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RESEARCH PAPER

Effects of phylogenetic associations on environmental and temporal niche partitioning among sympatric mammals

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ABSTRACT

Mammals have evolved to occupy spatial and temporal niches in order to optimize resource utilization and minimize predation risk or competition. Subsequently, niche partitioning may be influenced by phylogenetic associations, which could have substantial consequences for ecosystem structure and function. We use the output from occupancy models based on camera trapping data to construct a tri-partite network describing the environmental and temporal partitioning of activity among twelve sympatric mammals in the Apennine Mountains of central Italy. We further evaluate if there were any effects of phylogenetic associations on the contributions of species to the properties of this spatio-temporal network. The Apennines form a pristine region in central Italy with a relatively intact Mediterranean mammal fauna. The mammal community in our study consisted of species ranging in size from 300 gs to over 200 kg, and included herbivores, omnivores and predators. There was limited structuring of the network describing environmental and temporal niche use. Furthermore, we did not find any phylogenetic signal in species contributions to network structures, and phylogenetic relatedness among species was not associated with their similarities in environmental or spatial niche use. However, animals appeared to have partitioned environmental niches more than temporal ones, suggesting that spatial variation in resource availability may have been more important than temporal avoidance of predation risk or competition in shaping activity within this mammal community. Our study highlights the need to evaluate under which conditions evolutionary history is influencing contemporary ecological processes.

Introduction

Animals have evolved to occupy spatial, trophic and temporal niches in order to optimize resource utilization and minimize predation risk or competition (Leibold, 1995; Chase & Leibold, 2003). A species' ecological niche is defined by its requirements in environmental conditions and its role or function in the environment. It can be broadly

generalized into a multidimensional space defined by different aspects of the resources required by a species (Hutchinson, 1957). Spatial niche use is closely tied to the ecological niche, and describes the habitat or areas utilized by a given species (Grinnell, 1928). However, ecological niches may not only be realized in different patterns of activity in space, but also in time (Kronfeld-Schor & Dayan, 2003). As with spatial niches, temporal niches may relate to resource acquisition and associated

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competition (Schoener, 1974), thermal constraints (Bennie et al., 2014) and to a minimization of predation risk (Valeix et al., 2009).

Ecological niches are generally dictated by animals' resource requirements, classically named as "the fundamental niche" (Hutchinson, 1957). However, in ecological communities the fundamental niche may be constrained into a "realized" niche, where resource access and utilization have been restricted by species interactions such as competition or predation (MacArthur & Levins, 1967). Realized niches are intrinsically linked to species co-existence through two types of mechanisms (Letten, Ke, & Fukami, 2017): mechanisms reducing the average fitness differences among species ("equalizing mechanisms"), and mechanisms reducing niche overlap among species ("stabilizing mechanisms") (Chesson, 2000). In this context, variation in resource supply among species reflects an equalizing process, the magnitude of niche overlap a stabilizing process, and variation in the fundamental niches among species can reflect both a stabilizing and an equalizing process (Letten, Ke, & Fukami, 2017).

Phylogenetic processes may have wide-ranging effects on the niche utilization of co-existing species (Price, 1994; Wiens et al., 2010). It has long been recognized that species tend to retain phenotypic characteristics through evolutionary time (Derrickson & Ricklefs, 1988). This causes closely related species to exhibit similar phenotypic characteristics. Taxa may also be prevented from evolving expected traits within a specific clade, often referred to as phylogenetic constraints (McKittrick, 1993), which may further restrict the expressed phenotypes among organisms. For instance, phylogenetic history may influence temperature tolerance, and hence dictate the boundary conditions for species distribution ranges (Kellermann et al., 2012). Phylogenetic history has also been suggested to influence food web structure (Cattin et al., 2004), with subsequent effects on ecosystem stability (Rooney & McCinn, 2012). Despite strong support for the importance of including phylogenetic structure in studies comparing the ecological properties of different communities (Losos, 1996), the importance of phylogenetic relationships for niche partitioning within communities remains poorly tested (Davies, 2021).

Graph theory, a discrete class of mathematics focusing on networks formed by nodes (vertices) connected by links (edges), has been increasingly used for ecological applications (Dale, 2017). Graph theory allows for the quantification of network structures, or network topologies, which may hold important information about the processes maintaining the interactions in the network, as well as how the interacting agents influence each other and their environment (Sugihara, 1984). While much of our theoretical understanding of network topology comes from uni-partite networks, i.e. networks consisting of only one set of nodes, the nodes in ecological networks often form more than one set, e.g. predators and prey or plants and pollinators. Such networks can be described as bi-partite (two sets of nodes), tri-partite (three sets of nodes), or in theory any number of sets giving k-partite networks (West, 2001). Quantifying the structures and properties in such multi-partite networks constructed from ecological data may hold important information about ecosystem stability and function (Dale, 2021). Graph theory also allows for the quantification of the importance of individual nodes for the overall network properties, e.g. identification of keystone species or species with large importance for community stability (Miranda et al., 2013). While graph theory has been used to quantify several niche-related processes, such as the structures of trophic relationships (Miranda et al., 2013), landscape connectivity (Minor & Urban 2008) and animal space use (Lea et al., 2016), we are not aware of studies that have used multi-partite approaches to quantify spatial and temporal activity in communities of sympatric animals.

Quantifying how animals structure their activity in time and space may provide important insights into how ecological communities are assembled and maintained (Rosenzweig, 1995). Such insights may not only deepen our understanding of ecosystem functioning, but may also be paramount for our ability to develop sustainable management strategies for animal populations under ongoing and future environmental

changes (Shin et al., 2019).

