



The rhythm of the night: patterns of activity of the European wildcat in the Italian peninsula

Lorenzo Lazzeri¹ · Paola Fazzi² · Marco Lucchesi² · Emiliano Mori³ · Edoardo Velli⁴ · Nadia Cappai⁵ · Francesca Ciuti^{6,9} · Francesco Ferretti¹ · Federica Fonda^{7,14} · Chiara Paniccia⁸ · Marco Pavanello⁷ · Stefano Pecorella⁹ · Alberto Sangiuliano¹⁰ · Andrea Sforzi¹¹ · Antonino Siclari¹² · Arianna Spada¹³

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Abstract

The European wildcat is a threatened carnivore, whose ecology is still scarcely studied, especially in Mediterranean areas. In this study, we estimated activity rhythm patterns of this felid, by means of camera-trapping at three spatial scales: (i) whole country (Italy); (ii) biogeographical areas; (iii) latitudinal zones. The activity rhythms patterns were also calculated according to temporal scales: (1) warm semester; (2) cold semester and (3) seasonal scales. Lastly, we also tested whether the effect of moon phases affected the wildcat activity. We conducted the analysis on a total of 975 independent events collected in 2009–2021, from 285 locations, in ~65,800 camera days. We showed that the wildcat in Italy exhibits a > 70% nocturnal behaviour, with 20% of diurnal activity, at all spatial scales, and throughout the whole year, with peaks at 10.00 p.m. and 04.00 a.m. We observed a high overlap of wildcat activity rhythms between different biogeographical and latitudinal zones. The wildcat was mainly active on the darkest nights, reducing its activity in bright moonlight nights. Diurnal activity was greater in the warm months and decreased with the distance from shrubs and woodlands, most likely according to activity rhythms of its main prey, water presence in summer, the care of offspring and the availability of shelter sites. Conversely, the distance to paved roads seems to have no significant effects on diurnal activity, suggesting that, in presence of natural shelters, the wildcat probably may tolerate these infrastructures. We suggested limited plasticity in activity rhythm patterns of the wildcat, emphasizing the importance of dark hours for this species.

Keywords Activity rhythms · *Felis silvestris* · Mesocarnivores · Human disturbance · Moon phase · Nocturnality · Camera-trapping

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✉ Emiliano Mori
emiliano.mori@cnr.it

¹ Dipartimento Di Scienze Della Vita, Università Degli Studi Di Siena, Via P.A. Mattioli 4, 53100 Siena, Italy

² Viale Marina 6, 54038 Montignoso, MS, Italy

³ Consiglio Nazionale Delle Ricerche, Istituto Di Ricerca Sugli Ecosistemi Terrestri, Via Madonna del Piano 10Sesto Fiorentino, 50019 Florence, Italy

⁴ Istituto Superiore Per La Protezione E La Ricerca Ambientale, Area Per La Genetica Della Conservazione, Via Ca' Fornacetta 9, 40064 Ozzano dell'Emilia BO, Italy

⁵ Parco Nazionale Delle Foreste Casentinesi, Monte Falterona E Campigna, Via G.Brocchi 7, Pratovecchio Stia, AR, Italy

⁶ Via Pian di Bartolo 8, 51100 Pistoia, Italy

⁷ THERION Research Group, Loc. Castel San Mauro 1, 34170 Gorizia, Italy

⁸ Institute for Alpine Environment, Eurac Research, Drususallee/Viale Druso 1, 39100 Bolzano/Bozen, Italy

⁹ Canis lupus Italia ONLUS, c/o Museo del Paesaggio Storico Dell'Appennino, Moscheta, Firenzuola, Italy

¹⁰ Parco Nazionale del Pollino, Area Conservazione, Biodiversità E Ricerche, Complesso Monumentale Santa Maria Della Consolazione, 85048 Rotonda, PZ, Italy

¹¹ Museo Di Storia Naturale Della Maremma, Strada Corsini 5, 58100 Grosseto, Italy

¹² Citta Metropolitana Di Reggio Calabria, Piazza Italia, s.n., 89100 Reggio Calabria (RC), Italy

¹³ Dipartimento Di Scienze Ambientali, Informatica E Statistica, Università Ca' Foscari Venezia, Via Torino 155, 30170 Mestre Venice, Italy

¹⁴ Department of Life Science, University of Trieste, via L. Giorgieri 10, 34127 Trieste, Italy

Introduction

Ecological studies on elusive carnivores are particularly challenging, as these mammals are often threatened species that generally live in low population densities, with a fragmented distribution (Gese 2001). The European wildcat *Felis silvestris* is widely reported as a strictly nocturnal carnivore, living at low population densities throughout Europe and with a discontinuous distribution range (Daniels et al. 2001; Germain et al. 2008; Soyumert 2020; Anile et al. 2021; Migli et al. 2021). During daylight hours, the wildcat usually exploits resting sites, i.e., shelter structures, mainly at the limits of the forests (Jerosch et al. 2009). Some aspects of the wildcat ecology including population dynamics, population density (Anile et al. 2014, 2020; Kilshaw et al. 2015; Fonda et al. 2022) and spatial behaviour (Monterroso et al. 2009; Anile et al. 2019) have already been studied in detail, although large scale evaluations are still sparse. Conversely, the temporal activity level has been partially overlooked, in particular on a large scale (Anile et al. 2021; Migli et al. 2021). Indeed, patterns of the temporal behaviour of species may change with habitat, latitude, presence of competitors or mating opportunities (Pearman et al. 2008; Pratas-Santiago et al. 2016; Karanth et al. 2017). Moreover, geographic differences in genetic structure and ethological features (i.e.: valerian lures response) have been reported (Mattucci et al. 2013; Velli et al. 2015). Therefore, activity patterns need to be considered in different environmental contexts (e.g. Ashby 1972; Kerr 1997; Jordan et al. 2007; Brivio et al. 2017; Mori et al. 2020a). The European wildcat is fully protected over most of its range, under national and international legislations. This felid is included in CITES (Convention on International Trade of Endangered Species) Appendix II, listed in the European Union Habitats and Species Directive Annex IV and the Bern Convention Appendix II. Currently, some European wildcat populations are locally expanding, partially recovering the species' historical distribution range (Ragni and Mandrici 2003; Steyer et al. 2016; Tormen et al. 2020; Gavagnin 2021). The process of colonization or recolonization exposes wildcats to even greater consequences of direct and indirect anthropogenic threats, such as habitat loss and fragmentation, hybridization with domestic cats and direct persecution (Yamaguchi et al. 2015; Mattucci et al. 2013). Anthropogenic structures and disturbances might also influence the activity patterns of the wildcat (see Anile et al. 2021). For instance, roads have negative effects on wildlife, acting as barriers to movement and source of disturbance, injuries and mortality (Spellerberg 2002; Roedenbeck et al. 2007; Bastianelli et al. 2021).

