Acta Oecologica 130 (2026) 104153

Contents lists available at ScienceDirect

Acta Oecologica

journal homepage: www.elsevier.com/locate/actoec

Evaluating biotic interactions in a hard and fragile ecosystem: xerophilous land snails and epilithic cryptogram communities in rocky outcrops

Paula Gavarró[a], Vicenç Bros[b,c], Llorenç Sáez[a], Xavier Santos[d,e], Joan Real[f], Daniel Pons[c], Roger Puig-Gironès[f,*]

[a] Departament de Biologia Animal, de Biologia Vegetal i d'Ecologia (BABVE), Universitat Autònoma de Barcelona (UAB), Catalonia, Spain
[b] Departament de Ciències Ambientals, Universitat de Girona, C. Maria Aurèlia Capmany 69, 17003, Girona, Catalonia, Spain
[c] Servei de Gestió de Parcs Naturals, Diputació de Barcelona, Urgell 187, 08036, Barcelona, Catalonia, Spain
[d] CIBIO Research Centre in Biodiversity and Genetic Resources, InBIO, Universidade do Porto, Campus Agrário de Vairão. R. Padre Armando Quintas, 4485-661, Vairão, Portugal
[e] BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Campus de Vairao, 4485-661, Vairao, Portugal
[f] Equip de Biologia de la Conservació & Institut de la Recerca de la Biodiversitat (IRBIO), Universitat de Barcelona, Av. Diagonal 643, 08028, Barcelona, Catalonia, Spain

ARTICLE INFO

Keywords:
Terrestrial gastropods
Epilithic
Ecological requirements
Rock outcrops
Biodiversity conservation

ABSTRACT

In biodiversity hotspots like rocky outcrops, species distribution is shaped by environmental factors at multiple scales, with microhabitat characteristics like substrate composition and shelter playing key roles. These fragile ecosystems host a rich diversity of species, including endemic and endangered taxa. However, they remain underexplored in conservation research, despite their crucial role in sustaining xerophilic biodiversity. This study investigates the environmental drivers of xerophilous communities, specifically on land snails and epilithic cryptograms, in a Mediterranean Natural Park. Specifically, we examine how substrate composition influences species assemblages and their biotic relationship. Our field data and statistical models reveal that substrate heterogeneity, comprising conglomerates, pebbles, and sand, creates microclimatic conditions that support diverse communities. Land snails are particularly associated with larger pebbles that provide shelter and moisture retention, while epilithic species thrive on conglomerates and finer materials that stabilize micro-habitats. Minimal overlap in habitat preferences between snails and epilithic suggests niche partitioning and complex biotic interactions, highlighting the importance of substrate diversity in sustaining biodiversity. From a conservation perspective, we propose conservation strategies focussed on preserving substrate structural diversity within rocky outcrops to maintain vital habitat features for xerophilous species. Management policies should integrate microhabitat-scale considerations to enhance ecosystem resilience and mitigate disturbances from human and wildlife activities. This research not only advances our understanding of invertebrate ecology in extreme habitats but also offers valuable insights for the conservation of other biodiversity-rich ecosystems facing similar challenges.

1. Introduction

Rock outcrop ecosystems, though sharing common environmental challenges, exhibit considerable variation shaped by local and global drivers (Fitzsimons and Michael, 2017). Stressors such as climate change and forest encroachment threaten their ecological integrity (Santos et al., 2012). Climate change is particularly influential in mountainous areas, where shifting temperatures and changing precipitation regimes alter vegetation structure and biodiversity, especially in rocky habitats hosting highly specialized species (García et al., 2020). Their geological heterogeneity further complicates ecosystem responses to climate variability (Dong et al., 2023), while urbanization, agriculture, tourism, and invasive species exacerbate degradation (Michael et al., 2008; Franklin et al., 2016). Despite these threats, rock outcrops hold exceptional biodiversity and endemism, playing a critical role in ecosystem resilience and functioning (Wang et al., 2016; Fitzsimons and Michael, 2017; Corlett and Tomlinson, 2020).

