



## RESEARCH ARTICLE

# Camera-traps and the city: Spatiotemporal adaptations of wildlife to urban environments

Emiliano Mori<sup>1,2</sup>  | Lorenzo Lazzeri<sup>3</sup>  | Martino Maggioni<sup>2,4,5</sup>  | Andrea Viviano<sup>1</sup>  |  
 Giulia Guerri<sup>6</sup>  | Marco Morabito<sup>6</sup>  | Sofia Martini<sup>1</sup> | Olivia Dondina<sup>2,7</sup>  |  
 Davide Sogliani<sup>8</sup>  | Manuel Scarfò<sup>9</sup> | Leonardo Ancillotto<sup>1,2</sup> 

<sup>1</sup>Consiglio Nazionale Delle Ricerche, Istituto Di Ricerca Sugli Ecosistemi Terrestri, Florence, Italy; <sup>2</sup>National Biodiversity Future Center, Palermo, Italy; <sup>3</sup>Dipartimento di Scienze della Vita, Università degli Studi di Siena, Siena, Italy; <sup>4</sup>Dipartimento di Scienze della Terra e del Mare, Università di Palermo, Palermo, Italy; <sup>5</sup>Dipartimento di Biologia, Università degli Studi di Firenze, Florence, Italy; <sup>6</sup>Consiglio Nazionale delle Ricerche, Istituto per la BioEconomia (IBE), Florence, Italy; <sup>7</sup>Department of Earth and Environmental Sciences, Università degli Studi di Milano-Bicocca, Milan, Italy; <sup>8</sup>Istituto Zooprofilattico Sperimentale della Lombardia e dell'Emilia-Romagna (IZSLER), Brescia, Italy and <sup>9</sup>Studio Naturalistico Hyla Srl, Tuoro sul Trasimeno, Perugia, Italy

**Correspondence**

Olivia Dondina

Email: [olivia.dondina@unimib.it](mailto:olivia.dondina@unimib.it)**Funding information**

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**Abstract**

1. Urbanisation significantly reshapes ecosystems, affecting biodiversity and profoundly altering wildlife behaviour. Nonetheless, our understanding of the environmental drivers of behavioural changes, as well as the concurrent effects upon interspecific interactions, remains limited. Here, we investigated the spatiotemporal adaptations of wildlife to urban environments, with a focus on predator-prey dynamics in response to urban-specific environmental characteristics, adopting a year-round camera-trapping campaign within the metropolitan area of Florence, Italy.
2. Temporal and spatial activity patterns of predators, prey, humans and domestic animals, as well as their relative overlaps, were quantified, revealing a marked increase in nocturnal behaviour amongst most wildlife species compared to their conspecifics in rural areas.
3. A wide temporal overlap was recorded between predators and most of their prey (70%–93%), yet limited to night hours. Contrary to more natural settings, the effects of moon phases were negligible upon urban mammals, and the occurrence of humans was a strong driver of wildlife spatiotemporal behaviour. Species richness was also shaped by environmental factors, with artificial light negatively impacting diversity, whereas the presence of herbaceous edges enhanced the diversity of local mammal assemblages. Suburban regions emerged as biodiversity hotspots, highlighting the critical role of green corridors and thoughtful urban planning in mitigating biodiversity loss.
4. *Practical implication:* Our findings analysed the complex interface between human activity and wildlife in urban landscapes, showing how urbanisation reshapes

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predator–prey dynamics and ecological interspecific interactions. Camera trapping proved to be a fundamental tool, addressing observational challenges and providing an unbiased, detailed perspective on urban wildlife adaptations.

#### KEYWORDS

activity rhythms, prey–predator interactions, remote cameras, spatiotemporal adaptation, temporal partitioning, urban ecology, urbanisation

## 1 | INTRODUCTION

The ongoing rapid urbanisation is reshaping ecosystems worldwide, threatening biodiversity (Acuto et al., 2018; Alberti, 2015; McKinney, 2008; Piquet et al., 2025). By 2050, urban populations will increase by over 50% from now, intensifying habitat loss and resource exploitation, which are the major threats to global biodiversity (Ancillotto et al., 2024; Ancillotto, Guerri, et al., 2025; Ancillotto, Viviano, et al., 2025; Seto et al., 2010, 2012; Verrelli et al., 2022). These pressures create complex interactions between humans and wildlife, demanding a deeper understanding of urban evolutionary ecology which may in turn influence human wellness (O'Bryan et al., 2018; Soulsbury & White, 2015; Uchida et al., 2021; Verrelli et al., 2022). Urbanisation significantly impacts on the microclimate of cities, particularly urban surfaces affected by the well-documented surface urban heat island phenomenon (Morabito et al., 2021). The microclimate can become particularly critical and unlivable in some periods of the year, especially in late spring and throughout the summer due to the extreme temperatures recorded during the day. These conditions create substantial positive thermal anomalies that extend beyond central urban areas (Guerri et al., 2021).

Many wild species have developed a number of adaptations to thrive in human-modified environments, that is to survive in polluted and altered habitats and to limit encounters with humans and conflicts (Basak et al., 2023; Ferrari & Polidori, 2025; Lowry et al., 2013; Moll et al., 2018; Suraci et al., 2021; Viviano, De Meo, et al., 2024). A comprehensive meta-analysis of urban mammals has unveiled a consistent pattern of increased body sizes across all species (Santini et al., 2019). Other attributes such as body dimensions, higher behavioural adaptability (e.g. with broad tolerances and wide ability to modulate activity rhythms), and wider dietary breadth proved to be differentially advantageous amongst mammalian species, thus allowing to distinguish between urban-adapted and non-urban-adapted taxa (Santini et al., 2019). This variability underscores the complex and multifaceted nature of urban adaptation, likely reflecting the diverse ecological niches and functional roles that mammals can occupy within cities (Dondina et al., 2025; Magle et al., 2012). More in general, wildlife may avoid encounters with humans by means of spatial or temporal partitioning, and this would result in species-specific adaptations (George & Crooks, 2006; Raap et al., 2015; Shannon et al., 2016; Wereszczuk & Zalewski, 2023). For instance, some species may become more nocturnal to avoid humans or may

select thermally protective microsites in urban areas to reduce energy and thermoregulation costs and to thrive far from humans (Barrueto et al., 2014; Gaynor et al., 2018; Lovari et al., 2017; Suraci et al., 2021; Wereszczuk & Zalewski, 2023). Several small mammals (i.e. mostly nocturnal ones) are strongly affected by light pollution and heat island effects, thus failing to adapt to urban environments, whereas others find strategies to thrive even where light conditions at night are constant throughout the year (e.g. by increasing their use of sheltered habitats such as scrublands: Blackwell, 2024; Finch et al., 2020; Oosthuizen, 2024). Some species may tolerate human disturbance or be advantaged by living in direct contact with humans and in urban areas, as being fed and/or protected by predators or because of the occurrence of constant resource availability, level of food waste and weather conditions (e.g. Ancillotto et al., 2015; Cox & Gaston, 2018; Samia et al., 2015; Sogliani et al., 2021; Viviano, Mori, et al., 2024). Thus, also the influence and timing of human actions on the existence and well-being of urban wildlife are intricate and vary significantly across different species (Andreoni et al., 2021; Beasley et al., 2023; Łopucki & Kiersztyn, 2020; Thomas et al., 2018).

Camera traps offer a significant advantage over traditional focal observations, particularly in urban environments where wildlife is often elusive (Lovari et al., 2017; Okes & O'Riain, 2019; Young et al., 2019). Unlike human observers, camera traps allow for continuous monitoring, overcoming the limitations of time-restricted field studies and locations of limited accessibility (Beasley et al., 2023; Gelmi-Candusso et al., 2023; Steenweg et al., 2017). Besides, conducting camera-trap studies in urban environments presents unique logistical (e.g. permissions and access, theft and vandalism risk), environmental (urban noise, light pollution and urban heat island effect) and social (public perception and privacy concerns) challenges (Herrera, Moore, Tyler Flockhart, et al., 2021). In particular, conducting camera-trap studies in urban environments is logistically complicated due to the need for multiple permissions, restricted access and a high risk of theft or vandalism (Herrera, Moore, Tyler Flockhart, et al., 2021; Viviano, Ancillotto, et al., 2025). Environmental factors such as constant noise, light pollution and the urban heat island effect can interfere with wildlife behaviour and data collection (Herrera, Moore, Tyler Flockhart, et al., 2021). Additionally, researchers must navigate social concerns, including public suspicion, privacy issues and ethical implications of monitoring in densely populated areas (Viviano, Ancillotto, et al., 2025).