Camera trapping is being increasingly employed to estimate animal distribution and abundance, as well as local species richness (Tobler et al. 2008; O'Connell et al.

2011; Borchers et al. 2014; Kikuchi et al. 2020). This represents a reliable method to assess the temporal behaviour of animal species (Leuchtenberger et al. 2014; Mori et al. 2020a; Rossa et al. 2021). Activity rhythms of the wild cat can hardly be directly estimated by direct observations, as being nocturnal and elusive. Temporal activity patterns of this species have been estimated by camera-trapping at local study sites in Northern Spain (Monterroso et al. 2014), Anatolia (Soyumert, 2020), Central Bulgaria (Tsunoda et al. 2020) and Southern Italy (Mori et al. 2020b; Anile et al. 2021). Nevertheless, studies exploring wildcat activity patterns on a national scale are needed in order to effectively implement conservation strategies over wide areas.

In our study, we aimed at filling this gap, i.e., at determining patterns of the wildcat activity on the Italian national scale, in different bioclimatic regions.

We collected camera-trap data from several national Italian camera-trapping projects, which detected wildcats both as a target species and as a bycatch in monitoring programs of other medium to large-sized mammal species. We assessed the activity of the wildcat with the aim to assess whether the diurnal activity may be influenced by environmental and anthropogenic variables (e.g. distance from paved roads).

Calculating temporal overlap amongst contrasting ecological contexts would provide information on behavioural plasticity of the species in terms of temporal patterns of activity. This would in turn provide researchers with valuable information on the basic ecology of the species, which is pivotal to create successful conservation and management plans (O'Connell et al. 2011). For instance, temporal plasticity of each species should be assessed to determine its ability to cope with local touristic pressure and with global climatic change. Where environmental pressures change (e.g. predation/competition, food and shelter availability, anthropization), the same species may show different adaptations to thrive (e.g. the coypu *Myocastor coypus*: Mori et al. 2020a; the wild boar *Sus scrofa*: Brivio et al. 2017; Gordigiani et al. 2021). Following the literature available on the wildcat, we predicted that (1) the European wildcat would have been nocturnal in all study areas; (2) activity of European wildcat would not change in biogeographic regions and at different latitudes; (3) activity of European wildcat would change seasonally; (4) as most carnivores improve hunting abilities in bright moonlight nights, European wildcats might be most active in full moon nights (as in other small felids: Pentzerian et al. 2013; Huck et al. 2017; Bhatt et al. 2021); (5) the European wildcat would show some daylight activity with increasing distance from roads (as a proxy of human disturbance).

Materials and methods

Data collection and dataset preparation

We collected data gathered across research and monitoring projects using camera traps specifically centered on the European wildcat in Italy, or relevant to projects mainly targeted on other carnivore species. Analyses obtained through camera-trapping are accurate and precise as radio-tracking data, when events (i.e. photos or videos) of the target species are at least over 30 (Lashley et al. 2018). In contrast, the accuracy of estimates decreases when the sample size is lower than 30 detections (Lashley et al. 2018).

Overall, we obtained 1300 videos and photos of putative wild-living cats from 14 study areas from 2009 to 2021 (Table 1), with altitudes ranging from 0 to 1800 m above sea level, spanning from North-Eastern Italy to the most Southern regions (Fig. 1). Requirements for data to be included in our study were those specified by Lashley et al. (2018): (i) cameras should have been deployed on site according to a sampling design targeted to carnivores; (ii) one-month minimum monitoring time; (iii) records obtained from cameras kept active for the whole 24-h cycle. Furthermore, we identified European wildcats using a blind approach by at least three expert operators that independently analyzed the coat pattern of the species following the specific literature (Ragni and Possenti 1996; Beaumont et al. 2001; Kitchener et al. 2005). Only concordant identifications were included in the analyses. Discrimination between European wildcats and domestic cats has been proved to be achievable by means of morphological features, through *ad-hoc* keys (e.g. coat color pattern: Ragni and Possenti 1996; Devillard et al. 2014; Migli et al. 2021). We discarded records of domestic cats from our analyses, as well as doubtful *F. silvestris*/*F. catus* records (cf. Mattucci et al. 2016), i.e. those not fully respecting typical key pelage characteristics of the European wildcat (Jiménez-Albarral et al. 2021; Migli et al. 2021). We only used detections from the same camera station separated from each other by at least 30 min to limit the autocorrelation bias (Monterroso et al. 2014; Torretta et al. 2016; Mori et al. 2020b; Rossa et al. 2021). After filtering the initial dataset according to the above parameters, 975 nationally independent events from a total of 285 camera locations were included in our analyses with a total survey effort of 65,802 camera days (see the Table 1). In all cases the cameras were deployed on animal trails, footways, or forest roads and they had an average distance from the nearest camera of 1138 m (standard deviation = 1543 m).

For each event, we registered geographical coordinates (EPSG: 3035), latitudinal zones (North, Central and South,

see below for definitions), biogeographic areas (categories are: “Continental”, “Mediterranean”, “Alpine”), the solar hour of capture, date, season (categories are: “autumn”: October–December; “winter”: January–March; “spring”: April–June; “summer”: July–September), semester (categories are: “warm months”: April–September; “cold months”: October–March), type of habitat, assessed on the field during camera-trap deployment (deciduous forest; coniferous forest; shrubs; wetland; open land), lunar exact and percentage of the visible moon. The use of season allowed a better total year subdivision for our analyses; however, we also used the “semester” category to allow a reliable comparison with previously published studies which used this categorization (e.g. Mori et al. 2020b).

We used latitudinal zones subdivision to assess the patterns of activity based on similar conditions of light and latitude. We also considered a subdivision of the peninsula with three main latitudinal zones: (i) Northern Italy, above the 44° parallel; (ii) Central Italy, between 44° and 41° parallel; (iii) Southern Italy, under the 41° parallel, without isles (Fig. 1). Moreover, biogeographic regions categorization allowed us to elaborate data according to the main biocenosis distribution and climate conditions. They are described in the Supplemental Material.

