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Water sources shape drought effects on animal activity in Mediterranean woodlands

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Abstract:

Drought frequency and severity have notably increased in the Mediterranean basin throughout the 20th century, thereby impacting freshwater sources and forest regrowth, which are crucial for woodland mammal survival. We used camera trapping data collected from a mountain range in NE Spain from 2018 to 2023 (coinciding with an extreme drought event) to test whether freshwater sources, such as ponds and springs, act as biodiversity refuges for woodland mammals during extreme drought. Meteorological conditions during the study, such as accumulated precipitation, air temperature anomalies, air humidity and Standardised Precipitation-Evapotranspiration Index (SPEI), were used to predict mammal activity, richness and diversity using linear mixed-effect models. We detected eight common species including wild boar (*Sus scrofa*, 48% of all detections), roe deer (*Capreolus capreolus*, 28%) and red fox (*Vulpes vulpes*, 10%). Contrary to our expectation, mammal activity was unaffected by the presence of freshwater sources. Our findings show that the presence of freshwater sources did not generally alleviate negative effects of drought on animal activity and diversity. These results may emerge because traditionally permanent freshwater sources in Mediterranean ecosystems (such as springs and ponds) have dried up during the extreme 2021 – 2023 drought, halting its function as biodiversity refugia for woodland mammals. Our results highlight the impact of extreme weather conditions on mammal activity and will help managers create more effective conservation strategies for mammals under increasingly dry conditions.

Key words: Climate change · SPEI · Mammals · Camera trapping · Time series analysis · Freshwater sources.

Introduction

Global Mediterranean climate regions are among the ecosystems most threatened by drought (Mekonnen and Hoekstra 2016; Cramer et al. 2018). Drought is common in Mediterranean climates due to their warm, dry summers, mild winters, and a high variability in precipitation and temperature, both within (i.e., seasonally) and between years (Rundel et al. 2016). Mediterranean climates are intrinsically water limited, with the peak of aridity occurring during the hottest period of the year. Drought severity has increased during the 20th century in most western and central Mediterranean regions, with the exceptions of northwestern Iberia and

most of Turkey (Sousa et al. 2011), because of global warming (Cawdrey 2023). In addition, future climate projections for the Mediterranean basin suggest a potential decrease in precipitation by 2100, with mean annual rainfall expected to be 15%-20% lower, and an increase in rainfall variability (Seker and Gumus 2022). Global mean surface air temperature (and thus evapotranspiration) is also projected to rise by approximately 2°C relative to 1990 (Masson-Delmotte et al. 2021). As a result, drought frequency in the Mediterranean basin is projected to increase during the 2021-2060 period, with drought conditions expected to prevail for 12–25% of the time within this timeframe (Essa et al. 2023).

Precipitation in the Mediterranean basin is highly variable across years (Martin-Vide et al. 2022) which promotes highly variable water availability in Mediterranean's hydrological systems. However, the lack of regular water supply does not stop the Mediterranean basin from hosting varied and abundant animal populations. In fact, the Mediterranean region is widely considered as a global hotspot of biodiversity (Myers et al. 2000; Medail and Quezel 2001). Among these, woodland mammals play crucial roles in ecosystem functioning, including for seed dispersal, pest control, and nutrient cycling (Innes et al. 2004; Matías et al. 2010; Lacher et al. 2019). Mediterranean woodland mammal communities are rich in smaller animals, particularly rodents and shrews ("Mediterranean Basin – Species" 2024). Common species include the Eurasian red squirrel (*Sciurus vulgaris*), house rat (*Rattus rattus*), and yellow-necked and long-tailed field mice (*Apodemus flavicollis* and *A. sylvaticus*) (IUCN 2024). Tree-dwelling bats like Natterer's bat (*Myotis nattereri*) are also present (IUCN 2024). Carnivores typical of Mediterranean woodlands include the common genet (*Genetta genetta*), stone and pine martens (*Martes foina* and *Martes martes*), European badger (*Meles meles*), least weasel (*Mustela nivalis*), and western polecat (*Mustela putorius*) (IUCN 2024). Larger mammals such as wild boar (*Sus scrofa*), red deer (*Cervus elaphus*), and roe deer (*Capreolus capreolus*) are also common.

More severe droughts and increasing aridity due to climate change could potentially have negative effects on terrestrial mammals in Mediterranean ecosystems (Fuller et al. 2016). For

example, spring droughts have been related to poor crop sizes in Mediterranean oaks, thus lowering food availability (Fernández-Martínez et al. 2015). The availability of oak acorns has been seen to affect wild boar and small mammal population dynamics (Cahill and Llimona 2004; Bieber and Ruf 2005; Llanos-Guerrero et al. 2024). Roe deer population dynamics are also negatively impacted by reduced precipitation and poorer forage quality (Toïgo et al. 2006). Droughts can also harden the ground, making it difficult for wild boars to dig up roots and insects (Massei et al. 1997; Ruf et al. 2021). Additionally, droughts have been shown to alter mammal distributions. Both roe deer and wild boar home ranges increase during dry summers, when natural food availability is scarce (Cahill et al. 2012; Morellet et al. 2013).

In Mediterranean ecosystems we can find both perennial freshwater sources (i.e., those with a more constant flow, usually connected to groundwater, such as springs), and temporary freshwater sources (i.e., those with intermittent water flow throughout the year, depending on environmental conditions such as precipitation patterns) (Larned et al. 2010). The presence of freshwater sources can affect animal abundance and biodiversity and their responses to drought. For instance, in Mediterranean perennial springs, during dry phases, alpha diversity may increase because organisms that typically do not rely on water from those sources, such as some mammals and birds, may be drawn to them during droughts (Fernández-Martínez et al. 2023). When the dry phase subsides, alpha diversity slowly returns to its previous values, since these species can rely on other freshwater ecosystems that have been replenished (Fernández-Martínez et al. 2023). Climate change, however, is displacing the environmental conditions of Mediterranean ecosystems, making perennial freshwater bodies more prone to becoming temporary freshwater sources (Larned et al. 2010; Fernández-Martínez et al. 2023). In addition to these meteorological changes, various forms of anthropization, like aquifer overexploitation, is affecting quantity and quality of groundwater (Leduc, Pulido-Bosch and Remini 2017). Given the important function of these perennial freshwater sources as biodiversity refuges during drought, their loss during extraordinarily severe droughts could negatively impact animal communities. Understanding and predicting when and how mammal

communities might change following severe droughts is crucial for effective conservation and management. While studies, such as those by Catling (1988), Duncan et al. (2012) and Maiorano et al. (2011) have explored how drought affects Mediterranean woodland mammals, the responses of these populations to multi-year, extremely severe droughts remain poorly understood, and empirical studies are lacking. Hence, there is a need to study extreme droughts and their impact on animal communities to help managers and conservationists to develop strategies to help these communities cope with severe drought events.

In this study, we aimed to investigate the temporal dynamics of woodland mammal activity and their relationship with environmental conditions, specifically weather variability and presence of freshwater sources, in the context of a severe drought. To achieve this, we used camera traps to measure monthly activity of mammals in Mediterranean woodlands from 2018 to 2023. Data were gathered from four different sites, ranging from the bottom to the top of Furiosos' watershed in Montnegre mountain range (NE Iberian Peninsula), which has undergone a severe drought since October 2020. We hypothesised that during this severe drought, fauna detections will proportionally increase in sites with access to freshwater sources compared to those lacking freshwater sources. Our study also represents a comprehensive monitoring program for the mammal communities found in the Montnegre-Corredor Natural Park, offering valuable insights into which mammal species may require increased conservation efforts.