Mediterranean rock landscapes, characterized by severe temperature

---

* Corresponding author.
E-mail address: roger.puig.girones@gmail.com (R. Puig-Gironès).

https://doi.org/10.1016/j.actao.2025.104153
Received 24 October 2025; Received in revised form 11 December 2025; Accepted 22 December 2025

fluctuations and shallow soils, provide habitats for xerophilic communities adapted to arid conditions (Blondel et al., 2010; Mazzoleni et al., 2004; Puig-Gironès et al., 2023a; Zavala et al., 2010). These landscapes promote the presence of endemic and relict species, particularly land snails, plants and epilithic cryptograms, whose distributions are shaped by microhabitat conditions and limited mobility (Moreno-Rueda, 2007; Bros, 2011; Abeli et al., 2018; Puig-Gironès and Real, 2018; Thompson, 2020). Understanding the environmental factors shaping these communities is therefore essential for conservation.

Land snail distribution arise from multiscale processes (Labaune and Magnin, 2001; Astor, 2014; Gheoca et al., 2021), including moisture (Martin and Sommer, 2004), temperature (Cameron, 1970), altitude (Labaune and Magnin, 2001), soil calcium (Hotopp, 2002), and rock type (Nekola, 1999), as well as microhabitats elements like shelter and humidity retention (Kemencei et al., 2014; South, 1965). Microhabitats under rocks, logs, or litter protect snails against desiccation and predation (Örstan and Pearce, 2006). Although most land snails are herbivores, suggesting links to specific vegetation (Grime and Blythe, 1969), their diets also include lichens and cyanobacteria, as shown for *Chondrina clienta* in limestone habitats (Fröoberg et al., 2011). Feeding patterns often relate less to specific food types and more to microhabitat availability (Beyer and Saari, 1977; Hoffmann et al., 2011; South, 1965), though species-specific lichen preference exist (Fröberg et al., 1993). Despite some evidence for specialization (Grime and Blythe, 1969; Shachak and Steinberger, 1980), snail diets remain poorly understood, emphasizing the central role of microhabitats in determining snail distribution.

In temperate regions, while forests are typical habitats for land snails due to stable micro- and meso-climates, and structural heterogeneity (Dvoøáková and Horsák, 2012), some species also thrive in ruderal habitats (Le Gall and Tooker, 2017) or xeric open areas with limited moisture and shelter (Johnson, 2011; Moreno-Rueda, 2014). Even in seemingly inhospitable environments like rock outcrops or acidic (siliceous) habitats, high richness and specialized communities have been documented (Nekola, 1999, 2010). Rocky habitats also host epilithic communities (bryophytes, lichens, and cyanophytes) (Bros and Llobet, 2011) that play key ecological roles, like soil stabilization (Anderson et al., 1982), rock weathering (Adamo and Violante, 2000), and water retention (Verrecchia et al., 1995). These also serve as a food source for other species (Shachak and Steinberger, 1980), influence microbial-mediated nutrient cycling (Darnajoux et al., 2017; Grube and Berg, 2009; Raghoebarsing et al., 2005), and facilitate plant succession (Spitale and Nascimbene, 2012). Microhabitat preferences (rock, soil, or organic matter) also influences their composition and diversity (Autumn et al., 2020; Brodo, 1973; Spitale & Nascimbene,2012).

Land snails in turn contribute to decomposition, nutrient cycling (Astor, 2014; De Oliveira et al., 2010; Shachak and Steinberger, 1980; Wolters and Ekschmitt, 1997), and serve as a calcium-rich food source (Mänd et al., 2000). They are valuable bioindicators of heavy metal pollution (Baroudi et al., 2020) and environmental health due to their diversity, functional importance, small size, and limited dispersal capacity (Gerlach et al., 2013; Nica et al., 2013). However, interactions among snails, epilithic communities, and habitat structure remain poorly studied in temperate rocky systems.

This study was conducted in the Sant Llorenç del Munt i l'Obac Natural Park (NE Spain), a Mediterranean area with conglomerate and sandstone outcrops supporting rich xerophilous communities (Santos et al., 2012), like other similar regions (Wang et al., 2016; Fitzsimons and Michael, 2017; Corlett and Tomlinson, 2020). This park hosts endemic species such as the sandwort *Arenaria fontqueri* subsp. *cavanillesiana* and the endangered terrestrial gastropod *Xerocrassa montserratensis* (Bros and Llobet, 2011; Martínez-Ortí, 2011; Martinez-Ortí and Bros, 2017), which is restricted to rocky outcrops of NE Iberia. Given the ecological importance and vulnerability of these systems, our aim is to improve understanding of how environmental factors shape xerophilous land snail and epilithic cryptogram communities, with implications for conservation and management. Specifically, we seek to: (i) determine how environmental factors influence the abundance and richness of epilithic and snail communities, (ii) explore potential associations between snail species and epilithic types, (iii) assess whether snail distribution patterns linked to biotic and abiotic factors, (iv) characterize the habitat preferences of *X. montserratensis* to better understand conservation needs, and (v) provide management recommendations to preserve the biodiversity and interactions of rock outcrop ecosystems.