Patterns of activity rhythms

We used RStudio version 4.0.3 (RStudio Team 2020; R Core Team 2021) to estimate wildcats’ temporal activity patterns using the non-parametric kernel density estimation (Meredith and Ridout 2014).

Then, we also estimated 95% confidence intervals of activity patterns as percentile intervals from 1000 bootstrap samples (Ridout and Linkie 2009). We used package ‘overlap’ (Meredith and Ridout 2014) to draw the overlap plots between temporal activity patterns assessed in different biogeographic areas, latitudinal zones, seasons and semesters temporal overlap. Considering the similar results between the two temporal scales (seasons and semesters), we have been parsimonious and have considered only “semester”.

Bearing in mind that this work does not follow an homogeneous sampling designs for all study sites, and the events of wildcat have been collected in the framework of different projects, we checked for sampling sites that could weigh more than others due to potential differences in sample size across them, by comparing activity patterns between the full dataset ($N=975$ events) and a subsample of randomly selected events homogeneously distributed across sites ($N=312$, with 18 random events per site, i.e., the number of events coming from the site with the smallest sample size). We compute the Watson’s two-sample test of homogeneity to evaluate the uniformity of the two distributions (Lund et al. 2017). We used the

Table 1 Study areas, with a synthetic description about generic coordinates, target species, and study periods, mean distance between cameras with SD, sampling effort

Biogeographic regions	Latitudinal zones	Sites	Coordinates EPGS: 3035	Study period	Survey effort	Detections	Camera-sites recording wildcat	Target species	CT mean distance (DS)	MCP area surveyed Km ²
Alpine	Northern Italy	Dolomiti Bellunesi National Park	4492473, 2574872	2014;2015;2018; 2019;2020;2021	7314	46	24	Wildcat and mesocarnivores	448 (520)	9,08
Alpine	Northern Italy	Carnic, Pre-alps	4540007, 2574994	2014; 2015	7302	49	16	Wildcat and wolf	1106 (750)	18,19
Alpine	Northern Italy	Giulie Prealps	4593190, 2570044	2018;2019;2020	1415*	83	5	Mesocarnivores	3819 (1748)	17,34
Continental	Northern Italy	Gorizia, Torre and Malina municipal park	4588306, 2539562	2012;2013;2018; 2019;2020	476*, 233	24	20	Faunal inventory-wildcat	2798 (3021)	331,31
Continental	Central Italy	North Apennine PO-PT	4406542, 2322927	2014;2017;2018; 2019	3600*	23	9	Wolf	1068 (1026)	24,98
Continental	Central Italy	Foreste Casentinesi National Park	4464561, 2304810	2009;2010;2011; 2012; 2013; 2014; 2015 2018;2019;2020	15,068	328	87	Wildcat and wolf	1067 (1172)	563,56
Mediterranean	Central Italy	Alta Val di Cecina	4388083, 2242055	2014;2015;2017;2020	3272	37	9	Faunal inventory and wolf	1917 (2122)	77,22
Mediterranean	Central Italy	Montioni Regional Park	4383803, 2213109	2013;2014;2015;2016;2017;2019	5200*	21	9	Wolf	790 (614)	7,9
Mediterranean	Central Italy	Poggi di Prata	4401436, 2219997	2015-2016	2824	42	7	Faunal inventory	771 (497)	2,3
Mediterranean	Central Italy	Maremma Regional Park	4409940, 2169934	2017;2018;2019;2020	6687	77	27	Mammal community	744 (475)	44,51
Alpine	Southern Italy	Monte Genzana Alto Gizio Nature Reserve, Feudo Intramonti Reserve, Chiarano-Sparvera Forest L'Aquila	4645080, 2095011	2018;2019;2020	2347*	39	19	Wildcat	2250 (1946)	229,31

Table 1 (continued)

Biogeographic regions	Latitudinal zones	Sites	Coordinates EPGS: 3035	Study period	Survey effort	Detections	Camera-sites recording wildcat	Target species	CT mean distance (DS)	MCP area surveyed Km ² *
Mediterranean	Southern Italy	Cassino	4644829, 2057888	2020;2021	2050*	18	12	Faunal inventory	1159 (1618)	42,80
Mediterranean	Southern Italy	Pollino National Park	4847490, 1896375	2012–2017	3564	83	14	Mammal community	1878 (1337)	82,08
Mediterranean	Southern Italy	Aspromonte National Park	4849989, 1704812	2013;2014;2016;2017;2018;2019	4450*	105	34	Wolf	1527 (2515)	633,06
Total					65,802	975	285			

Total survey effort, detections and camera-sites in bold

*Indicates an approximate number of trap days

overlap coefficient Δ_4 to compare the two samples and to verify their concordance. We calculated the Δ_4 estimator coefficient since our sample was > 75 events (Linkie and Ridout 2011; Meredith and Ridout 2014). Overlap was defined as “low” when it was < 0.50, “intermediate” when included between $0.50 \leq \Delta \leq 0.75$, “high” with $\Delta > 0.75$ (Monterroso et al. 2014; Mazza et al. 2020; Mori et al. 2020b). We calculated the 95% confidence intervals for overlap coefficients as percentile intervals from 1000 bootstrap samples (Meredith and Ridout 2017).

