RESEARCH ARTICLE

Integrating remote sensing data on habitat suitability and functional connectivity to inform multitaxa roadkill mitigation plans

Francesco Valerio · Sérgio Godinho · Pedro Salgueiro · Denis Medinas · Giovanni Manghi · António Mira · Nuno M. Pedroso · Eduardo M. Ferreira · João Craveiro · Pedro Costa · Sara M. Santos

Abstract

Context Road impacts on biodiversity are increasing worldwide. Few attempts have been made to integrate multiple taxonomic groups into roadkill mitigation plans, while using remotely sensed habitat suitability and functional connectivity.

Objectives We pinpoint high-risk road locations (road planning units) for 19 woodland species from different taxonomic groups (non-flying mammals, birds, and bats) to enhance prioritisation and versatility of roadkill mitigation plans.

Methods In Southern Portugal, we collected species occurrence data, roadkill, and high-resolution satellite imageries, along 15 years. We identified remotely sensed habitat metrics, in turn weighted together with functional connectivity models and road metrics to estimate roadkill vulnerability, using random forests. The roadkill cumulative risk across species is then estimated, as well the likelihood variation within and between taxonomic groups to verify prediction consistency.

Results Remote sensing information thoroughly explained habitat suitability, identifying similar metrics within each group, and non-uniform environmental tolerance across species. Functional connectivity and habitat suitability significantly explained

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mortality, highlighting connected woodlands and neighbouring matrices. The roadkill cumulative risk endorses a conspicuous prioritisation of road planning units for implementing mitigation structures useful for multiple species, with high precision and low probability variation within each group. Some discrepancies in prediction consistency still emerge after group comparisons regarding bats.

Conclusions We provide novel insights for multi-taxa ecological responses and roadkill evaluations, demonstrating a possible spatial prioritisation in mortality patterns from species with different traits. The identified road units support resilience and multifunctionality over long-term, enabling to assist cost-effective mitigation plans. Findings ultimately offer versatility during the mitigation planning phase throughout the identification of road sub-optimal units, and opportunity costs given their potential for different taxa.

Keywords Multiple species · Roads · Mortality risk · Remote sensing · Landscape connectivity · Species distribution models · Wildlife crossing · Fencing

Introduction

Landscapes, with associated ecosystems and species, exert a major positive influence on life quality of human societies, given the variety of benefits they provide (Díaz et al. 2018), although on the contrary human activities often clash with the welfare of ecosystems and landscape multifunctionality. In particular, the pervasiveness of some landscape elements such as roads, as well their expansion, are affecting ecosystems and ecological communities around the world, contributing to the impoverishment of terrestrial biodiversity and nature sustainability (Laurance et al. 2014). This global proliferation of the infrastructure network can lead to increased fragmentation and traffic volumes, in turn exacerbating direct wildlife mortality through collisions with vehicles, commonly known as roadkill (Forman and Alexander 1998; Grilo et al. 2009). Over the past two decades, increasing mortality rates have been reported, prompting unprecedented research efforts to understand and mitigate road-related wildlife casualties (Pagany 2020). Yet on European roads alone, around

194 million birds and 29 million mammals are killed annually (Grilo et al. 2020), a significant loss that possibly threatens the viability of populations (van der Grift 2017; Oddone Aquino 2021), even though this may vary according to species and location (Grilo et al. 2009). To both reduce wildlife mortality and to restore connectivity ("the degree to which the landscape facilitates or impedes movements"; Taylor et al. 1993), mitigation structures (e.g over and underpasses; fences) are being designed and planned along roads (Clevenger and Huijser 2011; van der Grift 2017). However, structures are routinely criticised for having limited effectiveness, being most frequently directed to a particular taxonomic group (Rytwinski et al. 2016).

To ensure long-term sustainability, landscape approaches have been developed at the interface between biodiversity conservation and human development goals, and several principles have been proposed for future improvements: the need to deal with landscape dynamic processes, to include resilient and multifunctional solutions, as well to move towards more adaptative and negotiable strategies (Sayer et al. 2013). Among landscape approaches, roadkill risk models (RRMs) are being used as guidance to effectively enhance sustainability by applying mitigation measures at mortality hotspots (i.e. "segments of roads with particularly high animal-vehicle collision rates"; Santos et al. 2015) and/or movement corridors of target species (Gunson et al. 2011; Fabrizio et al. 2019). Decisions about site implementation are crucial during the strategic planning phase, and determine the effectiveness of mitigation structures. Such decisions are yet a challenge for prioritisation plans when targeting multiple species with distinct habitat requirements and movement abilities (Polak et al. 2019). When informing strategic plans, a key habitat, as well as functional connectivity, can be approximated for a wildlife group without relying on ecological information, through a so-called species-agnostic framework (*sensu* Marrec et al. 2020). In road ecology, this analytical approach may offer advantages as multifunctional roadkill proxy whenever a wide range of species is examined for planning initiatives (Koen et al. 2014). Still, it has long been argued that functional connectivity may diverge between species (Zeller et al. 2012), with research efforts still requiring to address multiple habitats and corridors (Brennan et al. 2020). Undoubtedly, wildlife is unevenly

distributed across landscapes in light of diverse ecological requirements and movement capabilities. Such an ecological perspective makes defining multifunctional corridors a demanding task, but one deserving greater consideration in spatial conservation prioritisation (Brennan et al. 2020; Salgueiro et al. 2021), especially when multiple taxa are taken into account (Marrec et al. 2020). Furthermore, a second neglected theoretical issue is that even if studies have extensively focused on habitat elements as main mortality drivers within RRMs (Gunson et al. 2011; Pagany 2020), road-related mortality might also be expected from dispersal movements in non-habitat matrix (Vasudev et al. 2015). This suggests that when relating roadkill to multifunctional corridors, various movement costs should be accommodated, since species' willingness to move within the matrix, such as during dispersal, may differ than within habitat (Zeller et al. 2012). Therefore, to bridge this knowledge gap and improve the efficiency of mitigation measures, it is crucial to approach functional connectivity with a focus on dispersal capabilities (Vasudev et al. 2015; Diniz et al. 2020), as well as to disentangle the effects of habitat and functional connectivity on RRMs (e.g Fabrizio et al. 2019).

In addition to the need to account for multifunctional solutions, another relevant aspect for enhancing the prioritisation of site selection for mitigation structures concerns to deal with landscape dynamic processes over long periods (Clevenger and Huijser 2011). From an ecological standpoint, dealing with landscape dynamics has been gradually recognised as an important step in conservation planning and management since the last decade, although it has still limited integration in road ecology (Oddone Aquino 2021). Indeed, while this issue has been recently explored in some study cases (e.g Medinas et al. 2021), most RRMs-based studies have still focused on a spatio-temporally limited representation of a landscape, namely through categorical land cover classes (Gunson et al. 2011; Pagany 2020). Some authors (Cushman et al 2010; Herrera et al. 2016) have also questioned categorical landscape conceptualisations to be able to represent the complexity of biological communities, while others have pointed to an underestimation of unique habitat elements (Kerr and Ostrovsky 2003; Coops and Wulder 2019). To overcome these drawbacks, as well as to incorporate landscape dynamics over time, a turning point is possible

thanks to continuous and more informative landscape descriptors from satellite remote sensing data (Coops and Wulder 2019), and to pixel-based methods preserving unique spectral/radar information (Schulte to Bühne and Pettorelli 2017). Despite these advantages and the increased available information from online repositories, a limitation remains in how to combine satellite against field data to determine key habitat elements, resulting in an interdisciplinary area with little consensus (Pettorelli et al. 2014).