2. Material and methods

2.1. The study area

Sant Llorenç del Munt i l'Obac Natural Park (NE Spain; Fig. 1), part of the Catalan Pre-coastal Mountain Range, covers an area of 13.694 ha and is characterized by an isolated massif of conglomerates and sandstone. This mid-altitude mountain ranges (300-1104 m asl) has a subhumid Mediterranean climate, with 2006–2021 data showing 355.8–897.9 mm annual precipitation ranges and average temperatures of 12.4–14 °C (Puig-Gironès et al., 2023b). The massif comprises a 1000-m-thick sequence of alternating conglomerate and clayey sandstone layers. Cliffs are dominated by well-cemented calcareous pebbles up to 20 m thick, while flatter areas are more clayey and less carbonated (Panareda and Pintó, 1997). Water-driven erosion dissolves clay cement and disaggregates pebbles, shaping the park's distinctive relief, including narrow valleys, caves, deep crevices, and sharp monoliths (Anglés i Vila & Maestro i Maideu, 2012).

Rock outcrops (Fig. 1), typically found on hills and mountain tops above 700 m, have a thin soil layer and combined with the local climate, shape a unique xerophilic community of fauna and flora. Although covering just 4.3 % of the park's total area, these often-isolated outcrops, surrounded by Holm oak forest, contribute significantly to their biodiversity (Santos et al., 2012).

2.2. The study species

The entire Natural Park hosts a diverse gastropod community, with over 90 species, mostly forest and saxicolous specialists (Bros, 2000). Rock outcrops shelter several land snails, which find shelter underneath pebbles or in the scarce vegetation that grows in the area. Notable endemic species include *Abida secale bofilli*, *Chondrina soleri*, *Montserratina bofilliana*, and *X. montserratensis*, all endemic to Barcelona Province, alongside 20 other Iberian endemism (Bros, 2000).

The vegetation in these outcrops is dominated by vascular plants such as *Arenaria fontqueri* subsp. *cavanillesiana*, *Erodium glandulosum*, *Sedum album*, *Narcissus assoanus*, *Dipcadi serotinum* subsp. *serotinum*, and *Thymus vulgaris* (Panareda and Pintó, 1997; Sáez and Aymeric, 2021). The epilithic community, though understudied, includes bryophyte (acrocarpous mosses) from various genera, such as Trichostomum, Bryum, Syntrichia, Tortella, and Grimmia; lichens with diverse thallus morphologies, including fruticose (Cladonia aggr. subrangiformis), squamulose mats (Cladonia aggr. convoluta and Squamarina), and gelatinous (Collema); and gelatinous cyanobacteria such as Nostoc sp. (Gavarró & Sáez, personal observation, March 2024).

2.3. Sampling design

Land snail and vegetation data were obtained from four rock outcrop sites within the park, each with a 1000 m^2 (100 × 100 m) Permanent Sampling Plot (PSP) established within 50 m of the habitat margins to minimize edge effects (Supplementary Fig. S1). These plots have been used since 2019 by the Biodiversity Monitoring Centre of the Mediterranean Mountains (CMBMM) for long-term biodiversity monitoring aimed at detecting changes and guising conservation efforts (Puig-Gironès and Real, 2018). To monitor both vegetation and snails,