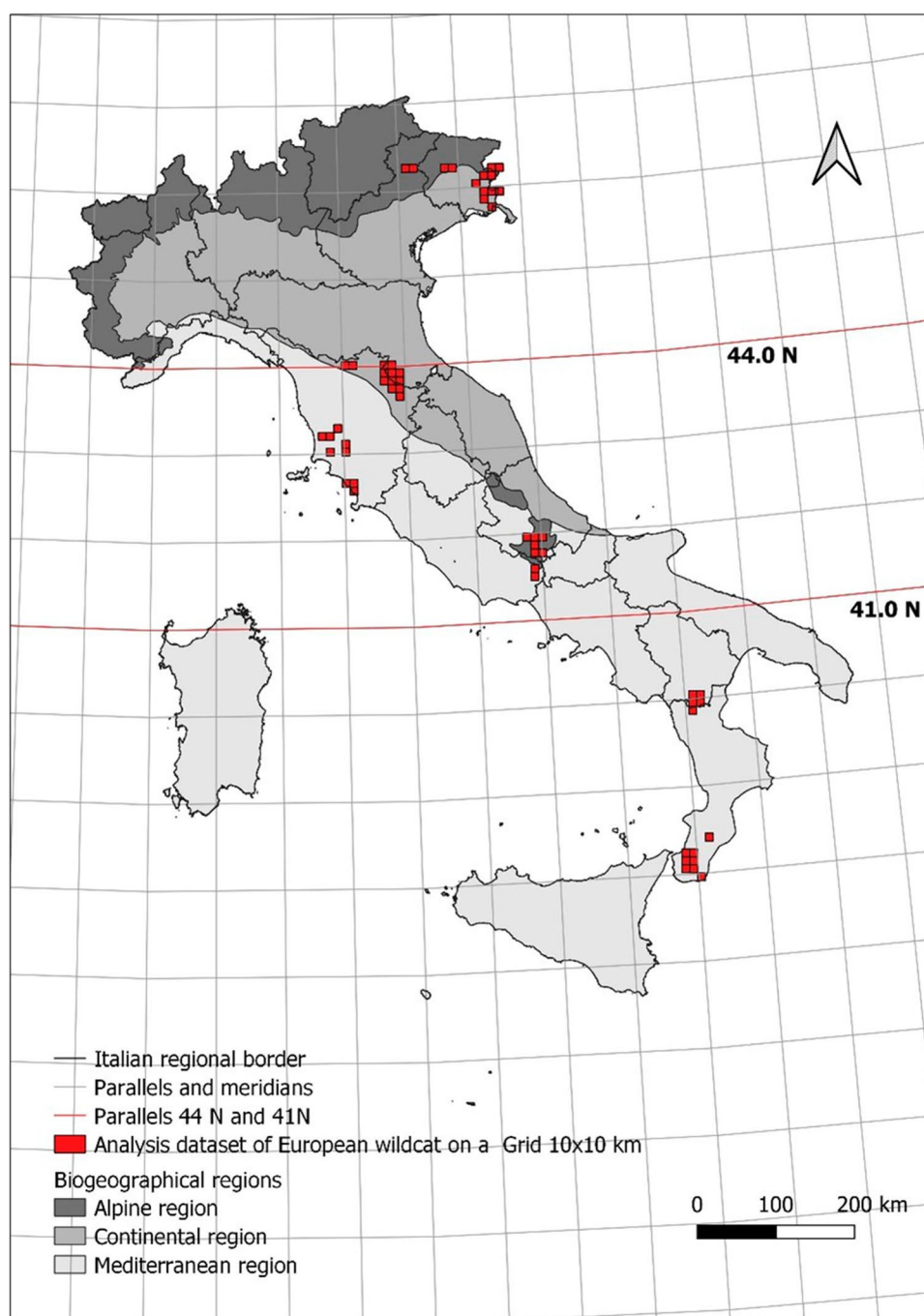
Ambiental light and activity

We tested through a chi-square test whether the activity of wildcats was concentrated during night, crepuscular hours, or daylight (Sokal and Rohlf 2012). A Cramer’s V index was calculated to test for the size effect of the variables on wildcat detections. We considered as crepuscular hours the range time between the nautical dawn (sun is 12° below horizon) to sunrise (sun is 0.833° below horizon) and between nautical dusk (sun is 12° below horizon) to sunset (sun is 0.833° below horizon). The nautical dawn and dusk begin ~ 24 min before and after the civil dawn and civil dusk, equal to the time it takes for the earth to rotate 6°. We calculated the times of sunset and sunrise for each camera site using a specific algorithm by Meeus (1991), implemented in a VBA (visual basic for application) script, including coordinates and dates of each wildcat event. In the same way, we also classified surveyed nights following moon phases and epact, to test the effect of night sky brightness on the activity of the wildcat. Nights were classified as it follows: (1) epact days = 0–3, 26–29; (2) epact days = 4–6, 21–25; (3) epact days = 7–9, 17–20; (4) epact days = 10–16 following the approach by Mori et al. (2020b). Then, we conducted a chi-squared test on numbers of nocturnal events (i.e. excluding from this analysis diurnal and crepuscular events) in each of these moon phases, to assess if they were uniform throughout the lunar cycle (Mori et al. 2020a).

Diurnal behaviour

We set a generalized mixed linear model (GLMM) through the package ‘glmmTMB’ (Brooks et al. 2017) and ‘lme4’ (Bates et al. 2015). We created a dichotomous dependent variable using binomial errors (link: logit), labelling daylight events (after sunrise, when the sun is 0.833° below horizon, and before sunset, when the sun is 0.833° below the horizon) as “1” and darkness events (before sunrise and after sunset) as “0”. We chose these sunset and sunrise, because we wanted to include only events with a substantial daylight and not borderline events. Running this model, we aimed at figuring out the diurnal activity of the species based on

Fig. 1 Biogeographic regions (shades of grey), 10×10 km cells selected for analyses (in red, $N = 85$) and latitudinal zones (whose borders are marked by parallels, highlighted in red). Cells have been identified when at least one detection of wildcat was inside the border of cell. Our map excluded Sardinia, where the African wildcat *Felis (silvestris) lybica* is present. All data were projected on the grid identified by Regulation (EU) No 1089/2010 and the INSPIRE Directive 2007/2/EC (ETRS 89/Laea-EPGS-3035)



our detections, outside major peaks of activity during the darkness hours.