Camera traps provide ideal data for quantification of spatial and temporal activity patterns in sympatric species (O'Connell et al., 2011; Frey et al., 2017). However, raw camera trapping data may suffer from biases associated with imperfect detection. These biases can effectively be minimized through occupancy models, which first quantify the probability of detection of a given species, and then use these detection probabilities to quantify conditional probabilities of patch occupancy (Mackenzie et al., 2002). The combination of data from camera trapping surveys and occupancy models have revolutionized modern community ecology, and this combination is seeing an increasing use for different applications in terrestrial ecological research (Rovero & Zimmermann, 2016).

Here we use the results from occupancy models, based on data from a camera trapping survey, to construct a tri-partite network describing the environmental and temporal partitioning of activity in a mammal community from the Apennine mountains of central Italy. We specifically evaluate if there were any effects of phylogenetic associations on the contributions of species to the properties of this spatio-temporal network. The Apennines form a relatively undeveloped region where some of the largest European predators still co-exists. The Italian mammal community that we investigated consisted of species ranging in size from 300 gs to over 200 kg, and included species at different trophic levels: herbivores, omnivores and predators. They range in phylogenetic relatedness from relatively closely related species within the same family (i.e., Canidae, Mustelidae, & Cervidae) to distant relatives that have been separated for long evolutionary times (Upham et al., 2019). We tested the following predictions: (i) phylogenetic clustering of ecological niche requirements will generate a modular structure of networks describing environmental niche use; (ii) convergence into common temporal niches will generate nested structures in which the activity of species with a narrow activity window is using the same time slots as species with a broader range of diel activity; (iii) there will be phylogenetic signals in species contributions to network properties; (iv) similarity in environmental and temporal niche use will subsequently be related to the phylogenetic associations among species. Although phylogenetic effects may dissipate rather rapidly with decreasing relatedness, this is not necessarily true for all traits (Wiens et al., 2010). Hence, we believe that our community-based approach will be informative (e.g., Cattin et al., 2004). A strong phylogenetic component in niche use would suggest that the evolutionary legacy within phylogenetic lineages has influenced the spatial and temporal partitioning among sympatric mammals (Wiens & Graham, 2005; Wiens et al., 2010). We expect that such niche conservatism causes a negative monotonic relationship between phylogenetic relatedness and similarity in environmental niche use, whereas competition combined with predator avoidance cause a humpbacked relationship between phylogenetic relatedness and similarity in temporal niche use.

Materials and methods

Study area

The study area includes three reserves of the Central Apennines, Italy, within the Abruzzo and Molise regions (13.94°E; 41.84°N, Fig. 1). The area is characterized by mountain ranges covering elevations between 900 and 2500 m above sea level. The dominant habitat is deciduous forests (35 % of the land area), consisting mainly of beech (*Fagus sylvatica*), followed by interspersed agricultural crop lands (27 %), pastures (16 %) and scrubland (11 %). Pastures (16 %) and rocks (2 %) are mainly occurring on higher elevation ridges whereas olive-tree groves, orchards and vineyards (4 %) as well as urban areas and villages (2 %) occur at lower elevations and along the valley bottoms. The presence of scrubland is related to re-colonization of abandoned pastures and cultivations and from forest degradation. Lakes and rivers, wetlands and perennial snowfields occupy the rest of the study area. The

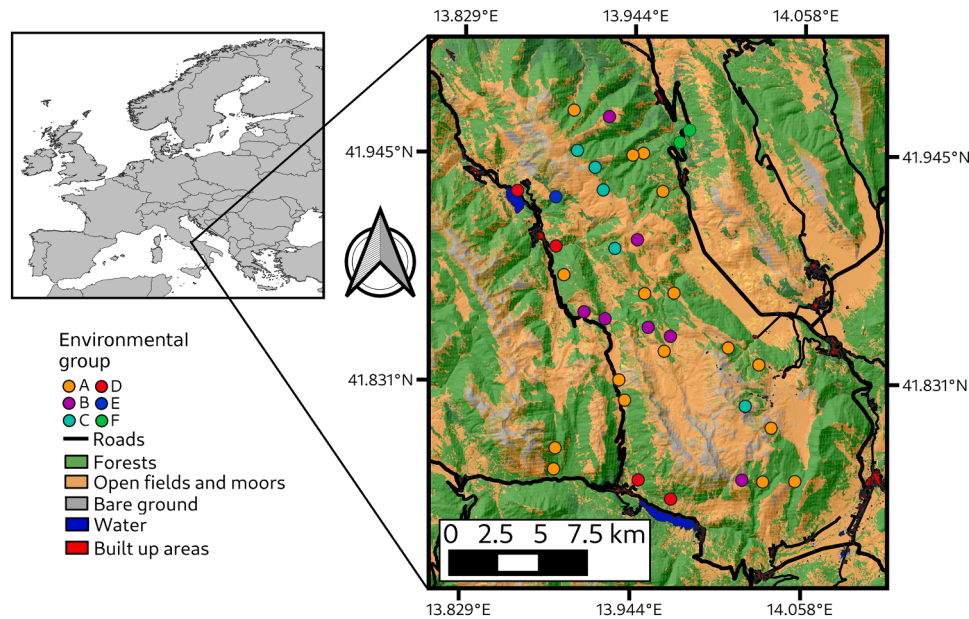


Fig. 1. Location of the study area in central Italy as well as the location of camera traps within the study area, color-coded by the environmental groups identified used to describe environmental niche use. These groups were derived from a from a cluster analysis based on the biological, geophysical, climatic and geographic characteristics at each camera site.