Material and methods

Study area

This study was carried in the Furiosos' stream watershed, located in Montnegre mountain range (NE, Iberian Peninsula). This study area is located within the Montnegre-Corredor Natural Park, which is managed by the Council of Barcelona (Torre, Arrizabalaga and Flaquer 2003). Montnegre is characterized by steep terrain and a diverse composition of plant communities, combining both Mediterranean and Central European plants. The dominant tree

species is the holm oak (*Quercus ilex*), accompanied by cork oak (*Q. suber*) and several species of deciduous oaks, such as *Q. pubescens* and *Q. canariensis*. Pine species, particularly stone pine (*Pinus pinea*) and Aleppo pine (*P. halepensis*), are common at lower to mid-altitudes. At higher elevations, the vegetation includes cherry trees (*Prunus avium*) and chestnut plantations (*Castanea sativa*) (Torre et al., 2003).

Montnegre has a sub-humid Mediterranean climate. The rainfall regime presents notable interannual variations with the average precipitation being 610 mm annually (Meteocat 2024). Heavy rainfall, particularly during the autumn months, frequently leads to flooding, especially in the drainage basins located on the southern slopes of the massif. Pluviometry data from this area indicate that rivers are mostly sporadic or seasonal. The main river is La Tordera which collects water from the many streams in the mountain range such as the streams of Vallgorguina, Olzinelles, Montnegre, Ramió and Fuirosos, the latter being our study area.

Wildlife monitoring

To monitor the activity of mammals in the area we used camera traps, a non-invasive technique that allows for long term monitoring. These cameras collect a lot of data at a relatively low cost, enabling researchers to estimate the abundance of terrestrial vertebrates (Gilbert et al. 2021), as well as their movement and behaviour (Caravaggi et al. 2017; Niedballa et al. 2019). Unlike other techniques, they can also detect rare, nocturnal, and elusive species (Rovero and Zimmermann 2016). The monitoring was conducted using four trail cameras (Browning Strike Force HD Pro X, Birmingham, AL), equipped with motion sensors and an infrared flash with invisible LED light. The cameras captured a burst of three high-resolution images (20MP) when motion was detected, facilitating the identification of moving animals. All four cameras were placed on the northern slope of Montnegre mountain range (Fig. 1) and were placed in woods with the same main vegetation, making the major difference between localities the presence or absence of freshwater sources. These water sources have permanently had water for decades, but they have recently had periods of dry out during the peak of the severe drought

of 2023. Camera data were collected approximately once a month. The lowest camera (POND) was installed on August 6, 2018. It was installed in an oak grove at an altitude of 235 meters above sea level (m.a.s.l.) above the Brinxà reservoir, next to an intermittent stream that dries out most summers and feeds a pond that, until the recent drought, have had water permanently throughout the year. The second camera (SPRING) was installed on 2 July 2021 near a country house (Can Ponet), within a hazel and oak grove adjacent to a spring that forms a muddy area at an elevation of 415 meters above sea level (m.a.s.l.). Like pond described above, this spring has been permanently pouring water until the peak of the drought in 2023. The third camera (DRY MID) started working on the 15th of December 2018 in an oak grove close to Sant Martí of Montnegre church at 508 m.a.s.l, situated in the middle of the mountain range. Finally, the highest camera (DRY TOP) was installed on 1st of July 2018 in an oak forest near the mountain peak of Turó Gros, at an altitude of 715 m.a.s.l. (Table 1).

Data processing

Photographs were visually inspected to identify animal species. When animal species could not be confidently identified, photographs were not considered in the analyses. In photographs where multiple animals of the same species appeared—a situation very common with wild boars and, to a lesser extent, roe deer—they were not individually counted but were considered a single detection. As a result, our findings may underestimate wild boars, and to a lesser extent, roe deer activity. Animals detected at very low frequencies (e.g., bats, rodents, common weasel) and domestic animals (e.g., sheep, dogs, cats) were excluded.

The photographs were then processed using R (v. 4.3.2) (R Core Team 2024) using several packages. The *fs* package (v. 1.6.3) (Hester, Wickham and Csárdi 2024) was used for file manipulations like listing files from directories. The *lubridate* package (v. 1.9.3) (Grolemund and Wickham 2011) facilitated date-time manipulations such as creating date-time objects, extracting specific temporal components, etc.. The *exifr* package (v. 0.3.2) (Dunnington and Harvey 2021) was employed to read EXIF data from the photographs, while the *dplyr* package (v. 1.1.4) (Wickham et al. 2023) was used for data manipulation. Photographs of individuals

from the same species captured within a 15-minute interval were treated as one single detection. This approach minimized the likelihood of multiple counts of the same animal, which could occur due to extended stays in the area, or the three-photo burst triggered by the camera in response to a single instance of movement.

As a result of this data processing, we constructed a database containing the total count of observations for each animal species, organized by month and locality. To correct the data for periods of camera malfunctions (such as theft, being switched off, etc.), we calculated monthly average observations accounting for the total number of days that the camera operated. For instance, if 10 observations were recorded in a given month but the camera was active for only 20 days, the corrected monthly average would be 0.5 observations per day. This measurement is also known as trapping rates (Wearn and Glover-Kapfer 2017). In addition to calculating the monthly trapping rates, we also determined the proportion of days with detections by dividing the number of days detections occurred by the total number of days the camera was operational. For example, if detections of a specific animal occurred on 10 days during a month in which the camera was operational for 20 days, the corrected proportion would be 0.5 detection days per operational day. Species richness for each site and month was calculated using basic R built-in functions (R Core Team 2024), while Shannon diversity was computed using the *vegan* R package (v. 1.6.3) (Oksanen et al. 2022).

Mean monthly temperature (°C), precipitation (mm) and humidity (%) data were obtained from the Dosrius - PN Montnegre Corredor weather station, provided by the Meteorological Service of Catalonia (2024). The dataset was used to calculate accumulated precipitation over one (Precipitation-1), three (Precipitation-3), and six (Precipitation-6) month period. Additionally, Standardized Precipitation Evapotranspiration Index (SPEI) was calculated with *SPEI* R package (v. 1.8.1) (Beguería and Vicente-Serrano 2023) as a measure of drought intensity. SPEI is calculated as the difference between precipitation and potential evapotranspiration (PET). Positive values of the SPEI indicate above-average wet periods and negative values indicate drought. We selected timescales of one (SPEI-1), three (SPEI-3), six (SPEI- 6), nine

(SPEI- 9) and twelve (SPEI- 12) months. SPEI was calculated for different time scales since animal activity may present a lagged response to prolonged drought periods. This approach also allows for the examination of both short-term and long-term drought effects, each of which can have significant ecological impacts (Sperry and Weatherhead 2008).

The enhanced vegetation index (EVI) serves as a robust indicator for tracking both temporal and spatial changes in leaf area and green biomass. within the spring weather, it can predict seed production of Mediterranean oaks (Fernández-Martínez et al. 2015; Vergotti et al. 2019), a food resource for the animal species within the study area. EVI was incorporated into the analysis to assess its impact on animal detection rates. EVI values were extracted from the Terra MOD13Q1 product of MODIS for the period between 1st of July 2018 and 31st of December 2023. These values, with a 16-day periodicity and a spatial resolution of 0.25 x 0.25 km², were obtained for the pixel adjacent to each camera site.

To assess the influence of water availability, a categorical variable was integrated into the database, called water presence. This categorical variable considered POND and SPRING as points where water was present, whereas DRY TOP and DRY MID were considered dry spots. A time index variable representing the number of months that have passed since the beginning of the study was added to evaluate overall trends over time, along with a seasonal variable representing winter, spring, summer, and autumn. To evaluate the impact of temperature on animal activity, we included a variable that estimates temperature anomalies. This variable was calculated by subtracting the average monthly temperature (from 2018-2023) from the observed temperature of each corresponding month. Temperature anomalies were calculated to address multicollinearity issues, as the mean monthly temperature variable and the season variable were highly correlated, making it difficult to distinguish the effect of each variable.

Statistical analysis

Descriptive statistics were calculated using basic R built-in functions and visualised with the *ggplot2* R package (v. 3.5.1) (Wickham 2016). Linear models, followed by Analysis of variance

(ANOVA) were used to detect differences between localities using the *stats* R package (R Core Team 2024) (v. 4.3.2).