So far, besides studies to improve methods (Herrera, Moore, Hermann, et al., 2021; Nagy, 2012), camera traps have been

rarely used to assess wildlife behaviour entirely in urban areas (McCallum, 2013), with several studies conducted at the interface between rural and urban areas, including only outskirts (e.g. Anton, Hartley, Geldenhuis, & Wittmer, 2018; Grade et al., 2022; Nickel et al., 2020). Moreover, urban studies with camera traps, which clearly specify in the paper text the amount of human settlement cover, the study period and all the camera-trapped species, have been conducted over a limited time period (often less than 1 year) or focused on a few species (Table 1). Even if the peak of urban biodiversity is often located in the city outskirts (Aronson et al., 2014; Grade et al., 2022; Magle et al., 2014; Sogliani et al., 2021), city centres may also host important habitat types for wildlife including urban parks, nature reserves, cemeteries and yards (Belair et al., 2014; Gallo et al., 2017; Grade et al., 2022; Magle et al., 2019). Despite this, up to now, very few studies have studied animal behaviour for long periods in city centres, that is where human pressure is supposed to be the highest (Fidino et al., 2021; Grade et al., 2022; Lovell et al., 2021; Magle et al., 2012). Amongst those, Lu et al. (2024) conducted a systematic study in an urban area of northern China but only focused on six species, including two domestic carnivores (*Felis catus* and *Canis familiaris*).

The spatiotemporal behaviour of different animal species may vary throughout the year and across seasons, as well as human pressure on different urban areas (e.g. green parks and industrial areas: Lovell et al., 2021; Mori, Andreoni, et al., 2020). Therefore, a comprehensive long-term dataset is essential to understand how various species adapt to diverse urban ecosystems and modify their behaviour in these areas compared to natural environments.

In this context, the metropolitan area of Firenze (i.e. Florence, central Italy) may serve as a model study site. Firenze represents an ideal setting for this kind of study, due to its wealth of historical data preserved by the oldest natural history museum open to the public in Europe, the availability of recent records on the distribution of mammals, the presence of a clear rural–urban gradient and a high density of historic villas and gardens which may have acted as refugia for diverse mammal species (Ancillotto, Guerri, et al., 2025; Ancillotto, Viviano, et al., 2025; Dondina et al., 2025). This resulted in a higher mammal diversity with respect to other Italian cities (e.g. Rome: Ancillotto et al., 2024).

Given the increasing urbanisation and its associated threats to biodiversity, this research aimed to document the spatiotemporal behaviour of wildlife species in various urban habitat types within the metropolitan area of Firenze and to compare the behaviour of wildlife species in urban environments to their behaviour in natural habitats. Based on the existing literature and the specific context of the metropolitan area of Firenze, we hypothesise that urban wildlife will shift spatial and temporal behavioural patterns in a heavily urbanised setting. Specifically, we predicted that (i) species will feature modified activity patterns that minimise contacts with humans (i.e. will be more nocturnal, as in Gallo et al., 2022); (ii) overlaps of activity rhythms between predators and relevant prey and intraguild overlaps will reflect those observed in non-urban environments, as all species would show similar adaptation to urban ecosystems (e.g.

Nardotto, 2022); (iii) activity rhythms of urban mammals will change according to light pollution and the heat island effect, as well as to more natural landscape elements such as the type of green space, occurrence of linear elements and tree cover (Richardson et al., 2025); (iv) spatiotemporal overlaps would be the lowest when comparing species well-adapted to urban environments (i.e. 'urban dwellers' sensu Santini et al., 2019) with species only occasionally using metropolitan areas (i.e. 'urban visitors' sensu Santini et al., 2019).

This study will not only fill a critical gap in understanding how wildlife responds to intense urbanisation in a highly developed European city (see Ancillotto, Guerri, et al., 2025), but it may also inform future conservation strategies and urban planning efforts aimed at promoting biodiversity in city environments. By providing fine-scale data on mammalian behaviour and distribution in different urban contexts, our findings can guide the development of more wildlife-friendly cities and improve coexistence between humans and urban fauna.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area

We conducted our analyses in the metropolitan area of Firenze (central Italy), comprising 11 municipalities (Firenze, Sesto Fiorentino, Calenzano, Campi Bisenzio, Fiesole, Impruneta, San Casciano Val di Pesa, Scandicci, Lastra a Signa, Empoli and Bagno a Ripoli; Permits number 140520/2023). This area includes severely anthropised sites ranging from 35 to 700m above sea level (overall covering approximately 15,000ha) and hosting a human population of 937,000 inhabitants in 2023 (<http://www.comuni-italiani.it>; accessed on 12.02.2024).

The study area is medium-flat (180m a.s.l.) even if in some municipalities it can be medium hilly above 200m above sea level (Bagno a Ripoli, San Casciano Val di Pesa, Sesto Fiorentino, Fiesole, Calenzano). According to the Köppen–Geiger climate classification (Rubel & Kottek, 2010), the study area has a borderline Mediterranean (Csa) and Humid subtropical climate (Cfa), with a moderate influence of the sea and warm summers. The study area is characterised by several classes of local climate zones (LCZ, Stewart & Oke, 2012), a classification system used to describe the physical characteristics of urban and rural environments based on their influence on local climate (LCZ, Demuzere et al., 2022). The prevalence of artificial surfaces, namely open midrise and lowrise (LCZ 5 and 6), and large lowrise (LCZ 8) built types, affected the local microclimate, exacerbating positive thermal anomalies within the Florentine metropolitan area (Guerri et al., 2021). In particular, land consumption was a critical cover affecting the whole area, especially Florence (42%), followed by Campi Bisenzio (32%) and Sesto Fiorentino (20%) (Munafò, 2023).

Our study area was mostly covered with human settlements (buildings and industrial areas: 38%), followed by urban parks and green areas with ornamental tree species such as *Platanus* spp., *Quercus* spp., *Pinus pinea* L., *Celtis australis* L., *Magnolia grandiflora* L., *Liquidambar styraciflua* L., *Cupressus sempervirens* L. and several palm species (Arecaceae)

**TABLE 1** Studies involving camera traps of mammals in urban areas published in the last 25 years and found by searching ('camera traps in urban areas') on Google Scholar, which include focal species, time period of each study and number of camera-trap locations.

Study	City	Focal species	Time period	N camera-trap locations
Hegglin et al. (2004)	Zurich (Switzerland)	<i>Vulpes vulpes</i>	9 days	48
Magle et al. (2014); Murray et al. (2021)	Chicago (USA)	<i>Odocoileus virginianus</i> and <i>Canis latrans</i>	~4 months (one month/season)	88
Jordan and Lobb-Rabe (2015)	Seattle (USA)	Mesocarnivores	~2 months	32
Elizondo and Loss (2016)	Stillwater, Oklahoma (USA)	<i>Felis catus</i>	~4 months	15
Hansen et al. (2018)	Charteris Bay (New Zealand)	<i>Felis catus</i>	6 months/year for 2 years	31
Anton, Hartley, Geldenhuis, and Wittmer (2018); Anton, Hartley, and Wittmer (2018)	Wellington (New Zealand)	All mammals, invasive mammals	~3 months	20 (in urban areas)
Herrera and Cove (2020)	Washington DC (USA)	<i>Buteo jamaicensis</i> and <i>Carphophis amoenus</i>	Single record	1
Łopucki and Kiersztyn (2020)	Lublin (Poland)	<i>Apodemus agrarius</i>	~1 month	15
Fidino et al. (2021)	Austin, Texas, Chicago, Illinois, Denver, Colorado, Fort Collins, Colorado, Iowa City, Iowa, Indianapolis, Indiana, Manhattan, Kansas, Madison, Wisconsin, Orange County, California and Wilmington, Delaware (USA)	All mammals	~12 months	569
Herrera, Moore, Tyler Flockhart, et al. (2021)	Washington DC (USA)	<i>Felis catus</i>	~10 months in 3 years	148
Lovell et al. (2021)	London (UK)	<i>Vulpes vulpes</i> and <i>Meles meles</i>	2 months/year for 3 years	211
Park et al. (2021)	Gwanggyo (South Korea)	All species	~2.5 months	20
Grade et al. (2022)	Urban areas of Massachusetts (USA)	All species	16 summer days /year for 3 years	36
Nardotto (2022)	Outskirts of Padova (Italy)	<i>Vulpes vulpes</i> and potential prey	~5 months	4
Beasley et al. (2023)	Hampstead Heath (London, UK)	All species	~2.5 months	26
Gelmi-Candusso et al. (2023)	Toronto (Canada)	<i>Vulpes vulpes</i> , <i>Canis latrans</i> and their potential prey	12 months	33
Viviano et al. (2024)	Sesto Fiorentino (Firenze, Italy)	<i>Pica pica</i>	~3 months	3
Li et al. (2023); Lu et al. (2024)	Tianjin (China)	<i>Canis familiaris</i> , <i>Felis catus</i> , <i>Erinaceus amurensis</i> , <i>Lepus tolai</i> <i>Mustela sibirica</i> and <i>Meles leucurus</i>	~24 months	60
Viviano, Ancillotto, et al. (2025)	Empoli (Firenze, Italy)	<i>Myocastor coypus</i> and relevant predators	12 months	1

Note: Studies using camera traps in urban environments were excluded if they did not clearly report the duration of the project, did not provide a species list or specify focal species, used baits to attract mammals or if they reanalysed data already included in our table using a different analytical framework.

(27%), cultivated areas (including also vegetable gardens, olive groves and vineyards: 21%), riverine habitats along Arno, Mugnone, Zambra and Pesa rivers (mostly covered with *Populus nigra* L., *Populus tremula* L. and *Salix alba* L.: 9%) and urban 'forests' (mostly composed by *Populus nigra* L., *Quercus ilex* L., *Q. cerris* L. and *Robinia pseudoacacia* L.: 5%).