climate is generally of Mediterranean type varying from meso- to sub-Mediterranean with elevation. The fauna is rich and typical of the Mediterranean mountainous biome. Wild ungulates include red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*), wild boar (*Sus scrofa*) and on steep mountain cliffs the Apennine chamois (*Rupicapra pyrenaica ornata*). Several species of larger rodents, such as the crested porcupine (*Hystrix cristata*) and the red squirrel (*Sciurus vulgaris*) also occur, as well as three lagomorphs: the European hare (*Lepus europaeus*), the mountain hare (*L. timidus*) and the Corsican hare (*L. corsicanus*). Meso-carnivores are abundant and include red fox (*Vulpes vulpes*), badger (*Meles meles*), European pine marten (*Martes martes*) and stone marten (*Martes foina*), stoat (*Mustela erminea*), least weasel (*Mustela nivalis*) and wild cat (*Felis sylvestris*). Larger carnivores include the Apennine brown bear (*Ursus arctos marsicanus*), the Italian grey wolf (*Canis lupus italicus*) and the Eurasian otter (*Lutra lutra*).

Camera trapping

For the entire study area, a grid consisting of 2.5×2.5 km cells was established. Within this grid, coordinates were generated for camera trap placement in the centroid position of the respective cell, resulting in the selection of 33 grid coordinates corresponding to the placement of 33 camera traps placed within an area covering approximately 350 km². The camera traps were ScoutGuard (SG560K-18mHD and SG2060-X) or Browning (BTC-8E-HP4 and BTC-5HDP). They were activated between early June and late October 2019. Cameras were placed 1–1.5 m. above the ground and positioned with a 10° angle towards it. They were set-up in photographic mode to capture three photos, 20 s apart for each event. Delay time was set to 15 min. In order to maximize trapping effort for the only elusive feline within the study area, the wild cat, a pole was positioned in front of each camera and sprayed with a tincture based on *Valeriana officinalis* and ethanol. Since the scent was used consistently over both space and time, we argue that it did not influence our estimates of either spatial or temporal occupancy, although it could have affected the relative detectability among species. This would, however, not cause biases in our case since we fitted separate detection functions for each species. The camera trap data were stored via the open-source software Wild.ID (<https://github.com/ConservationInternational/Wild.ID>), with specific identification features, number of individuals, time,

camera trap code, and date annotated.

The data analyses were restricted to observations of wild large mammals defined as any species larger than 300 gr. All photographs of domestic species, livestock and species smaller than 300 gr were discarded. For the remaining photographs, we identified each observation to species except for martens (*Martes* sp.) and hares (*Lepus* sp.), which were only identified to the genus level. We only considered photographs taken more than 30 min apart of the same species or taxon and at the same station as independent observations, and only included species or taxa with at least five independent observations in our analyses (Greco et al., 2021).

Categorization of environmental niches

To estimate environmental niches, we grouped all camera stations based on similarity in nine variables related to environmental characteristics: percent cover of deciduous forest, coniferous forest, herbaceous vegetation and moorland, heterogeneity in land cover, distance to the nearest water body, distance to the nearest road, primary productivity, elevation, terrain ruggedness, temperature and precipitation. These variables are frequently used to define the ecological niches of a diverse set of organisms (e.g., Sillero et al., 2021). Following the niche concept of Hutchinson (1957), they reflect different living requirements such as predator refugia, availability of food resources and hunting habitat, as well as environmental protection (Chase & Leibold, 2003). For all variables except the distance measures, we used values within a circular buffer with a radius of 150 m centered around each camera station (giving an area of 28.3 ha). Land cover was derived from a land cover classification from 2017 Sentinel-2 imagery with 10 m resolution (Malinowski et al., 2020). Percent cover of the four most abundant land cover classes was estimated within each buffer, and land cover heterogeneity was calculated as the Shannon index of the relative surface area covered by all classes within each buffer. We extracted all water bodies larger than one ha from the land cover map, and calculated the distance from each station to the nearest water body. Distance to the nearest road was estimated as the distance from each station to the nearest primary, secondary, and residential road identified by the OpenStreetMap project (OpenStreetMap, 2017). We used the Normalized Difference Vegetation Index (NDVI) as a proxy for primary productivity. We calculated the

index from Sentinel-2-based imagery with 10 m resolution. The index was estimated as the average value for seven days within July and August 2019, all with a cloud cover of less than 5 % (Appendix A, Table S1). Elevation and terrain ruggedness was estimated from the EU-DEM version 1.1 Digital Elevation Model (DEM), which was provided with a 1'' (~30 m) resolution (García Gonzales, 2015). Elevation and terrain ruggedness were both estimated as the average value within each buffer. Terrain ruggedness was estimated from the DEM as the mean difference in elevation between each pixel and its surrounding cells. Temperature and precipitation were estimated from WorldClim2 raster maps of 1 km resolution, consisting of annual averages between 1970 and 2000 (Fick & Hijmans, 2017), and calculated as the average values of each buffer area. All providers and sources for the original spatial data are given in Appendix A, Table S1.

We compiled all environmental information into a matrix, scaled all continuous variables to unit variance and created a pairwise distance matrix using Euclidean distances (Sokal & Rohlf, 1981). We clustered the distance matrix into a dendrogram using unweighted average linkage clustering, since this method provided the highest cophenetic correlation among five evaluated algorithms ($R^2 = 0.73$, Appendix A, Table S2), and cut the dendrogram into six clusters (Appendix A, Fig. S1A). This solution was the most favored among 30 different indices identifying optimal number of cluster groups (Charrad et al., 2014, Appendix A, Fig. S1B). The subsequent grouping provided good separation in a principal component space (Appendix A, Fig. S2), where the most important dimensions were influenced by temperature, elevation, distance to nearest road, and vegetation variables (Appendix A, Table S3).