First, we used Quantum Geographic Information System (QGIS) version 3.10 ‘A Coruña’ to calculate environmental predictors. We used the MMQGIS-Hub distance plugin and data from Corine Land Cover © European Union, Copernicus Land Monitoring Service, European Environment Agency (EEA) and open street map (<https://www.openstreetmap.org>) to calculate minimum distances to woodland (broad-leaved forest, coniferous forest, mixed

forest), shrubs (moors and heathland, sclerophyllous vegetation, transitional woodland/shrub), natural and semi-natural open areas (arable land, heterogeneous agricultural areas), discontinuous urban fabric and paved roads. According to the classification of the roads provide from Open Street Map, we excluded to our analysis the pathways and “minor road” (forest roads, residential roads, pedestrian roads) and we included only principal paved roads (“major roads”: motorway and highway). In the analyses we only considered environmental predictors that had

a distance within 2500 m (hence our sample is reduced to $N = 729$) using as reference the approximate average radius of largest home-ranges of European wildcats in Italy (males and females) in literature (Anile et al. 2017). Moreover, the average daily home-range from radio-tracking data was similar, i.e., 2.26 km (Sarmiento et al. 2006; Monterroso et al. 2009). Since more of 50% of our camera-trapping stations ($N = 285$) were farther than our limit distance to natural and semi-natural open areas and discontinuous urban fabric we did not consider these land use categories as predictors in our model. We used the ‘raster sampling’ plugin and DEM at an accuracy of 20 m (data from National Environmental Information System Network of the Italian National Institute for Environmental Protection and Research: ‘SinaNet-ISPRA’, www.mais.sinanet.isprambiente.it/ost/) to calculate the elevations of each camera-trapping station.

Overall, in our global model, we considered as predictors: (i) season, (ii) % of visible moon, (iii) elevation, (iv) distance to the nearest paved road, (v) distance to the nearest shrubs, (vi) distance to the nearest woodland, (vii) type of habitat at each camera-trap site. As random effects, we selected the year and the study areas. We assessed collinearity among predictors through correlations using the Pearson and Spearman correlation coefficient for each possible couple of predictors, using a threshold of 0.51 (Crawley 2007).

A global model was initially evaluated for this analysis with all predictors. Subsequently, all possible models were calculated with the different combinations of considered predictors, evaluated through model selection procedure based on comparison of AIC scores (Akaike Information Criterion). We identified as the best model the most parsimonious one, i.e., the one having the lowest AICc (Burnham and Anderson 2002; Richards et al. 2011). Moreover, we selected for inference all models with $AICc \leq 2$ (Burnham and Anderson 2002; Harrison et al. 2018) and among these, those which were not more complex versions of the simpler model (Richards et al. 2011); we used the selection model with nesting rule to avoid retaining overly complex models (Richards et al. 2011; Harrison et al. 2018). Model selection was conducted through the R package ‘MuMIn’ (Barton 2012). We estimated parameters (95% confidence intervals and B coefficients, which is the degree of change in the response variable for every 1-unit of change in the predictor variable) of the best model by using the R packages ‘glmmTMB’ (Brooks et al. 2017) and ‘lme4’ (Bates et al. 2015). Then, the best model was validated by visual inspection of the distribution of residuals (Zuur et al. 2009) through the ‘DHARMA’ package (Hartig 2021). Model weight was standardized within the subset of selected models.

For our best model we also performed a post-hoc analysis for the categorical season predictor.

Results

Activity rhythm patterns on the national scale

We included in our analyses a total of 975 events (warm, $N = 524$; $N = 451$). The comparison between the random sample generated and our total sample underlined high overlap between two distributions (Fig. 2a–b). The Watson two test was not significant (Fig. 2c); thus, we used the total sample for the followed analyses. The European wildcat activity peaked at night on an annual level, with two main peaks around 10:00 pm and 04:00 am (Fig. 2a–c).

In the warm months, the wildcat activity increased from 07:00 pm, with a maximum peak between 02:00 and 04:00 am. In the cold months, the greatest activity was recorded between 05:00 pm and midnight, with a second peak at about 05:00 am (Fig. S1 in Supplementary Material).

Patterns of activity rhythms at the biogeographic scale

The overlap in all cases (Fig. S2–3 in Supplementary Material), between the activity of the wildcats in the three different biogeographic contexts, on a yearly scale was high. Nonetheless, some minor differences could be observed (Fig. 3a–c). The highest peak in the Continental area was at 10:00 pm with a second lowest peak at 05:00 am, whereas, in the Mediterranean area, the maximum peak was at 05:00 am and a second one after 11:00 pm. The wildcat had a little activity also during the daylight, with two small peaks at midday and at 04:00 pm. In the Alpine area, the activity began to increase around 04:00 pm with a peak around 11:00 pm with a plateau until 03:00 am. As to the analyses of two semesters (cold and warm), the intra-area overlap was high for the Alpine and Mediterranean areas and intermediate for the Continental area (Fig. S3 in Supplementary Material). There was a slight peak of activity in diurnal hours for the Alpine and Mediterranean areas in the warm period but not in the cold one.

Patterns of activity rhythms at the latitudinal zones scale

In the northern area, the major peak was recorded around 10:00 pm, but the activity kept being high until 05:00 am. In central Italy the wildcat had two highest peaks of activity at 10:00 pm and 04:00 am. In southern Italy, the activity of wildcat began to increase around 06:00 pm reaching the highest peak at about 03:00 am (Fig. 4a–c).

The overlap was high in all cases (Fig. S4–5 in Supplementary Material), on a yearly scale (Fig. S4 in Supplementary Material), at the semester scale (warm and cold months), at the intra-area and the inter-area levels (Fig. S5 in Supplementary Material), underlining a substantial activity overlap among the three different latitudinal zones. The peaks of activities during cold months were anticipated with respect to warm months in all latitudinal zones. Moreover, a slight increment of wildcat diurnal activity in the warm months was observed, with respect to the cold ones.

Ambiental light and activity

The wildcat activity resulted significantly dependent from night-day phases being recorded for 70.2% of our events in night ours, for 20% during daylight and for the remaining 9.8% during the twilight ($\chi^2 = 914.87$, $df = 2$, $P < 0.001$; Cramer's $V = 0.56$). Nocturnal activity of the wildcats was not constant in different moon phase nights (year: $\chi^2 = 66.54$, $df = 3$, $P < 0.01$; warm months: $\chi^2 = 30.83$, $df = 3$, $P < 0.01$; cold months, $\chi^2 = 86.85$, $df = 3$, $P < 0.01$; Cramer's $V = 0.57$), decreasing from darkest nights (78.25% nocturnal records) to full moon nights (21.75% nocturnal records).