There is still limited empirical evidence on whether similar ecological responses to satellite-derived habitat metrics can be expressed across a group of wildlife species with similar characteristics, which could be beneficial in RRM approaches. This is because a road may impact different species in similar ways, resulting in similar ecological responses (Santos et al. 2016a; Polak et al. 2019). Implications for connectivity, which are typically considered species-specific (Zeller et al. 2012), may also arise, arguably converging for a group of species with similar environmental preferences and characteristics, as well as dispersal capabilities. The main advantage here lies in prioritising conservation measures on planning units (e.g., pixels; see Margules and Pressey 2000) along roads (road planning units; RPUs), by capitalising on the capacity for 'mortality prevention' within a wildlife taxonomic group, even though this condition may not hold when considering groups of species with divergent ecological needs and movement capabilities. To ensure the effectiveness of mitigation measures, in addition to understanding the relative importance of habitat, functional connectivity, and anthropogenic pressures (e.g., road traffic) influencing road mortality, it is also imperative to ascertain whether quantitative models can accurately represent this exposure risk for various species from different groups, as their comprehensive integration into management plans continues to be neglected today (Polak et al. 2019).

In this study, conducted in southern Portugal, we make use of long-term (15 years, from 2005 to 2020) monitoring datasets on species occurrences and roadkill to optimise RRMs that offer support and guidance in identifying high-priority road locations for multispecies to implement concrete and effective mortality mitigation measures. We selected 19 vertebrate species belonging to three taxonomic groups: non-flying mammals, birds, and bats, each ranging from habitat specialists to generalists. In detail, to

ameliorate prioritisation and versatility of roadkill mitigation plans, we aimed to: (1) evaluate the utility of remotely sensed habitat metrics in describing species occurrence; (2) quantify the relative contribution of species-specific habitat, functional connectivity and road metrics in explaining spatial patterns of road mortality; and (3) identify priority road locations with the highest agreement in long-term mortality risk predictions, for the greatest number of species in each group and across groups.

Materials and methods

Study area

The study area is located in the Évora district (≅110 km E from Lisbon; Fig. 1) and it is bisected by a highway corridor linking Lisbon to Madrid. The area, characterised by a Mediterranean climate, encompasses more than 621,000 ha of a topographically gentle terrain, with a landscape dominated by the so-called *montado* agroforestry system, composed of a mosaic of open areas (pastures) and evergreen forests (mostly *Quercus suber* and *Quercus rotundifolia*) (Godinho et al. 2018; Pinto-Correia and Godinho
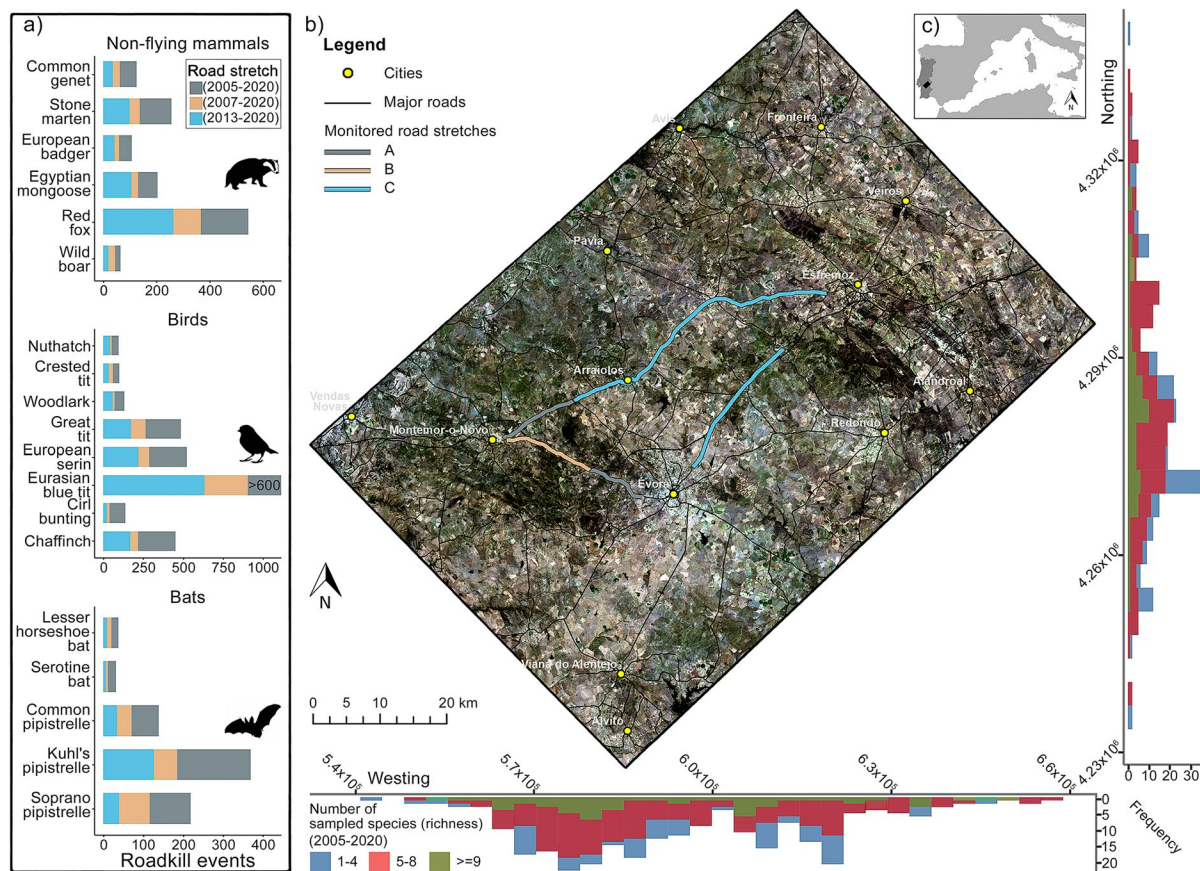
Fig. 1 Map of the study area. **a** The three left panels illustrate the number of roadkill events per species and monitored periods for each road stretch. **b** The road stretches, defined according to sampling effort, are layered with cities, and with a true-color satellite image composition (Landsat path 203 rows 33 and 34, and path 204 row 33 footprints). While occurrence sampling events are not directly depicted within the map, the distribution of sampled species is shown in the marginal histograms, in turn geographically covering the entire area following the longitudinal (South-North) and latitudinal (West–East) axes. Here, marginal histograms are depicted according to the number of sampled species (richness) pooled into three classes (1–4, 5–6 and >=9 species), and the frequency of such classes. **c** Location of the study area within SW Europe

2013). The *montado* is classified as "High Nature Value farming system", meaning that it holds high biodiversity, while also being of remarkable socio-economic value (Pinto-Correia and Godinho 2013). Other land uses present in the study area include olive groves and vineyards, while pine and eucalyptus plantations occur sparsely.

Major threats to the *montado* system are some landscape dynamic processes attributable to the intensification of agricultural practices, but also inappropriate forest management. Along with roads, this is leading to increased disturbance, fragmenting the landscape and compromising functional connectivity (Carvalho and Mira 2011; Pinto-Correia and Godinho 2013; Machado et al. 2020).

Methodological framework

A framework conceived the prime methodology (Fig. 2).

Data acquisition

Environmental information relied on high-resolution Landsat satellite imagery (Online Appendix S1.2; Fig. 2a). Occurrence data for the selected species were gathered for the entire study area encompassing the roads on which roadkill events were monitored (Fig. 1b). Collection of each data source (remotely sensed data, species occurrences and roadkill) was carried out over a long-time span, from 2005 to 2020 by the University of Évora team, and same persons when applicable for systematic surveys (e.g., Santos et al. 2015). We targeted different taxonomic groups (non-flying mammals, birds, and bats), corresponding to 19 focal forest-dwelling species (Online Appendix S.1.1), with varying degrees of habitat specialisation and dispersal capabilities. Non-flying mammals occurrence data was mostly obtained from linear transects targeting species' presence signs (e.g., footprints) and from camera traps (Herrera et al. 2016). Bird occurrences were obtained from 10 min point counts conducted during the breeding season at early dawn and with suitable weather conditions (Salgueiro et al. 2018).