We assessed the effects of the SPEI, freshwater source presence and its interaction with SPEI, temperature anomalies, precipitation, humidity, EVI, season, and the time index variable (all considered as fixed effects) on animal activity (quantified through trapping rates and the proportion of days with detections), species richness and diversity. We used one linear mixed-effects model (LMM) for each species and response variable. To account for the non-independence of the data grouped at the site level, the camera identity was specified as a random effect. Temporal autocorrelation was accounted for by including a continuous autoregressive correlation structure at lag 1. All models were fitted using the Maximum Likelihood (ML) estimation method. To fit linear mixed-effect models, we used the *lme* function in the *nlme* R package (v. 3.1-163) (Pinheiro et al. 2024). The Akaike Information Criterion (AIC) (Akaike 1998) method was employed to identify the best-performing model among the candidate models. To do this, we followed a stepwise model selection procedure (backwards-forward) using the *stepAIC* function, from the *MASS* R package (v.7.3-60) (Venables and Ripley 2002), starting with the saturated model including all fixed predictors. The *visreg* R package (v. 2.7.0) (Breheny and Burchett 2013) was used to visualize the estimated effects of the predictors and generate partial residual plots.

To meet model assumptions (normality and homoscedasticity in model residuals), trapping rates and the proportion of days with detections were transformed using either a square root or a logarithmic transformation, ensuring that the data adhered to these necessary conditions. The models for both the European badger and the European hare (*Lepus europaeus*) did not meet these assumptions and were therefore not used in this study.

Results

Animal species detected, differences between localities and trends over time

During the studied period, between the 1st of July 2018 and the 13th of December 2023, over 138,000 photographs were obtained. In these photographs, eight mammals appeared regularly, accounting for a total of 12,012 independent observations. The average trapping rates (detections/observations day⁻¹) in all four localities were: 0.96 ± 0.87 SD for wild boars, 0.57 ± 0.53 SD for roe deer, 0.21 ± 0.22 SD for red foxes (*Vulpes vulpes*), 0.08 ± 0.11 SD for stone martens, 0.07 ± 0.13 SD for genets, 0.045 ± 0.11 SD for red squirrels, 0.04 ± 0.11 SD for European badgers and 0.02 ± 0.06 SD for European hares (see percentage of total observations in the Fig. A). The proportion of animals per locality can be seen in (Fig. 2). Statistical differences in trapping rates among the four localities were observed for all eight mammals (Fig. 3). Differences among locations were inconsistent across animal species and they were not clearly related to proximity of freshwater sources. Mean species richness over the whole study period also significantly differed between localities ($F_{3,204} = 12.31$, $p < 0.001$; Fig. B). Similarly, mean Shannon diversity values were significantly different among localities ($F_{3,204} = 39.41$, $p < 0.001$; Fig. B). However, the presence of freshwater sources did not have a significant effect on either species richness or diversity, with the best model to predict animal richness not including the presence of freshwater variable, and its effect on diversity not being statistically significant.

For all the analysed animals, time series revealed fluctuations in trapping rates throughout the years, with various peaks and lows (Fig. C). Our analyses indicated that roe deer trapping rates increased by 280% over the study period (Fig. 4a; see model output details in the Table A). Conversely, modelled trapping rates declined for the stone marten (82% decline), common genet (99%) and red squirrel (73%) (Figs. 4.b, 5.c and 5d); see model output details in the Supplementary Material Table S1). All other animal trapping rates did not undergo statistically significant changes throughout the study period. All animals showed little or no seasonal patterns. Among the species showing slight seasonal variation, wild boars had a peak of

trapping rates during winter, while stone martens showed higher trapping rates during late spring and throughout summer. Animal richness and diversity also experienced a significant decline from 2018 to 2023 (30% decline; $\beta = -0.30 \pm 0.06$ SE; $p < 0.001$ and 29% decline; $\beta = -0.26 \pm 0.09$ SE; $p < 0.001$ respectively). This was mainly driven by the fact that roe deer trapping rates, the second most frequently observed species in this study, increased over time, while trapping rates of less frequently observed species (e.g., stone marten, common genet, red squirrel) declined over the same period.

Trapping rates and their relation to freshwater sources and environmental variables

Accumulated precipitation over 6- or 3-months had a significant negative effect on trapping rates of roe deer ($\beta = -0.47 \pm 0.09$ SE; $p < 0.001$) and the common genet ($\beta = -0.17 \pm 0.06$ SE; $p < 0.001$) respectively (Table S1). Wild boar had significantly higher trapping rates at higher relative humidity levels ($\beta = 0.17 \pm 0.07$ SE; $p = 0.01$). The proportion of days with wild boar detections (number of days with wild boar detections/total number of operational days) significantly increased with Enhanced Vegetation Index (EVI) ($\beta = 0.20 \pm 0.09$ SE; $p = 0.03$). However, no significant relationship was found between EVI and wild boar trapping rates ($\beta = 0.11 \pm 0.09$ SE; $p = 0.25$).

Drought conditions, estimated using the Standardised Precipitation-Evapotranspiration Index, had a statistically significant impact on trapping rates of all animals except the red fox and the red squirrel. However, no consistent patterns in response to drought were observed among the analysed species. Trapping rates of wild boars were significantly higher during drier-than-normal periods, as denoted by the SPEI-6 ($\beta = -0.40 \pm 0.06$ SE; $p < 0.001$) (Fig. D). We found statistically significant interactions between drought and the presence of freshwater sources for the trapping rates of roe deer, stone marten, and the common genet (Table S1). Roe deer trapping rates significantly decreased with drought only at locations with no water sources (Fig. 5a, see figure for statistics) while stone marten significantly decreased with drought only at locations with water sources (Fig. 5b, see figure for statistics). The common genet trapping

312 rates, instead, significantly increased with drought at locations with no water sources (Fig. 5c,
313 see figure for statistics). All results are consistent for both trapping rates and the proportion of
314 days with detections. Shannon's diversity also significantly decreased with drought, but only at
315 locations with presence of water sources (Fig. 6, see figure for statistics). For species richness,
316 neither the water presence nor SPEI was selected in the best model.

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Discussion

Effect of extreme drought on mammal activity

In this study, we examined the varying responses of mammal species to environmental and meteorological conditions, with a particular focus on drought, as estimated by SPEI. Animal activity responded to a range of meteorological variables. SPEI and precipitation were the meteorological variables most selected in models, with drought significantly affecting trapping rates for all mammals except the red fox and red squirrel. These results highlight the importance of precipitation and water availability to explain population dynamics of Mediterranean woodland mammals. Additionally, we assessed how the availability of permanent water sources influences the effect of drought on trapping rates of the different species. Contrary to our hypothesis, we found that animal trapping rates did not consistently decline with increasing drought in dry habitats, and they did not increase in habitats close to springs or ponds.

The variation in trapping rates across these mammal species in response to drought may be attributed to their behavioural patterns and/or food and water requirements. For example, wild boar trapping rates, the most abundant species in our study, increased during drought conditions, regardless of whether there were freshwater sources nearby or not. However, the significant increase in wild boar populations in recent years—particularly in Montnegre, which has one of the highest densities of wild boars in Catalonia—may have confounded the effect of drought in our analysis. The wild boars heightened activity during drought could be attributed to how they lack functional sweat glands (Gourdine et al. 2006) and thus cannot sweat to regulate their temperature during dry conditions. This makes them seek shaded areas to stay cool (Blackshaw and Blackshaw 1994), which, as all camera traps were in groves, could have resulted in a higher trapping rates, and therefore activity, for all four localities compared to open areas that we did not include in our study. For the common genet, its activity increased

with drought only in areas lacking nearby freshwater sources. This animal originated from northern Algeria or Arabian Peninsula —regions featuring drylands with hyper-arid and rainless climates (Gaubert et al. 2009). Therefore, they should have lower water requirements compared to other mammals. This adaptation could explain its increased activity during drought periods, as these conditions resemble its native environment. However, that explanation would not account for why this behaviour occurs only in areas lacking freshwater sources. Lastly, in areas with freshwater sources, drought decreased stone marten's activity. This could be due to the stone marten's seasonal variations in its diet. Stone marten has a higher intake of plants, such as fruits, during the summer compared to other seasons (Bakaloudis et al. 2012). The Mediterranean climate, characterized by its driest period in the summer, coincides with this dietary shift. Given the high water content in plants, particularly some fruits that are consumed by the stone marten (e.g. from *Rubus ulmifolius* and *Prunus laurocerasus*) (Pereira et al. 2019), it is possible that this animal meets its water requirements through their diet during the summer, reducing their dependence on permanent water sources. In contrast, during wet seasons, the stone marten may be more likely to gather around water sources to meet their hydration needs.