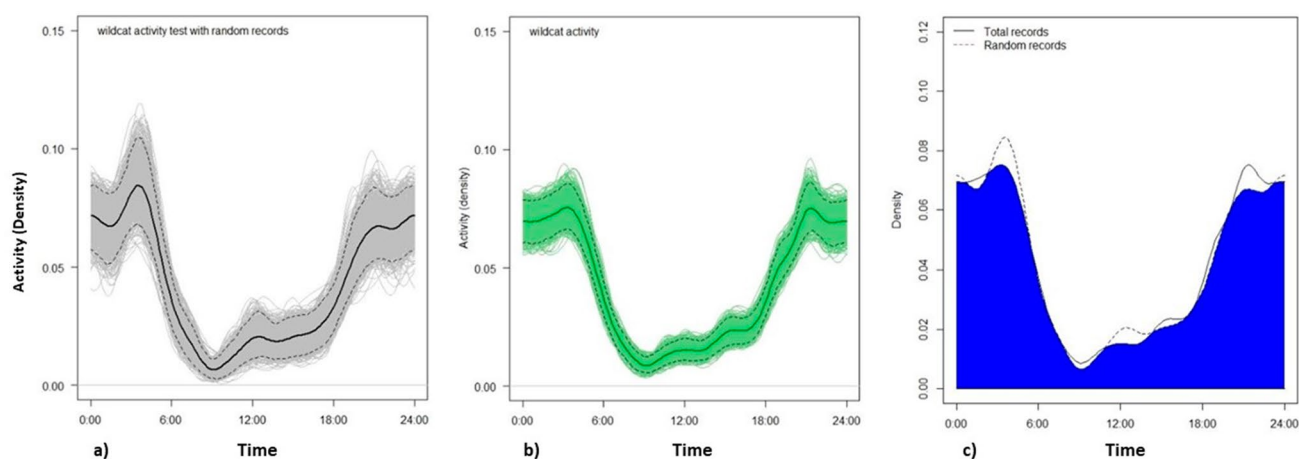


Fig. 2 **a** Total activity rhythms of the wildcat in Italy; **b** activity rhythms estimated through a random subset of wildcat records; **c** overlap between **a** and **b** $\Delta_4 = 0.96$; 95% confidence intervals = 0

.89–0.96; Watson test: $W < 0.001$, $P > 0.10$. Coloured lines represent bootstrapped estimates of activity patterns; dashed black lines represent 95% confidence intervals

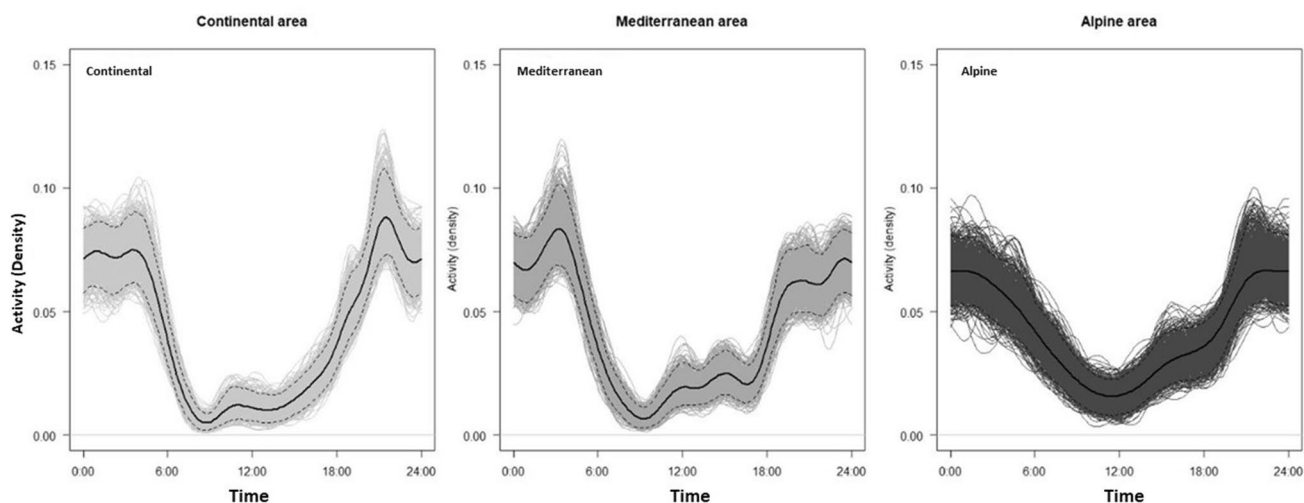


Fig. 3 Temporal activity patterns of wildcat in the three biogeographic regions: **a** Continental, **b** Mediterranean, **c** Alpine. Coloured lines represent bootstrapped estimates of activity patterns; dashed black lines represent 95% confidence intervals

Diurnal behaviour

In the global model none of the predictors were correlated and they could all be included.

In the best model we considered the follow predictors: (i) distance to the nearest shrub woods; (ii) elevation; (iii) season.

The probability of wildcat detection in daylight was favoured by a minor distance to shrubs and low altitudes (Table 2; Fig. S6 in Supplementary Material). Moreover, the model underlines that the probability of wildcat detection in daylight is higher in spring and summer compared to the autumn. Conversely, the human structures, i.e., paved roads—seem not to influence the diurnal activity of the species, since this variable was not selected to be part of the best model (Table S1 in Supplementary Material).

Discussion

In all our outcomes and pairwise comparisons, the European wildcat confirmed a predominantly nocturnal habit as also reported in other studies (Daniels et al. 2001; Germain et al. 2008; Soyumert 2020; Anile et al. 2021; Migli et al. 2021), with over 70% events falling in dark hours. Furthermore, the wildcat seemed not to select the transition period between night and daytime (only less than 10% of events were in crepuscular hours). Surprisingly, we found a 20% of our detections fell during daylight. One reasons could lie in the sample size of our study being significantly larger with respect to most of other works, carried out mostly on local or regional scale (Germain et al. 2008; Can et al. 2011; Anile et al. 2021; Migli et al. 2021) and that might have

better detected this phenomenon. Moreover, our data come from a more representative geographic range that could have intercepted hidden differences in prey typology and abundance with a consequent shift in feeding habits for some individuals. Indeed, in areas where some wildcat preys are diurnal (e.g. voles), wildcats may show some diurnal activity (cf. Jiménez–Albarral et al. 2021). Inter-season activity differences showed shifts in the peaks, in line with differences in sunrise and sunset time, suggesting a preference toward total darkness.