Bat activity data came from surveys that combined linear transects, point counts conducted after dusk, and roost surveys (Medinas et al. 2013, 2021). Bat detectors were used in these campaigns, followed by a classification of echolocation calls for species identification.

Regarding data acquisition and primary processing steps, further details are provided in Supporting information (Online Appendix S.1.2–S.1.5).

Remote sensing-based habitat metrics

Intra-annual time series of habitat metrics were developed to secure spatio-temporal information on landscape patterns (Fig. 2a). Metrics were pooled into six predictor groups: "Spectral bands" (Online Appendix S1.2), given the efficiency in optical spectral properties for identifying landscape elements at high spatial resolution (Valerio et al. 2020); "Spectral indices", describing vegetation phenological patterns such as biomass (BNDVI, NDVI, EVI, MSAVI2), water content (NDII, NDWI, MSI) and senescence (PSRI, SWIR32); and "Thermal infrared", utilised to infer land surface temperature (LST). Also, horizontal vegetation complexity was characterised to reflect habitat heterogeneity in more open *montado* areas (Herrera et al. 2016), in the form of second-order "Textural indices" (GLCM_H, GLCM_E, GLCM_M; Haralick 1979), and parameterised according to Godinho et al. (2018). Finally, radar-derived predictors were identified as "Topographic", describing wetness index (TWI), as well "L-band SAR polarisations" through the PALSAR predictors (HH, HV), that allow to penetrate the vegetation overstorey to infer vertical vegetation complexity (Le Toan et al. 1992). This portfolio dataset of remotely sensed habitat metrics covered prime biogeophysical aspects of the *montado* agro-forest ecosystem (Godinho et al. 2018; Valerio et al. 2020), including ecological inferences on the target wildlife species, in geographically close areas (Santos et al. 2016b; Medinas et al. 2021). Time series were repeatedly collated within each year using the median across habitat metrics, resulting in 315 fine-grained predictors (21 metrics per year), developed in GEE and stored as data cube (Fig. 2a). Metric details are provided in Supporting information (Online Appendix S1.6).
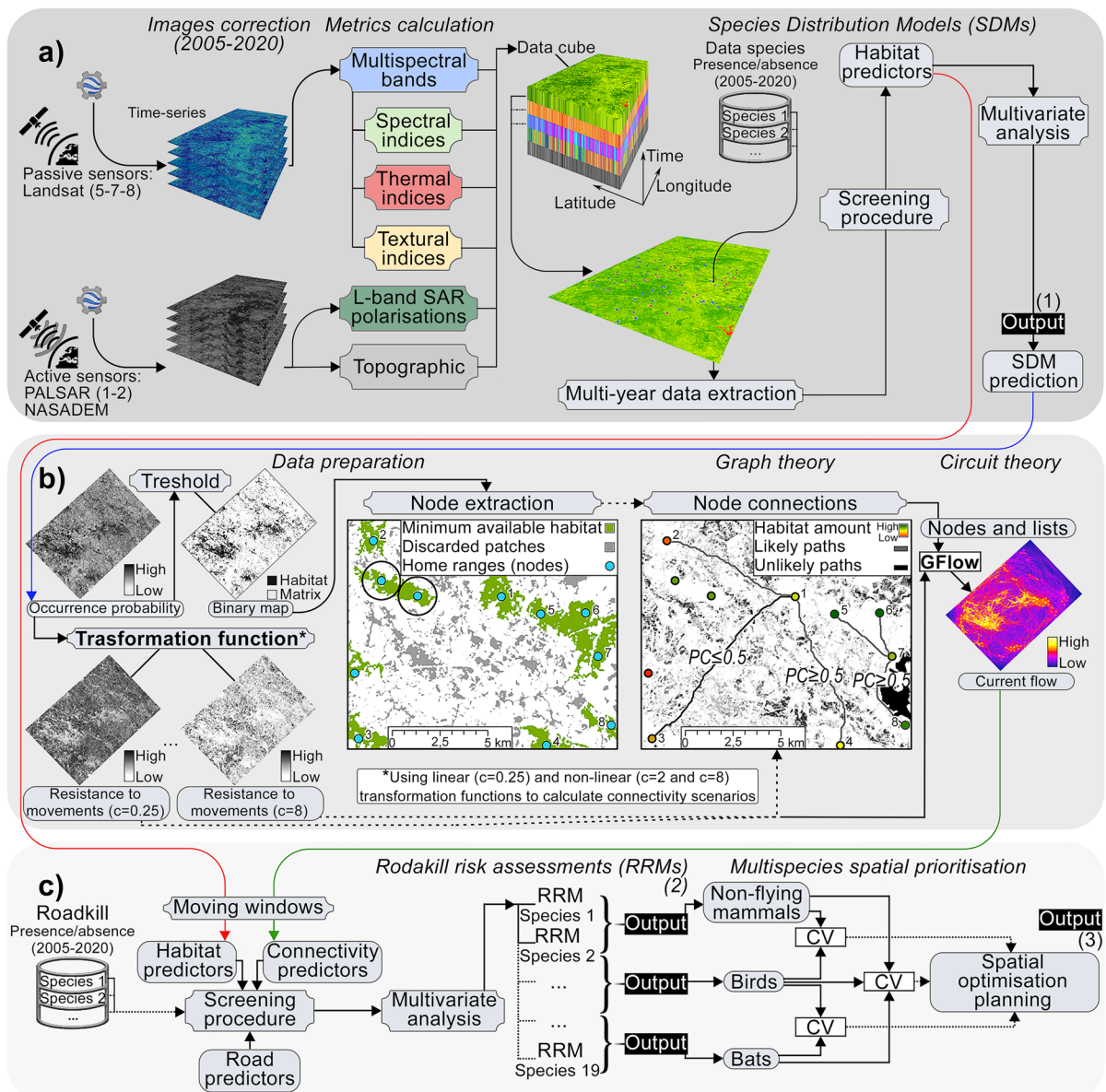
Fig. 2 The schematic methodological framework, with arrows guiding the development of the three main sub-tasks (**a**, **b**, **c**). The upper scheme (**a**) illustrates the satellite data processing, habitat metrics calculation, and data modelling for SDMs. The central scheme (**b**) illustrates the preparation of input data for functional connectivity models, namely nodes, resistance surfaces, along with lists of connected nodes, to compute func-tional connectivity scenarios. The lower scheme (**c**) illustrates the final task, namely the preparation of roadkill data and RRMs analysis including species-specific habitat, functional connectivity, and road predictors; then, the processing of road-kill risk overlap and probability variation (CV) within and between taxonomic groups. The numbers (1,2,3) in the figure refer to the three main goals of the research

Determining significant habitat metrics for species and taxonomic groups

Quantifying species-specific meaningful habitat metrics involved building species distribution models (SDMs; Fig. 2a; Elith and Leathwick 2009; Synes et al. 2016) with Random Forests classifiers (Brei-man 2001). These were performed in R statistical environment (v.3.6.3; R Core Team 2016) using "*Boruta*" (v.7.0.0) and "*randomForest*" (v.4.6-14)

packages. The response variable (species occurrence data, namely presence/absence set with 0.5 of prevalence; Online Appendix S1.7) temporally matched remotely sensed habitat metrics during data extraction (Fig. 2a). Then, to identify significant metrics describing habitat suitability, Boruta calculation was applied to 'confirm' or 'reject' predictors (Kursa and Rudnicki 2010), through 2000 runs with as many trees, and by a mean Z-score (0.01 P-value threshold; Valerio et al 2020). Predictors' significance was assessed by comparison with their randomised copies (Kursa and Rudnicki 2010). Multicollinearity problems were reduced by discarding predictors until values of Variance Inflation Factor (VIF) were negligible (VIF $\leq$ 5), and Pearson correlation coefficient indicated no strong correlation among predictors ($|r| < 0.9$) (Christophe 2011; Millard and Richardson 2015). Following a parameter tuning for SDMs interesting best number of trees (*ntree*) and the number of available predictors split at each tree node (*mtry*) (detailed in Supplementary material; Fig. 2a), then sensitivity, specificity, error rate (%), and area under the receiver operating characteristic curve (AUC; Fielding and Bell 1997) were estimated through 10-fold cross-validation runs, to assess the performance of the multivariate Random Forests models. We employed AUC threshold scores of $0.6 \geq AUC \geq 0.7$, $0.7 \geq AUC \geq 0.8$, and $AUC \geq 0.9$, to define model discrimination capacity as 'acceptable', 'excellent' and 'outstanding', respectively. The relative contribution was obtained from each SDM to determine the top-performing predictors influencing species occurrence. In addition, we selected the average of relative contribution between predictors to identify those potentially useful for further analysis (RRMs). Partial dependence plots were also computed, to assess the species' ecological responses to predictors (response curves).