## 2.2 | Data collection

Camera trapping activities were conducted within the Florence metropolitan area under specific permits (Fondazione Capellino Project 'Monitoring and Mitigation of Climate change and promotion of biodiversity: the Florence model' Prot. N. 26581 of 31 January 2023; Comune di Calenzano, Document 140520/2023; Comune di Sesto Fiorentino, prot. Comunale col. n. 22101/2023). To ensure compliance with national and international privacy laws (Legislative Decree 196/2003 and European Regulation 2016/679), informative panels were installed at park entrances. These panels detailed the camera-trapping project, its objectives and the procedures for handling recorded data. A QR code linked to project documentation and provided a direct contact for visitors to report any concerns or request the immediate deletion of videos containing human subjects. All such videos were removed from both SD cards and data storage systems within 72h of recording. Station selection involved identifying areas with similar structural habitats (habitat patches) surrounded by dissimilar urban environments (i.e. urban matrix; Forman & Godron, 1981) using QGIS 3.28 (QGIS Development Team, 2019). Field verification ensured site accessibility and suitability for camera-trap placement.

To prioritise human privacy, we adhered to the guidelines outlined by Herrera, Moore, Tyler Flockhart, et al. (2021). Camera traps were strategically placed near animal paths and fence openings, avoiding narrow pathways where capturing humans was inevitable (Herrera, Moore, Tyler Flockhart, et al., 2021). Camera traps were positioned away from traffic to limit disturbance due to camera lights and were never aimed at house windows. Additionally, camera traps in public areas were always installed at knee height to minimise human facial captures (Gelmi-Candusso et al., 2023). To foster community involvement and reduce the risk of camera-trap theft and other urban environment challenges, we engaged private citizens with gardens or fenced green areas by directly knocking on their doors and showing them our project (Herrera, Moore, Tyler Flockhart, et al., 2021). Direct outreach (Herrera, Moore, Tyler Flockhart, et al., 2021) encouraged participation and strengthened local support for the project.

## 2.3 | Camera trapping

A total of 35 stations were monitored by camera traps (© Browning SpecOps) across the study area (Figure 1).

To select sites, we adopted a standardised sampling design by overlaying a 1×1 km<sup>2</sup> grid on the metropolitan area of Firenze. For

each cell, we quantified green area size and fragmentation using FRAGSTATS and the 2021 ISPRA national land cover maps (Dondina et al., 2025). Cells were classified into four size classes and four fragmentation classes based on the Aggregation Index (AI), resulting in 16 combined categories (Dondina et al., 2025). Sampling cells were selected to cover the full range of urbanisation and fragmentation variability within the city. Within each selected cell, we identified accessible green areas, prioritising private properties where landowners consented to camera trap deployment. This approach allowed access to much of the city green space, which is predominantly private, while reducing theft risk. The selected cells are part of a broader network used in multiple studies under the NRRP and the National Biodiversity Future Center, ensuring data comparability across the 2022–2025 triennium, throughout a number of Italian cities (Alba et al., 2025; Ancillotto, Viviano, et al., 2025; Dondina et al., 2025; Viviano, Ancillotto, et al., 2025).

Cameras were placed at a height of ~30–80 cm from ground level and were activated for 24h/day to take one 60s video/event, with a 5s interval between videos. The cameras were left unattended throughout the sampling period. Data collection was conducted between March 2023 and May 2024, for a total of 388 nights; three camera-trap stations were active only for 42, 52 and 53 days, as they were vandalised. Camera traps were placed at fixed georeferenced locations (i.e. trees or street-lamps) where each camera trap was tied with ropes and chains. Stations were separated by at least 800m from one another to minimise the risk of pseudoreplication (O'Connell et al., 2011). Cameras were checked once a week to download data and replace batteries.

## 2.4 | Spatiotemporal behaviour of urban wildlife

Collected data were inserted in a data set including: 'species', 'date', 'hour', 'day phase' (i.e. diurnal or nocturnal or crepuscular) and 'station'. We discarded all videos where species determination was not possible (4.3%) and species with less than 30 records were removed from the dataset (Lashley et al., 2018). To avoid pseudoreplicates, records of the same species occurring at the same camera-trap station within less than 30 minutes were collapsed into a single observation (Monterroso et al., 2014). Then, we reported dates and hours (solar time) of capture directly shown on each video in the dataset. We defined the night as the period included between 1h after sunset and 1h before sunrise (Carnevali et al., 2016). Dawn and dusk were defined by the period of astronomical/circadian twilight and were calculated through the R package *NightDay* (Hughes-Brandl, 2018). Diel phenotypes (such as crepuscular, nocturnal, diurnal and cathemeral) were assigned to each species using the *Diel.Niche* R package, applying the 'general' hypothesis set, which distinguishes standard diel categories based on activity levels across diel periods and allows differentiation between bimodal and trimodal patterns (Gerber et al., 2024).

We analysed patterns of activity of wildlife species through the package *overlap* (Meredith & Ridout, 2014) for R vers. 4.1.2 (R Core

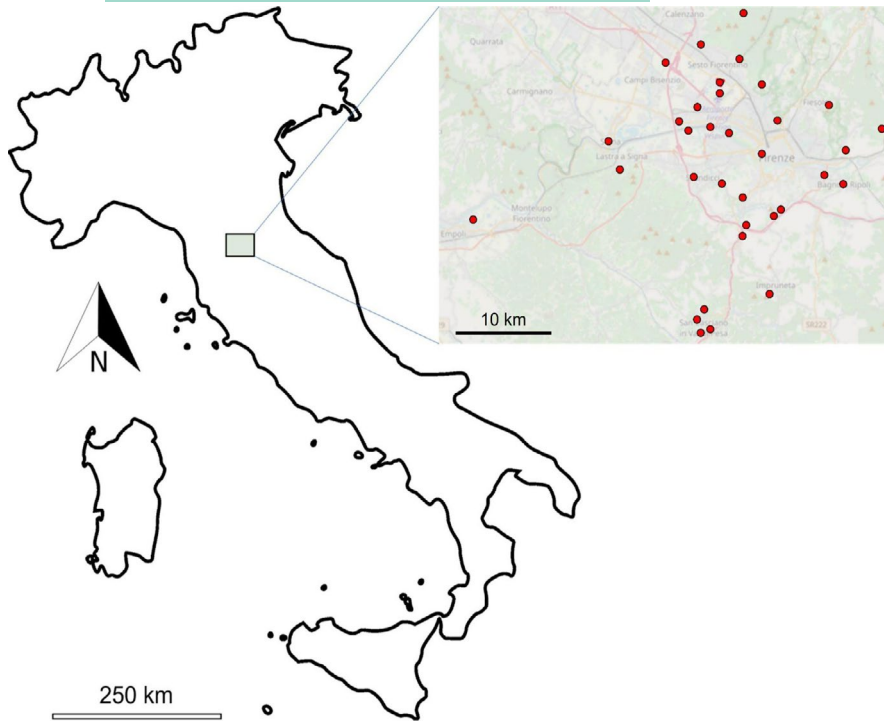


FIGURE 1 Location of camera-trap stations (red dots).

Team, 2018). The overlap coefficient of temporal activity patterns ( $\Delta$ ) was computed for predators and relevant prey, and amongst species sharing the same guild (i.e. amongst all predators, all lagomorphs and all ungulates). As to small mammals, we considered the intraguild overlap amongst large-sized species (coyupu *Myocastor coypus* and crested porcupine *Hystrix cristata*) which may share the same food habits and shelter sites (Amori et al., 2009), and all the possible pairwise combinations of small-sized species, sharing similar niches (Eurasian red squirrel *Sciurus vulgaris*, Western hedgehog *Erinaceus europaeus*, wood mouse *Apodemus* sp., black rat *Rattus rattus* and brown rat *Rattus norvegicus*: Amori et al., 2009).

We used  $\Delta_1$  estimator when records for at least one species in each pairwise comparison were less than 75, and  $\Delta_4$  when records of both species were over 75 (Monterroso et al., 2014). We considered a moderate delta value between 0.50 and 0.75, high when  $>0.75$  and very high when  $>0.90$  (Mori, Bagnato, et al., 2020). We then estimated the 95% confidence intervals (hereafter, CIs) for  $\Delta$  as percentile intervals from 999 bootstrap samples (Monterroso et al., 2014).

The Mardia Watson Wheeler (MWW) test was used to compare the same species pair overlaps of activity rhythms between urban and rural areas (where camera-trap data have been collected in the framework of similar projects on mammal communities), which were selected as areas far  $\geq 50$  km from metropolitan city centres (e.g. Metalliferous hills, Monte Rufeno Nature Reserve, 'Poggi di Prata' Natura2000 site and Merse river in Tuscany: Mori & Menchetti, 2019; Mori, Andreoni, et al., 2020; Mori, Mazza, et al., 2022; Palombi et al., 2024; Panzeri et al., 2021; Viviano et al., 2021; see Supporting Information).

We used the Hermans–Rasson test (HR test) to estimate whether a random activity pattern was exhibited by wildlife species round the clock (Landler et al., 2019).

