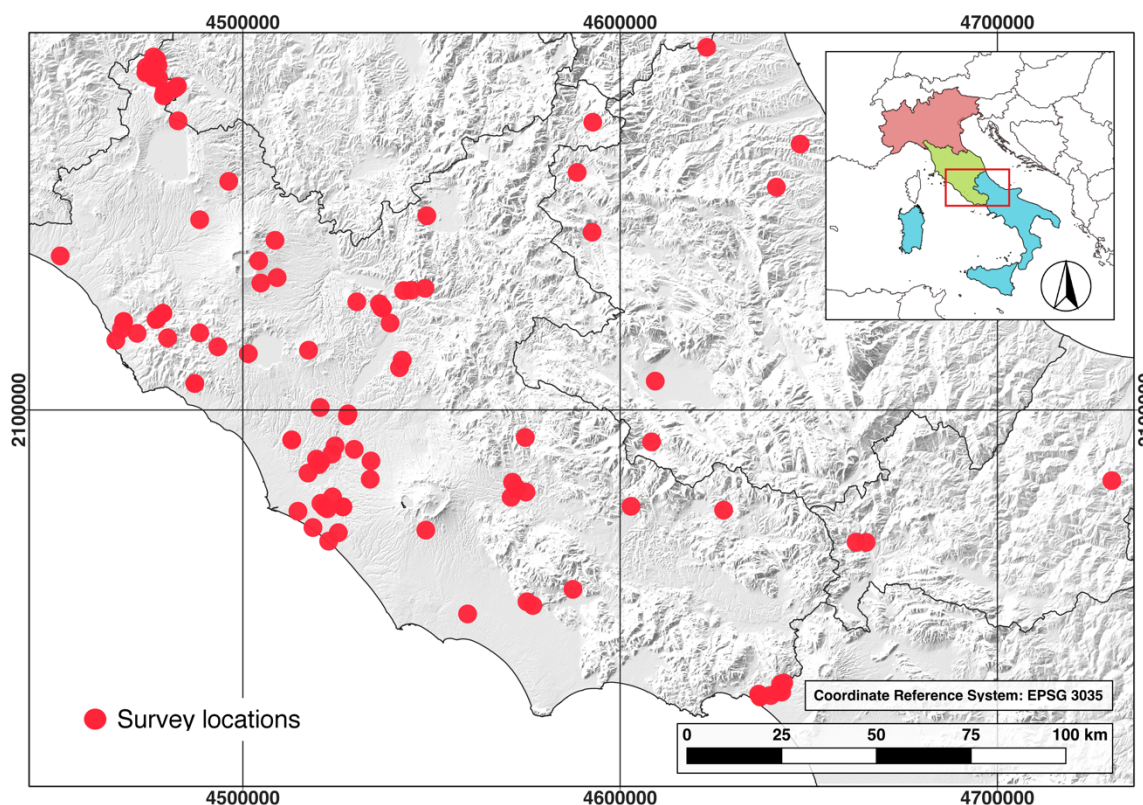


Figure 1. Location of study area along with the nesting or roosting sites of Common Barn-owl (*Tyto alba*). At the top right corner, the colors identify: Northern Italy (light red), Central Italy (light green), and Southern Italy (light blue)

Small mammal data

Small mammal data were extracted directly from OpenMICE (Paniccia et al. 2018a) which is a standardized georeferenced database of small mammal occurrences, abundances, and functional traits data derived from owl pellets. We extracted a set of georeferenced sites for

pellets of Common Barn-owl (*Tyto alba*) collected in south-central Italy in the period 1979 – 2013. We considered only the sampling sites with more than 50 prey individuals in order to detect the overall small mammals' community composition occurred in each area (Bond et al. 2004). For each sampling site, we analyzed the species abundance and the specific morphological, functional and ecological traits (see Table 1).

Traits data

In our study, we considered 21 small mammal species occurring in south-central Italy (10 Rodentia and 11 Euliphotypla).

A preliminary trait selection was done based on biological relevance for the species ecology in the focal small mammal communities. Particular attention was given to the selection of traits that are broadly relevant and crucial to describe the ecology of the species able to assure the ecological realism of our study.

Traits data consists on a set of functional and ecological characteristics describing the different small mammal species available on OpenMICE (Paniccia et al. 2018), and collated from relevant sources, such as databases, review papers, books, and primary literature (see Table 1).

Body mass, measured as the mean mass (g) across sexes is strongly correlated with the specific metabolic demand and constitutes a key trait for describing the resource acquisition behavior (e.g. foraging and predation rates) and at the same time the vulnerability towards changes in environmental conditions (Ryall and Fahrig 2006; Barnes et al. 2014).

We used trophic level in form of feeding type (Carnivore (predominantly eating animals), Herbivore (predominantly eating plants), Omnivore (feeding on both animals and plants)), as another essential trait providing insights about resource acquisition and species-specific affect on energy fluxes in ecosystems (Gravel et al. 2016). Additionally, feeding type relates to vulnerability of a species in changing environmental conditions and altered resource availability (Santini et al. 2016).

To connect the behavior and the habitat use of a species, activity pattern (activity of species throughout day and night, e.g. diurnal, cathemeral, polyphasic, nocturnal, etc.), pattern of torpor (e.g. hibernation, daily torpor), breeding site (location used for breeding, e.g. arboreal, underground, etc.), prevalent habit (above ground, arboreal, fossorial, semi-aquatic) were included (Table 1). To understand individual species effect on community and population

dynamics the social system (degree to which individuals tend to associate in social groups and form cooperative societies, solitary or group-living) is measured (Lukas and Clutton-Brock 2017).

Variable	Description	Data type
Activity pattern	Daily activity cycle of the species. Categories are: Diurnal (obligate diurnal), Nocturnal (obligate nocturnal), Cathemeral (irregularly active at any time of night or day) or Cathemeral-Polyphasic (cathemeral pattern with several short-term activity cycles per 24h), according to (Halle and Stenseth 2012)	categorical
Body mass	Mean mass (grams), which refers to the mean mass of individuals (age unspecified) of the species	decimal
Breeding site	Location used as breeding site of the species. Categories are: Arboreal or Underground	categorical
Pattern of torpor	Classified according to Ruf and Geiser (2015). Categories are: Daily torpor, Hibernation	integer
Prevalent habit	The prevalent habit of a species. Categories are: Above ground, Arboreal, Fossorial Semi-aquatic	categorical
Social system	Degree to which individuals tend to associate in social groups and form cooperative societies. Categories are: solitary or group-living	categorical
Trophic level	The trophic level of species. Categories are: Carnivore (predominantly eating animals), Herbivore (predominantly eating plant material), Omnivore (feeding on both animals and plants)	categorical

Table 1. List of functional and ecological traits considered in this study

Land-cover data and landscape pattern

Land-cover data describing landscape characteristics of the pellet sites were obtained from land-cover maps (European CORINE – CLC, relative to the years 1990, 2000, 2012), freely available at a European level (<https://land.copernicus.eu/pan-european/corine-land-cover>). CLC data is available with a geometric accuracy of 100 m resolution and a minimum mapping unit (MUM) of 25 ha and 100 meters minimum mapping width (Copernicus 2019).

In order to assure the temporal correspondence among pellets collection and land-cover maps as well as obtain coeval land-cover patterns, we distinguished samples site based in steps of ten years: 1979-1989 samples referred to the 1990 map, 1991-1999 samples to the year 2000 and finally, the 2001-2013 samples to the 2012 cover map (see for details Table S 3).

Maps and georeferenced data were managed with QGIS 2.18 (QGIS Development Team 2016).

The original CLC categories were grouped into 9 classes that are meaningful in terms of small mammals habitat requirements with and expert-based outline theorized by Rondinini et al. (2011) (Table 2).

We have measured a set of 14 pattern metrics at class and landscape level for each sampling site within a circular moving window with a radius of 1000 m determined by *T. alba* hunting territory radius (Paniccia et al. 2018). Spatial metrics were calculated using FRAGSTATS (McGarigal et al. 2002).

In order to avoid redundant information, and correlated variables the 14 landscape metrics were sub-selected considering a Variance Inflation Factor (VIF) < 5 (Guisan et al. 2017). Thus, we selected the following set of not correlated landscape metrics: Shannon's Evenness Index (SHEI), Patch Richness Density (PRD), Interspersion & Juxtaposition Index (IJI), Contrast-Weighted Edge Density (CWED), Percentage of landscape (PLAND for 9 classes; for details see Table S 2).