The only species that partially exhibited the expected response by our hypothesis was the roe deer, with its activity levels decreasing during drought in areas lacking freshwater sources. Roe deer are income breeders, relying on energy gained during the reproductive period rather than stored energy for reproduction (Andersen et al. 2000). Since they are income breeders, they adjust home range size continuously to temporal variation in food resources (Morellet et al. 2013). During periods of extreme drought, it would be expected that these herbivores would leave areas where water is scarce in search for areas with availability of water such as the ponds and spring studied here.

Effect of extreme drought on mammal diversity

We found that the presence of freshwater sources mediated the effect of drought on mammal diversity. However, this mediating effect was inconsistent across species and overall does not support our prediction that the presence of water sources alleviates the negative effects of drought on mammal diversity. Shannon's diversity index decreased with drought at localities with water sources, but not at localities without water sources. These results could be attributed to the fact that historically permanent freshwater sources are becoming temporary because of global change (Fernández-Martínez et al. 2023). Extreme drought periods, such as the one observed in this study area and period, coincide with these temporary springs and ponds drying out (Pinto-Cruz et al. 2023), a phenomenon that was observed during the monthly revisions of the cameras during 2023. Several species that depend on these water sources may temporarily disappear during the dry phases in search for other sources of water. Once drought periods end and water sources are replenished, local diversity is expected to return to previous levels. This provides a feasible explanation for the observed decrease in local diversity at the water sources during drought.

Effect of greenness and other meteorological variables on mammal activity

Our study investigated the effect of other meteorological variables such as humidity and precipitation and their impact on mammal trapping rates. As anticipated, an increase in humidity was associated with a higher trap rate of wild boars, the only animals in the study that have a rooting behaviour. This is potentially due to high humidity promoting early root growth, a primary component of the wild boar's diet (Woodland Trust 2024), whilst also making the soil easier to dig favouring the efficiency of wild boar olfactory sense (Lemel et al. 2003). Consequently, these conditions likely stimulate rooting activity, thereby increasing wild boar movement and trapping rates. Regarding precipitation, we found that accumulated precipitation negatively affected the activity of the common genet. Common genets are

reported to inhabit areas characterized by reduced rainfall (Virgós, Romero and Mangas 2001). This distribution may be explained by the fact that mountainous areas with higher precipitation are also colder, which could be disadvantageous for common genets due to their African origins. Finally, green biomass, assessed through Enhanced Vegetation Index (EVI), was also included as a proxy of Mediterranean oak acorn production (Fernández-Martínez et al. 2015; Vergotti et al. 2019). Higher EVI was found to significantly increase wild boar proportion of days with detections, indicating that seed production influences wild boar activity. However, EVI did not have a significant effect on the activity levels of any other animal species. This is supported by the fact that wild boars go to urban areas when food sources in their natural habitats are low (Cahill et al. 2012). Therefore, when there is high acorn production, it is expected that wild boar activity increases within forested areas. This trend was likely observed exclusively in the wild boar, as it is the only species in the study, aside from the red squirrel, for which acorns constitute a significant portion of the diet.

Trends in animal activity, richness and diversity from 2018 to 2023

The results of this study also provide data to monitor the long-term trends in animal activity, diversity, and richness in the Montnegre Natural Park from the period preceding the drought (2018-2020) through to the last year of this study, during which the drought continues (2023). During the study period, roe deer trapping rates have more than doubled. Before the 90s, this species of cervid had nearly disappeared in Catalunya, leading to different reintroduction projects in the coastal massifs, including Montnegre (Generalitat de Catalunya Departament d'Agricultura 2013). Since then, the roe deer has expanded widely throughout Catalunya (Griffiths Romano et al. 2017). This expansion is likely facilitated by the species' limited predation pressure, as natural predators such as wolves (*Canis lupus*) are absent in areas like Montnegre Natural Park. Additionally, the roe deer demonstrates reproductive plasticity, adjusting the timing and number of offspring in response to environmental cues (Flajšman et al. 2013; Griffiths Romano et al. 2017). Conversely, there has been a big decline in carnivorous

mammals, such as the stone marten (82% decrease) and the common genet (becoming very marginal in 2023). This decline may be linked to their dependence on rodents as a food source, with rodent populations being influenced by the availability of evergreen and deciduous oak acorns (Llanos-Guerrero et al. 2024) which, in turn, are directly affected by drought conditions, particularly during spring (Fernández-Martínez et al. 2015). The increase in the activity of the second most common mammal in the study, combined with the decline of species that were already rare, led to a substantial reduction in both mammal richness and diversity, with a decrease of approximately 30% over the study period.

Conclusions

Our results suggest that drought has important effects on abundance and diversity of Mediterranean mammals, and that the nature and magnitude of those effects, as well as the mediating effect of permanent water sources, vary across species. In this study we suggest that permanent water resources are transitioning into seasonal water bodies due to climate change, a phenomenon supported by previous studies (Fernández-Martínez et al. 2023; Kazemi-Garajeh et al. 2024). Further research is needed to assess changes in the quality of these habitats. Our findings offer further insights into the adaptive responses of mammal species to these environmental shifts. The distinct responses to drought and other meteorological variables among various mammal species highlight the necessity to investigate the underlying mechanisms of these activity shifts. Our findings will help managers to assess better management practices to deal with fauna under increasingly dry conditions. Overall, this study demonstrates the urgent need for immediate action to preserve woodland Mediterranean ecosystems, ensuring the protection and restoration of their ecological value.

Data and code availability

All data used in this study, and the R code to reproduce our results, can be found at Figshare:

<https://doi.org/10.6084/m9.figshare.27941691>

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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642 **Tables**

643 **Table 1.** Coordinates, locality, altitude, most abundant plant species and operational dates of each site.

644 The most abundant plant species included: evergreen oaks (*Quercus ilex*), sessile oaks (*Quercus*
645 *petraea*), cork oak (*Quercus suber*) and the common hazel (*Corylus avellana*).

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	POND	DRY TOP	DRY MID	SPRING
Coordinates	Latitude: 41.6749 Longitude: 2.5908	Latitude: 41.6619 Longitude: 2.5802	Latitude: 41.6714 Longitude: 2.5677	Latitude: 41.6813 Longitude: 2.5520
Locality	La Brinxà reservoir	Turó Gros	Sant Martí de Montnegre	Can Ponet
Freshwater source located near the camera trap	Small pond	Dry area	Dry area	Spring
Meters above sea level (m.a.s.l.)	235	715	508	415
Most abundant plant species	Oak grove primarily composed of	Oak grove composed of	Oak grove composed of	Oak and hazel grove composed of

	evergreen oaks and sessile oaks	evergreen oaks and sessile oaks	evergreen oaks and cork oaks	the common hazel evergreen oaks
Operational dates	6/8/2018- 13/12/2023	1/7/2018- 13/12/2023	15/12/2018- 13/12/2023	2/7/2021- 13/12/2023

Figures

Fig. 1. Location of the four camera traps within Montnegre Corredor Natural Park. The map images were obtained from Google Earth (Google Earth, 2024).