Pairwise spatial overlap between wildlife species pairs was computed through the Pianka index (Pianka, 1974; Mori, Bagnato, et al., 2020), which ranges between 0 (no overlap) and 1 (total overlap). This index is calculated by considering the proportion of records of each species pair at different camera-trap stations (Pianka, 1974):  $O_{jk} = (\sum p_{ij} \times p_{ik}) / (\sum p_{ij}^2 \times p_{ik}^2)^{1/2}$ , where  $p_{ij}$  is the proportion of records of species 'j' and  $p_{ik}$  is the proportion of records of the species 'k'. The Pianka index was computed for all pairwise combinations already used for temporal overlaps. We computed Pearson's correlations to test whether the number of independent records detected by each camera trap was related to the time since first urbanisation of the camera-trap site (straight line).

Detected species were classified as 'urban dwellers' (i.e. species relying entirely on urban areas, including urban green spaces, for breeding and foraging) and 'urban visitors' (urban species which regularly move into nearby natural habitats for resources) (Santini et al., 2019). In particular, following the classification by Santini et al. (2019), we conducted our analyses on 15 urban dwellers, characterised by broad behavioural plasticity (see Loy et al., 2025), and five urban visitors, whose spatial and trophic ecology is more demanding (Table S1). The Mann–Whitney *U*-test was used to compare spatiotemporal overlaps between urban dwellers, between urban visitors and between urban visitors and urban dwellers.

## 2.5 | Impacts of lunar light

We assessed the potential role of the lunar brightness for the locomotory activity of most detected nocturnal species in urban contexts. First, the dataset was restructured by defining noon as the

start of a new day, ensuring that detections spanning two calendar days were treated as part of the same nocturnal event (Lazzeri et al., 2025; Lazzeri, Ferretti, et al., 2024). We used the *sunalc* R package (Thieurmél et al., 2019) to calculate sunrise and sunset times for each detection, classifying them as either nocturnal or diurnal events (following Carnevali et al., 2016), and then, we discarded the daytime detections, using in this analysis only the nocturnal ones (Lazzeri et al., 2025). In this analysis, we used just the nocturnal events for species showing the highest number of detections.

The analysis utilised generalised linear mixed models (GLMMs) with Tweedie errors (Dunn & Smyth, 2005) to explore the effects of lunar illumination on the nocturnal spatiotemporal activity of species filmed. These models were implemented using the *glmmTMB* (Brooks et al., 2017) R package. To ensure robust statistical analyses and avoid issues related to small sample sizes, we included in GLMMs only species with a total number of detections exceeding 100 across all camera traps. This threshold was set to ensure sufficient data for reliable parameter estimation and to minimise biases related to small sample sizes, as suggested by Zuur et al. (2009) in the context of GLMMs. The analysis was limited to species with at least 100 independent detections to ensure robustness in biological inferences and reduce the risk of results reflecting random variation, given the low frequency of detections on some nights. The response variable was defined as the detection rate of each target species per hour of darkness at each camera station and for each night. To account for seasonal variation in night length, detections were standardised by the number of hours between sunset and sunrise for each date (Lazzeri et al., 2025).

The models included the following variables: (i) the brightness index, (ii) the Bortle index, (iii) shrub cover around the camera in a 100 m radius, (iv) tree cover around the camera in a 100 m radius, (v) season. Random effects accounted for camera locations.

The 'brightness index' was subsequently developed by multiplying the moon phases (phase 1 [0.125], from new moon to  $\frac{1}{4}$ ; phase 2 [0.375], from  $\frac{1}{4}$  to  $\frac{1}{2}$ ; phase 3 [0.625], from  $\frac{1}{2}$  to  $\frac{3}{4}$ ; phase 4 [0.875], over  $\frac{3}{4}$ ) by the 'sky clearness', i.e. the inverse of cloud cover (in percentage with a 10% accuracy) (Gordigiani et al., 2022). To avoid zeros in calculations, any values of '0' for cloudiness were replaced with '0.001'.

The 'Bortle Index' is a numerical scale (ranging from 1 to 9) used to quantify the level of light pollution in a specific location, affecting the visibility of astronomical objects. It is usually determined by observing the visibility of celestial objects with the naked eye (Gronkowski et al., 2018). A lower Bortle value (e.g. 1 or 2) indicates a dark sky with minimal light pollution, while higher values (e.g. 8 or 9) correspond to urban areas with significant artificial light interference. We obtained the 'shrub cover' and 'tree cover' through visual assessment in a buffer around the camera of 100 m radius. The Bortle index was determined by visually observing key features in the night sky (milky way, zodiacal light, artificial light glow, celestial objects) and matching them to the descriptions for each class (Gronkowski et al., 2018).

We calculated the variance inflation factor (VIF) with a threshold of 3 to test the multicollinearity (Zuur et al., 2009). Model validation was conducted through visual inspection of residual distributions using the *DHARMA* package (Hartig, 2021), following Zuur et al. (2009).

## 2.6 | Impacts of urban context

To assess the impact of anthropogenic disturbance, environmental type and urban context on mammal species diversity detected through camera traps, we used a generalised linear model (GLM) with a negative binomial error distribution. The dependent variable was the number of species detected at each site over the entire monitoring period. We selected the negative binomial distribution after evaluating the fit of different candidate distributions to our data using the *fitdistr()* function (MASS package), which indicated that the negative binomial provided a better fit than the Poisson distribution due to overdispersion in the count data. The independent variables considered to account for anthropogenic disturbance were:

- Artificial light index: This variable was inferred using the nine-level Bortle index scale, which classifies night sky brightness from class 1 (excellent dark sky site) to class 9 (inner-city skies with extreme light pollution) (Crocker, 2021; Gronkowski et al., 2018).
- Human presence: This was estimated by calculating the proportion of camera-trap captures in which people were detected. Specifically, the number of human detections was divided by the total number of independent captures recorded by each camera-trap. This normalised measure serves as an index of human activity at the site, controlling for differences in overall camera-trap effort and detection rates.

Both these environmental measures are known to potentially shape mammals' responses, for example by fostering antipredatory behaviours and, thus, elicit changes in spatiotemporal activity patterns (nocturnal lights: Sordello et al., 2025; human presence: Mirante et al., 2024).

The independent variables used to assess the effect of the environmental type included:

- Type of green area: This categorical variable describes the general setting of each camera trap, classified into three types: woodland patch, riparian strip or recreational urban park. These categories reflect different habitat structures and degrees of human management. In detail, woodland patches were defined as vegetated areas dominated by tree canopy cover with limited public access and minimal built infrastructure; riparian strips were linear green areas adjacent to rivers or streams, primarily characterised by their proximity to water bodies and functioning as ecological corridors; recreational urban parks were areas primarily designed for public recreation, typically containing open lawns,

paths, playgrounds or sports facilities, even if they included tree-covered zones. In cases where green spaces exhibited mixed characteristics (e.g. urban parks containing woodland elements), classification was based on the primary intended use and management focus (Ancillotto, Viviano, et al., 2025). Given the relatively limited numbers of locations in the present study and the relative homogeneity of habitat types in the green spaces of Florence, we are confident that our classification, despite homogenising some more subtle differences, efficiently captures the main categories present in the area (Ancillotto, Guerri, et al., 2025).

- **Local climate zone (LCZ):** LCZs are standardised urban climate classifications based on land cover, structure and surface properties (Demuzere et al., 2022; Stewart & Oke, 2012). LCZs are widely used to study urban heat islands and land-atmosphere interactions (Guerri et al., 2023). In this study, LCZ classification provided a consistent way to account for the broader urban morphological context of each site. The LCZ map used for classification was generated from spatial data primarily derived from satellite and airborne sources. These included variables such as vegetation cover and tree height, as well as building height and density. Specifically, we used (i) the national land consumption (i.e. the conversion of non-urban land into built-up areas due to population growth) and land cover dataset provided by the Institute for Environmental Protection and Research of Italy (ISPRA) and (ii) the Digital Surface Model and Digital Elevation Model from the Regional LIDAR dataset of the Tuscany Region.
- **Vegetation structure:** This was assessed through three visually estimated variables within a 100-m radius buffer around each camera trap: (i) the percentage coverage of the tree layer; (ii) the percentage coverage of the shrub layer; (iii) the abundance of herbaceous edges, categorised as either localised or widespread. This last variable refers to the presence and distribution of herbaceous margins (e.g. grassy strips, unmanaged edges) and was used as a proxy for the structural connectivity of green areas.

All these variables represent environmental descriptors of ground-level conditions at the sampled locations, a key aspect that may affect species' occurrence as well as their activity patterns, especially in the case of non-volant mammals (temperature: Owen, 1990; vegetation structure: Lindenmayer et al., 2008; type of park: Nielsen et al., 2014).

Finally, the variables considered to account for the urban context of each camera-trap site were:

- **Time since urbanisation:** a continuous variable representing how long ago that area transitioned from non-urban (e.g. natural or rural land) to urban use (e.g. residential, industrial, infrastructure: see Ancillotto, Guerri, et al., 2025).
- **Type of urban fabric:** a categorical variable visually estimated within a 100-m radius buffer and classified into four categories: central continuous fabric, peripheral continuous fabric, discontinuous fabric and industrial areas. This variable reflects differences in building density, infrastructure and land use.