Level 1	CLC classes	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. Urban
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. Forest 3.2. Shrubs and herbaceous vegetation associations 3.3. Open spaces with little or no vegetation	3.1. Forest 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
5. Water bodies	5.1 Inland waters 5.2 Marine waters	

Table 2. Reclassification classes for the CORINE Land-cover map based on CLC2012.
 Source: <https://land.copernicus.eu/pan-european/corine-land-cover>

Statistical analysis

All statistical analyses were performed using R programming language (R Development Core Team 2018). Shapiro–Wilks tests revealed that small mammal abundance data were not normally distributed ($p\text{-value} = 4.11\text{e-}12$). The data were normalized using standard transformations ($\log_{10}(x + 1)$), to improve normality and homoscedasticity, and therefore, parametric analyses were performed on ranked data (Conover 1999).

Then the relation among small mammal communities and landscape pattern was explored by analyzing 108 sites per five pattern metrics using Canonical Correspondence Analysis (CCA). CCA stresses patterns in relative abundances and is particularly useful for species data with many zero abundances (Palmer 1993).

To determine the factors that significantly constrained the structure of small mammal communities, a forward selection model with Monte Carlo permutation tests was performed with the function ‘*ordistep*’ in the ‘*vegan*’ package (Oksanen et al. 2016) to select a parsimonious set of significant landscape metrics on basis of their permutational p values, and on Akaike Information Criterion (AIC) in case of ties (Borcard et al. 2011).

Then, in order to describe the trait/environment relationships and to provide an intuitive matrix of environment by trait interactions we performed a fourth-corner model (Dray and Legendre 2008). The fourth-corner model allows to relate species traits (e.g. mass, to landscapes attributes by fitting a predictive model of species abundance as a function of matrices of land-cover types and species traits and their interaction (‘*mvabund*’ R package; Wang et al. 2012).

Fourth-corner models in community ecology are models that examine the effects of species traits on their abundance (Warton et al. 2015a, b). While standard community ecology models study predictor-by-species effects (e.g. how are small mammal species affected by vegetation density, habitat connectivity, etc.), fourth-corner models focus on predictor-by-trait effects (e.g. how does species size affect its abundance along landscape or temperature gradients).

The fourth-corner coefficients were plotted using the ‘*lattice*’ R package (Sarkar 2018), also we used the ‘*traitglm*’ function in the R package ‘*mvabund*’ (Wang et al. 2012) to apply multivariate generalized linear models with a negative binomial distribution.

Finally, to test the statistical significance of the overall relationship between land-cover metrics and trait variables we computed a Monte-Carlo randomization test with 999 permutations (Dray and Legendre 2008).

3. Results

From the analysis of the Common Barn-owl pellets collected on 108 sites we identified 27,539 specimens belonging to 2 orders (Rodentia and Euliphotypla), 5 families and 21 species (Table S 4). The most common species were: *Microtus savii* and *Mus domesticus* (11,746 and 3,136 specimens, respectively) followed by *Apodemus sylvaticus*, *Crocidura suaveolens*, *Crocidura leucodon*, and *Suncus etruscus* (ranging between 2,912 and 1,501 specimens; Table S4, Figure S1). The less common species were the Mediterranean Mole, *Talpa caeca*, the Edible Dormouse, *Glis glis*, and the Eurasian water Shrew, *Neomys fodiens* (between 2 and 8 total specimens). *Muscardinus avellanarius*, a species of conservation concern in Europe (Appendix IV of European Habitats Directive 1992/43/EEC), was the most common species of Gliridae (1,134 specimens). Among the species of conservation concern (Table S4), we found four species listed as “Data Deficient” in the Italian Red List (Rondinini et al. 2013): *Talpa caeca* (n = 2), *Sorex antinorii* (n = 121), *Neomys fodiens* (n = 8), *Neomys milleri* (n = 14) and two species listed as “Near Threatened”: *Arvicola italicus* (n = 94) and *Eliomys quercinus* (n = 11; for details, see Table S4).

Community structure

The Canonical Correspondence Analysis (CCA) is statistically significant ($p < 0.001$) and land-cover-cover variables explain about 24.21 % of variance in small mammal community composition. The significance of the first canonical axis and the significance of all canonical axes together were tested using Monte Carlo permutation tests under the full model (unrestricted permutations = 999). The first (eigenvalue = 0.1790) and second (eigenvalue = 0.0427) canonical axes captured most of the variance; therefore, subsequent axes are not discussed.

CCA based on abundance matrix of each small mammal species at 108 sites sampled by Common Barn-owl is shown in Figure 2. Fourth-corner model (DF.diff = 66; Deviance = 380.1; $p = 0.001$) showing the association between species traits and land-cover metrics. Functional traits significantly explained the species-habitat relationship.

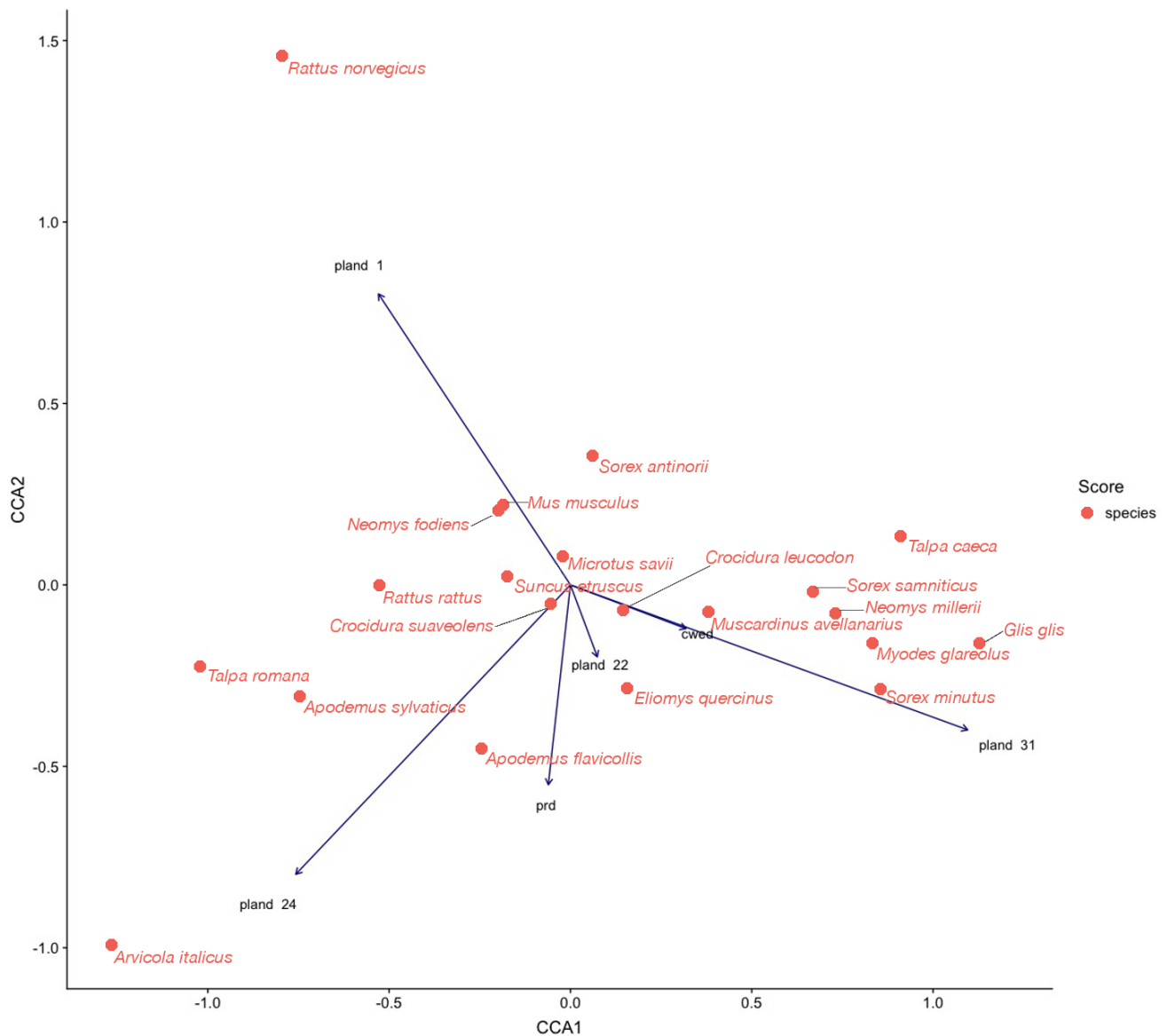


Figure 2. Canonical Correspondence Analysis (CCA) scatter plot of species distributed along the first two canonical axes. Arrows point in the direction of an increase in the magnitude of the respective environmental parameter. Land-cover metrics: PLAND 1: %Urban; PLAND 22: %Permanent crops; PLAND 24: %Heterogeneous agricultural areas; PLAND 31: %Forest; CWED: Contrast-Weighted Edge Density; PRD: Patch Richness Density

The fourth-corner analysis of trophic level revealed that omnivores have a positive association with artificial surfaces, herbivores tend to prefer forested areas, whereas carnivores occurred in homogeneous landscape with a low value for patch richness density (Figure 4). The distribution of body mass is positively related to the artificial gradient, with heavier species in urban areas, as well as areas with high values of Contrast-Weighted Edge Density (as a proxy of fragmented landscapes), while small and lightweight species were restricted to forested areas.