Wildcats show several physical and physiological adaptations to nocturnal or crepuscular activity, mainly involving hunting and courtship behaviour. These adaptations include an acute auditory sense, an improved tactile sense from vibrissae and other hair tufts, and an acute sense of smell for maximizing the activity at dark (Tabor 1983), which may explain why they are mostly reported as nocturnal species. Furthermore, wildcats have large eyes with a high proportion of rods in the retina for better vision in poor low-light vision (Tabor 1983).

Amongst mammals, the activity of predators is often synchronized with the activity of their prey (Daan and Aschoff 1981; Zielinski et al. 1983; Monterroso et al. 2013), or shaped by the need of avoidance of humans or other competitors (Wang et al. 2015; Mori et al. 2020b; Murphy et al. 2021). As a matter of fact, nocturnal activity is one of the strategies that wildlife adopts to avoid encounters with humans (Gaynor et al. 2018; Nickel et al. 2020). Differently from our hypotheses, our results suggested that nocturnal activity of the wildcat was the lowest in bright moonlight nights. This behaviour might be explained in relation to the temporal behaviour of its main prey. Rodents and lagomorphs tend to avoid bright moonlight nights (Mori et al.

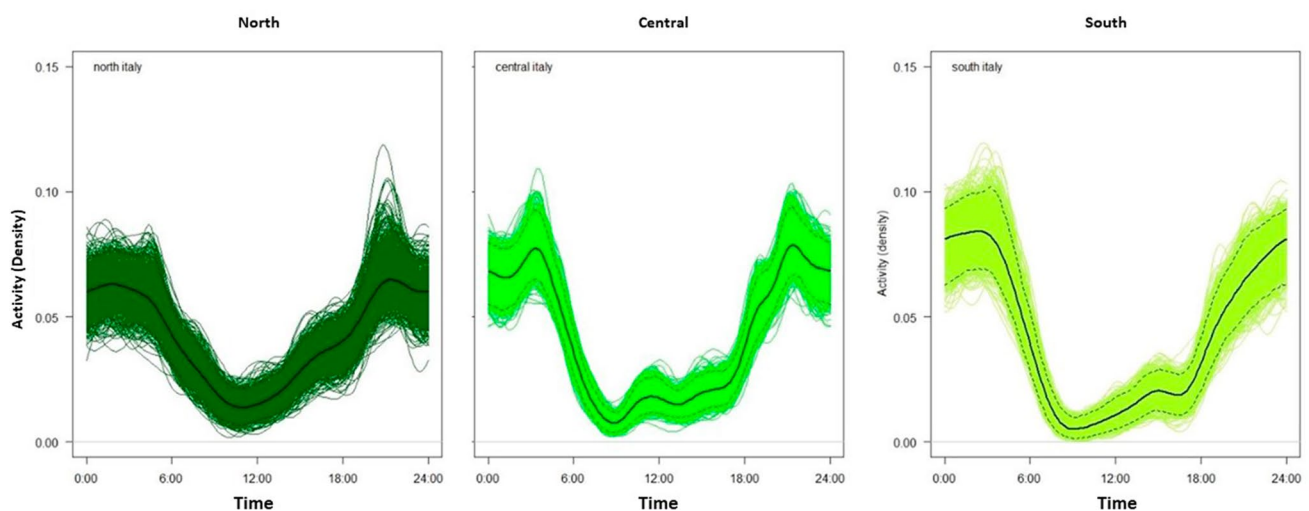


Fig. 4 Temporal activity patterns of wildcats in the three latitudinal zones: **a** northern, **b** central, **c** southern. Coloured lines represent bootstrapped estimates of activity patterns; dashed black lines represent 95% confidence intervals

Table 2 Model selection for diurnal activity, estimated through generalized linear mixed models

Post-hoc analysis	Variables	<i>B</i>	SE	95% CIs	<i>P</i>	
	Spring (autumn)	0.976	0.301	[0.202, 1.750]	0.006	
	Summer (autumn)	0.939	0.300	[0.169, 1.708]	0.009	
	Winter (autumn)	0.381	0.303	[-0.398, 1.159]	0.589	
	Summer (spring)	-0.037	0.259	[-0.702, 0.628]	0.999	
	Winter (spring)	-0.595	0.288	[-1.334, 0.144]	0.163	
	Winter (summer)	-0.558	0.272	[-1.255, 0.139]	0.168	
Best model	Variables	<i>B</i>	SE	95% CIs	<i>z</i>	<i>P</i>
Diurnal activity	Intercept	-1.887	0.257	[-2.391, -1.383]	-7.338	<0.001
	Distance to the nearest shrub	-0.301	0.100	[-0.498, -0.105]	-3.003	0.003
	Elevation	-0.200	0.093	[-0.381, -0.018]	-2.155	0.031
	Season [Spring]	0.976	0.301	[0.385, 1.567]	3.238	0.001
	Season [Summer]	0.939	0.300	[0.351, 1.526]	3.132	0.002
	Season [Winter]	0.381	0.303	[-0.213, 0.975]	1.256	0.209

Effects of predictors included in best model are shown: model coefficients (*B*), their standard error (SE), 0.95 confidence intervals (CIs), zeta-value (*z*), and *p* value (*P*). For our best model we included also a post-hoc analysis for the categorical season predictor

2014; Penteriani et al. 2013; Pratas-Santiago et al. 2016; Viviano et al. 2021), with ranging movements mostly concentrated in concealed habitats or during the darkest nights. Therefore, it is likely that the wildcat synchronized its movements with those of its main prey, e.g., by decreasing its activity in bright moonlight nights. Another reason for which the wildcat avoids bright moonlight nights could be related to the fact that increased visibility would make it less effective in predatory activity (Prugh and Golden 2014). Moreover, the avoidance of bright moonlight could also be related to the presence of apex predators, i.e., the grey wolf *Canis lupus*, which is present and abundant throughout Italy, and the lynx *Lynx lynx*, only present with few individuals in the Alps (Loy et al. 2019). Accordingly, apex predators are mostly active in bright moonlight nights, potentially forcing mesocarnivores to be active mostly in the darkest nights (e.g. Theuerkauf et al. 2003; Penteriani et al. 2013). Several other small-sized carnivores coexist with the wildcat and may compete with this species for diet and/or spatiotemporal behaviour (cf. Mori et al. 2020b). Our result seems to agree with Di Bitetti et al. (2006), as they examined feline activity on the trails in Argentina and found that ocelots *Leopardus pardalis* were predominantly nocturnal with no significant differences between males and females and more active during dark sky periods (new moon near periods). However, ocelots are adapted to thrive in environments with abundance of larger carnivores (e.g. pumas *Puma concolor* and jaguars *Panthera onca*). Conversely, where the mesocarnivore guild is composed by a lower number of species or in areas where wolves are a rare occurrence, no effect of moonlight is observed in wild cats (Migli et al. 2021).