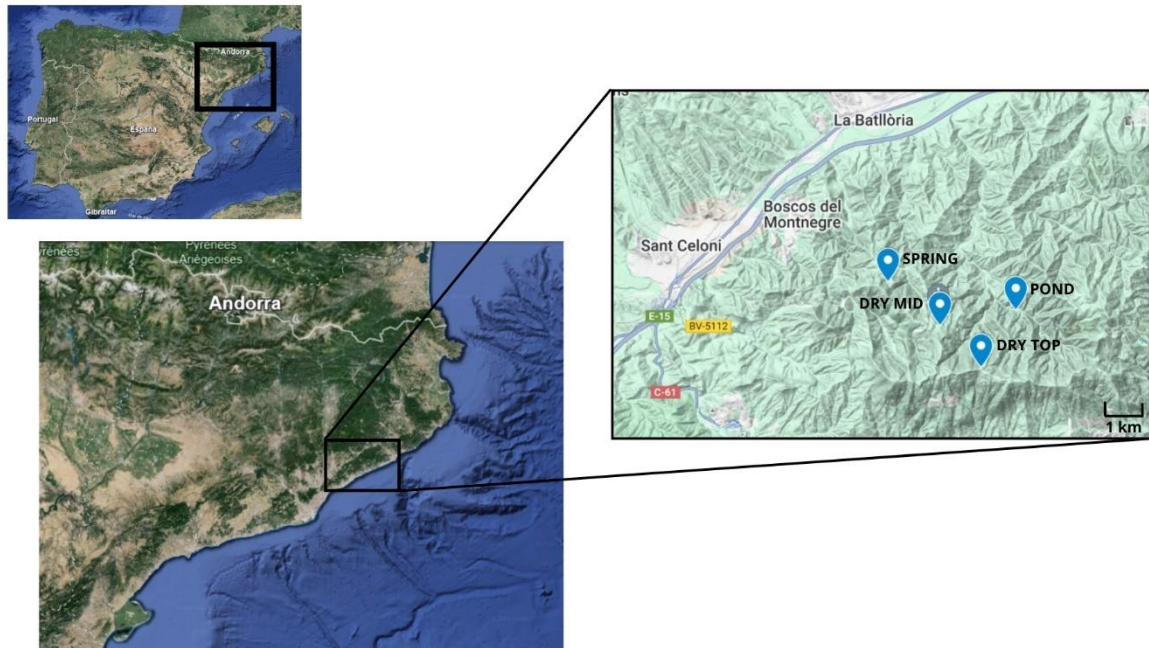


Fig. 2. Total independent observations of wild boar (*Sus scrofa*), roe deer (*Capreolus capreolus*), red fox (*Vulpes vulpes*), stone marten (*Martes foina*), common genet (*Genetta genetta*), red squirrel (*Sciurus vulgaris*), European badger (*Meles meles*), European hare (*Lepus europaeus*) at each locality. Localities POND and SPRING were next to freshwater sources, and localities DRY TOP and DRY MID had no freshwater sources nearby.

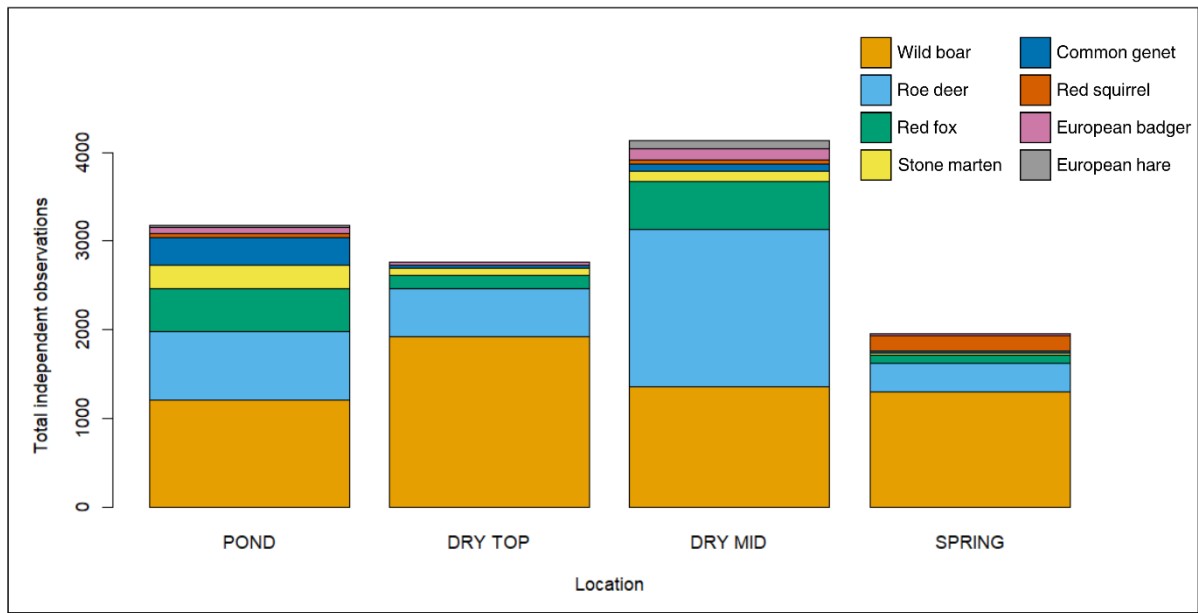


Fig. 3. Average trapping rates (observations day⁻¹) for wild boar *Sus scrofa*, roe deer *Capreolus capreolus*, red fox *Vulpes vulpes*, stone marten *Martes foina*, common genet *Genetta genetia*, red squirrel *Sciurus vulgaris*, European badger *Meles meles*, European hare *Lepus europaeus* per locality. Panel **a** shows the four most common animals, while panel **b** displays the rest of the animals. Error bars indicate standard error (SE). Letters denote the outcomes of pairwise comparisons of Estimated Marginal Means (EMM) among the four localities for each animal.