Functional connectivity analysis

We performed inter-annual collations of habitat metric time series by using their median. This allowed species-specific SDMs' predictions to integrate, over the entire 15-year period, spatiotemporal environmental variability of landscape dynamic processes. Remote sensing was incorporated into connectivity via SDMs, from whose resistance surfaces and nodes were constructed (Fig. 2b). In detail, regarding resistance surfaces, linear and non-linear transformation functions (Eq. S1.1; Trainor et al 2013) were employed to assess potential connectivity (*sensu* Fletcher et al. 2016). Those functions were applied on the SDMs at 3-degree scores ($c = 0.25$, $c = 0.5$, $c = 8$; Valerio et al. 2019), which represent movement scenarios reflecting progressively reduced costs on resistance surfaces, such as within matrix during dispersal (Diniz et al. 2020). Second, regarding nodes, those were derived from habitat patches by converting each SDM into a categorical, species-specific binary (habitat/matrix; Fig. 2b) classification (Online Appendix S1.8) (Moilanen 2011). The "*SeSpeql*" approach was selected as threshold, thereby softening the absolute difference between sensitivity and specificity (Nenzén and Araújo 2011). The connectivity analysis for each species was performed in a two-step process. First, a graph-based approach analysed the landscape spatial configuration, identifying the strength of connections between each pair of habitat nodes (Diniz et al. 2020). The probability of connectivity (*PC*) (Equations S1.2; Saura and Pascual-Hortal 2007) between each pair of nodes was calculated in Conefor-Sensinode (v.2.2; Saura and Torné 2009), by weighing the habitat amount within a node and species dispersal distances (Online Appendix S1.9), and the functional distance between nodes, in turn dependent on the selected resistance surface (Fig. 2b; e.g., Salgueiro et al. 2021). Using this procedure, only resulting linkages with PC > 50% were retained for further analyses, and compiled as a list of pairwise linked nodes. Second, following the omniscape method, with circuit-theoretic analysis (McRae et al. 2008) we evaluated multiple alternative routes as current flow between the list of linking nodes (Salgueiro et al. 2021). Current was set to flow between each set of linked nodes subjected to the resistance surface (Fig. 2b) using GFlow (v.0.1.7; Leonard et al. 2016). In total, we produced 57 fine-grain potential connectivity models (19 species * 3 movement cost scenarios).

Quantifying intra and inter-group roadkill risk optimisation efficacy

RRMs multiscale models were performed to spatially prioritise road planning units (RPUs), and examine the agreement in mortality predictions within and between taxonomic groups. Roadkill events were used

as a response variable (presences and pseudo-absences; Online Appendix S1.10) and independent validation dataset (Synes et al. 2016) to quantify the relative contribution of species-specific selected "Habitat predictors", "Connectivity predictors" and "Road predictors" in explaining spatial mortality patterns. "Road predictors" (Fig. 2c) included road and culvert features (traffic density percentage, culverts density percentage, distance from culverts, and road width) (Carvalho and Mira 2011; Medinas et al. 2013; Online Appendix S1.11). To identify the functional scale at which road-kill occur, multiple scales were systematically applied through moving windows over "Habitat predictors" and "Connectivity predictors" (Fig. 2c), with windows of 3×3 ($\approx$100m) and 16×16 ($\approx$500m) sizes according to previous studies (Carvalho and Mira 2011; Medinas et al. 2013). The modelling procedure was performed using Boruta, as previously mentioned. Multivariate Random forests classifications to perform RRMs were conducted with "*randomForest*" (v.4.6-14) package (Fig. 2c). We determined the top-performing predictors, and correspondent predictor group, by calculating their relative contribution to the models. Predictors were then screened for multicollinearity and model evaluation was performed as for SDMs (Fig. 2c). Within each taxonomic group (Fig. 2c), the binary RRM maps (see Online Appendix S1.10 for the thresholding procedure) were overlaid to obtain a cumulative distribution frequency of RPUs, to spatially inform about the maximum number of species subject to high roadkill risk, here conceived as mortality richness and utilised as priority ranking method. Secondly, by using the previous threshold, high-risk probability values from RRMs were aggregated to analyse RPUs agreement in covering mortality for multiple species and taxa (e.g., intra- and inter-groups). For this purpose, we only considered RPUs where at least one species of each taxonomic group was identified with high risk. To ensure versatility in spatial planning, the variation in risk probability (RRMs), within each group, was assessed by using the coefficient of variation percentage (%CV; Fig. 2c). The lower the variability in the probability of RRMs, the higher the agreement among species and the higher the intra-group flexibility of mitigating impacts beyond prioritised RPUs. That said, for this study, we considered a CV of 30% as an 'acceptable' flexibility threshold. Statistical differences in %CV of RRMs probabilities within RPUs were further investigated for inter-group

flexibility in spatial mitigation planning, utilising the D'AD test (Feltz and Miller 1996) in the R package "*cvequality*" (v.0.2.0, Marwick and Krishnamoorthy 2019), wherein a $P \leq 0.05$ was set to reject the hypothesis of no difference in variance between groups.

Results

Habitat suitability drivers among wildlife taxonomic groups

SDMs, based on remotely sensed habitat metrics, resulted in good performances for most of the selected species. Non-flying mammals achieved 'excellent' accuracy scores (AUC $\mu = 0.75$; error rate $\mu = 31.42\%$), together with birds (AUC $\mu = 0.7$; error rate $\mu = 35\%$), whereas bats had the lowest, albeit still 'acceptable' scores (AUC $\mu = 0.67$; error rate $\mu = 38.16\%$) (Online Appendix S2.1). "Spectral indices" predictors (MSAVI2, EVI, NDVI, BNDVI, NDWI, NDII) were all identified as top-performing for describing occurrence patterns in non-flying mammals, followed by "L-band SAR polarisations" predictors (HV) (66.6% of species). The latter group was also the most representative for birds (62.5% of species), followed by "Spectral indices" (PSRI and SWIR32) (62.5% of species)."Thermal infrared" (LST) was the top-performing predictor for bats (Fig. 3) (80% of species), followed by "Spectral indices" (PSRI and SWIR32) (80% of species).

We found similar ecological responses among species in each group (Fig. 4).