However, the fourth-corner model suggests that fossorial species avoid forested areas and prefer artificial surfaces, semi-aquatic species show a clear preference mainly in heterogeneous agricultural areas and non-fragmented landscapes. In contrast, arboreal species avoid artificial surfaces and anthropogenic landscapes while preferred spatial heterogeneity in diversify and varying land-cover classes. Concerning the breeding site, the results do not show any significant trends; only flimsy preferences to species that using burrows in homogeneous landscape was observed. Polyphasic species preferred forested areas and heterogeneous landscapes, while nocturnal species were abundant in urban areas. Cathemeral species not show a significant pattern of occurrence but they avoid urban areas. Pattern of torpor showed a significant relationship with the land-cover pattern, even if these ecological traits are scarcely linked to landscape characteristics, was evidenced that species that use the strategy of hibernation lives usually in forested areas. Social system not showed a clear and significant pattern of correlation, solitary species were weakly linked to heterogeneous landscapes, and group-living species to forested areas.

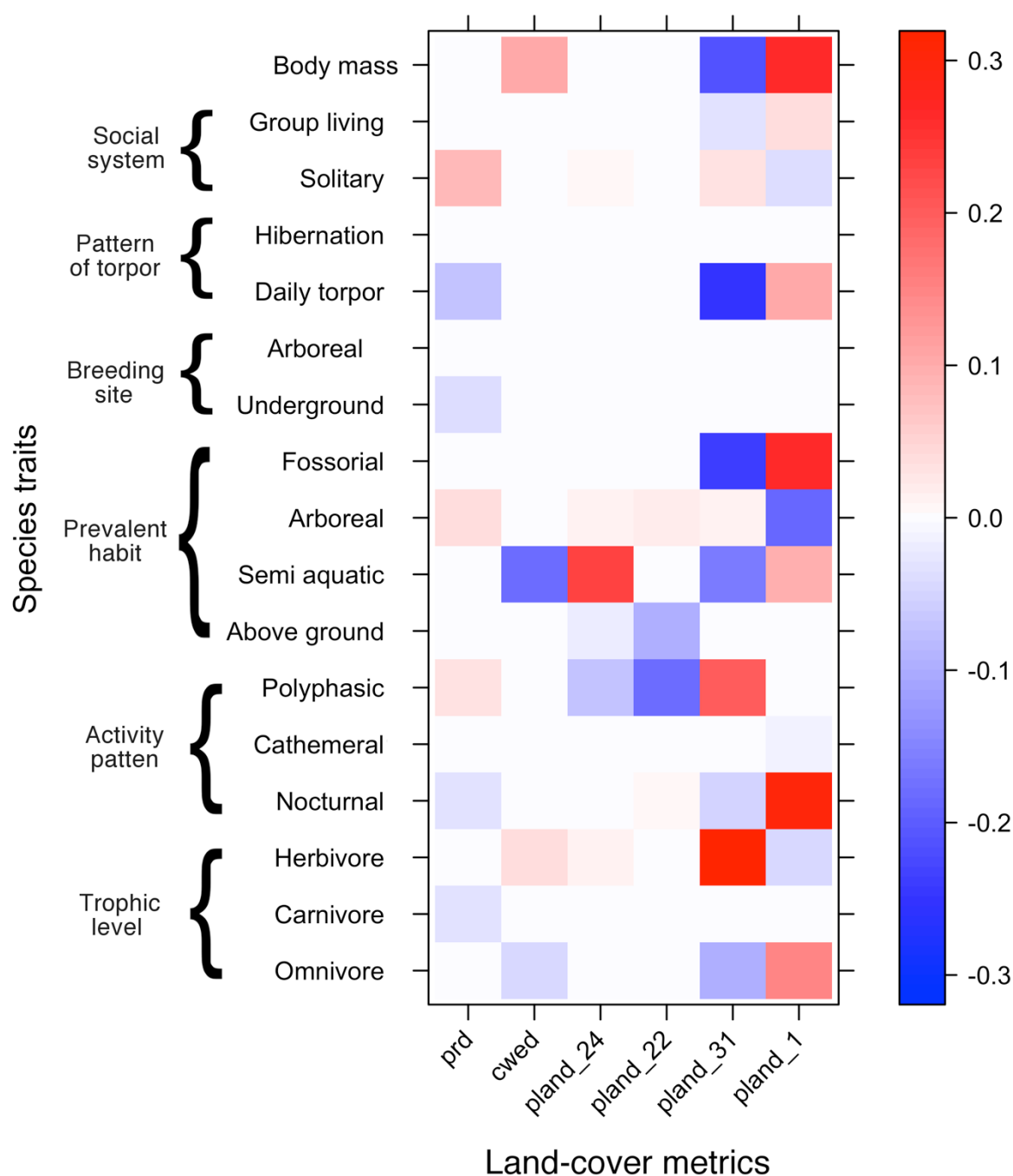


Figure 3. Fourth-corner interaction coefficients for the relationship between small mammal traits and land-cover types. Statistically significant relationships are indicated in red (positive) and blue (negative); the shade of the color represents the strength of the association. Trophic level: The trophic level which the given species belongs. Categories are: Carnivore (predominantly eating animals), Herbivore (predominantly eating plant material), Omnivore (feeding on both animals and plant); Prevalent habit: The prevalent habit of a species. Categories are: Above ground, Arboreal, Fossorial Semi-aquatic; Social system: Degree to which individuals tend to associate in social groups and form cooperative societies. Categories are: Solitary or Group-living; Breeding site: Location used as breeding site by the

species. Categories are: Arboreal or Underground; Body mass: Mean mass (grams), which refers to the mean mass of individuals (age unspecified) of the species; Activity pattern: Daily activity cycle of the species. Categories are: Diurnal (obligate diurnal), Nocturnal (obligate nocturnal), Cathemeral (irregularly active at any time of night or day) or Cathemeral-Polyphasic (cathemeral pattern with several short-term activity cycles per 24h), according to (Halle and Stenseth 2012). For details on functional and ecological traits used in the analysis see Paniccia et al. 2018. Land-cover metrics: PLAND 1: %Urban; PLAND 22: %Permanent crops; PLAND 24: %Heterogeneous agricultural areas; PLAND 31: %Forest; CWED: Contrast-Weighted Edge Density; PRD: Patch Richness Density.

4. Discussion and Limitations

Past research have pointed out the usefulness of owl pellets in the evaluation of small-mammal communities composition (Yalden and Morris 2003; Bond et al. 2004; Meek et al. 2012). While numerous studies are focused on live-traps data (de la Peña et al. 2003; Mortelliti and Boitani 2009), pellets are considered a useful tool to study and investigate elusive, furtive species that are difficult to trap (Mortelliti et al. 2007).

Relative to the objectives of this study, the methodology has allowed us to use abundance data at a relatively large spatial scale over a prolonged time period, that would require huge trapping efforts associated with prohibitive costs.

In our study pellet sampling was conducted through various seasons, so seasonal variations in abundance are unlikely to affect our data.

Community composition

Nevertheless, these valuable results combined with landscape characteristics, could provide valuable insights in determining species distribution, segregation as well as species diversity. In fact, the Canonical Correspondence Analysis (Figure 2) explained most of the data variation and pointed out several important ecological relationships. Two arboreal rodents, hazel dormouse (*Muscardinus avellanarius*) and the edible dormouse (*Glis glis*) were closely linked to forested areas. A difference in habitat specialization between this two similar species was confirmed: hazel dormouse showed a generic preferences for forests, other wooded areas or shrubs (Amori et al. 2008), while edible dormouse was more selective on strictly forest land-cover (Capizzi et al. 2003; Paniccia et al. 2018b). The yellow-necked mouse (*Apodemus flavicollis*) preferred heterogeneous agricultural areas (that contain 'Annual crops associated with permanent crops', 'Complex cultivation patterns', 'Land principally occupied by agriculture, with significant areas of natural vegetation', and 'Agro-forestry areas'); and a diverse predilection respect the wood mouse (*Apodemus sylvaticus*) to more heterogenous landscapes (Benedek and Sîrbu 2018).