Categorization of temporal niches

We based the estimation of species temporal niches on the time stamp of each camera observation. Based on the solar zenith angle, we defined each observation to have occurred during one of six time categories: dawn (−12 to 0°), early day (0° to solar noon), late day (solar noon to 0°), dusk (0 to −12°), early night (−12° to nadir) and late night (nadir to −12°). With these definitions, we included both civil and nautical twilight in the dawn and dusk categories. Solar angles for each time stamp were calculated using formulas implemented in Thieumel and Elmarhraoui (2019). We opted to use sun angles rather than raw times to define time categories since they better account for seasonal shifts in light regimes.

Occupancy analyses

We used the single season occupancy models initially proposed by MacKenzie et al. (2002) to estimate the relative utilization of environmental and temporal niches. We fitted separate models for each species. To estimate environmental niche use, we added the environmental group, as defined above, as a discrete site-specific co-variate to each station, and extracted the predicted occupancy for each species and each environmental group from the models. To estimate temporal niche use, we regarded each time bin as a separate capture event, so that each camera station was regarded as having been present during six events during a 24-hour period. We then added the time bin as a site-specific co-variate, so that each site got entered 6 times, one for each time period, during a 24-hour period. Although this approach may be at odds with the spatial nature of the concept of site-specific co-variables, spatial and temporal dimensions could be regarded as analogues analytically (e. g., Dalerum et al., 2017). The output from this parametrization is also fully interpretable, in that the occupancy estimate for each time bin represents the estimated occupancy across our whole study area for each of the six diel time periods. We opted for this approach to quantify temporal niche use over the more commonly used kernel estimator of diel activity (Ridout & Linkie, 2009), since the latter would have been confounded by seasonal changes in light regimes. We pooled

observations by weeks for all models to avoid excessive number of zero values and associated poor precision in estimated detection probabilities (Rovero & Spitale, 2016). We did not include observation level co-variables. Estimated occupancy for each environmental group and time bin are given in Appendix A, Tables S4 and Table S5. We did not have sufficient numbers of observations to determine occupancy for each environmental group within each time bin.

Estimation of phylogenetic relationships

Phylogenetic relationships were estimated from a complete dated mammal phylogeny consisting of 5911 mammal species (Upham et al., 2019). We generated 1000 random subsets pruned to the 12 taxa included in our study (Fig. 2), and calculated the mean edge length of the consensus tree and forced it to be ultrametric using the “nnls” method (Revell, 2012).

Network construction

We created a tri-partite network using taxa, environmental niches and temporal niches as vertices and weighted the edges based on the estimated occupancy of a given taxon for an environmental and temporal niche. In addition, we projected the full tri-partite network (containing both environmental and temporal niches), as well as the separate bi-partite networks for environmental and temporal niches into uni-partite networks describing the relationships among species in the different niche dimensions.

Data analysis

We estimated the following network-level metrics to separately describe the bi-partite networks representing temporal and environmental niche: connectance, specialization, nestedness and modularity. Network connectance describes the number of observed interactions in relation to the number of possible interactions, and is an index of network complexity (Dunne et al., 2002). We used a weighted connectance index calculated as the linkage density divided by number of species included in the network (Bersier et al., 2002). We used the network-wide specialization index H'_2 (Blüthgen et al., 2006), which describes how specific species are in their partner choice. Nestedness describes a utilization pattern where the niche use of species with the broadest niche use also encompasses the niches of the most specialized ones (Patterson & Atmar, 1986). We used the Weighted-Interaction Nestedness Index (WIN, Galeano et al., 2009), which we for ease of interpretation present in its normalized form (WINE), where values of zero indicate no deviation from random expectations, negative WINE values are possible indications of anti-nestedness, i.e. that the composition of a community is less nested than random predictions, whereas positive values suggest a more nested pattern than random predictions. A WINE value of one indicates perfect nestedness. Modularity describes the extent to which species form discrete sub-communities (compartments), and where the majority of interactions takes place within compartments (May, 1973). We estimated the degree of modularity using the QuaBiMo algorithm (Q), based on a hierarchical random graphs approach adapted for weighted bi-partite networks (Dormann & Strauss, 2014). Q ranges from 0, indicating that links within modules are not higher than expected by chance, to a maximum value of 1 when modules are discretely delimited. For both environmental and temporal niche use, we evaluated the significance of network specialization, nestedness and modularity by comparing our observed values to expected values from 1000 randomized matrices where we had randomly shuffled the cell values (i.e. a quantitative version of the first null model presented by Fortuna and Bascompte (2006)). We did not evaluate the significance of connectance, since this was the same for the observed and the randomized matrices. For significant metrics, we also computed D values as the deviation from each random expectation and the observed