Diurnal activity occurred in about 20% of our events and was reported especially in the warm season (spring and

summer) perhaps due to the activity of diurnal prey such as arthropods, reptiles, squirrels, birds (Apostolico 2003; Apostolico et al. 2005; Ragni et al. 2014), or due to, most likely, the reduced prey availability during summer which, in the Mediterranean climate, represents the limiting season. Therefore, the wildcat may switch prey to maximize hunting opportunities, considering also that during summer the daylight hours are more represented during the day. This behaviour has never been reported for the wildcat. A similar behaviour has been observed in the jaguar, which exploit diurnal hours to search for peccaries when nocturnal turtle abundance was the lowest (Carrillo et al. 2009). Furthermore, the warm period coincides with the weaning of offspring and consequently with an increase in the physiological demand for additional food resources. Accordingly, Migli et al. (2021) confirmed a peak of activity in night hours in radio-tracked wildcats in Greece, with a peak in diurnal activity of reproductive breeding females in warm months.

Diurnal movements are negatively correlated with increasing distance from shrubs, but not with forests. Thus, we suggest the importance of shrubs for the species probably due to a greater preference for protection, shelter, and the abundance of prey (Monterroso et al. 2009; Lozano et al. 2010; Ferretti et al. unpublished data). A preference for these habitats has also been revealed by wildcat monitoring in the Polish Carpathians (Okarma et al. 2002). Conversely, Anile et al. (2019) reported a preference for mixed forests in a volcanic environment of Southern Italy. In this area, the shelter provided by shrub is largely overwhelmed by the local abundance of natural cavities typical of the volcanic soil. This particular situation is related to the volcanic area and to a wildcat population which is genetically isolated

from the peninsular population. Our study, including data from the whole of the Italian peninsula, stresses that shrublands are important for the species, in agreement with other studies carried out in the Mediterranean.

Wildcat occupancy has been reported as negatively affected by altitude (Anile et al. 2019). Our results hence showed that diurnal activity decreases with increasing altitude (i.e., up to 1800 m a.s.l.). Nevertheless, the interpretation of this result requires further investigation.

The presence of paved roads seemed not to affect the diurnal activity of wildcats, even though the transit of vehicles generally increases during the day. This result suggests that in presence of natural shelters, such as shrubs and other protection elements, which sometimes occur on paved road sides, this species can tolerate these anthropogenic infrastructures (Jerosch et al. 2009; Wening et al. 2019). Klar et al. (2008) highlighted how human infrastructures such as roads and villages are usually avoided by the wildcat although over a certain distance (i.e., ca. 200 m for single streets and houses, ca. 900 m for villages). Thus, human infrastructures do not seem to influence the wildcat ranging movement patterns, further suggesting that a small number of main roads can be tolerated within the home-range of a wildcat, despite being an important mortality factor (Klar et al. 2009). Many of our study areas are protected areas that are in natural and rural zones with roads usually not too busy, hence further ad hoc study could be required to confirm the result. Moreover, this result could be affected by a gender factor as highlighted in Jerosch et al. (2018) suggesting a gender difference, with females avoiding the areas near roads more than males.

In conclusion, our insights shed lights on some basic ecology elements of wildcat behaviour in Italy, for the first time with a national-scale perspective and at different latitudes, including some novel information about its diurnal movements. These aspects are pivotal for the conservation and effective management of this endangered species that has been poorly studied on a large scale. Nonetheless, we are aware that gathering data from different monitoring projects, carried out with heterogeneous designs, even though complying with fundamental requirements, could lead to some inaccuracies that could be taken into consideration. We, therefore, think it should be advisable to standardize as much as possible the camera-trapping protocols and to tend to national-scale coordination in wildcat monitoring in Italy. Several in-depth analyses will be necessary for the future, holding into consideration the behaviour of wildcat prey and/or direct potential competitors, including *Martes* spp., red foxes *Vulpes vulpes*, apex predators (wolves and lynxes), golden jackals *Canis aureus* and, locally, alien species too (e.g., the racoon *Procyon lotor* and the genet *Genetta genetta*). Moreover, another element to investigate is the

spatio-temporal behaviour of wildcats in relation to climate change scenarios, particularly in the context of the Mediterranean region, with drought currently lasting longer than in the past, and potentially leading to behavioural modulation changes.

To conclude, the data collected during this study made it possible to highlight that the currently known distribution of the species is lacking and needs further nationwide studies, essential to properly describe the range of the European wildcat in the Italian territory.

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distribution (Fig. S8 in Supplementary Material) since, among all data collected by us or belonging to other unpublished personal archives (including detections not comprised in the above analyses), some were interesting for their collocation in areas not yet included in the currently formal national distribution of the species. Authors acknowledge Prof. Marco Bologna (University of Roma Tre), Silvia Castelli and Nicole Marini for their support in the surveys in the Foreste Casentinesi National Park, and Federica Mattucci, Romolo Caniglia and Nadia Mucci (ISPRA), for their advice and experience. Authors would like to thank three anonymous reviewers for their useful comments on our manuscript.

Author contribution LL, PF, ML, EM, EV and Asp: conceived, planned the study and requested the data of the study areas. LL: collected data for Val di Cecina; PF and ML: collected data for Casentinesi State Natural Reserve; EM: collected data for Prata's hills; EV and NC: collected data for Foreste Casentinesi National Park; FC: collected data for Pistoia's Apennine; ASi: coordinated the projects in Aspromonte National Park; FFO, MP and SP: collected data for Friuli Venezia Giulia. ASa: collected data for Pollino National Park; FFe: collected data in Maremma Regional Park; ASF: participated in data validation for Maremma Regional Park; Asp: collected the data for Dolomiti Bellunesi National Park and Torre and Malina municipal park; CP: collected the data for Abruzzo region. LL and EM: conducted statistical analyses. PF and Asp: conducted the GIS analyses. LL, PF, ML, EM, EV and Asp: wrote the first draft; all authors participated in writing the final manuscript.

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Declarations

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

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