Apodemus sylvaticus is a generalist species that preferred various habitats (Macdonald et al. 2000; Tattersall et al. 2001), as well as is particularly successful in exploiting farmland mosaics (Ouin et al. 2000). In our study, the wood mouse show a preference to high heterogeneous landscapes and different land cover types, it is strictly related to Heterogeneous agricultural areas and occur also in urban areas while avoid high fragmented landscapes (high values of CWED) (Figure S 3), that would prove, as well highlight by Tattersall et al. (2001), it was being linked to natural landscapes characterized by ecotones and field margins.

The presence and abundance of *M. glareolus* was correlated with the forest land-cover, i.e. the tree and shrub layer covers. The connectivity of suitable habitats plays an important role for *M. glareolus* (Sozio and Mortelliti 2016), whereas the species had the strongest positive response to tree cover being a forest specialist, and occur frequently sparse in forests or rock areas covered by shrubs or canopies (Amori et al. 2008).

Overall, for south-central Italy, our study revealed a remarkably association between *Mus domesticus*, *Rattus norvegicus*, and *Rattus rattus* with the artificial surfaces (Figure 2 and S 4) and a strong connection though the Savi's pine vole (*Microtus savii*) with pastures and permanent crops (Ranchelli et al. 2016). *Sorex samniticus* is present and even abundant in forests and woodland patches (Mortelliti et al. 2007), to date only few research has been carried out on the ecology of *Sorex samniticus*, particularly in the Italian Peninsula. *Sorex samniticus* in our study is linked to forest area, this result confirmed that the species is a forest dependent (Mortelliti and Boitani 2009).

Fourth-corner analysis

Our results revealed that differences in species composition and trait distributions are related to land-cover pattern and that composition in particular seem to play the most important roles in determining such differences.

In particular, there was evidence of a pronounced change in species composition along different land-cover gradient, with a clear assemblage of species adapted to artificial and urban areas (e.g. *Mus domesticus*, *Rattus norvegicus*, *Rattus rattus*) and groups of species living in forested areas (e.g. *Myodes glareolus*, *Muscardinus avellanarius*, *Neomys milleri*, *Sorex samniticus*, *Sorex minutus*).

The fourth-corner analysis revealed some significant associations between individual small mammal traits and land-cover types and configuration, some associations were found in forested areas with positive relationship between herbivores, solitary and polyphasic small mammals. However, other associations were showed, in particular, omnivores with high values of body mass, fossorial or nocturnal species were positively related with artificial surfaces (Figure 3).

Habitat requirements and limitation across spatial scales

In the European Union, the most important initiative with respect to the building of an LULCC database is CORINE Land-cover (CLC; EEA 2012). CLC has been largely used by planners and researchers but is a big debate about the use of CLC in Ecology and Conservation Biology (Santos et al. 2016). There is no doubt CLC provides highly valuable information on land-use and its evolution in European Union countries. Its average scale (1:100,000) is suitable for analyzing land-use dynamics at a national or even regional level. Its use is inappropriate, however, for local studies. I have calculated numerous fragmentation and diversity indices (i.e. Shannon diversity index, Simpson

diversity index, Contrast-Weighted Edge Density, Interspersion and Juxtaposition Index) by using FRAGSTATS (McGarigal et al. 2002) on CLC at each sampled site (buffer area approximately 1000 m). Unfortunately, through time (45 years) landscape indices were not significantly changed, while the total percentage of land-cover (PLAND) have been changed.

It is recommended to proceed with caution when using this source because it not will very powerful to detect changes through time for a fine-scale resolution (such as for fragmentation and spatial configuration indices). Generally, functional traits and abundance data have fitted good relationships in specie-habitat requirements. However, these allow us to observe large-scale processes and capture only macro-phenomena. In this context, the use of different remote sensing variables that are proxy for landscape diversity (e.g. NDVI, EVI, etc.) may provide more accurate in shaping mammal distribution from a large spatial-scale to a small spatial scale (Pettorelli et al. 2014; He et al. 2015; Turner et al. 2015).

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4.1.2 Supplementary material

	Tropic level			Activity pattern			Prevalent habit				Breeding site		Pattern of torpor		Social system		Body size
Scientific name	Omnivore	Carnivore	Herbivore	Nocturnal	Cathemeral	Polyphasic	Above ground	Semi-aquatic	Arboreal	Fossorial	Underground	Arboreal	Daily torpor	Hibernation	Solitary	Group-living	Body mass
<i>Apodemus flavicollis</i>	1	0	0	1	0	0	1	0	0	0	1	0	1	0	1	0	26.70
<i>Apodemus sylvaticus</i>	1	0	0	1	0	0	1	0	0	0	1	0	1	0	1	0	21.90
<i>Arvicola italicus</i>	0	0	1	0	1	0	0	1	0	0	1	0	1	0	0	1	150.89
<i>Crocidura leucodon</i>	0	1	0	1	0	0	1	0	0	0	1	0	1	0	1	0	10.88
<i>Crocidura suaveolens</i>	0	1	0	1	0	0	1	0	0	0	1	0	1	0	1	0	7.35
<i>Eliomys quercinus</i>	1	0	0	0	1	0	0	0	1	0	0	1	0	1	1	0	114.61
<i>Glis glis</i>	1	0	0	1	0	0	0	0	1	0	0	1	0	1	1	0	128.09
<i>Microtus savii</i>	0	0	1	0	1	0	0	0	0	1	1	0	1	0	0	1	20.00
<i>Mus domesticus</i>	1	0	0	1	0	0	1	0	0	0	1	0	1	0	1	0	19.30
<i>Muscardinus avellanarius</i>	1	0	0	1	0	0	0	0	1	0	0	1	0	1	1	0	27.50
<i>Myodes glareolus</i>	0	0	1	0	1	0	1	0	0	0	1	0	1	0	1	0	20.73
<i>Neomys fodiens</i>	0	1	0	0	0	1	0	1	0	0	1	0	1	0	1	0	20.73
<i>Neomys milleri</i>	0	1	0	0	0	1	0	1	0	0	1	0	1	0	1	0	13.19
<i>Rattus norvegicus</i>	1	0	0	1	0	0	1	0	0	0	1	0	1	0	0	1	282.89
<i>Rattus rattus</i>	1	0	0	1	0	0	0	0	1	0	0	1	1	0	0	1	142.68
<i>Sorex antinorii</i>	0	1	0	0	0	1	1	0	0	0	1	0	1	0	1	0	7.70
<i>Sorex minutus</i>	0	1	0	0	0	1	1	0	0	0	1	0	1	0	1	0	4.32
<i>Sorex samniticus</i>	0	1	0	0	0	1	1	0	0	0	1	0	1	0	1	0	8.50
<i>Suncus etruscus</i>	0	1	0	1	0	0	1	0	0	0	1	0	1	0	1	0	2.26
<i>Talpa caeca</i>	0	1	0	0	0	1	0	0	0	1	1	0	1	0	1	0	71.08
<i>Talpa romana</i>	0	1	0	0	0	1	0	0	0	1	1	0	1	0	1	0	92.50

Table S 1. List of functional and ecological traits in this study, data was derived from (Paniccia et al. 2018a)