Non-flying mammals held positive relationships with higher vegetation biomass (MSAVI2, EVI, NDVI, and BNDVI) and structure (HV), while higher habitat suitability was observed with areas of low vegetation water stress (lower values of NDWI and NDII). The occurrence of birds responded positively to vegetation structure (HV), as well to low vegetation stress and senescence (lower values of NDWI, PSRI and SWIR32). Bats responded negatively to high temperatures (LST), while again showing a similar response to non-flying mammals and birds for stressed areas (PSRI and SWIR32). Also, for analogous metrics detected in each group, differences in environmental tolerance (amplitude) are observable, showing varying habitat specialisations.
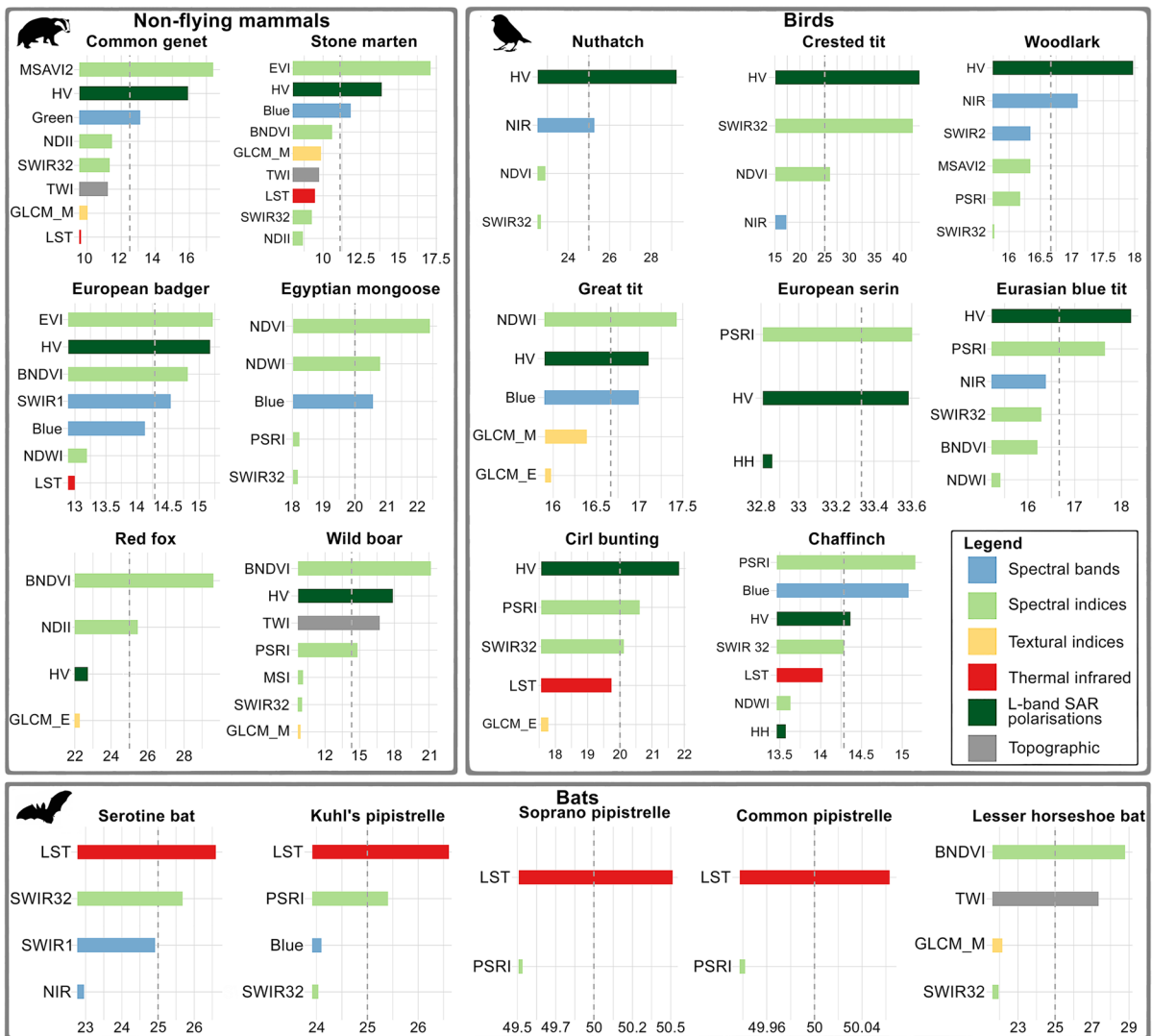
Fig. 3 The relative contribution (%) of predictors in explaining species occurrence: non-flying mammal, bird, and bat species. Bar colours indicate the predictor group, while the vertical dashed lines (averaged importance values) were used to discriminate predictors to use for further RRMs analysis (the ones at the right side of the line)

Disentangling habitat, connectivity and anthropogenic influence on roadkill

After retaining the best scales from uncorrelated predictors (see Online Appendix S2.2 in the RRMs section), evaluation metrics for the RRMs models indicated 'excellent' performances in predicting roadkill, with slight differences detected between species (AUC μ = 0.84 and error rate μ = 22.3; further details in Online Appendix S2). "Habitat predictors", which were selected as influencing species occurrence (SDMs), were also significant for predicting roadkill patterns (RRMs) (in Online Appendix S2.2). Similar ecological responses to those observed in SDMs were detected in RRMs, along with positive responses for the two most important predictors considered, namely "Connectivity predictors" and "Road predictors" (Online Appendix S2.2). As depicted in Fig. 5, "Connectivity predictors" were the best performers in explaining roadkill for non-flying
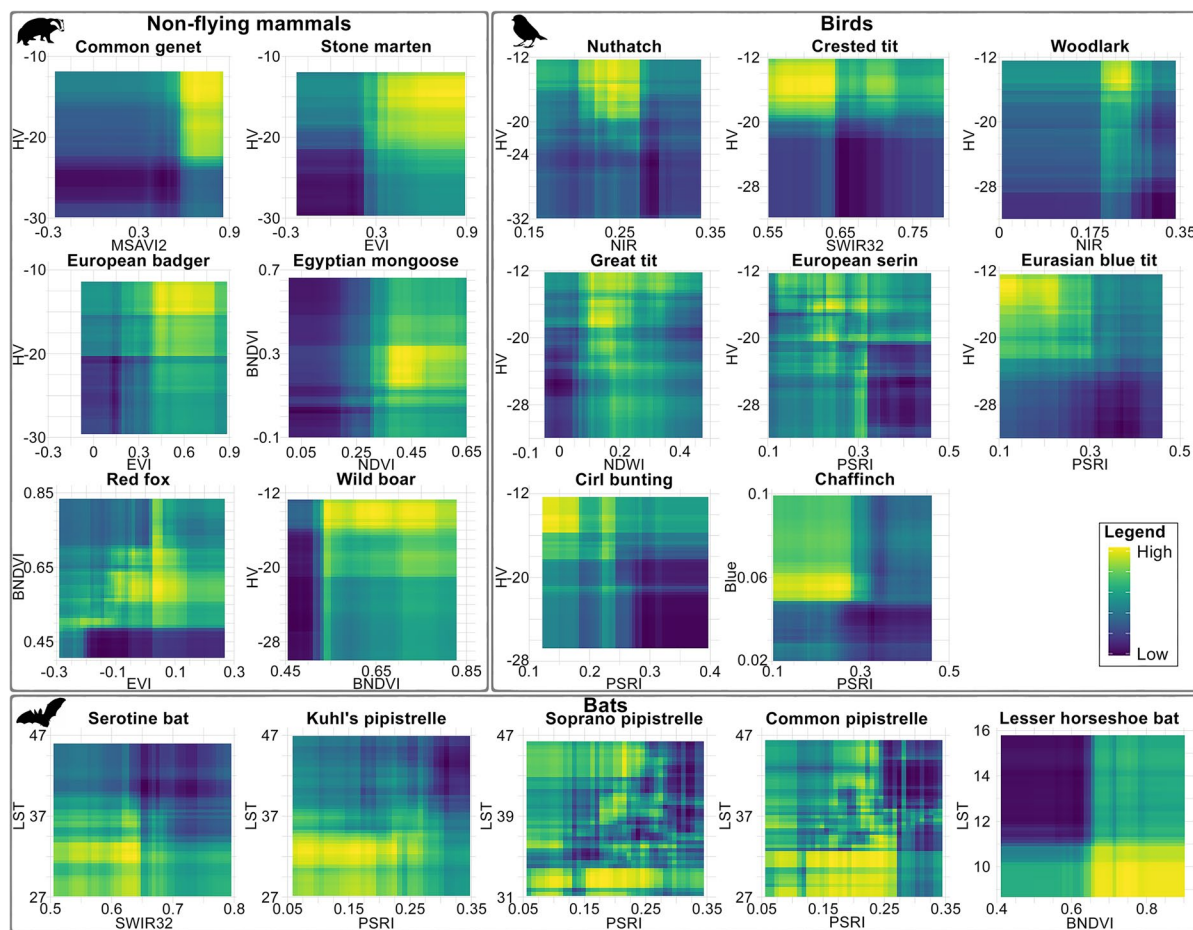
Fig. 4 Partial dependence plots, scaled on occurrence probability (SDMs), showing interactions between the two most important habitat metrics for non-flying mammal, bird, and bat species. High probabilities of species occurrence are coded in yellow, while low probabilities are coded in dark blue. Further details on the response curves for relevant predictors pertaining SDMs are supplied in Online Appendix S2.1