Given the dynamic nature of urban land cover and the limitations of available GIS data, microhabitat conditions were assessed in the field using a standardised approach commonly adopted in applied ecology (Ancillotto, Viviano, et al., 2025). While we recognise that a degree of subjectivity is inherent in field-based habitat assessments, this approach is widely accepted in applied ecology, particularly when aiming to capture fine-scale microhabitat conditions at the level of individual camera traps (Ancillotto, Viviano, et al., 2025; Lovari & Rolando, 2004; O'Connell et al., 2011).

Both these latter variables may represent key drivers of local mammal diversity, since both the time dimension of urbanisation (Ancillotto et al., 2024; Ancillotto, Guerri, et al., 2025) and type or density of urban fabric (Ancillotto et al., 2015; Baker et al., 2003) have been shown to shape species and communities' responses in cities.

We centred and scaled each independent continuous variable. Given the low ratio between the number of observations (i.e. the number of camera-trap sites) and the number of independent variables included in the analysis, we applied a variable selection procedure to reduce model complexity and avoid overfitting. Prior to model selection, we assessed multicollinearity amongst predictors in the global model by calculating the VIF, using a threshold of 3 to identify potentially collinear variables (Guisan et al., 2002; Zuur et al., 2009). To select the most important variables affecting mammal species richness, we adopted an information-theoretic model selection approach based on Akaike's Information Criterion corrected for small sample sizes (AICc; Burnham & Anderson, 2002). A global model was fitted including all predictors, and model selection was conducted using the *dredge* function from the MuMIn package in R (Barton, 2023), which generates all possible submodels and ranks them by AICc. Models with  $\Delta\text{AICc} < 2$  were considered equally supported and used for model averaging with the *model.avg* function. To evaluate model fit while accounting for model uncertainty, we computed the pseudo- $R^2$  for each model with  $\Delta\text{AICc} < 2$  as one minus the ratio between residual deviance and null deviance and then calculated the AICc-weighted average of these values.

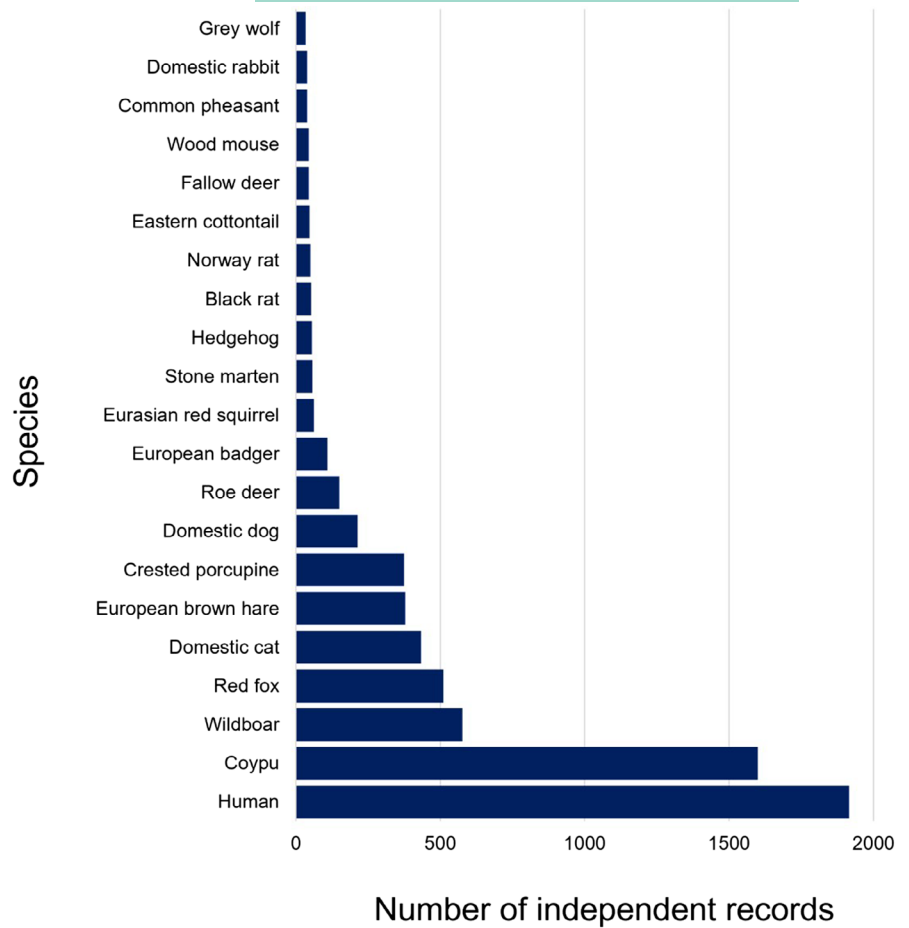
## 3 | RESULTS

### 3.1 | Spatiotemporal overlap amongst wildlife species

We collected a total of 7880 independent videos belonging to 72 species. The most recorded species were humans ( $N=1916$  independent videos), followed by the coypu *Myocastor coypus* ( $N=1600$ ), the wild boar *Sus scrofa* ( $N=581$ ) and the red fox *Vulpes vulpes* ( $N=511$ ). For 33 species, we obtained over 30 videos (Figure 2; Figure S1). Amongst birds, we only kept the common pheasant *Phasianus colchicus* for temporal and spatial analysis, as it is almost a ground-dwelling species sufficiently recorded.

We recorded a moderately strong, negative linear relationship between the number of independent records per site and time

**FIGURE 2** Number of videos of each species in the metropolitan area of Florence included in spatiotemporal analyses.



since urbanisation (Pearson's  $r = -0.539$ ,  $p = 0.00043$ ). Most species showed nocturnal behaviour, with only six species being diurnal and four species being cathemeral (Table 2). The overlap of rhythms of monitored species in urban and non-urban areas was moderate to high (Table 3).

Temporal overlap analyses revealed several differences between urban and non-urban settings for predator-prey and interspecific interactions (Table S2). Predator-prey pairs involving the grey wolf, such as wolf-wild boar ( $\Delta = 0.79$ ), wolf-roe deer ( $\Delta = 0.72$ ) and wolf-fallow deer ( $\Delta = 0.75$ ), showed moderate to high temporal overlap in the urban context. Mann-Whitney  $U$ -tests revealed non-significant differences compared to natural areas ( $p > 0.05$ ), except for wolf-fallow deer ( $p = 0.02$ ), where overlap was significantly reduced in the urban setting. Similarly, wolf-coypu ( $\Delta = 0.81$ ) and wolf-crested porcupine ( $\Delta = 0.76$ ) pairs showed temporal overlaps comparable to those in rural contexts, with no significant shifts detected ( $p > 0.05$ ), suggesting the persistence of nocturnal predator-prey synchrony despite urbanisation. In contrast, wolf-fallow deer and wild boar-fallow deer exhibited significantly lower overlap in urban environments compared to non-urban ones ( $p = 0.02$ ). Similarly, roe deer-fallow deer showed a significant reduction in synchrony ( $\Delta = 0.41$ ,  $p = 0.02$ ). Amongst mesopredators, red fox-brown rat ( $\Delta = 0.82$ ) and red fox-coypu ( $\Delta = 0.83$ ) overlaps did not significantly differ from those observed in rural areas ( $p > 0.05$ ). Conversely, red

fox-crested porcupine and red fox-European brown hare also showed high overlap values ( $\Delta > 0.74$ ), with no statistical differences compared to non-urban contexts, reflecting stable nocturnal foraging activity. For the European badger, temporal overlap with the crested porcupine was extremely high ( $\Delta = 0.92$ ), again not differing from natural areas ( $p > 0.05$ ). Wild boar ( $\Delta = 0.19$ ), red fox ( $\Delta = 0.31$ ), European badger ( $\Delta = 0.17$ ) and crested porcupine ( $\Delta = 0.16$ ) all showed significantly reduced overlap with humans in urban environments, lower than in non-urban areas (Table S2). In general, predators and prey tend to exhibit high temporal overlap (often nocturnal) and low spatial overlap. However, this pattern does not typically apply to domestic predators (dogs and cats), which show high spatial overlap with their prey but low temporal overlap, as these predators are predominantly diurnal or cathemeral (Figure 3).

Intraguild spatiotemporal overlap was moderate-high for ungulates (lower for pairwise comparisons involving fallow deer), low-moderate for lagomorphs and for small mammals, low-high for carnivores (Figure 4; Supporting Information). Temporal overlaps were the lowest when pairwise comparisons involved one diurnal species.

Spatial and temporal overlaps were significantly lower when comparing 'urban dwellers' with 'urban visitors' (Mann-Whitney  $U$ -test:  $U = 947-1692$ , respectively, for spatial and temporal overlaps;  $p < 0.001$ : Supporting Information). A very high spatiotemporal

**TABLE 2** Peak of activity rhythms of monitored species and associated Herman-Rasson test's significance,  $p < 0.05$  indicate non-random patterns.