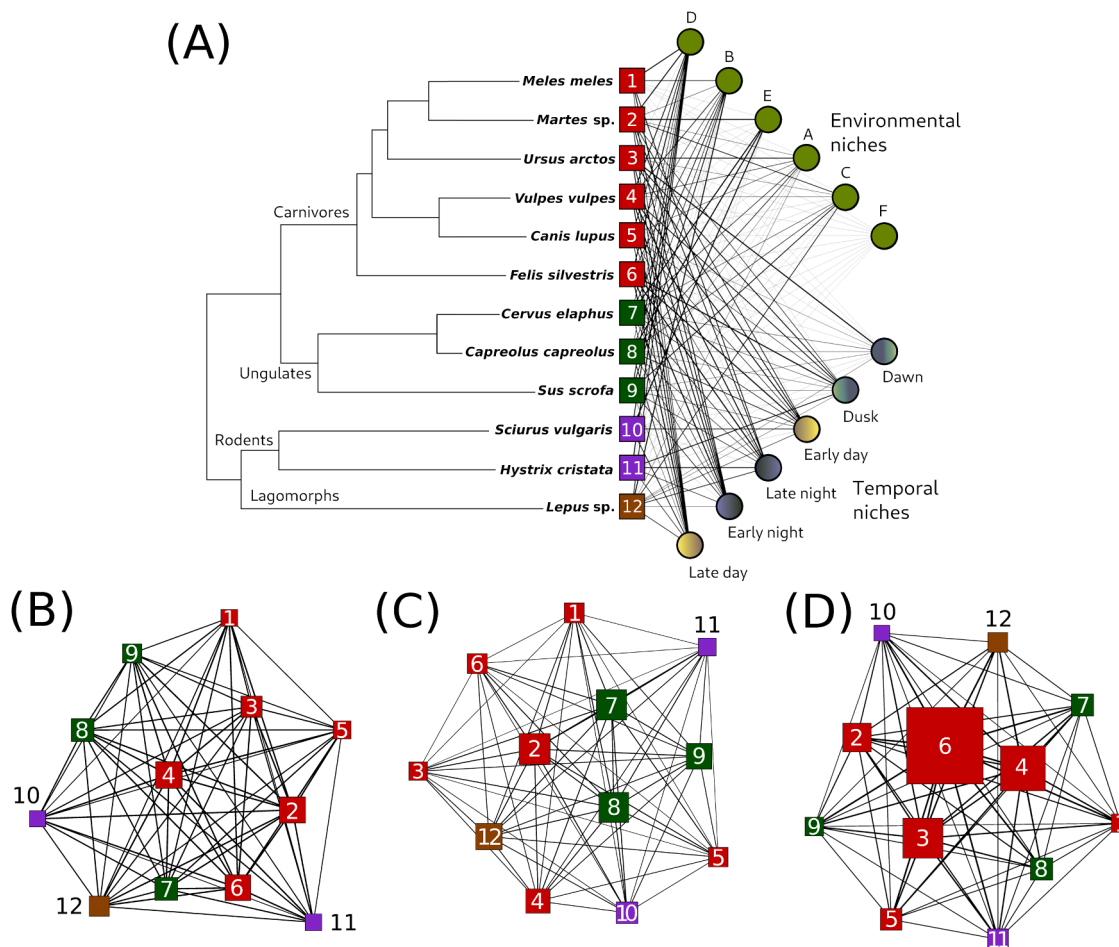


Fig. 2. Phylogenetic relationships among all taxa included in the study superimposed on the observed tri-partite network describing the utilization of environmental or temporal niches (A), as well as uni-partite projections describing the relationships between species in combined environmental and temporal niche use (B) and in environmental (C) and temporal (D) niche use separately. In the tri-partite network, edge thickness reflects estimated utilization of each niche for a particular taxon, and the niches are sorted so those with the most intense utilization, based on the sum of the occupancy estimates for that niche, are placed closest to the phylogeny. In the uni-partite projections, edge thickness reflects the strength of shared niche utilization (calculated as the sum of the estimated occupancy for shared niches), vertex size reflects closeness centrality, and the networks are also structured so that species with higher centrality measures are placed closer to the centre of each network (Fruchterman & Reingold, 1991). Phylogenetic relationships were estimated from a dated mammal super tree, and niche uses were calculated as estimated occupancy values based on camera trapping data.

value (Manly, 1997), and compared the D values between environmental and temporal niche use using a two sample permutation test (Hothorn & Hornik, 2021).

To evaluate the relative importance of each species or taxon in the structure of niche utilization, we calculated weighted degree centrality and weighted closeness centrality for each species from each of the uni-partite networks. Weighted degree centrality was calculated as the sum of the edge weights going in and out of the node (i.e. node strength, Barrat, Barthelemy, Pastor-Satorras, & Vespignani, 2004), and weighted closeness centrality as the inverse of the sum of the weights of all edges connecting a node to other nodes in the network (Newman, 2001). For our data, degree centrality represents how similar the niche utilization of a species or taxon was in relation to that of other species or taxa, whereas closeness centrality represents how distant a species or taxon was to other species or taxa in the utilized niche space. While these two indices obviously are related, we believe that they hold additive information, as shown previously (Jordán et al., 2007). We also calculated a weighted specialization index (d') for each species and niche dimension from respective bi-partite networks, which measured how specialized a species or taxon was in its utilization of environmental and temporal niches. This index was adopted from Blüthgen et al. (2006), and is a species-level equivalent to the network wide index described above.

Each of these indices were evaluated against random expectations for each species using 1000 randomized matrices where the cell values had been randomly shuffled. We evaluated the phylogenetic signal in each of these species level indices using the K statistic (Blomberg, Garland, & Ives, 2003), which is based on the variance of phylogenetically independent contrasts relative to randomized shuffling of the terminal tip values.