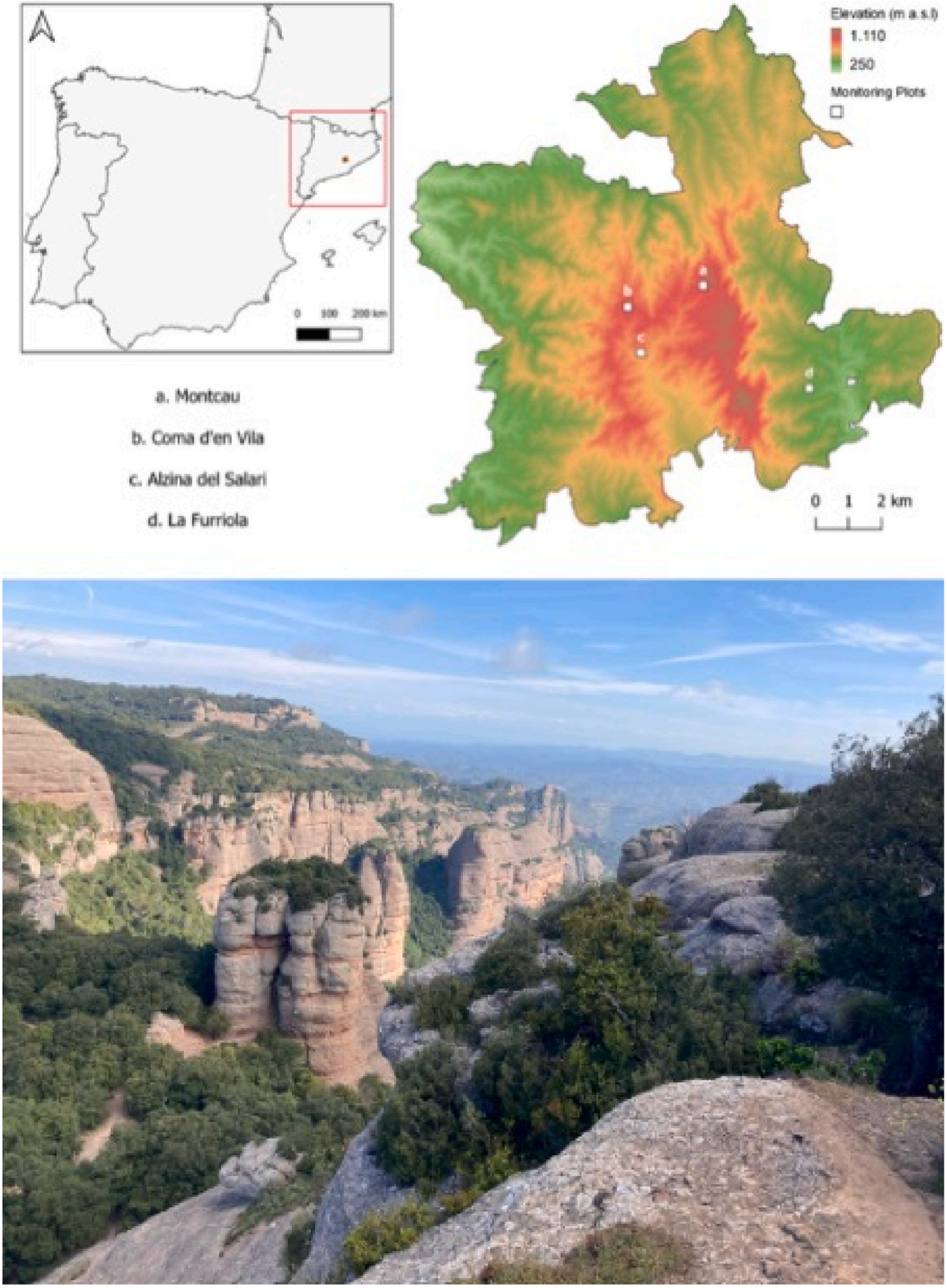

Fig. 1. Geographical location of the four monitoring plots in the Sant Llorenç del Munt i l'Obac Park, Catalonia (Spain): a) Montcau, b) Coma d'en Vila, c) Alzina del Salari, and d) La Furriola. Below, an image of the park landscape, courtesy of Marc Oriol Orpinell (May 2021), highlighting typical monolithic structures found throughout the massif.

five 10 × 10 m sub-plots were randomly placed within each PSP in the first year, with annual resampling, resulting in a total of 20 sub-plots (Fig. 1). Subplots were spaced at least 40 m apart to minimize spatial autocorrelation and were located in homogeneous rock outcrop conditions (>80 % exposed rocky surface). This distance and habitat uniformity reduce the likelihood of pseudoreplication, as each subplot represents an ecologically independent sampling unit within the same outcrop type.