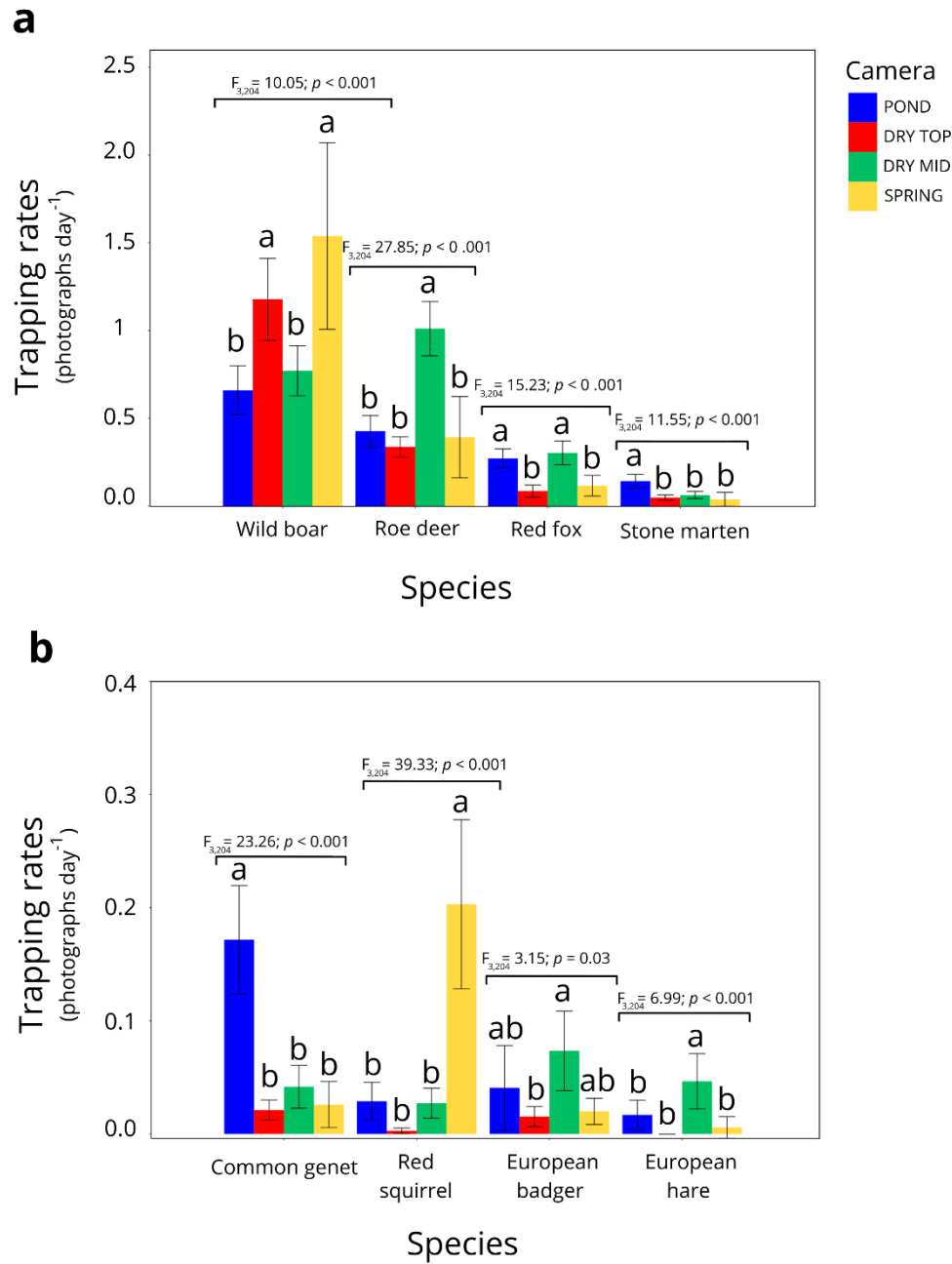
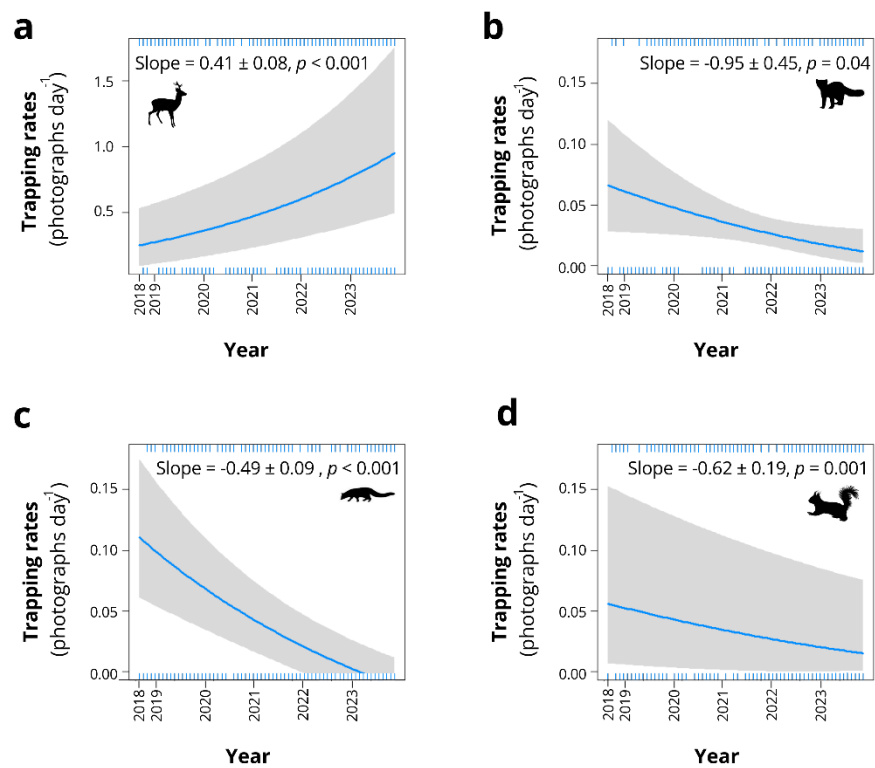


Fig. 4. Temporal trends of trapping rates (observations day⁻¹) from July 2018 to December 2023 for the roe deer *Capreolus capreolus* (a), the stone marten *Martes foina* (b), the common genet *Genetta genetta* (c) and the red squirrel *Sciurus vulgaris* (d). Regression lines and 95% confidence intervals are shown. The blue ticks inside the figure represent the partial residuals. Outputs of the models underpinning these results are provided in the Supplementary Material Table S1.



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Fig. 5. Drought effects on trapping rates (observations day⁻¹) of roe deer *Capreolus capreolus* (a), stone marten *Martes foina* (b) and the common genet *Genetta genetta* (c), in areas with either presence or absence of freshwater sources. Regression lines and 95% confidence intervals are shown. Negative SPEI values signify drought conditions, while positive values indicate wetter conditions. The blue ticks inside the figure represent the partial residuals. Outputs of the models underpinning these results are provided in the Supplementary Material Table S1.

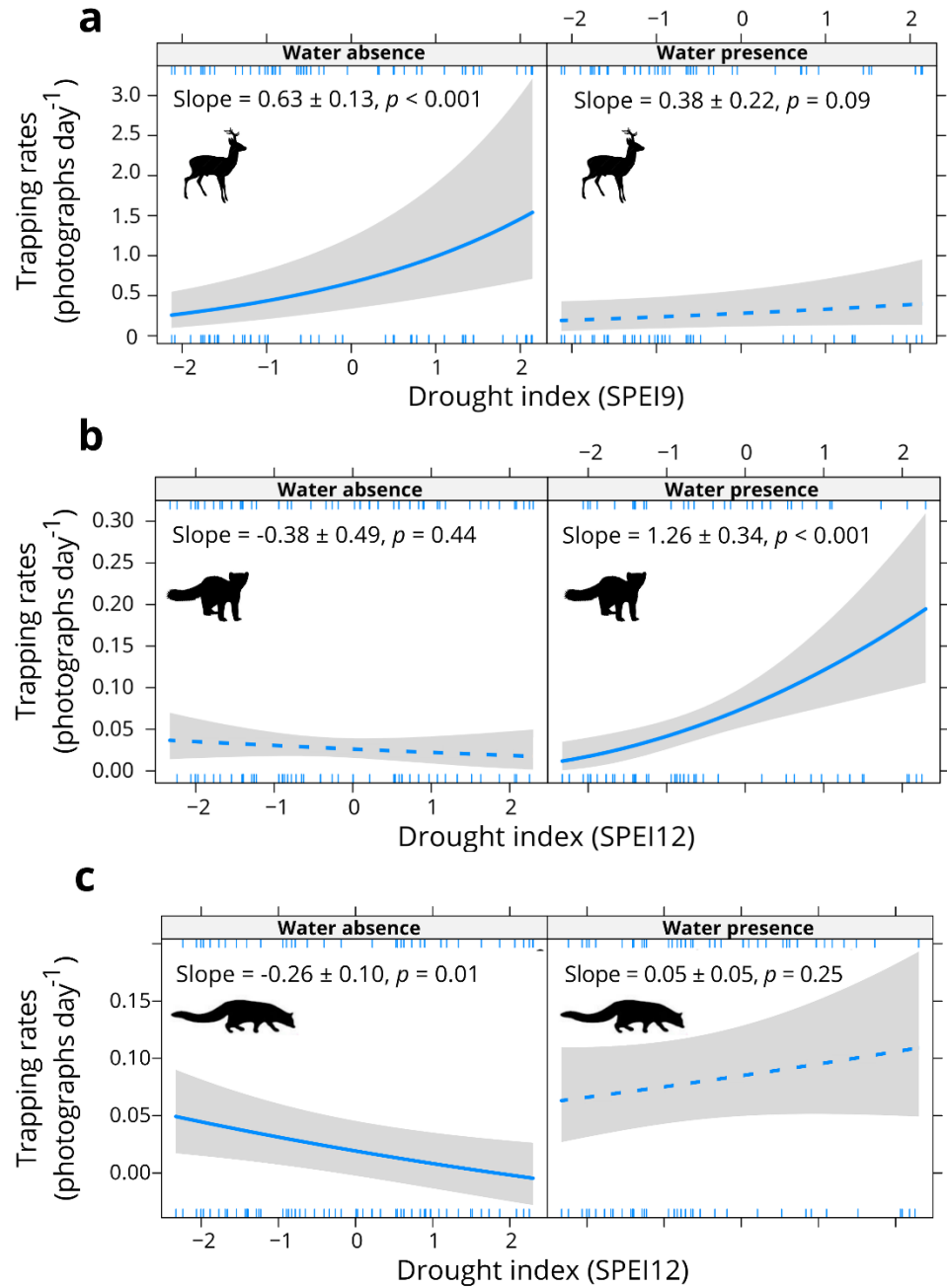
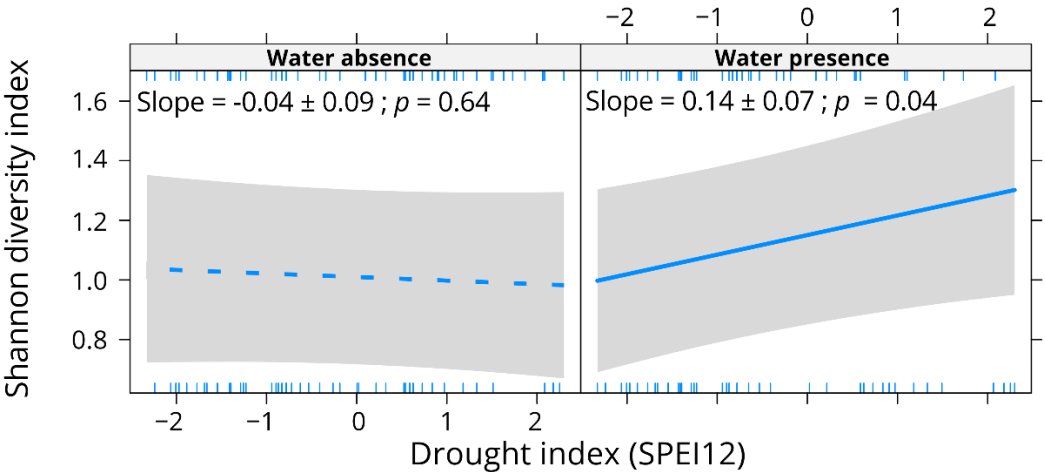