To further evaluate phylogenetic patterns in niche utilization, we used Mantel tests based on Pearson's correlation coefficient to quantify associations between phylogenetic distances among species or taxa and differences in their environmental, temporal or combined environmental and temporal niche use. The Mantel tests were conducted on a phylogenetic distance matrix consisting of the pairwise phylogenetic distances between each species based on the branch length separating them as well as one of three matrices describing differences between species in combined environmental and temporal, environmental, and temporal use. These three matrices were based on the Jaccard dissimilarity index (Legendre & Legendre, 2012), calculated on the estimated occupancy for each taxon in each environmental and temporal niche.

All data analyses were done in the statistical environment R version 4.1.2 compiled for the Linux system (<http://www.r-project.org>), using the contributed packages ape (version 5.0, Paradis & Schliep, 2019),

bi-partite (version 2.16, Dormann et al., 2009), cluster (version 2.1.2, Maechler et al., 2021), exactRankTests (version 0.8–34, Hothorn & Hornik, 2021), igraph (version 1.2.11, Csardi & Nepusz, 2006), NbClust (version 2.0.3, Charrad et al., 2014), unmarked (version 1.1.1, Fiske & Chandler, 2011) and vegan (version 2.5.7, Oksanen et al., 2020).

Results

During a total of 5161 individual camera trapping days we made 950 independent observations of 12 species or taxa from four mammalian orders (Appendix A, Table S6); Carnivora: Eurasian badger, martens, brown bear, red fox, grey wolf, Eurasian wild cat; Cetartiodactyla: red deer, roe deer, wild boar; Rodentia: red squirrel, crested porcupine; Lagomorpha: hares.

The most intensively utilized environmental niches ("D" and "B", Fig. 2) were characterized by conifer forest and large landscape heterogeneity (environmental niche "D"), as well as high precipitation, high elevation, large distance to roads and herbaceous or moor vegetation (environmental niche "B", Appendix A, Fig. S2B, C). The most utilized temporal niches were late day and early night (Fig. 2A).

The bi-partite network representing environmental niche use had lower connectance than the bi-partite network representing temporal niche use (Table 1). Both environmental and temporal niche use were less specialized than random expectations (Table 1), and temporal niche use was significantly less specialized than environmental niche use (mean difference in d values = -0.05 , $z = 31.1$, $p < 0.001$). There were no significant nested structures for either environmental or temporal niche use (Table 1). However, the structure of temporal niche use was less modular than random expectation (Table 1), and also significantly less modular than environmental niche use (mean difference in d values = 0.05 , $z = 36.0$, $p < 0.001$).

No species deviated from random expectations in either degree or closeness centrality, neither for the uni-partite networks representing partitioning in combined environmental and temporal niche use (Fig. 2B) nor the network representing partitioning in environmental niche use (Fig. 2C) (Appendix A, Table S7). However, wild cat had higher (observed degree=79.87, expected degree=66.50, $Z = 1.81$, $p = 0.008$) and red deer lower (observed degree=50.88, expected degree=66.56, $Z = -2.15$, $p = 0.031$) degree centrality than random expectations in the uni-partite network representing temporal niche use (Fig. 2D), and there was a trend for red fox to have higher than expected degree in this network (observed degree=79.87, expected degree=66.50, $Z = 1.80$, $p = 0.070$). Wild cat also had higher closeness

centrality than random expectations in the network representing temporal niche use (observed closeness=0.10, expected closeness=0.03, $Z = 6.21$, $p < 0.001$), together with the red fox (observed closeness=0.06, expected closeness=0.03, $Z = 2.55$, $p = 0.011$) and the brown bear (observed closeness=0.05, expected closeness=0.03, $Z = 2.02$, $p = 0.043$). Squirrels had higher specialization values than random expectations for their interactions based on combined environmental and temporal ($d'_{\text{obs}}=0.28$, $d'_{\text{exp}}=0.12$, $Z = 3.35$, $p = 0.001$) and temporal niche use ($d'_{\text{obs}}=0.27$, $d'_{\text{exp}}=0.09$, $Z = 3.18$, $p = 0.001$), and brown bear had higher specialization values than random expectations for their interactions based on combined environmental and temporal ($d'_{\text{obs}}=0.22$, $d'_{\text{exp}}=0.12$, $Z = 1.96$, $p = 0.050$) and environmental niche use ($d'_{\text{obs}}=0.33$, $d'_{\text{exp}}=0.16$, $Z = 1.96$, $p = 0.050$) (Appendix A, Table S7).

There was no phylogenetic signal in either degree centrality (combined environmental and temporal niche use: $K = 0.30$, $Z = 0.67$, $p = 0.727$; environmental niche use: $K = 0.40$, $Z = -0.50$, $p = 0.339$, temporal niche use: $K = 0.48$, $Z = -0.56$, $p = 0.363$), closeness centrality (combined environmental and temporal niche use: $K = 0.27$, $Z = 1.06$, $p = 0.862$; environmental niche use: $K = 0.39$, $Z = -0.41$, $p = 0.386$, temporal niche use: $K = 0.51$, $Z = -0.66$, $p = 0.336$), or specialization (environmental niche use: $K = 0.63$, $Z = -1.16$, $p = 0.163$, temporal niche use: $K = 0.57$, $Z = -0.91$, $p = 0.181$).

Similarly, there were no significant correlations between phylogenetic distances and differences in the utilization of either combined environmental and temporal niches ($R = 0.10$, $p = 0.324$, Fig. 3A) nor between phylogenetic distances and the use of environmental ($R = 0.08$, $p = 0.334$, Fig. 3B) or temporal niches ($R = 0.17$, $p = 0.205$, Fig. 3C).