Vegetation data was collected in March 2024 from each sub-plot using five random 50 cm diameter circles, each with a 625 cm^2 square at the centre (i.e., the sample unit). The square was divided into ten 25 cm^2 grid units, and coverage was assessed by counting the number of grid units where bryophyte, lichen or cyanophyte species covered at least 50 %. A picture of each sample unit (circle and square) was taken (Supplementary Fig. S2), and bryophyte samples were collected for lab identification. Bryophyte were identified using the dichotomous keys of Casas et al. (2020), as only mosses were observed. No liverworts or hornworts were found, due to the habitat's unfavourable conditions. Moss nomenclature follows Hodgetts et al. (2020). Coverage data for fruticulose, gelatinose or foliaceus lichens, as well as *Nostoc* sp., were also collected. Species were identified in the field at the genus level, except for *Cladonia*, where two groups (*C. foliacea* and *C. rangiformis*) were recognized.

Gastropod data were collected in spring and autumn of 2020 and 2022 from each sub-plot. The CMBMM's methodology for monitoring rock outcrop snail species, many of which are endemic and protected (Puig-Gironès and Real, 2018), is non-lethal. Due to minimal or absent soil in the habitat (Supplementary Figs. S1 and S2), monitoring relied on visual searches in different microhabitats, including under rocks and dead logs, and within herbaceous and shrubby vegetation. Sampling lasted 30 min per 10 × 10 m sub-plot with one collector or 15 min with two. Individuals were categorized as alive, recently dead, or long dead (Soler Brugués et al., 2025). Recently dead individuals were identified by body partially or completely inside the shell and/or with intact shell coloration, whereas long-dead individuals lacked the body and showed partially or completely discoloured shells. Deceased shells were crushed and left in place for ongoing tracking, helping to correlate mortality with factors like droughts. One individual of the species that could not be identified in the field were collected for laboratory identification. Micro-snails were not targeted because suitable microhabitats (humus, litter, fine soil) are virtually absent in these rocky outcrops, and methods for detecting them involve destructive sampling, which was avoided.

Abiotic variables, relevant to species habitat preferences and their impact on vegetation and microhabitat structure, included slope, orientation, and substrate characteristics (Labaune and Magnin, 2001; Örstan and Pearce, 2006). These variables were measured at the subplot scale to capture microhabitat heterogeneity. Slope (steepness of the terrain), affecting water drainage, soil erosion, and substrate stability (Panareda and Pintó, 1997), was measured with an inclinometer app, providing the angle of inclination for each sample unit. Steeper slopes tend to have faster water runoff, leading to drier conditions, while softer slopes may retain more moisture, supporting different vegetation types and microhabitats (Örstan and Pearce, 2006). Orientation or aspect (the slope's direction, e.g., north, south, east, west), influencing sunlight exposure, soil temperature & therefore moisture levels (Örstan and Pearce, 2006), was measured using a compass app, ensuring precise data for each sample unit. South-facing slopes in the Mediterranean region receive more sunlight, leading to warmer and drier conditions, while north-facing slopes are cooler and moister. On boulders, both aspect and slope are key predictors for bryophyte and lichen presence, affecting light and moisture availability (Spitale and Nascimbene, 2012).

Substrate categories (the surface material covering the ground), were quantified for each sample unit: 1) conglomerate coverage (areas whit large and well-cemented rock fragments); 2) large pebble coverage (areas with pebbles ≥10 cm^2, which provide shelter for snails and affect moisture retention); and 3) small pebble coverage (finer particles like smaller pebbles, sand or clay, supporting different plant and snail species). Substrate analysis was conducted using ImageJ software (Schneider et al., 2012). Field photographs were manually colour-classified by the substrate categories, and ImageJ quantified the coverage for the three categories based on the size of known objects (e.g., circle diameter) (Supplementary Fig. S3). Substrate composition determines the type of vegetation supported (Brodo, 1973) and is crucial for land snails, affecting their movement, shelter, and egg-laying behaviour (Baur, 1988; Moreno-Rueda, 2007).

Lastly, wild boar (*Sus scrofa*) activity was recorded as a potential disturbance indicator. Both vegetation and snail species in the habitat, such as *X. montserratensis*, are mainly threatened by habitat destruction (Altonaga et al., 2011; Bros, 2008). Wild boars can significantly alter the microhabitat by uprooting the scares bulbous vegetation, compacting soil, and changing substrate structure, which may affect snail populations and vegetation cover (Barrios-Garcia and Ballari, 2012).