mammals (66.6% of species), while for bird and bat species, "Connectivity predictors" and "Habitat predictors" shared the same importance.

Functional connectivity performed better when high function scores ($c = 8$; lower movement cost) were applied for non-flying mammals (75% of species), while for birds and bats the function scores that performed better were low ($c = 0.25$; higher movement cost) (60% of species) and medium-high ($c = 2$ and $c = 8$) (50% of species), respectively. Regarding the importance of "Road predictors", traffic density percentage, was the most important in explaining mortality only for two species, red fox and Kuhls' pipistrelle.

RPUs prioritisation and roadkill risk uncertainties assessment between wildlife taxonomic groups

RPUs with the highest richness scores, which pinpoint high-risk locations across taxonomic groups, were predominantly found in the southern part of the study area (road N114), as well as in the south-western and, to a lesser extent the northern areas (road N4), with the lowest risk values occurred in the eastern area (road N18) (Fig. 6a).

All groups showed a decreasing trend in RPUs frequency as richness increases, where RPUs with maximum species richness represented a remarkably small proportion compared to others (9.1% for non-flying mammals, 8.9% for birds, whilst 11.6% for bats)
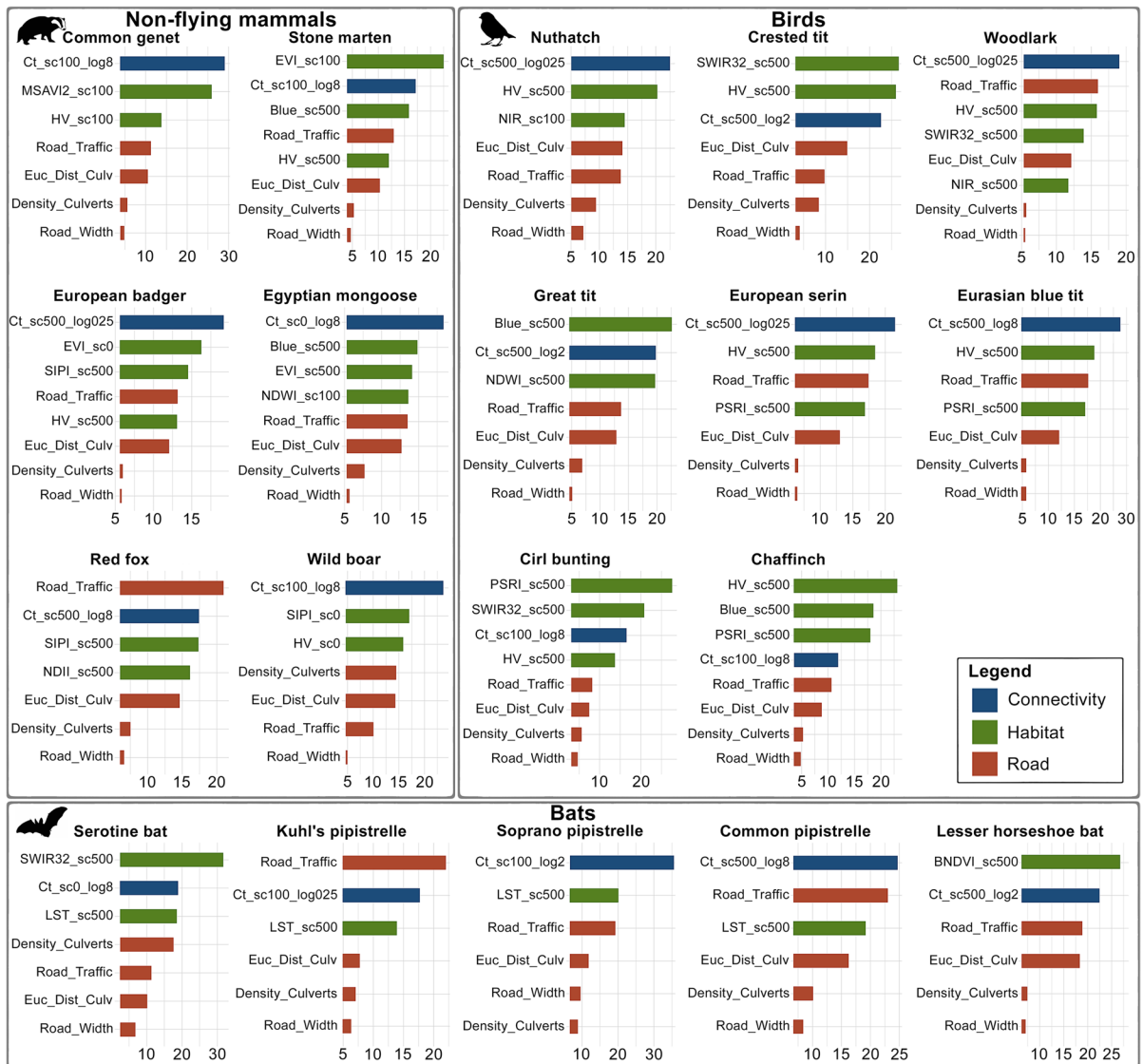
Fig. 5 The relative contributions (%) of Habitat, Connectivity and Road predictors in explaining roadkill patterns (RRMs) of non-flying mammal, bird and bat species. Bar colours indicate the typology of the predictors, listed in order of importance. In the predictors' name, the "*Ct*" prefix indicates that a species-specific connectivity scenario was used, with the score of the "*log*" suffix corresponding to the selected degree of the transformation function (0.25, 2, 8). The "*sc*" suffix is relative to the selected spatial scale (0, 100, 500), which is applicable to both habitat and connectivity predictors