Pattern metrics	Description	Level
Patch Richness (PR)	Measures the number of patch types present	Landscape
Patch Richness Density (PRD)	Standardizes richness to a per area basis that facilitates comparison among landscapes	
Simpson's Diversity Index (SIDI)	SIDI equals 1 minus the sum, across all patch types, of the proportional abundance of each patch type squared. Note, P_i is based on total landscape area (A) excluding any internal background present	
Shannon's Evenness Index (SHEI)	SHEI equals minus the sum, across all patch types, of the proportional abundance of each patch type multiplied by that proportion, divided by the logarithm of the number of patch types. In other words, the observed Shannon's Diversity Index divided by the maximum Shannon's Diversity Index for that number of patch types. Note, P_i is based on total landscape area (A) excluding any internal background present	
Simpson's Evenness Index (SIEI)	SIEI equals 1 minus the sum, across all patch types, of the proportional abundance of each patch type squared, divided by 1 minus 1 divided by the number of patch types. In other words, the observed Simpson's Diversity Index divided by the maximum Simpson's Diversity Index for that number of patch types. Note, P_i is based on total landscape area (A) excluding any internal background present	
Shannon's Diversity Index (SHDI)	SHDI equals minus the sum, across all patch types, of the proportional abundance of each patch type multiplied by that proportion. Note, P_i is based on total landscape area (A) excluding any internal background present	
Area-weighted mean patch size (AREA_AM)	AM (area-weighted mean) equals the sum, across all patches in the landscape, of the corresponding patch metric value multiplied by the proportional abundance of the patch [i.e., patch area (m^2) divided by the sum of patch areas]. Note, the proportional abundance of each patch is determined from the sum of patch areas rather than the total landscape area, because the latter may include internal background area not associated with any patch	
Area-weighted mean patch shape index (SHAPE_AM)	AM (area-weighted mean) equals the sum, across all patches of the corresponding patch type, of the corresponding patch metric value multiplied by the proportional abundance of the patch [i.e., patch area (m^2) divided by the sum of patch areas]	
Interspersion & Juxtaposition Index (IJI)	IJI equals minus the sum of the length (m) of each unique edge type divided by the total landscape edge (m), multiplied by the logarithm of the same quantity, summed over each unique edge type; divided by the logarithm of the number of patch types times the number of patch types minus 1 divided by 2; multiplied by 100 (to convert to a percentage)	

Percentage of landscape (PLAND)	PLAND equals the sum of the areas (m ²) of all patches of the corresponding patch type, divided by total landscape area (m ²), multiplied by 100 (to convert to a percentage); in other words, PLAND equals the percentage the landscape comprised of the corresponding patch type. Note, total landscape area (A) includes any internal background present	Class
Total Edge Contrast Index (TECI)	TECI equals the sum of the lengths (m) of each edge segment in the landscape multiplied by the corresponding contrast weight, divided by the total length (m) of edge in the landscape, multiplied by 100 (to convert to a percentage). Edge segments along the landscape boundary are treated like background (as specified in the edge contrast weight file) unless a landscape border is present, in which case the boundary edge types are made explicit by the information in the border	
Contrast-Weighted Edge Density (CWED)	CWED equals the sum of the lengths (m) of each edge segment in the landscape multiplied by the corresponding contrast weight, divided by the total landscape area (m ²), multiplied by 10,000 (to convert to hectares). Edge segments along the landscape boundary are treated like background (as specified in the edge contrast weight file) unless a landscape border is present, in which case the boundary edge types are made explicit by the information in the border. Note, total landscape area (A) includes any internal background present	
Number of Patches (NP)	NP equals the number of patches of the corresponding patch type (class). Number of patches of a particular patch type is a simple measure of the extent of subdivision or fragmentation of the patch type	
Fractal Dimension Index (FRAC)	FRAC equals 2 times the logarithm of patch perimeter (m) divided by the logarithm of patch area (m ²); the perimeter is adjusted to correct for the raster bias in perimeter	

Table S 2. List of land-cover metrics calculated on CLC

Id	Year	Latitude	Longitude	CLC	Id	Year	Latitude	Longitude	CLC
1	1987	41.24737	13.75588	1990	55	1985	42.8033	11.88872	1990
2	1987	41.24579	13.75702	1990	56	1985	42.80972	11.90794	1990
3	1987	41.24777	13.7908	1990	57	1985	42.75941	11.96927	1990
4	1987	41.25263	13.75302	1990	58	1985	42.83102	11.89413	1990
5	1987	41.2563	13.81411	1990	59	1985	42.82425	11.90448	1990
6	1987	41.25469	13.82569	1990	60	1991	42.2540100	12.6769000	2000
7	1987	41.27375	13.82358	1990	61	1997	41.6606400	12.4133700	2000
8	1987	41.27658	13.83357	1990	62	1997	41.6800199	12.4446700	2000
9	1980	41.47486	12.84544	1990	63	1997	41.6944200	12.3648500	2000
10	1979	41.49841	13.03444	1990	64	1997	41.7344099	12.3185400	2000
11	1979	41.52368	13.18125	1990	65	1997	41.7381600	12.4120399	2000
12	1987	41.679111	12.722306	1990	66	2000	41.7415799	12.4618300	2000
13	1989	41.69674	13.66863	1990	67	1999	41.7415799	12.4618300	2000
14	1988	41.716260	13.375760	1990	68	1997	41.7518900	12.3922899	2000
15	1981	41.75000	12.99644	1990	69	1997	41.7426999	12.4029600	2000
16	1985	42.779150	11.909450	1990	70	1999	41.7661299	12.4297100	2000
17	1979	41.489	13.05252	1990	71	1991	41.8055400	12.5510199	2000
18	1982	41.84913	12.55533	1990	72	1999	41.8251899	12.3542200	2000
19	1984	41.87822	12.50322	1990	73	1992	41.8446100	12.3888800	2000
20	1987	41.89161	13.04849	1990	74	1992	41.8579099	12.3823399	2000
21	1980	41.9055	12.3053	1990	75	1999	41.8688000	12.4316900	2000
22	1980	41.959043	12.484535	1990	76	1997	41.8680000	13.4493610	2000
23	1980	41.963837	12.487210	1990	77	1999	41.8877999	12.4427200	2000
24	1988	42.01295	13.46937	1990	78	1996	41.9809699	12.3989400	2000
25	1981	42.087722	12.665139	1990	79	1997	42.0472499	12.0013700	2000
26	1979	42.15808	11.91808	1990	80	1991	42.1775560	12.6303330	2000
27	1980	42.19988	11.77876	1990	81	1999	42.2036939	11.8855830	2000
28	1979	42.203694	11.885583	1990	82	1991	42.2140100	12.6074100	2000
29	1984	42.214010	12.60741	1990	83	1991	42.2309600	12.5261200	2000
30	1979	42.21718	11.9049	1990	84	1991	42.2542600	12.7009700	2000
31	1980	42.21718	11.9049	1990	85	1991	42.2575599	12.7456900	2000
32	1984	42.22448	12.59827	1990	86	1999	42.1707899	11.8210300	2000
33	1981	42.283170	12.220520	1990	87	2010	41.604060	14.083120	2012
34	1982	42.29504	12.27339	1990	88	2006	41.714530	14.903590	2012
35	1984	42.33624	12.21577	1990	89	2009	41.761050	13.044120	2012
36	1980	42.36008	11.58002	1990	90	2010	41.771020	13.014780	2012
37	1982	42.38423	12.26995	1990	91	2009	41.785720	13.002710	2012
38	1988	42.43095	12.7594	1990	92	2002	41.85093	12.39577	2012
39	1980	42.43866	12.03008	1990	93	2007	41.9055	12.3053	2012
40	1988	42.46237	13.88486	1990	94	2010	41.60229	14.11500	2012

41	1987	42.52863	12.12647	1990	95	2007	42.04725	12.00137	2012
42	1988	42.52005	13.24715	1990	96	2001	42.069861	12.655667	2012
43	1982	42.63844	13.30408	1990	97	2008	42.11504	12.17448	2012
44	1985	42.67662	11.96831	1990	98	2006	42.11903	12.36725	2012
45	1985	42.74094	11.93025	1990	99	2007	42.13361	12.07799	2012
46	1985	42.73744	11.92333	1990	100	2006	42.15539	11.75263	2012
47	1985	42.74843	11.92665	1990	101	2007	42.18166	11.7712	2012
48	1985	42.75505	11.9618	1990	102	2008	42.16806	12.02112	2012
49	1985	42.78234	11.89339	1990	103	2007	42.19988	11.77876	2012
50	1985	42.79356	11.86797	1990	104	2006	42.20286	11.88236	2012
51	1985	42.79405	11.87474	1990	105	2007	42.203694	11.885583	2012
52	1980	42.80471	13.68159	1990	106	2010	42.21581	12.60397	2012
53	1985	42.80675	11.86987	1990	107	2013	42.375611	13.287417	2012
54	1985	42.80819	11.88783	1990	108	2013	42.56228	13.96788	2012

Table S 3. Sampling sites for Common Barn-owl and related CLC maps used to calculate landscape metrics. Id = Sampling site code; Latitude = Latitude in decimal degrees: EPSG 4326; Longitude = Longitude in decimal degrees: EPSG 4326; CLC = year referred to CLC