	% Diurnal	% Crepuscular	% Nocturnal	Classification	HR test/ $p$
Black rat	1.90	7.50	90.60	Nocturnal	<0.001
Brown rat	27.59	43.10	29.31	Cathemeral	<0.001
Common pheasant	77.10	22.90	0.00	Diurnal–crepuscular	0.03
Coypu	15.75	26.25	58.00	Cathemeral	0.453
Crested porcupine	0.00	7.10	92.90	Nocturnal	<0.001
Domestic cat	7.21	20.49	72.30	Crepuscular–nocturnal	0.689
Domestic dog	64.02	28.50	7.48	Diurnal–crepuscular	0.02
Domestic rabbit	25.23	70.09	4.68	Diurnal–crepuscular	<0.001
Eastern cottontail	8.51	14.89	76.60	Nocturnal	<0.001
Eurasian red squirrel	93.65	6.35	0.00	Diurnal	0.03
European badger	0.00	0.00	100.00	Nocturnal	<0.001
European brown hare	29.02	14.78	56.20	Cathemeral	0.774
Fallow deer	0.00	2.22	97.78	Nocturnal	<0.001
Grey wolf	11.76	14.71	73.53	Crepuscular–nocturnal	0.04
Hedgehog	0.00	14.55	85.45	Nocturnal	0.02
Human	77.15	15.70	7.15	Diurnal	0.04
Red fox	7.63	20.94	71.43	Crepuscular–nocturnal	<0.001
Roe deer	40.40	19.20	40.40	Cathemeral	0.564
Stone marten	0.00	12.28	87.72	Nocturnal	<0.001
Wildboar	1.89	19.79	78.32	Nocturnal	0.03
Wood mouse	0.00	15.56	84.44	Nocturnal	<0.001

overlap was also observed amongst semifossorial species, i.e. the European badger with the crested porcupine and the coypu (Supporting Information).

Humans spatially overlapped at 100% (Pianka index) with all monitored species, whereas temporal overlaps were low–moderate with most species, apart from domestic taxa, roe deer and Eurasian red squirrel (Figure 5; Supporting Information).

### 3.2 | Impacts of lunar light

The results of the GLMMs with a Tweedie distribution for factors influencing the standardised detection rate of focal species are shown in Table S3. Analyses were conducted for coypu *Myocastor coypus*, red fox *Vulpes vulpes*, European badger *Meles meles*, crested porcupine *Hystrix cristata*, European brown hare *Lepus europaeus* and wildboar *Sus scrofa*. 'Season' was a significant factor influencing nightly detections for several species. *Myocastor coypus* showed lower detections in spring ( $B = -0.391$ , 95% CI:  $-0.729$ ,  $-0.053$ ,  $p = 0.023$ ) and winter ( $B = -0.466$ , 95% CI:  $-0.774$ ,  $-0.158$ ,  $p = 0.003$ ) compared to autumn. A similar trend was observed for *H. cristata*, with detections significantly lower in both summer ( $B = -1.302$ , 95% CI:  $-2.448$ ,  $-0.155$ ,  $p = 0.026$ ) and winter ( $B = -0.428$ , 95% CI:  $-0.745$ ,  $-0.111$ ,  $p = 0.008$ ) compared to autumn. In contrast, *S. scrofa* had significantly higher detections in spring ( $B = 0.732$ , 95%

CI:  $0.097$ ,  $1.366$ ,  $p = 0.024$ ) relative to autumn, while *L. europaeus* showed increased detections in winter ( $B = 0.622$ , 95% CI:  $0.143$ ,  $1.101$ ,  $p = 0.011$ ).

'Tree cover' significantly negatively affected detection for *H. cristata* ( $B = -1.130$ , 95% CI:  $-2.247$ ,  $-0.013$ ,  $p = 0.047$ ). Similarly, 'Shrub cover' had a significant negative effect on *L. europaeus* ( $B = -1.619$ , 95% CI:  $-2.814$ ,  $-0.424$ ,  $p = 0.008$ ).

The 'Bortle index', which measures light pollution, significantly negatively affected detection for several species. *V. vulpes* showed a negative effect ( $B = -0.762$ , 95% CI:  $-1.441$ ,  $-0.083$ ,  $p = 0.028$ ), as well as *M. meles* ( $B = -1.292$ , 95% CI:  $-2.232$ ,  $-0.351$ ,  $p = 0.007$ ) and *L. europaeus* ( $B = -2.408$ , 95% CI:  $-3.939$ ,  $-0.877$ ,  $p = 0.002$ ). In contrast, no significant positive associations existed with the Bortle index for any species.

The 'Brightness index' did not significantly influence any species analysed.

### 3.3 | Impacts of urban context

Model selection based on AICc identified a set of three models with  $\Delta AICc < 2$ , which were included in the model averaging procedure. The averaged model revealed a significant negative effect of the artificial light index and a significant positive effect of the presence of widespread herbaceous edges (reference level: localised herbaceous

**TABLE 3** Overlap of activity rhythms of monitored species between urban and non-urban areas.

Species	$\Delta_4$	95% CIs
Human	0.78	0.69–0.79
Wildboar	0.81	0.78–0.89
Roe deer	0.58	0.51–0.72
Fallow deer	0.64	0.61–0.72
European brown hare	0.69	0.32–0.74
Eastern cottontail	0.84	0.76–0.86
Domestic rabbit	NA	NA
Wood mouse	0.86	0.82–0.92
Black rat	0.88	0.86–0.98
Brown rat	0.59	0.52–0.77
Eurasian red squirrel	0.75	0.32–0.74
Hedgehog	NA	NA
Crested porcupine	0.91	0.85–0.96
Coypu	0.57	0.42–0.63
Grey wolf	0.79	0.70–0.84
Red fox	0.77	0.70–0.78
European badger	0.83	0.77–0.87
Stone marten	NA	NA
Domestic cat	0.83	0.81–0.86
Domestic dog	0.92	0.83–0.98
Common pheasant	0.89	0.85–0.99

Note: Non-urban rural areas used for each species is reported in [Supporting Information](#).

Abbreviations: NA, not available;  $\Delta_4$ , coefficient of temporal overlap.

edges) within a 100-m radius buffer (Table 4; Figure 6). The averaged pseudo- $R^2$  across the supported models was estimated at 0.379, indicating that the averaged model explained approximately 38% of the deviance in species richness.

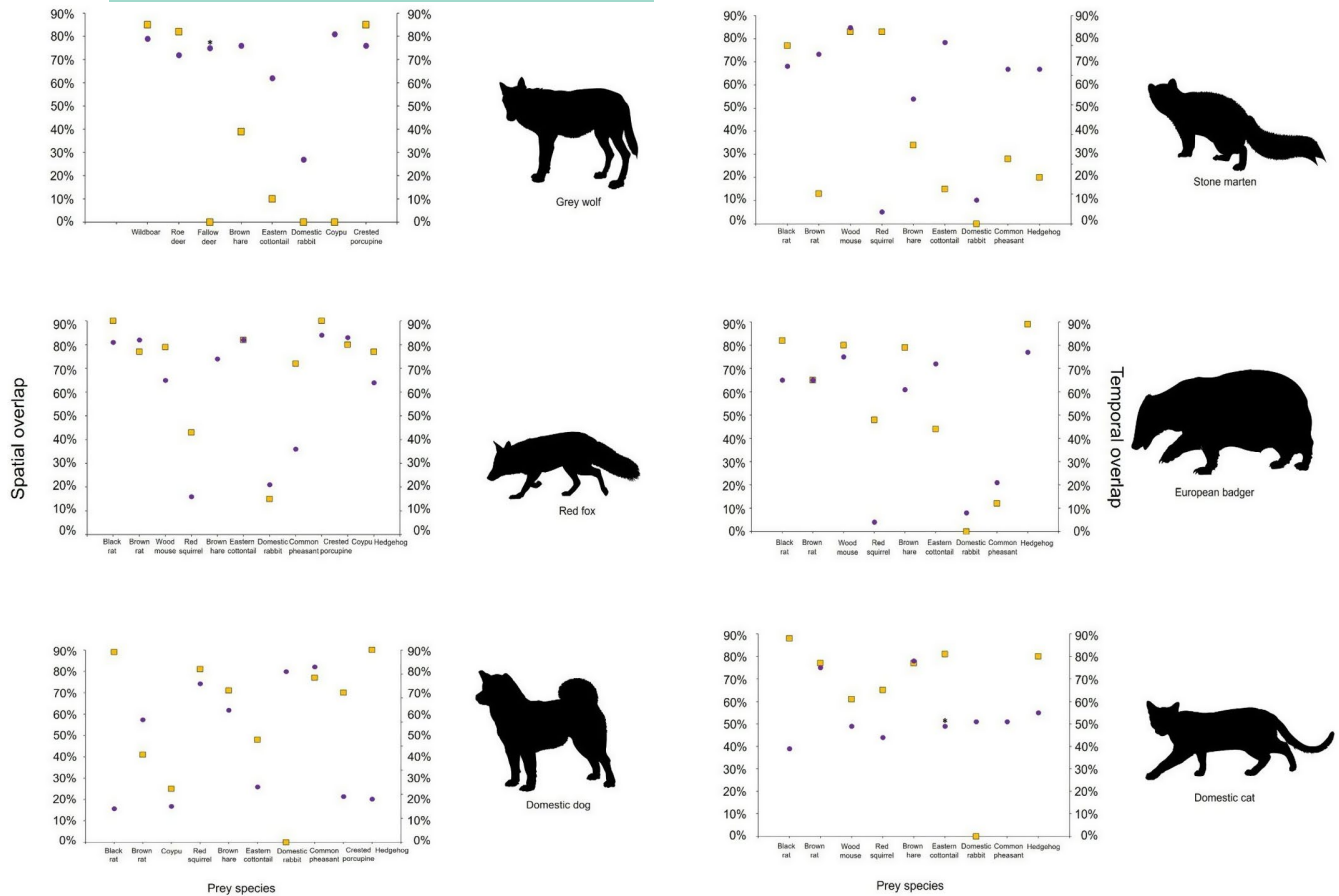
## 4 | DISCUSSION

In this study, we investigated the spatiotemporal interactions between wildlife, humans and urban environments through the use of camera traps in a metropolitan area of central Italy characterised by increasing fragmentation and urbanisation (cfr. Dondina et al., 2025; Vaccari et al., 2013). Our results revealed that urbanisation significantly reshapes animal behaviour and distribution, driving species-specific spatiotemporal adaptations and promoting interspecific coexistence (Łopucki & Kiersztyn, 2020; Ritzel & Gallo, 2020).