Discussion

We found limited structure in our network describing environmental and temporal niche use. Similarly, we did not find any phylogenetic signal in species contributions to network structure, nor any significant relationships between phylogenetic relatedness and similarities in either environmental or temporal niche use. These results contradict our predictions and suggest a remarkable lack of segregation in space and time among the diverse mammal species included in our study, as well as limited influences of phylogenetic history on the observed activity patterns. However, taxa appeared to have partitioned environmental niches more than temporal ones. These observations suggest that spatial variation in resource availability was more important than temporal avoidance due to predation risk or competition in shaping the activity within this mammal community.

Although species that share common ancestry often exhibit similar morphological, physiological and behavioral traits (Blomberg & Garland, 2002; Wiens & Graham, 2005), species contributions to networks describing environmental and temporal niche partitioning did not seem to have been influenced by the phylogenetic associations among species. Similarly, we did not find any relationships between phylogenetic distances between species and their differences in environmental and temporal niche use. Some of these results could have been caused by the lack of closely related species in our analyses, as phylogenetic signal in niche use may not be uniformly occurring (Knouft et al., 2006; Losos, 2008; Olalla-Tárraga et al., 2017). However, we suggest that our data indicate that evolutionary history may have had limited influence on niche use in this mammal assembly. Since phylogenetic signal has been found in the spatial distribution of both living and fossil mammals (Carotenuto et al., 2010), we interpret our results as support for both scale and context dependencies in the importance of evolutionary history for niche partitioning among sympatric mammals. Such an interpretation would mirror suggestions of context dependencies in other behavioral and ecological processes, e.g., non-lethal effects of predation risk (Wirsing et al., 2021), and highlight that understanding context dependencies may be as or more important for ecology than to search for broad, general rules in empirical ecological systems (Catford et al.,

Table 1

Observed and random expectations of four metrics of the bi-partite networks describing the utilization of environmental and temporal niches among sympatric mammals; connectance - describing the weighted number of network links out of all possible links as a measure of network complexity, specialization (H'_2) - a measure of how specialized the species are on average in their interactions, nestedness (WINE) - describing how nested the structures in the networks are, and modularity (Q) - describing how clustered the species are in their interactions. Significant deviations from random expectations, based on 1000 randomly shuffled interaction matrices for each niche dimension, are indicated in bold font.

	Observed	Expected	Z	P
Environmental niche use				
Connectance	0.36			
Specialization (H'_2)	0.22	0.30	-3.51	<0.001
Nestedness (WINE)	0.19	-0.01	1.08	0.438
Modularity (Q)	0.23	0.21	1.04	0.466
Temporal niche use				
Connectance	0.41			
Specialization (H'_2)	0.09	0.12	-3.85	<0.001
Nestedness (WINE)	-0.05	-0.01	-0.28	0.924
Modularity (Q)	0.11	0.15	-3.38	<0.001

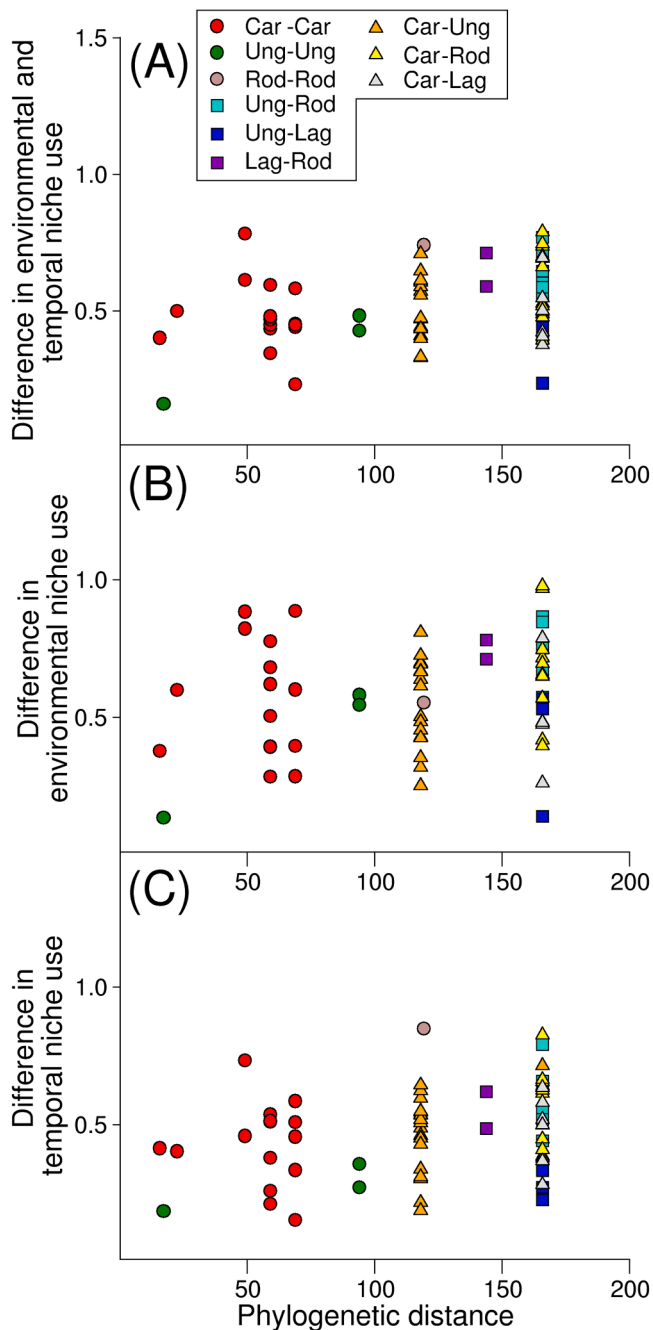


Fig. 3. Relationships between pairwise phylogenetic distances among species and species differences in environmental and temporal niche use (A), as well as between phylogenetic distances and differences in the environmental (B) and temporal (C) niche use only. Phylogenetic distances were estimated as the branch length separating two species in a dated mammal super tree, and differences in niche use by the Jaccard dissimilarity index calculated on estimated occupancy in environmental and temporal niches. Data points are color-coded based on the orders of evaluated species (Car - Carnivora, Ung - Cetartiodactyla [ungulates], Rod - Rodentia, Lag - Lagomorpha).