2.4. Data analysis

Total epilithic species abundance and species richness per sub-plot were modelled using general linear mixed models (GLMM) with the lme4 package (Bates et al., 2015) in R software (R Core Team, 2023). Six explanatory variables were included: orientation, slope, conglomerate coverage, large pebble coverage, small pebble coverage and signs of wild boar damage. Epilithic abundance was modelled a square-root transformed normal distribution to meet normality and homoscedasticity assumptions (Zuur et al., 2009). Species richness followed a log-linear Poisson error structure, suitable for count data (Zuur et al., 2009). GLMMs were fitted with random intercepts for PSP/outcrop to account for hierarchical structure. Epilithic models included only abiotic predictors, avoiding causal inference with snail data. Snail models included only invariant abiotic variables; epilithic cover was used in exploratory analyses with non-causal interpretation. Collinearity among variables was assessed using the variance inflation factor (VIF) with the function "check_collinearity" (Lüdecke et al., 2021). Large pebble coverage, showing moderate correlation (VIF >7) with other variables, was removed (Brodo, 1973).

A permutational multivariate analysis of variance (PERMANOVA) was used to explore spatial patterns in epilithic species composition. This method tests variance based on a distance or dissimilarity measure, using permutations to generate p-values (Anderson, 2001). Bray-Curtis distances were calculated with 999 random permutations using the vegan R package (Okansen et al., 2024). A Mantel test (Mantel, 1967) analysed the correlation between the Bray-Curtis similarity matrix and geographical distance, revealing no significant spatial structure. Consequently, the sampling plot (PSP) was included as a random factor in the GLMMs.

Epilithic abundance variables (moss, lichen, and cyanophyte species coverage) were included in the snail community analysis, adapted to the snail sampling scale (10m × 10m) by averaging data across five sub-plots, resulting in 80 observations (four replicates per sub-plot, two in 2020 and two in 2021). Environmental variables considered were: orientation, slope, conglomerate coverage, large pebble coverage, small pebble coverage, wild boar damage, and epilithic abundance. Two GLMM were fitted for the two response variables, total snail abundance and species richness per sub-plot. Following a collinearity check (Lüdecke et al., 2021), the small pebble coverage variable was excluded due to its low significance in providing suitable shelter for snails (Bros, 2011; Cook, 2001). Total abundance was modelled, with a square root transformation using the predictor variables, and species richness was modelled using a log-linear Poisson error structure. The sampling plot was included as a random factor, based on results from a PERMANOVA and a Mantel Test.

To explore snail community distribution and organization, a partial redundancy analysis (RDA) was performed. This ordination method revealed relationships between species community composition and environmental variables while controlling for spatial effects (Legendre and Legendre, 2012). Hellinger-transformed species abundance data were analysed using the *vegan* R package (Okansen et al., 2024) to reduce the influence of highly abundant species. The predictor matrix included abiotic variables (standardized to a mean of 0 and a standard deviation of 1) and epilithic coverage, also Hellinger-transformed. The PSP was treated as a covariate, and the RDA significance was assessed using ANOVA-like permutation tests (999 iterations).

The endemic and protected species *X. montserratensis*, accounting for over 45 % of sightings and present in all outcrops but not in every subplot, was further analysed. Its abundance was modelled using the same GLMM approach applied to the total snail abundance with a square root transformation. Because zeros occurred at the subplot level, we used a zero-inflated Poisson error structure to account for excess zeros.

3. Results

3.1. Epilithic data analysis

In the study area, a diverse assemblage of epilithic species were identified (Supplementary Table S4). The bryophyte community within the class Bryopsida included the species *Trichostomum crispulum*, *Bryum sp.*, *Tortella squarrosa*, *Syntricha montana*, and *Grimmia orbicularis*. Lichenized fungi (phylum Ascomycota, class Lecanoromycetes) also contributed to the epilithic diversity with members of the *Cladonia* group, specifically *C. convoluta* and *C. subrangiformis*, as well as *Collema* sp. and *Squamarina* sp. alongside cyanobacteria from the genus *Nostoc* sp.