Scientific name	Family	Order	Count	IUCN National Status	Habitat Directive
<i>Apodemus flavicollis</i>	Muridae	Rodentia	63	LC	IV All.
<i>Apodemus sylvaticus</i>	Muridae	Rodentia	2912	LC	
<i>Arvicola italicus</i>	Cricetidae	Rodentia	94	NT	
<i>Crocidura leucodon</i>	Soricidae	Eulipotyphla	1639	LC	
<i>Crocidura suaveolens</i>	Soricidae	Eulipotyphla	1679	LC	
<i>Eliomys quercinus</i>	Gliridae	Rodentia	11	NT	
<i>Glis glis</i>	Gliridae	Rodentia	3	LC	
<i>Microtus savii</i>	Cricetidae	Rodentia	11746	LC	
<i>Mus domesticus</i>	Muridae	Rodentia	3136	NA	
<i>Muscardinus avellanarius</i>	Gliridae	Rodentia	1134	LC	
<i>Myodes glareolus</i>	Cricetidae	Rodentia	877	LC	
<i>Neomys fodiens</i>	Soricidae	Eulipotyphla	8	DD	
<i>Neomys milleri</i>	Soricidae	Eulipotyphla	14	DD	
<i>Rattus norvegicus</i>	Muridae	Rodentia	65	NA	
<i>Rattus rattus</i>	Muridae	Rodentia	543	NA	
<i>Sorex antinorii</i>	Soricidae	Eulipotyphla	121	DD	
<i>Sorex minutus</i>	Soricidae	Eulipotyphla	345	LC	
<i>Sorex samniticus</i>	Soricidae	Eulipotyphla	1621	LC	
<i>Suncus etruscus</i>	Soricidae	Eulipotyphla	1501	LC	
<i>Talpa caeca</i>	Talpidae	Eulipotyphla	2	DD	
<i>Talpa romana</i>	Talpidae	Eulipotyphla	25	LC	

Table S 4. Scientific name along with their relative Family and Order of the analyzed species. Count: number of specimens; IUCN National Status: The current conservation status, following the IUCN Italian Red List Rondinini et al. (2013). Categories are: Extinct (EX), Extinct in the wild (EW), Endangered (EN), Regionally Extinct (RE), Critically endangered (CR), Vulnerable (VU), Near Threatened (NT), Least Concern (LC), Data Deficient (DD), Not applicable (NA). Habitat Directive: Number of Annex in which the species is listed under the Habitats Directive (1992/43/EEC)

Model	AIC _c
log1p(sm) ~ prd + cwed + pland_24 + pland_22 + pland_31 + pland_1	326.75
log1p(sm) ~ pland_31 + pland_24 + pland_1 + pland_22 + cwed	327.23
log1p(sm) ~ cwed+ pland_24+pland_22+pland_21+pland_31	327.52
log1p(sm) ~ cwed+shei+pland_24+pland_22+pland_21+pland_31	327.59
log1p(sm) ~ iji + cwed + pland_24 + pland_22 + pland_31 + pland_1	327.69
log1p(sm) ~ pland_31 + pland_24 + pland_1 + pland_22	328.51
log1p(sm) ~ prd+cwed+iji+shei+pland_24+pland_22+pland_21+pland_31+pland_1	329.33
log1p(sm) ~ pland_31 + pland_24 + pland_1	329.58
log1p(sm) ~ prd+cwed+iji+shei+pland_24+pland_32+pland_22+pland_21+pland_31+pland_1	329.76
log1p(sm) ~ pland_31 + pland_24	331.31
log1p(sm) ~ pland_31	334.01
log1p(sm) ~ pland_31+pland_22+pland_21+pland_23+pland_22+pland_33 +pland_24+shei+iji+cwed+prd	344.52

Table S 5. Top ranked model derived from the model selection procedure. The presented variables are obtained by automatic forward selection with Monte Carlo tests (999 permutations). AIC: Akaike weight of each model

Mod_f = cca(formula = log1p(sm) ~ prd + cwed + pland_24 + pland_22 + pland_31 + pland_1)				
Variable	Df	ChiSquare	F	Pr(>F)
%Forest	1	0.12872	14.5531	0.001 ***
%Heterogeneous agricultural areas	1	0.04461	5.0435	0.001 ***
%Urban	1	0.03409	3.8538	0.004 **
%Permanent crops	1	0.02713	3.0678	0.009 **
Contrast-Weighted Edge Density	1	0.02823	3.1915	0.005 **
Patch Richness Density	1	0.02071	2.3416	0.020 *

Table S 6. Term effects of land-cover pattern on small mammal communities computed by the forward-selection in the CCA

		Land-cover					
		Arable land	Forest	Heterogeneous agricultural areas	Permanent crop	Shrubs and herbaceous vegetation	Urban
Species abundance	<i>Apodemus flavicollis</i>	32	20	11	0	0	0
	<i>Apodemus sylvaticus</i>	1304	132	1086	347	5	38
	<i>Arvicola italicus</i>	25	10	59	0	0	0
	<i>Crocidura leucodon</i>	895	455	194	81	2	12
	<i>Crocidura suaveolens</i>	568	466	490	86	3	66
	<i>Eliomys quercinus</i>	2	3	2	4	0	0
	<i>Glis glis</i>	0	3	0	0	0	0
	<i>Microtus savii</i>	4641	2913	1292	1601	22	1277
	<i>Mus domesticus</i>	1895	431	184	67	10	549
	<i>Muscardinus avellanarius</i>	379	442	24	286	0	3
	<i>Myodes glareolus</i>	136	627	42	71	0	1
	<i>Neomys fodiens</i>	8	0	0	0	0	0
	<i>Neomys milleri</i>	6	8	0	0	0	0
	<i>Rattus norvegicus</i>	14	2	0	0	0	49
	<i>Rattus rattus</i>	160	35	192	49	0	107
	<i>Sorex antinorii</i>	111	9	0	1	0	0
	<i>Sorex minutus</i>	126	213	0	4	0	2
	<i>Sorex samniticus</i>	519	885	5	207	0	5
	<i>Suncus etruscus</i>	813	206	317	50	0	115
	<i>Talpa caeca</i>	0	1	0	1	0	0
	<i>Talpa romana</i>	7	2	14	0	0	2

Table S 7. Species abundance (number of individuals) of small mammal find in owl pellets in the land-cover types