Notably, a shift towards nocturnal activity was observed in most wild mammalian species (e.g. the Eurasian badger, the crested porcupine, the Eastern cottontail, the wild boar and the fallow deer), consistent with prior research suggesting that nocturnality helps reduce human-wildlife conflicts in urban settings (e.g. Dowding et al., 2010; Lovari et al., 2017; Ritzel & Gallo, 2020)

and fulfilling our prediction (i). Diurnal species such as the Eurasian red squirrel and domestic dogs and rabbits retained their more diurnal behaviour in urban areas, reflecting their resistance to shift towards nocturnality, a behavioural trait shared with conspecific populations in non-urban ecosystems (Parker et al., 2019; Ramos et al., 2024; Sogliani et al., 2021; Wauters & Dhondt, 1987). Additionally, several invasive alien species, including domestic taxa, the brown rat and the coypu, exhibited some diurnal activity, as being mostly fed by humans (and by rubbish) in our study site (Viviano, Ancillotto, et al., 2025; Viviano, De Meo, et al., 2024; Viviano, Lazzeri, Vitale, & Mori, 2025). As well, European brown hares and roe deer are typically nocturnal species of glades and open areas, mostly avoiding human-modified habitats (Ciach & Fröhlich, 2019; Mori, Carbone, et al., 2022; Pagh et al., 2025). However, these species were often detected in our study site, in particular in open areas located at city outskirts, as well as in meadows surrounding urban parks, whereas being less detected in covered habitats. These urban environments tend to have fewer natural predators compared to rural areas (Møller, 2012), allowing hares and roe deer to safely shift some of their activity to daylight hours, where food and shelter may be more accessible (Ciach & Fröhlich, 2019). Furthermore, urban green spaces might offer better visibility and cover during the day, making hares and roe deer safe enough to forage or move around during daylight hours. To conclude, urban heat islands, with the exception of late spring and summer months (during which air and surface temperatures can reach extreme values), can create favourable conditions during the day, making daytime activity more energetically efficient for hares and roe deer (Hackländer et al., 2002; Weiner, 1977).

Predator-prey activity levels exhibited variable degrees of overlap, similar to those occurring in natural areas for most species pairs (Mori et al., 2019; Mori, Bagnato, et al., 2020; Nardotto, 2022; Palombi et al., 2024; Viviano et al., 2021), thus emphasising how urban landscapes may also maintain the same ecological interactions with respect to natural areas and fulfilling our prediction (ii). We only showed a low temporal overlap between the grey wolf and the roe deer, which remarkably differed from natural areas (Lazzeri, Pacini, et al., 2024). In particular, the predator was mostly nocturnal, likely to avoid contact with humans, whereas the roe deer were mostly active in the daylight and at sunrise and sunset, up to the first half of the night (Ciach & Fröhlich, 2019), whereas being more nocturnal in natural environments (Lazzeri, Pacini, et al., 2024). Furthermore, wolves may be drawn to urban areas due to the availability of anthropogenic food sources (Musto et al., 2021). As a result, the predator's tendency to maximise encounters with its natural prey is diminished. This alteration in foraging behaviour could weaken the strong temporal overlap typically observed in natural areas, where predator-prey interactions are primarily shaped by ecological dynamics (Lazzeri, Pacini, et al., 2024; Mori, Bagnato, et al., 2020). Domestic dogs showed the highest spatial overlap with their prey but also the lowest temporal overlap, as these predators are predominantly diurnal, whereas cats are crepuscular. Accordingly, diurnal and crepuscular prey species in urban areas are the most affected by predation events by domestic dogs and cats (Mori et al., 2019; Sogliani et al., 2023).

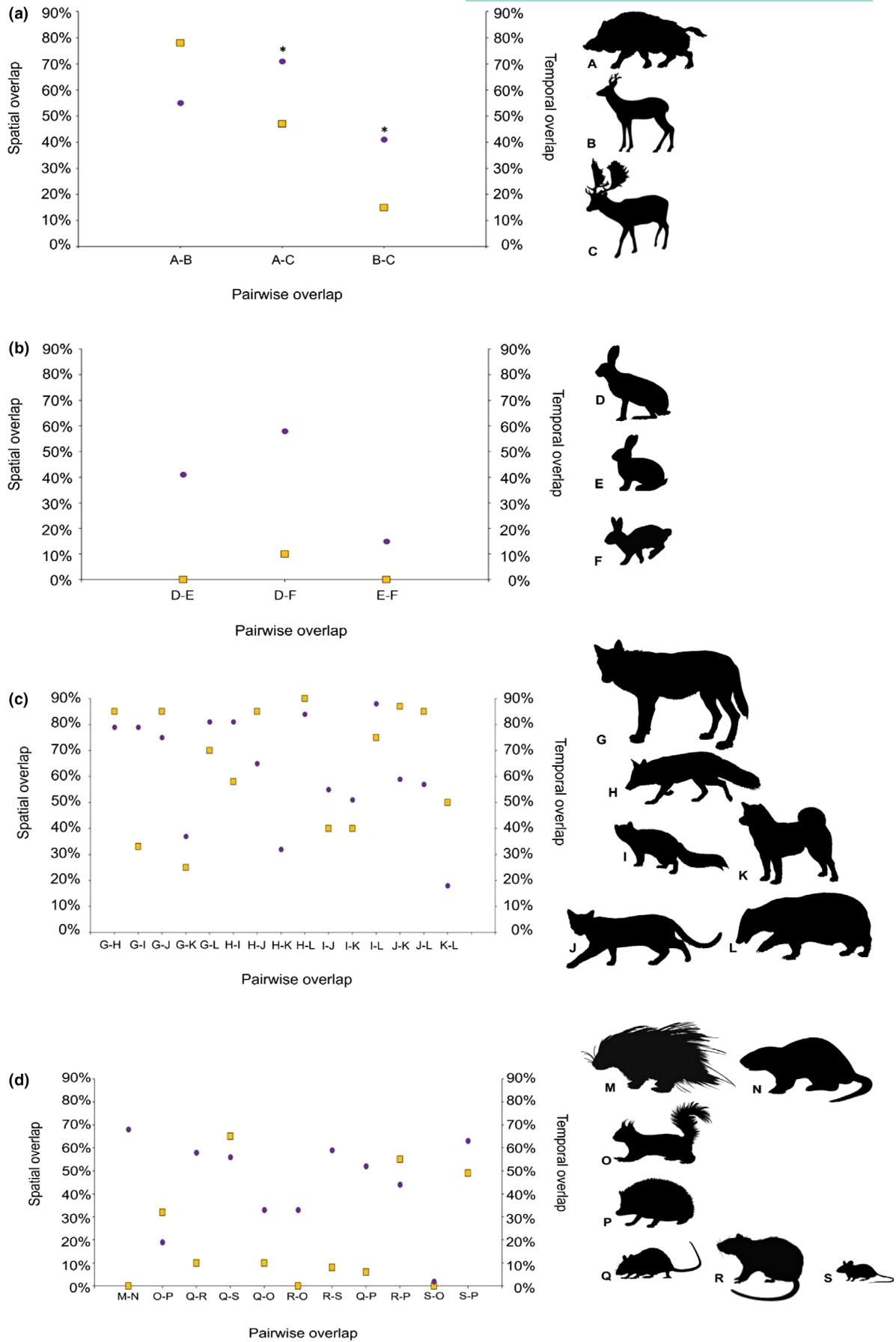


**FIGURE 3** Spatial (squares, Pianka index) and temporal (circles) overlap between predators and their potential prey species. Asterisks highlight different temporal overlaps with respect to non-urban areas (see [Supporting Information](#)).

Species sharing the same temporal activity pattern mostly showed a limited spatial overlap. On the contrary, species sharing the same food habits and habitat preferences (e.g. red fox and domestic cat) showed a moderate or low temporal overlap, to limit the potential for competition (Sogliani & Mori, 2019). These findings underscore how urban settings modify classical ecological relationships, with species adjusting their activity patterns to exploit anthropogenic resources while avoiding human presence. Our data also revealed significant spatial overlap between humans and all recorded species, reflecting how urban fauna coexist in shared spaces. Nevertheless, temporal overlaps were generally low, indicating effective avoidance strategies by wildlife (Mirante et al., 2024; Mori, Bagnato, et al., 2020; Oberosler et al., 2017). These findings support previous studies indicating that human activity affects both the spatial distribution and temporal activity patterns of wildlife, with a particularly strong influence on the latter (Beasley et al., 2023; Gaynor et al., 2018; Lovell et al., 2021).