The GLMM analysis showed that substrate composition variables, specifically conglomerate coverage and small pebble coverage, had a significant positive effect on epilithic abundance (Table 1). As the conglomerate coverage and the small pebble coverage increases, epilithic abundance also rises, as shown by positive estimated scores and 95 % confidence intervals that do not overlap zero (Fig. 2). For species richness, only conglomerate coverage had a significant positive effect (Table 1), suggesting its key role in influencing species richness in the study area. This is further supported by the confidence interval for conglomerate coverage remains entirely above zero (Fig. 2).

The PERMANOVA analysis showed a significant effect of plot on epilithic community structure ($F_{3,59} = 5.74, p = 0.001, R^2 = 0.226$), indicating that 22.6 % of the variation in community composition across sites is explained by plot. However, the Mantel test, comparing the Bray-Curtis dissimilarity matrix with geographical distance between plots, revealed no significant spatial pattern ($r = -0.51, p = 0.875$), suggesting that the observed differences were not driven by spatial pattern.

3.2. Snail data analysis

The gastropod community in the study area consists of both endemic and widespread species (Supplementary Table S5). Notable endemic species include *C. soleri*, *M. bofilliana*, *X. montserratensis*, and *Xerocrassa penchinati*, characteristic of the local fauna. Additionally, widespread species found in the Iberian Peninsula include *Chondrina tenuimarginata*, and *Graniberia braunii*. The most common species observed were *Cepaea nemoralis*, *Ferussacia folliculum*, *Granopupa granum*, *Jaminia quadridens*, *Pomatias elegans*, *Pseudotachea splendida*, and *Rumina decollata*. All species belong to the order Stylommatophora, except *P. elegans* which belongs to the order Littorinimorpha.

Table 1

Fixed Effect Estimates from the Linear Mixed-Effects Model for total epilithic abundance and species richness. The table presents the slop estimates, associated standard errors (SE), and p-values for each variable.

Fixed Effect	Epilithic abundance			Epilithic richness		
	Estimate	SE	p-value	Estimate	SE	p-value
Intercept	6.23	2.68	0.07	−0.17	0.39	0.66
Wild boars	1.03	2.98	0.74	−0.08	0.41	0.84
Orientation	−0.90	0.88	0.32	−0.15	0.10	0.13
Slope	0.48	0.65	0.46	−0.12	0.12	0.34
Conglomerate coverage	4.09	1.02	<0.001	0.42	0.20	0.04
Small pebble coverage	2.60	0.97	0.009	0.34	0.21	0.10

The fixed effect estimates from the snail abundance GLMM model indicate that large pebble coverage significantly positive effected snail abundance (Table 2), as shown by its confidence interval not crossing the zero line (Fig. 3). No other predictors showed significant effects. For species richness, the GLMM revealed no significant effects from any predictors (Fig. 3). The intercept in both models was significant, suggesting a baseline level of abundance and species richness that remains unexplained by the included predictors (Table 2).

The PERMANOVA analysis for the land snail dataset revealed a significant influence of plot on community structure ($F_{3,59} = 6.48, p = 0.001, R^2 = 0.205$), meaning that 20.5 % of the variation in community composition across sites is attributed to plot. However, the Mantel test comparing Bray-Curtis dissimilarity and geographical distance indicated that observed differences were not due to spatial patterns ($r = 0.308$, $p = 0.41667$).

The RDA analysis of the snail community data showed that environmental variables explained 12.76 % of the total variance in species composition, after accounting for spatial factors. The first axis (RDA1), which explains 34.2 % of the constrained variance, was statistically significant ($F = 9.12$, $p = 0.007$), indicating that habitat structure and disturbance-related factors may influence snail distribution. In contrast, the second axis (RDA2), explaining 19.7 % of the variance, was not significant ($p = 0.365$), suggesting weaker environmental gradients. Although the adjusted R^2 was low (0.114), the first axis explained 34.2 % and the second axis 19.7 % of the constrained variance, which is substantial for observational studies in complex natural habitats. Nevertheless, these associations should be interpreted with caution.

The ordination plot derived from the RDA (Fig. 4) reveals that *X. montserratensis* is weakly associated with slope and the presence of wild boars along RDA1, though the latter correlation is weaker. *X. montserratensis* shows also correlates positively with the moss *Bryum sp.*, the lichen *Squamarina sp.*, and, to a lesser extent, with *G. orbicularis* abundance, suggesting a preference of these epilithic types and same microhabitat characteristics. *G. granum*, by contrast, is strongly related with large pebble coverage along RDA2, although this axis is not significant. On RDA1, *G. granum* mirrors the associations of *X. montserratensis* but with weaker correlations, indicating a more generalized habitat preference.