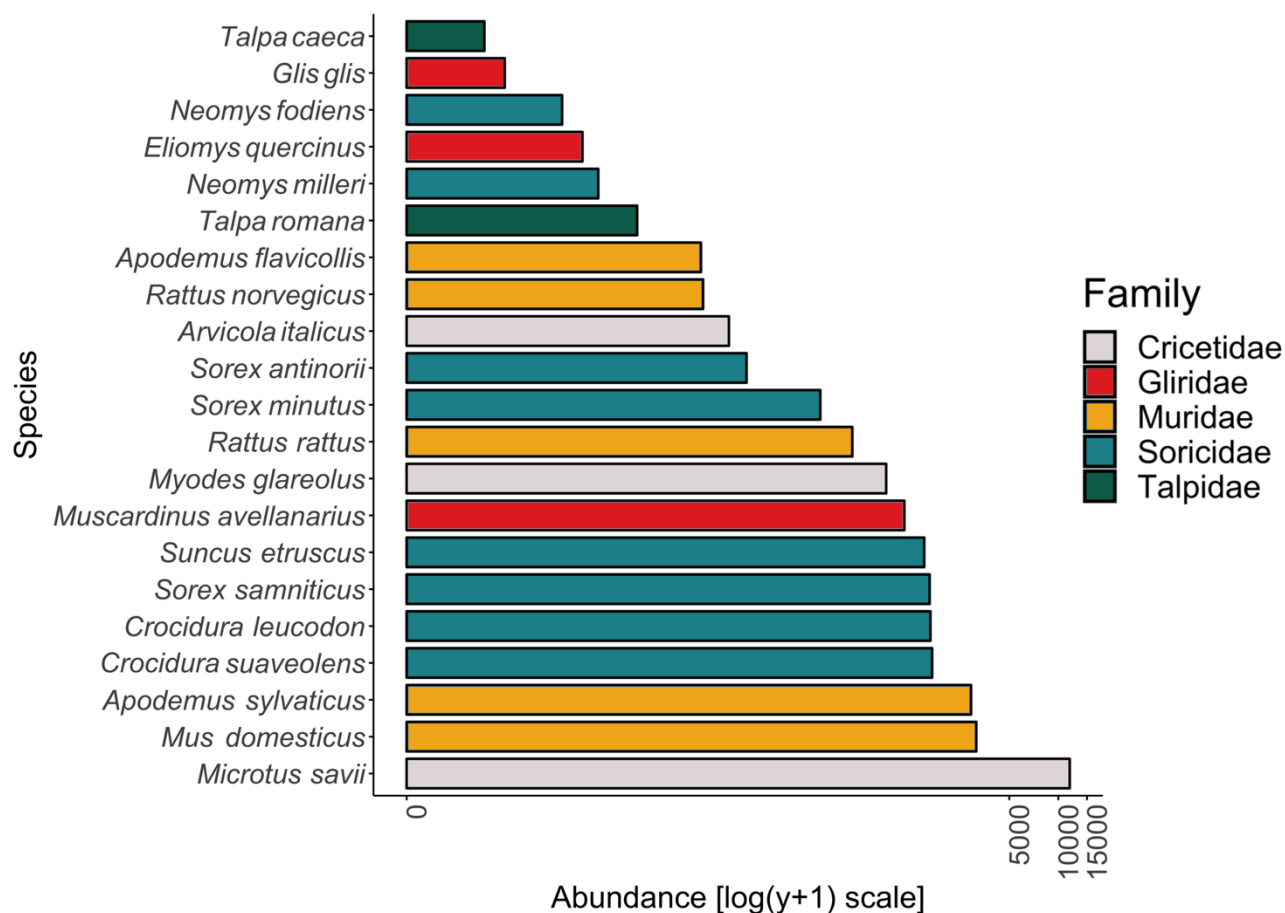


Figure S 1. Number of individuals per taxa. The number of specimens analyzed are shown within the bars. All abundances are log10 plus one transformed

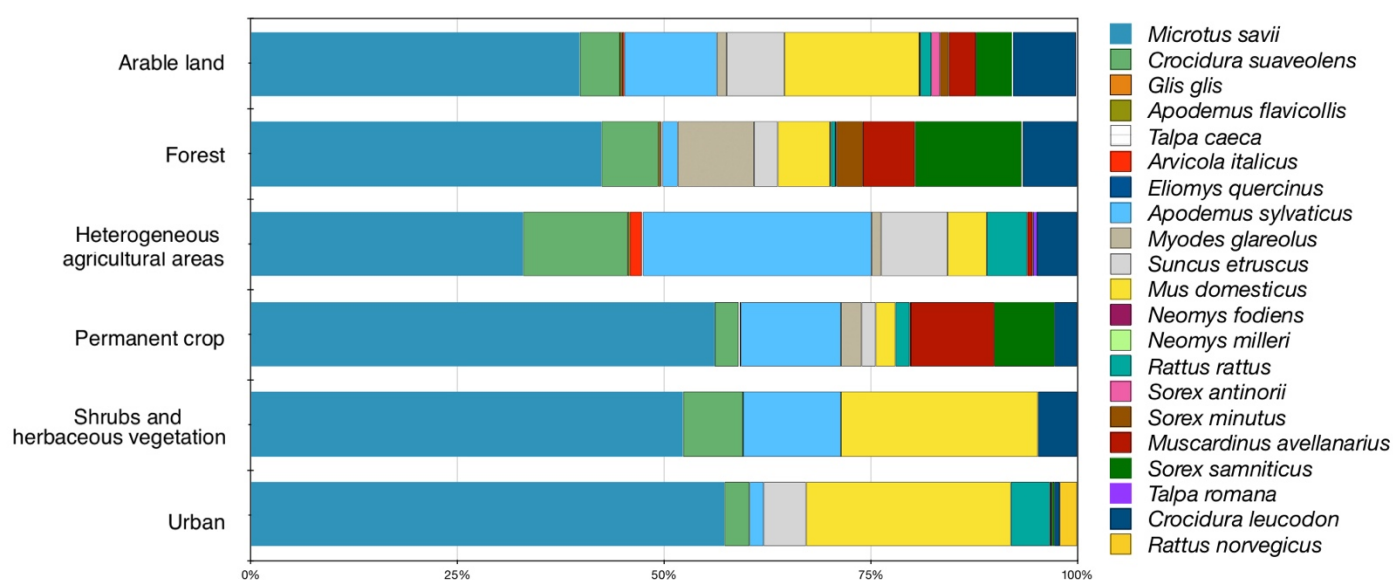


Figure S 2. The abundance (number of individuals) in the land-cover types

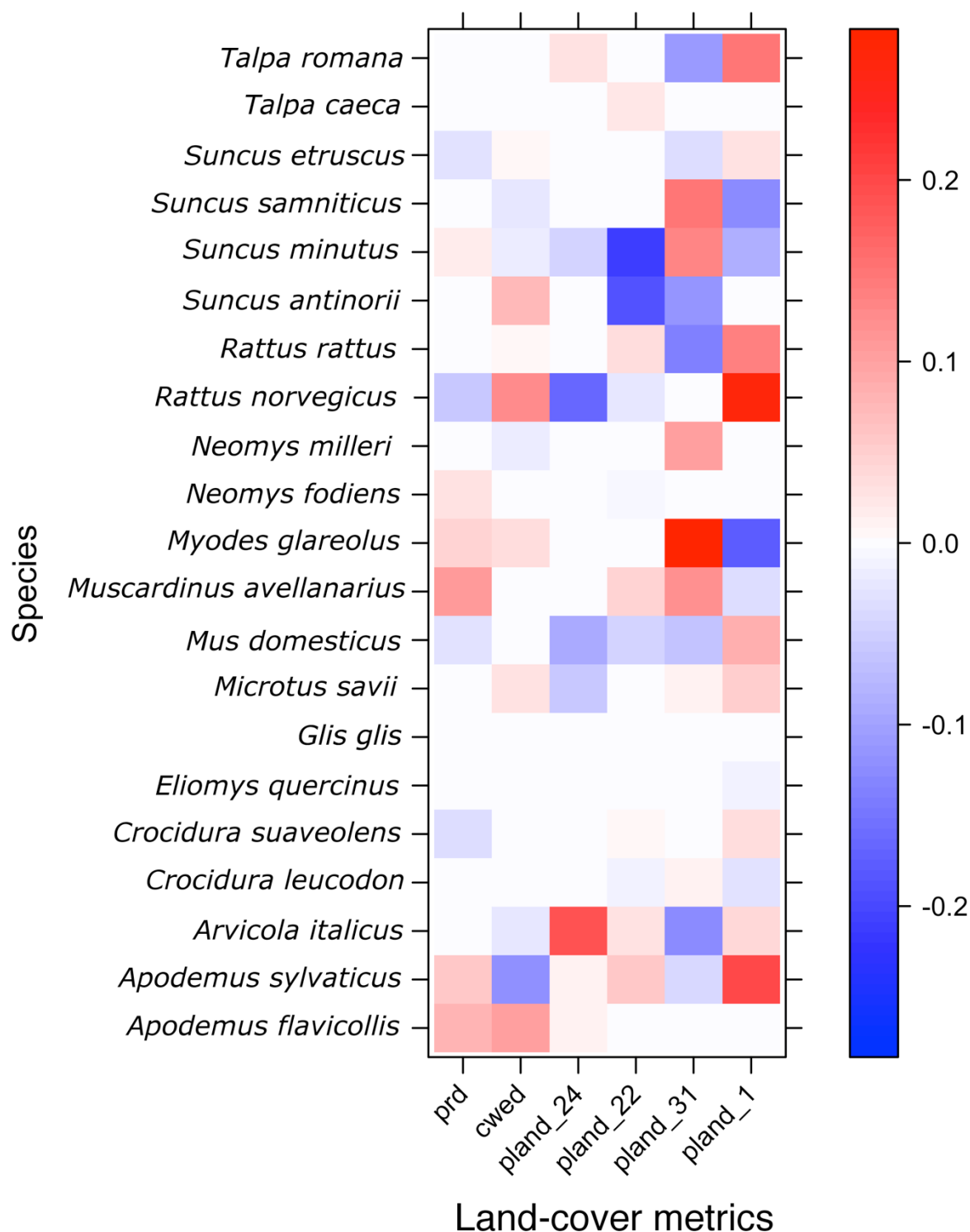


Figure S 3. Fourth-corner interaction coefficients for the relationship between small mammal species included in the study and land-cover metrics. Interaction coefficient are based on small mammal abundance data. Statistically significant relationships are indicated in red (positive) and blue (negative); the shade of the color represents the strength of the association. Land-cover metrics: Pland 1: Urban; Pland 22: Permanent crops; Pland 24: Heterogeneous agricultural areas; Pland 31: Forest; Cwed: Contrast-Weighted Edge Density; Prd: Patch Richness Density

CHAPTER V

Conclusion and perspectives

5.1 Conclusion

Three key objectives of this Ph.D. research were defined in the first chapter, in addition to various research aims that have been detailed in each of the research chapters presented (Chapter II, III, IV). These key objectives provided a rationale for three research papers.