Fig. 6. Drought effects on Shannon's diversity index, in areas with either presence or absence of freshwater sources. Regression lines and 95% confidence intervals are shown. Negative SPEI values indicate drought conditions, while positive values indicate wetter conditions than normal. The blue ticks inside the figure represent the partial residuals. Outputs of the models underpinning these results are provided in the Supplementary Material Table S1.



Supplementary information

Table A. Full output of the fitted models for each mammal. Models **a-f** predict trapping rates, while model **g** predicts species richness and model **h** predicts species diversity.

a) Wild boar trapping rates

Fixed effect	β (SE)	t-value	p-value
Intercept	0.00 (0.00)	-2.48	0.01
SPEI-6	-0.40 (0.06)	-6.46	< 0.001
Mean monthly relative humidity	0.17 (0.07)	2.46	0.01
Spring-Autumn	-0.25 (0.07)	-3.42	< 0.001
Summer-Autumn	0.24 (0.09)	-2.73	0.01
Winter-Autumn	0.06 (0.08)	0.72	0.47
EVI	0.11 (0.09)	1.16	0.24

b) Roe deer trapping rates

Fixed effect	β (SE)	t-value	p-value
Intercept	0.00 (0.00)	-0.70	0.49
Water presence (compared to no water presence)	-0.46 (0.26)	-1.78	0.22
SPEI-9 (water_presence = 0)	0.63 (0.13)	4.90	< 0.001

6 month accumulated precipitation	-0.47 (0.09)	-5.14	< 0.001
Time index variable (measured in passing months)	0.41 (0.08)	4.92	< 0.001
Interaction term between SPEI-9 and water presence (water_presence = 1)	-0.25 (0.07)	-3.51	< 0.001

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721 **c) Red fox trapping rates**

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Fixed effect	β (SE)	t-value	p-value
Intercept	0.00 (0.00)	-7.03	< 0.001
Spring-Autumn	0.02 (0.07)	0.24	0.81
Summer-Autumn	0.10 (0.07)	1.38	0.17
Winter-Autumn	0.20 (0.07)	2.72	0.007
6 month accumulated precipitation	-0.11 (0.06)	-1.74	0.08

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724 **d) Stone marten trapping rates**

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Fixed effect	β (SE)	t-value	p-value
Intercept	0.00 (0.00)	6.26	< 0.001
Water presence (compared to no water presence)	1.26 (0.31)	4.08	0.06

SPEI-12 (water_presence = 0)	-0.38 (0.49)	-0.78	0.44
Time variable index (measured in passing months)	-0.95 (0.45)	-2.11	0.04
Interaction term between SPEI-12 and water presence (water_presence = 1)	1.65 (0.36)	4.53	< 0.001

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729 **e)** Common genet trapping rates

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Fixed effect	β (SE)	t-value	p-value
Intercept	0.00 (0.00)	-11.05	< 0.001
3 month accumulated precipitation	-0.17 (0.06)	-2.80	0.006
Water presence (compared to no water presence)	0.43 (0.14)	2.98	0.10
SPEI-12 (water_presence = 0)	-0.26 (0.10)	-2.53	0.01
Time variable (measured in passing months)	-0.49 (0.09)	-5.56	< 0.001
Interaction term between SPEI-12 and water presence (water_presence = 1)	0.26 (0.07)	3.51	< 0.001

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f) Red squirrel trapping rates

Fixed effect	β (SE)	t-value	p-value
Intercept	0.00 (0.00)	2.98	0.003
Spring-Autumn	-0.39 (0.23)	-1.66	0.10
Summer-Autumn	-0.009 (0.23)	-0.04	0.97
Winter-Autumn	-0.61 (0.23)	-2.59	0.01
Time variable index (measured in passing months)	-0.62 (0.19)	-3.24	< 0.001

g) Species richness

Fixed effect	β (SE)	t-value	p-value
Intercept	0.00 (0.00)	14.58	< 0.001
Time variable index (measured in passing months)	-0.30 (0.06)	-4.62	< 0.001

h) Shannon's diversity index

Fixed effect	β (SE)	t-value	p-value
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Intercept	0.00 (0.00)	7.23	< 0.001
Time variable index (measured in passing months)	-0.26 (0.09)	-3.02	0.003
SPEI-12 (water_presence = 0)	-0.04 (0.09)	-0.47	0.64
Water presence (compared to no water presence)	0.19 (0.29)	0.65	0.58
Interaction term between SPEI-12 and water presence (water_presence = 1)	0.19 (0.07)	2.56	0.01

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Fig. A. Relative abundance of the total independent observations across different animal species. This figure incorporates independent observations from all four camera traps.

	Total independent observations	Percentage
Wild boar (<i>Sus scrofa</i>)	5779	48.02
Roe deer (<i>Capreolus capreolus</i>)	3421	28.43
Red fox (<i>Vulpes vulpes</i>)	1268	10.54
Stone marten (<i>Martes foina</i>)	483	4.01
Common genet (<i>Genetta genetta</i>)	445	3.70
Red squirrel (<i>Sciurus vulgaris</i>)	285	2.37
European badger (<i>Meles meles</i>)	237	1.97
European hare (<i>Lepus europaeus</i>)	117	0.97

Fig. B. Species richness (a) and diversity (b) between locations. The plots show the average species richness and diversity, calculated as the mean of all monthly values over the entire study period for each locality. Analysis of variance (ANOVA) revealed significant differences among all four locations for both variables. Letters denote the outcomes of pairwise comparisons of Estimated Marginal Means (EMM) among the four localities.