(Fig. 6b), corresponding to prioritised RPUs with an ameliorated focus for allocating resources for roadkill mitigation. Within RPUs representing the three groups with at least one species, priority locations for multitaxa mitigation planning were identified by considering the overall species richness across all groups (Fig. 6c). Also, the median %CV showed a relatively low variability for non-flying mammals and birds (%CV ≅ 14), which was higher for bats (%CV ≅ 27) (Fig. 6d). Generally, those values indicated an 'acceptable' score, and hence intra-group flexibility beyond prioritised RPUs for resource allocation. Between taxonomic groups, there were significant differences in variability (%CV) of RRMs probabilities between non-flying mammals and bats, and between birds and bats. Variability differences were not significant between non-flying
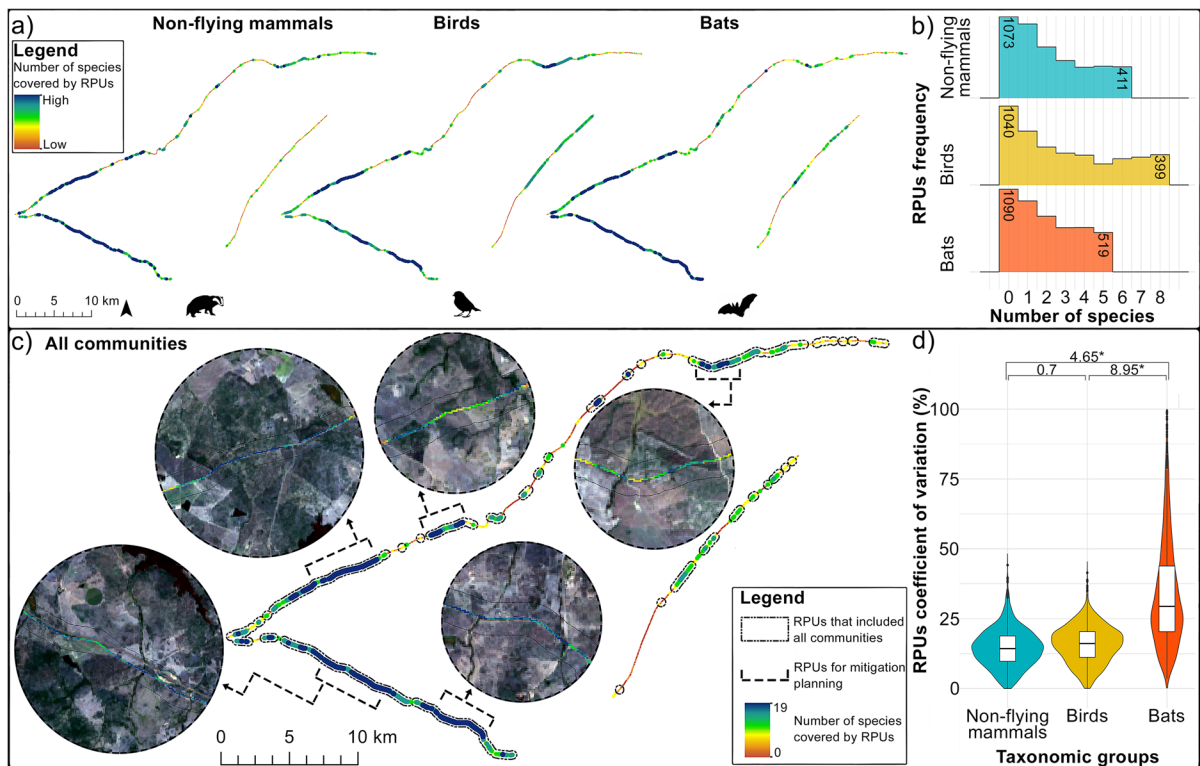
Fig. 6 RPUs with the number of species (richness) subject to high mortality risk (**a**), and histograms showing the RPUs frequency according to richness scores, for each group (**b**). RPUs covering all the taxonomic groups indicating multispecies mortality risk for mitigation planning, layered with RGB bands from Landsat (7/8) images. Darker areas, notably vegetated areas (e.g., forests, riparian habitats), correspond to higher roadkill risk locations for multiple species (dark violet) (**c**). For each group, %CV boxplots are depicted with the interquartile range, minimum, maximum, median, and outliers, together with D'AD scores, wherein the *symbol indicates $P \leq 0.05$, hence no agreement in variation between groups (**d**)

mammals and birds, here supporting inter-group flexibility for allocating resources beyond prioritised RPUs (Fig. 6d).

Discussion/conclusions

Usefulness of remotely sensed habitat metrics in describing species occurrence

By combining remote sensing information with wildlife occurrences, this study showed that SDMs can significantly benefit from the use of complementary habitat metrics derived from optical multispectral and radar data. Such data fusion approaches for mapping species distributions have recently been highlighted in the literature, yet their use is still in its infancy (Schulte to Bühne and Pettorelli 2017).

Here, for non-flying mammals, the use of spectral indices related to ecosystem productivity (MSAVI2, EVI, NDVI, and BNDVI) has been shown essential in explaining species occurrence. In general, higher values of MSAVI2, EVI, NDVI, and BNDVI are related to environments with high levels of productivity, which may reflect greater vegetation cover and resource availability (e.g., shelter and food; Kerr and Ostrovsky 2003; Pettorelli et al. 2011). Nevertheless, the relative importance of each vegetation index varied across species. For the common genet, a forest specialist, the low occurrence probabilities are predicted over a low range of MSAVI2 values, reflecting the reluctance of this species to occur in areas with scarce vegetation cover (Valerio et al. 2019). This was better captured by the MSAVI2 index than by EVI, NDVI, or BNDVI, likely due to its superior ability to minimise the influence of soil on the spectral signal

from the sparse vegetation cover component (Qi et al. 1994). The stronger relationship of the EVI index with the occurrences of stone martens and European badgers agrees with previous work (Santos et al. 2016b), and can be explained by their similarities in preferring forests with high canopy cover conditions, mixed with open habitat mosaics of lower cover conditions (Santos and Santos-Reis 2010). On this issue, species with more opportunistic habits, namely Egyptian mongoose, red fox, and wild boar, showed a higher tolerance to sparse vegetation conditions as evidenced by the importance of NDVI and BNDVI indices to explain their occurrence, where both indices are characterised by a weaker sensitivity to canopy density compared to EVI (Pettorelli et al. 2011). Forest vertical structural attributes, as described by the L-band SAR HV polarisation, showed a relevant predictive capacity for non-flying mammals. The positive relationship observed between HV backscatter values and the presence of these species may reflect a general favourability of mature forests, in the sense that the higher the HV values, the higher the trees, canopy cover, as well as aboveground biomass levels (Pettorelli et al. 2014; Yu and Saatchi 2016; Flores-Anderson et al. 2019). Bird occurrence is also greatly influenced by the L-band SAR HV index, showing a stronger forest dependence. This is particularly true in forest specialists (e.g., nuthatch, crested tits) when compared to more generalist species (e.g., great tit, European serin), which have a higher tolerance for lower HV values. These findings suggest that forest vertical structure relates to habitat requirements, demonstrating that the inclusion of radar information, in particular L-band HV polarisation, is useful in predicting the occurrence of bird species (Bergen et al. 2007). Despite this study being focused on using PALSAR's L-band backscatter data for SDMs, the obtained results highlight the relevance of the upcoming NASA Indian Space Research Organisation (ISRO) Synthetic Aperture Radar (NISAR) mission (to be launched in 2022), which will provide L-band data at a higher spatiotemporal resolution (NISAR 2020). The current findings additionally highlighted a general avoidance of stress areas (NDWI, PSRI, SWIR32), possibly attributable to drought stress in Mediterranean ecosystems (Santos et al. 2016b). Besides water-deficient areas, bats also avoided prohibitively warm areas (LST), for which the most generalist species (e.g., soprano, common pipistrelle) exhibited the greatest thermal tolerance. This raises the hypothesis that the warmest areas identified by LST might hold scarcer resources (Friedl 2002), and in Mediterranean regions, a higher favourability towards cooler areas may relate to greater water availability and woodland cover, but also with foraging opportunities and proximity to riparian habitats (Dietz and Kiefer 2016; Medinas et al. 2021). Overall, the first gap of knowledge that this research aimed to solve was that species belonging to the same taxonomic group responded similarly to a particular group of habitat metrics. Our data in this sense, constitutes a novel finding, supporting future multitaxa research in a plethora of contexts, in semi-arid Mediterranean areas and beyond. Also, some divergences emerged in environmental tolerance across metrics, supporting in the Iberian context, the theoretical perspective of landscapes as multi-dimensional gradients as opposed to mosaics of discrete units, being the former more adequate to describe multiple species' ecological responses (Herrera et al. 2016).