2021).

Despite a lack of phylogenetic signal, all species did not contribute equally to the networks describing environmental and temporal niche use. Two meso-carnivores, the red fox and the wild cat, occupied central positions in the networks describing interactions in temporal niche use, whereas one large carnivore (the brown bear) and one small herbivore (the squirrel) were specialized in their interactions describing environmental niche use. The central positions of the red fox and the wild cat

suggest that they had a relatively broad overlap in diel activity with the other sympatric mammals. In Europe, both red foxes and wild cat have previously been recorded as primarily nocturnal, albeit without a distinct activity peak during the night (e.g., Díaz-Ruiz et al., 2016; Martín-Díaz et al., 2018). We observed red foxes in all time slots, and wild cats in all time slots except during the dawn, which highlights that these two species may have been largely cathemeral in this Italian landscape. Red squirrels are tightly tied to the availability of food (Boutin et al., 2006), and we suggest that their high specialization in the network describing environmental niche use is caused by their space use being dictated by the availability of conifer forests. Brown bears, on the other hand, are highly omnivorous and are therefore likely not constrained in their environmental niche use by either food supply or competition. Brown bears in the central Apennines have previously been observed to prefer intermediate elevations as well as deciduous woodland, and to avoid agricultural areas and scrublands (Posillico et al., 2004). Our results corroborate these earlier findings, and suggest that the high interaction specialization of brown bears in their environmental niche use may be due to low tolerance to human activity (Mohorovic et al., 2017; Vicedo et al., 2023), and that this caused them to use a more restricted range of environmental niches compared to the other mammals in our study.

Although the study area is relatively pristine, at least part of our results may have been influenced by human activity. Recent studies from other southern European regions have found that human activity may drive spatio-temporal shifts in patterns of activity in medium-sized and large mammals, and that such shifts could cause an increased spatial or temporal niche overlap among species (Ciucci et al., 1997; Torretta et al., 2017; Mori et al., 2022; Vicedo et al., 2023). Shifts in activity could be caused either by the footprint of human activities or by direct human presence (Nickel et al., 2020). Humans have transformed almost all parts of the Earth's land areas (Williams et al., 2020), which has led to widespread habitat destruction for many species (Baisero et al., 2020). Such habitat transformation could lead to species being forced to live in similar environments. However, animals could also shift their activity due to behavioural risk avoidance, similarly to what frequently is done to evade predation risk (Frid & Dill, 2002). This could influence activity in both spatial and temporal dimensions. For instance, mammal species have shifted to more nocturnal behaviour across the globe (Gaynor et al., 2018; Nix et al., 2018), although a shift towards more distinct nocturnality does not seem to be uniform in all instances (Khatiwada et al., 2022).

While we regard our results to be robust, we provide some caveats to our study. First, despite basing the analysis on close to 1000 independent observations, limited sample sizes may have biased the estimated occupancy values for some species and specific niches. However, sample sizes would always be an issue for rarely utilized niches, and we regard our minimal threshold of 5 observations per species to be a reasonable compromise between maintaining a maximum number of species in the analyses while maintaining a reasonable accuracy in the estimation of detection. While Bayesian implementations of multi-species occupancy models have been suggested to partly overcome sample size problems for rare species (e.g., Dorazio & Royle, 2005), our own exploratory analyses using this class of models did not give sufficient improvements to warrant the increased analytical complexity of them. Similarly, we did not have enough observations to create fully resolved occupancy models in both space and time. This constraint may have masked context-dependent patterns in niche utilization, e.g., if a species was only using a specific environmental niche at a specific time, which could warrant further investigation. Furthermore, our study only included twelve species. Network structures such as nestedness may be sensitive to network size (Nielsen & Bascompte, 2007). However, we do not regard network size in our study to be constrained by sampling effort, but rather a characteristic of the study system. Finally, we highlight that our study was only carried out in a single season and, on a landscape scale, had an effective sample size of one (e.g., Hurlbert, 1984). We therefore

call for caution in generalizing the results from this study to other systems. However, we re-iterate that individual empirical studies do hold scientific value (Ríos-Saldaña et al., 2018), especially in the light of the need to identify appropriate contexts for the relative importance of different ecological processes (Catford et al., 2021).

Conclusions

Our results suggested limited structuring in the network describing environmental and temporal niche use within this mammal community, and that phylogenetic history appear to have been relatively unimportant for shaping patterns of niche utilization among these species. Hence, our study does not support any strong effects of phylogenetic niche conservatism or phylogenetic constraints on niche utilization, but rather indicates that both the relative niche differentiation and the phylogenetic influences on such differentiation may be scale- and context-dependent. However, environmental niches appear to have been more partitioned among species than temporal ones, suggesting environmental characteristics were more important than avoidance of inter-specific interactions in shaping the activity of these mammals.

Declaration of Competing Interest

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

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.baee.2023.12.002](https://doi.org/10.1016/j.baee.2023.12.002).

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