This section provides a short description of the achievement of the aforementioned objectives.

Objective 1) The database OpenMICE made widely available data usually accessible to a restricted audience. We obtained the first map of small mammal diversity for south-central Italy and find a gap of knowledge about this study area nor where the data available for a wide scientific community. This database is especially useful for those species that are endemic to Italy and little known (listed as DD – Data Deficient) in both the global and national IUCN red list (www.redlist.org; Rondinini et al. 2013). Despite biodiversity index remains low and stable in some areas, nevertheless guilds are always well represented, suggesting that decrease in species diversity is not always coupled with a decrease in functional roles of small mammals in ecosystems. Thus, guild diversity might be a better indicator of environmental health than species diversity, and used to guide and prioritize management and conservation actions.

Objective 2) At a fine-scale, our study emphasized how accounting for imperfect detection can improve the statistical significance and interpretability of niche overlap estimates based on presence/absence data. In a forest management context, an accurate quantification of niche overlap provides useful information to assess the effects of different management practices on the occurrence and abundance of these arboreal rodents, and consequently design a sustainable use of forests allow to maintaining forest mammal species diversity. Such approach allowed to identify alternative ecological strategies between the two forest dormice (i.e. habitat generalist vs habitat specialist). Our study shown that occupancy of edible dormouse was directly related with increasing values of stand basal area and mean tree height, as well as occupancy values increasing in high forests and coppices in conversion. Hence, this evidence supports the findings that edible dormouse is an arboreal species which lives on the canopy of mature broadleaved mature mixed woodlands. In contrast, the hazel dormouse shown high occupancy values for low standard deviations of tree height, high tree densities and beech stands. These conflicting outcomes suggest that hazel dormouse prefers a wide variety of forests with different stand characteristics, which, in the study area, include even-

aged, highly dense stands (typical of the coppice management system) as well as beech forests predominantly managed as high forests. Our study offered a methodological framework to assess forests naturalness and to explore possible effects of alternative forest management systems on stands' structure, for instance, towards natural evolution and the establishment of old-growth forests. Forest management strategies oriented at promoting high forests would likely favor both the specialist (edible dormouse) and the generalist (hazel dormouse), as the two species share a significant portion of their niches corresponding to forests with these specific characteristics. On the other hand, practices enhancing forest stands with different and heterogeneous characteristics would primarily have a positive effect on the occurrence of *M. avellanarius* and not necessarily on *G. glis*.

Objective 3) As there are community-level attributes and taxa most sensitive to habitat change than others, our results support a multi-taxonomic approach with a high diversity of community-level attributes to biodiversity assessments and conservation planning in human-modified landscapes. We were able to identify and quantify, how and if small mammal communities were related to landscape features or to land-cover configuration.

5.2. Limitations and caveats of research

In my study, small mammal occurrence data are derived from owl pellet remains, so the data correspond to the owl resting or nesting site. Therefore, the spatial accuracy of an occurrence datum is equivalent to the hunting range of the predator (Contoli 1975; Lovari et al. 1976). Despite these impediments and limitations, OpenMICE represents the best available dataset on the small mammals occurring in Italy. The outcomes from this dataset can detect gaps to improve the sampling of terrestrial mammals and facilitate the understanding of community composition and potential trophic cascades (Szpunar et al. 2008; Rugiero et al. 2012; Milana et al. 2016, 2018; Roulin 2016). Future studies based on this database will contribute to improved knowledge on how global changes (e.g. climate, land use – land cover) may act to rearrange species distributions and community assemblages, providing relevant information to develop adaptive strategies for preserving small mammal biodiversity.

On a landscape perspective, compare spatial scale is one of the biggest problems to solve in ecology (Pettorelli et al. 2014). Small mammal ecological relationships need to be compared with a fine grain, yet, remote sensing is a good way to investigate this relationship due to the high-resolution layers.

In my study, first I used the Corine Land Cover Map at a resolution of 250 m. Unfortunately, this approach has failed and did not detect land-use changes through time, in fact, the spatial resolution is not good enough to show fine land-use changes through time. Remote sensing data is for sure a good tool for mapping biodiversity changes throughout time. Hence, recent studies showed that indices (i.e. NDVI, EVI, LAI), as well as parameters relative to indices, may affect the quality of the species distribution models (Austin 2007).

In order to analyze community structure and diversity patterns, ecologists apply different measures, such as abundance (i.e. total and proportional abundance), species richness (i.e. raw number and/or corrected number of species) and species diversity (e.g. Fisher's α). Each of these measures may reflect different responses to environmental conditions and/or ecological constraints including landscape configuration parameters, climate gradient, etc.

While total abundance may reflect the biomass and food availability for all individuals regardless of their species identity (Srivastava and Lawton 1998; Dodson et al. 2000), species richness may correlate to the means by which different organisms utilize resources within a community (Title and Burns 2015; Pigot et al. 2016). Species diversity, on the other hand, may reflect the proportional use and subdivision of resources among the existing species, providing additional information about realized niches and interactions among a set of existing species (Hiltunen et al. 2006). In addition, each of these community measures might be scale-dependent in a different way, given that determinants of community structure and composition change with scale (Dumbrell et al. 2008).

Habitat suitability is widely used as a remotely sensed proxy for species distribution and richness. It mainly covers the composition sphere of biodiversity (He et al. 2015; Vihervaara et al. 2015). Though successful in many of the discussed examples, the micro-heterogeneity of an area required for many species does not always allow a discrete classification approach. Many species (e.g. generalist species) use more than a single distinct vegetation type and some non-herbivore species may show low strength of association with a habitat or vegetation type because many species, regardless of the degree of habitat specificity, do not occupy the full extent of their preferred habitat type that can be remotely sensed (Cardillo et al. 2005; Leyequien et al. 2007). Current habitat classification is based on discrete maps and the resulting representation of class boundaries may not capture the meaningful ecological functional variability for each species. Correspondence between field data and remotely sensed imagery aimed at species communities was found to be high in some studies (Müller

and Brandl 2009; Cavada et al. 2017), but limited in others (Leyequien et al. 2007). One factor limiting the accuracy in this approach appears to be the application of proxies at inappropriate spatial, spectral, and temporal resolutions. Remote sensing studies involving species diversity need to consider different levels of taxonomic resolution. Several studies used a higher or lower taxonomic resolution approach as proxy for estimating species richness for other taxa (Gotelli and Colwell 2001). Cross-taxon congruence in biodiversity across different groups of organisms was also investigated as potential surrogates for each other (Marsh CJ et al. 2010). However, correlations and congruencies in species richness among different taxonomic groups are difficult to generalize as they differ to environmental gradients. Accuracy of assessing species diversity in particular may further increase by adding environmental variables to the analysis.

5.3 Future challenges

In the near of future, the big amount of standardized and organized ecological database will improve the animal ecology researches, as well as the ways of sharing data by using open-access portals and services (Hampton et al. 2013). Furthermore, the use of remote sensing data is widely accepted as a powerful tool which different application in animal ecology (Pettorelli et al. 2014; Turner et al. 2015).

To date, however, most of the researches on small mammal ecology and distribution, carry out in Italy and in Europe, have been poorly implicated with remote sensing products, yet it can be an interesting topic to explore to support the science community.

- i) I'm interested in exploring the effects of different forest landscape features on arboreal rodent species, with a focus on a broad scale, due to the use of high-resolution images. The vast majority of small mammal species are characterized by a low dispersal rate, at a fine-scale, micro-habitat features may be influenced populations persistence as well population parameters, yet the most influence on diversity and distribution on arboreal rodents may be revealed by forest diversity, spatial heterogeneity and configuration (e.g. arboreal species diversity, canopy cover, cutting pressure, time since last harvesting event, etc.). Hence remote sensing has the potential to estimate structural properties and assess their heterogeneity. Most studies relating remote sensing derived structural properties to animal diversity have relied on height measuring technologies such as airborne lasers (i.e. airborne LiDAR) and Synthetic

Aperture Radar (SAR) (Leyequien et al. 2007), particularly on forest habitats (Jaime-González et al. 2017; Linnell et al. 2017).

- ii) On a community level prospective, I will analyze more in deep my preliminary results for understand and quantify how small mammal communities were modified throughout the combined effects of land-use and climate changes.

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Animal ecology is one of my best passion! It can be very satisfying for those who love to try through field research or laboratory analyses new discoveries on the life of wild animals. Unfortunately, this kind of research is often little rewarding from the economic standpoint and asks for many hours far from home, on the field, or chained to the laptop.

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