Environmental light is a main factor shaping temporal behaviour of wildlife. In non-urban ecosystems, nocturnal carnivores are usually well adapted to hunt in darkness and their success often increases on nights with brighter moonlight, such as during a full moon with clear skies (Bhatt et al., 2021; Cozzi et al., 2012; Harmsen et al., 2011; Lima Sabato et al., 2006). Conversely, prey species frequently counteract predator effectiveness by being more active on the darkest nights, such as during a new moon (Daly et al., 1992; Penteriani et al., 2013; Prugh & Golden, 2014). Urban environments mitigate natural factors like moonlight-induced activity changes, as artificial lighting reduces lunar brightness effects (Gordigiani et al., 2022; Prugh & Golden, 2014). In our study, this behavioural pattern was observed in carnivores such as the red fox and European badger, which showed diminished sensitivity to lunar phases compared to their conspecifics in rural sites. However, artificial light itself negatively impacted species richness, showing a barrier role for urban wildlife activity and fulfilling our prediction (iii). Species

**FIGURE 4** Intraguild spatial (squares, Pianka index) and temporal (circles) overlaps: (a) ungulates, (b) lagomorphs, (c) carnivores, (d) small mammals. Asterisks highlight different temporal overlaps with respect to non-urban areas (see [Supporting Information](#)). (A) Wildboar, (B) roe deer, (C) fallow deer, (D) European brown hare, (E) domestic rabbit, (F) Eastern cottontail, (G) grey wolf, (H) red fox, (I) stone marten, (J) domestic cat, (K) domestic dog, (L) European badger, (M) crested porcupine, (N) coypu, (O) Eurasian red squirrel, (P) hedgehog, (Q) black rat, (R) brown rat, (S) wood mouse.



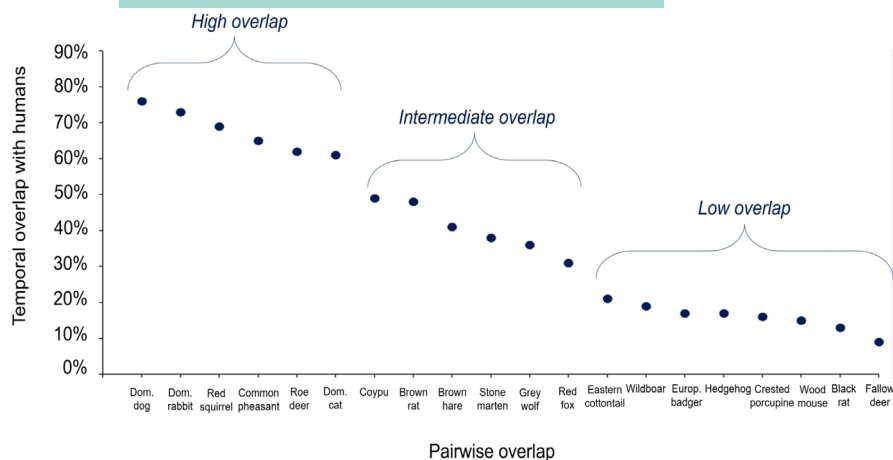


FIGURE 5 Temporal (circles) overlaps between humans and wildlife in urban areas.

Covariate	Estimate	Adjusted SE	z	Pr(> z )
(Intercept)	2.897	0.569	4.999	<0.001
Artificial light index	-0.217	0.057	3.820	<0.001
Time since urbanisation	-0.001	0.001	1.685	0.092
Herbaceous edges: widespread	0.545	0.274	1.988	0.047

Note: z is the Wald statistic for testing the hypothesis that the corresponding estimate is equal to zero (null hypothesis). Pr(>|z|) is the probability that the null hypothesis is true.

Abbreviations: AICc, Akaike's Information Criterion corrected; SE, standard error of estimates.

TABLE 4 Results from model averaging across candidate models with  $\Delta AICc < 2$  developed to identify the effect of anthropogenic disturbance, environmental type and urban context on mammal species richness.

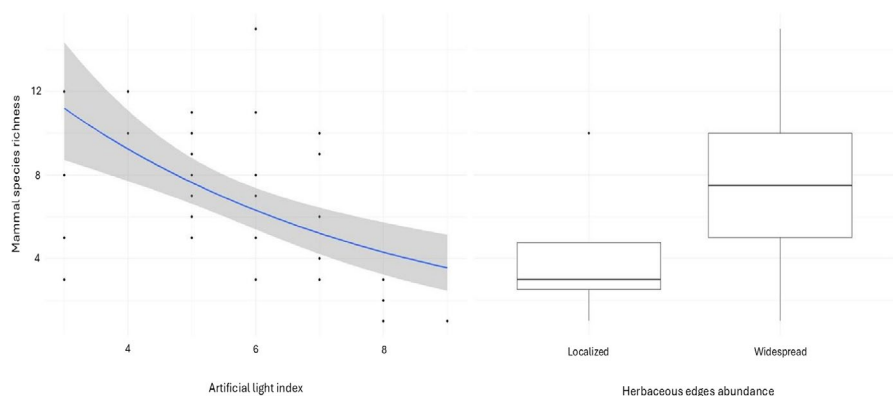


FIGURE 6 Relationship between mammal species richness, artificial light index and herbaceous edges abundance.

richness showed a slight increase with reducing time since urbanisation, although the effect was minimal and only marginally significant. The number of independent records also increased, with suburban and peri-urban areas acting as biodiversity hotspots and including also a higher number of passages of urban visitors, not well adapted to human-modified ecosystems (Santini et al., 2019). Moreover, species richness of urban mammals also increased with increasing herbaceous layers providing both food for herbivores and shelter for smaller species (Chernousova et al., 2014; Riem et al., 2012; Villaseñor et al., 2014). This trend supports the idea that managing green spaces, including herbaceous layers, and reducing artificial disturbances could mitigate biodiversity loss in heavily urbanised areas (Chen et al., 2020; Kang et al., 2015; Resemini et al., 2025).

Overall, our findings show that most mammalian species in the metropolitan area of Florence exhibit marked spatiotemporal

plasticity, enabling them to persist and even thrive in urbanised landscapes. These behavioural adjustments, including temporal segregation from humans, shifts towards nocturnality and spatial partitioning, highlight a multifaceted array of adaptation strategies promoting interspecific coexistence and underscore the resilience of urban wildlife in the face of ongoing anthropogenic pressure. While our research underscores the potential of urban landscapes to support diverse wildlife populations, limitations such as the focus on a single city suggest the need for broader, multi-city studies to deepen our understanding of urban ecology (Fidino et al., 2021; Grade et al., 2022). Ultimately, triggering citizen engagement, for example by placing camera traps in owned (fenced) urban areas and promoting sustainable urban planning may play important roles in ensuring coexistence between humans and wildlife in increasingly urbanised landscapes.

## AUTHOR CONTRIBUTIONS

Emiliano Mori conceived this study, collected most data and wrote the first draft; Olivia Dondina, Marco Morabito, Giulia Guerri and Lorenzo Lazzeri conducted statistical analyses; Leonardo Ancillotto, Andrea Viviano, Davide Sogliani, Martino Maggioni, Sofia Martini and Manuel Scarfò collected field data and participated in preparing the final dataset.

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## CONFLICT OF INTEREST STATEMENT

Authors certify that they have no affiliation with or involvement in any organisation or entity with any financial or nonfinancial interest in the subject matter or materials discussed in this manuscript. Therefore, they have no conflict of interest to declare.

## PEER REVIEW

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## DATA AVAILABILITY STATEMENT

Data are available from Mendeley Data <https://doi.org/10.17632/3htr438mcw> (Viviano, Lazzeri, Maggioni, et al., 2025) and from the Dryad Digital Repository <https://doi.org/10.5061/dryad.wdbrv162f> (Mori et al., 2025).

## ORCID

Emiliano Mori <https://orcid.org/0000-0001-8108-7950>

Lorenzo Lazzeri <https://orcid.org/0000-0002-9556-6204>

Martino Maggioni <https://orcid.org/0009-0004-1495-7476>

Andrea Viviano <https://orcid.org/0000-0002-2970-3389>

Giulia Guerri <https://orcid.org/0000-0001-5844-178X>

Marco Morabito <https://orcid.org/0000-0002-8799-4866>

Olivia Dondina <https://orcid.org/0000-0001-8097-1971>

Davide Sogliani <https://orcid.org/0000-0002-6455-7823>

Leonardo Ancillotto <https://orcid.org/0000-0002-8774-0671>

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## SUPPORTING INFORMATION

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

**Table S1.** Classification of urban-dwelling and urban-visitor mammal species detected in our study, following Santini et al. (2019) and Loy et al. (2025).

**Table S2.** Temporal overlaps amongst wildlife pairs, with relevant 95% CIs, comparison with non-urban areas and spatial overlap (Pianka index).

**Table S3.** Factors influencing nocturnal daily detection of our focal species estimated through generalised linear mixed models (GLMMs) with tweedie distribution. Estimates of model coefficients ( $B$ ), their standard errors (SE) and 95% confidence intervals (95% CIs) and  $p$  values for the linear predictor. In bold significant predictors.

**Figure S1.** Number of videos of each species in the metropolitan area of Florence.

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