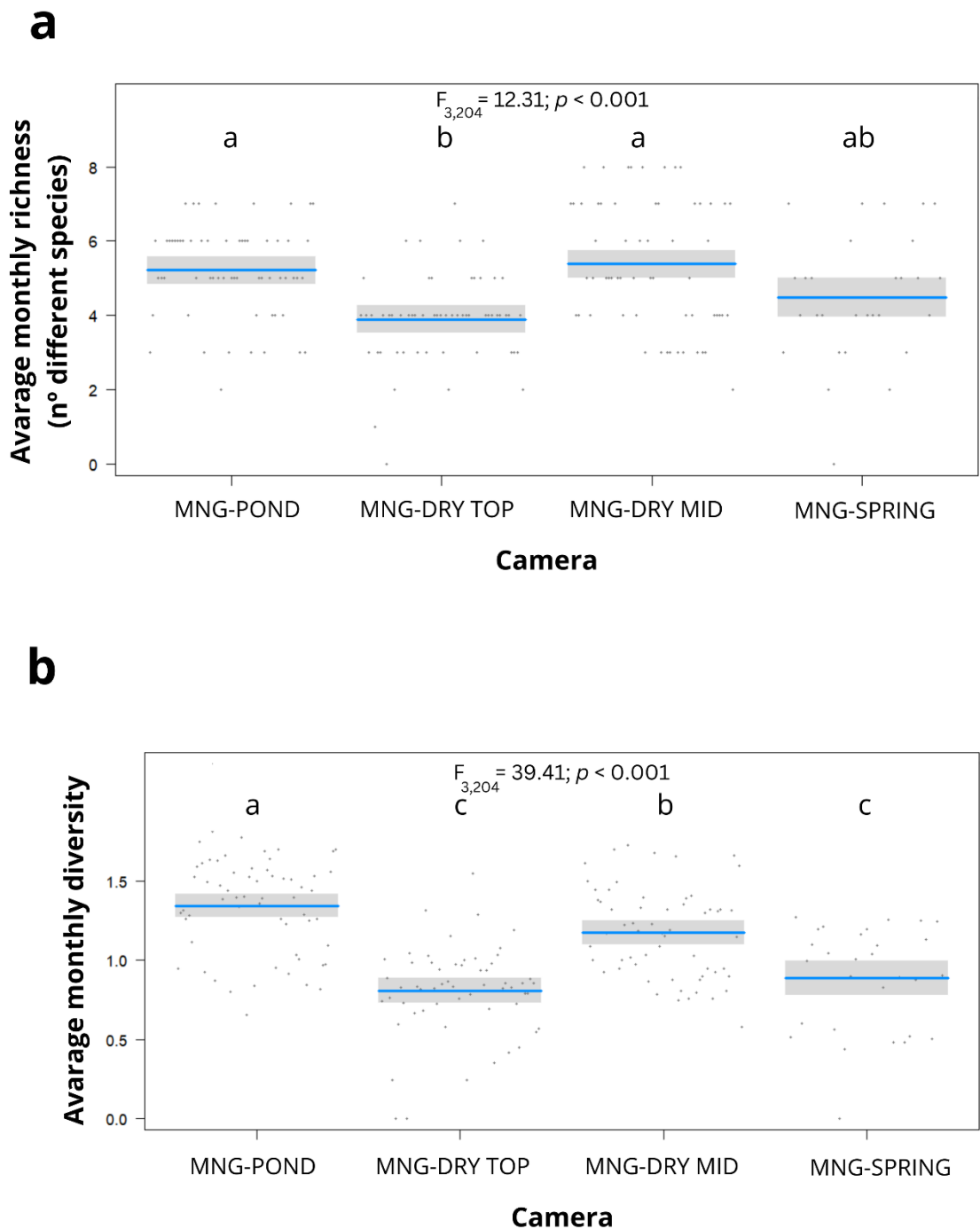


Fig. C. Trapping rates (observations day⁻¹) throughout July 2018 to December 2023 for all eight studied mammals. Wild boar *Sus scrofa* (a), roe deer *Capreolus capreolus* (b), fox *Vulpes vulpes* (c), stone marten *Martes foina* (d), the common genet *Genetta genetta* (e), the red squirrel *Sciurus vulgaris* (f), the European badger *Meles meles* (g), the European hare *Lepus europaeus* (h).

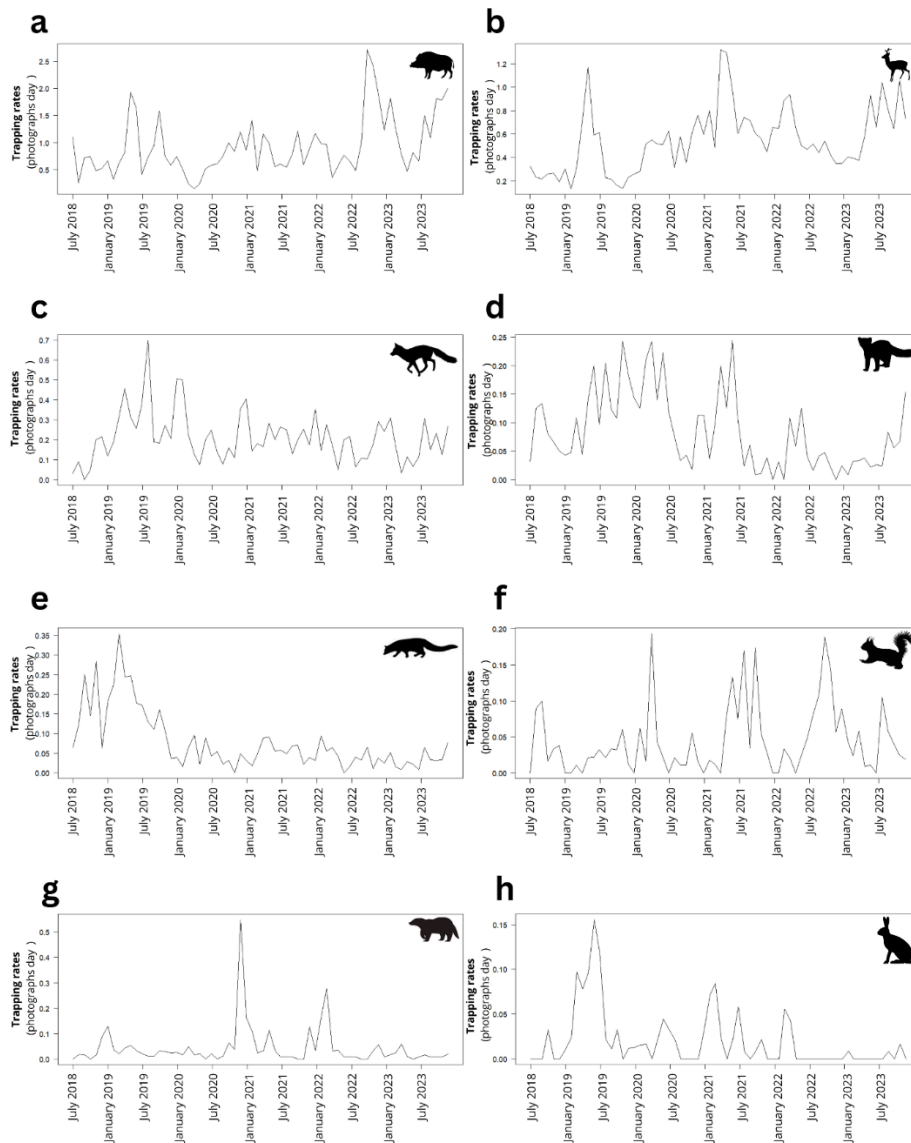


Fig. D. Wild boar trapping rates in relation to drought. Results obtained with wild boar's mixed effect model. Regression lines and 95% confidence intervals are shown. Negative SPEI values indicate drought conditions, while positive values show wetter than normal conditions.