Contributing factors to roadkill

Our findings revealed that roadkill patterns are not randomly distributed and can be predicted by different types of habitat and connectivity metrics. For non-flying mammals, the higher explanatory strength of low movement cost scenarios, from RRMs, can be associated with periods characterised by greater mobility, such as during dispersal (Grilo et al. 2009), with lower landscape resistance, and roadkill additionally occurring in non-habitat matrix (Vasudev et al. 2015; Diniz et al. 2020). In Mediterranean systems, this is explained for ungulates and mesocarnivores by a high roadkill risk that is not merely circumscribed to forest areas, but also to the surrounding matrix of more open areas (Malo et al. 2004). Birds showed stronger performances associated with higher movement cost scenarios, which may derive from a more pronounced matrix avoidance during road-crossing events. For some species (e.g., crested tit, great tit, chaffinch), the higher explanatory strength of habitat metrics may be explained by their foraging behaviour strategies near roads, namely foliage/bark gleaning, which was previously described in the literature as among the strongest roadkill drivers (Santos et al. 2016a). Regarding bats, for opportunistic species (e.g., common pipistrelle) we found roadkill events more

related to movements in non-habitat matrix (given the low movement cost scenarios), including open areas, also used for hunting (Dietz and Kiefer 2016). Conversely, for less generalist species (e.g., Soprano pipistrelle), mortality was more pronounced in areas of high connectivity closer to woodlands, as well as riparian corridors, since both are used as landmarks during flight orientation, and with a pronounced bat activity (Dietz and Kiefer 2016). For cases of higher mortality risk associated with habitats, this might be due to habitat elements influencing movements along roads, which may be the case for edge-adapted species (e.g., serotine bat) (Tink et al. 2014), and/or deriving by the difficult representation of suitable roosting conditions (e.g., lesser horseshoe bat; Dietz and Kiefer 2016). Road predictors (road traffic) were more relevant in explaining roadkill for some species (e.g., for red fox, Kuhls' pipistrelle), and despite this being an aspect deserving further investigation, it is possible that some characteristics, such as being generalists and common species with a wide distribution, may have softened the influence of landscape patterns in driving roadkill (e.g.; Santos et al. 2013). Our findings meet Fabrizio et al. (2019) remarks about the usefulness of integrating habitat, connectivity metrics, and road predictors within RRMs, extending this approach for more species. Our results were also in agreement with previous approaches investigating landscape characteristics and ecological scales in shaping wildlife roadkill of studied taxonomic groups (Malo et al. 2004; Carvalho and Mira, 2011; Gunson et al. 2011), even though we provided and described novel ecological insights from sensitive and continuous remote sensing products.

Mitigation optimisation of RPUs over long-term

This is the first attempt to predict road mortality across multiple taxa at a high resolution (30 × 30m pixels), and over a long study period. Results for each taxonomic group showed that for RPUs integrating both high mortality risk and richness scores, represent 9 to 12% (depending on the group) of all RPUs, hence effectively enhancing prioritisation of roadkill mitigation plans for species with different degrees of habitat specialisation, home-ranges and dispersal abilities. Additionally, to optimise resource allocation in mitigation structures and maximise financial return, overlap across all taxonomic groups identified RPUs

potentially offering comprehensive mortality protection, including species from all the three studied taxonomic groups. The simultaneous inclusion of different taxonomic groups represents an unprecedented step in road ecology that may also be of relevance in environmental impact assessment, particularly for other infrastructures-derived anthropogenic mortality, such as from railways, electric power lines, and wind turbines (Forman and Alexander 1998; Bernardino et al. 2018). This prioritisation step is fundamental when considering the need for broad biodiversity representation in conservation planning (Margules and Pressey 2000), and scarce mitigation resources should be applied rigorously and efficiently (Polak et al. 2019). Besides, when investigating the mortality risk prediction ability of RPUs, results revealed relatively low variation scores within each group. Moreover, no significant differences in variation were found between non-flying mammal and bird groups. Our findings suggest an intra and inter-group agreement in mortality prediction, which may be explained by an overlap between habitats in Mediterranean forest ecosystems (Santos and Santos-Reis 2010), combined with woodland connectivity that similarly accommodates species, at least those with 'medium' dispersal abilities (see Machado et al. 2020). Those results may increase the versatility of mitigation plans, offering opportunities during the strategic planning phase in implementing mitigation measures beyond best RPU sites, thus fostering negotiations between conservationists and road managers (Rytwinski et al. 2015; van der Ree et al. 2015). In fact, when allocating conservation resources, unexpected factors can influence the application of designed structures on desirable sites (van der Grift 2017), for example due to overlooked topographic conditions, or when it is more costly-efficient to adapt existing structures, such as culverts (Rytwinski et al. 2015; van der Ree et al. 2015). Culverts are often supplemented with fencing for non-flying mammal species (e.g., mesocarnivores; Clevenger and Huijser 2011), and results suggest that strategically applied fences can simultaneously help to reduce mortality for birds as well, factoring into advantageous opportunity costs for applied measures (Rytwinski et al. 2015; White et al. 2022). Nevertheless, further frameworks need to include opportunity costs with social costs and benefits (Kujala et al. 2018; White et al. 2022), whereas at the design level of structures, is required further support for post-hoc

mitigation effectiveness regarding multiple taxa (i.e., BACI; Rytwinski et al. 2016). Bats show greater, albeit acceptable, intra-group variation in mortality risk, but significant divergence emerged when compared to other groups. The latter may derive from the larger home-range sizes and travelled distances (Dietz and Kiefer 2016), which may have led to divergent mortality patterns. Overall, our method is applicable to define mitigation measures that benefit as many species as possible, while suggesting a degree of flexibility (*sensu* Rytwinski et al. 2015) in the logistic of mitigation plans for single or multi taxonomic groups without hindering the main goals of the conservation plan. Still, in specific cases when mismatches occur within or between taxonomic groups, prioritisation of RPUs with highest predicted richness is preferable, even at the expense of flexibility towards sub-optimal ones. We further advise caution towards species-agnostic connectivity frameworks, as this may not always be generalisable as mitigation guidance for multiple taxa.

The Mediterranean basin is a biodiversity reservoir (Pinto-Correia and Godinho 2013), and a social-ecological challenge remains to secure its resilience over long-term, notably through conservation planning efforts. Remote sensing information can help to address landscape dynamic processes and fragmentation effects, while its integration into fine-grain connectivity can enable the characterisation of habitats sufficiently large and persistent to infer immigration/emigration rates between wildlife populations, and thus viability. In our study, we were able to contextualise RPUs into a larger corridor network composed of multiple meaningful and durable pathways, which is key for optimal road mitigation planning for multiple species (Clevenger and Huijser 2011). Biodiversity can constitute a solid guideline for determining the conservation value of a planning unit during prioritisation (Margules and Pressey 2000), and the present systematic planning framework is practicable as conceived with cost-efficient data, which seems of special relevance in a world of limited funds for conservation. In Mediterranean habitats, we first recommend that conservation planners should consider landscape heterogeneity from *forest-to-open* gradients, in turn identified with top-performing habitat metrics, and consider them with connectivity and road predictors for more comprehensive RRMs evaluations. We then advocate to encompass

both developments from different research fields and encourage evidence-based territorial solutions for effective management optimisation, as well as to increase nature sustainability. This is here exemplified by the precise identification of resilient and multifunctional RPUs for mortality mitigation, encompassing woodlands and adjacent matrices, which also ensures planning versatility and opportunity costs, and supports scrutiny on models' predictions (Pressey et al. 2017). Finally, our findings incentivise transdisciplinary collaborations in wildlife ecology, conservation science, and remote sensing, as may be beneficial to guide practitioners, inform policy-makers, and improve transparency on uncertainty problems (Pettorelli et al. 2014; Rose et al. 2019).

Declarations

Conflict of interest The authors declare no competing interests.

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