On the negative side of the RDA1 axis, the snail species *C. soleri*, *C. tenuimarginata*, and *C. nemoralis* are closely associated with conglomerate coverage and orientation. This relationship extends to the epilithics, including the cyanophyte *Nostoc* sp., the lichens *Cladonia* group *convolute*, *Cladonia* group *subrangiformis*, and *Collema* sp., as well as the mosses *T. squarrosa*, and *T. crispulum*, indicating a preference for microhabitats with suitable substrate and orientation. These species are negatively related with slope, wild boar activity, and large pebble coverage. The remaining snail species in the study area do not exhibit clear associations with the environmental variables, as reflected by their central position in the ordination plot.

The GLMM analysis for *X. montserratensis* abundance revealed that none of the selected environmental variables had a significant effect, except for orientation, which approached significance (Table 2). However, the slop and the vegetation abundance were close to the signification. The model's intercept was highly significant, suggesting that unmeasured factors may play a key role in determining the abundance of this species in the study area.

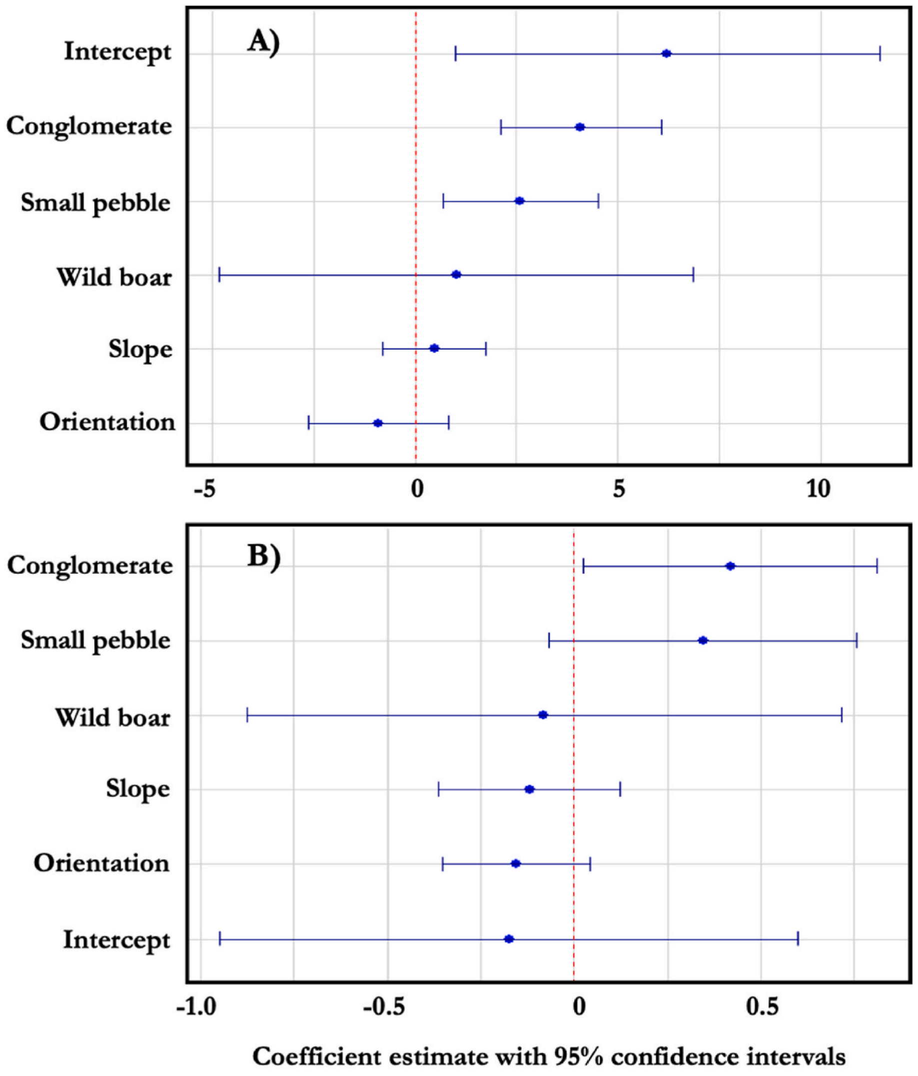

Fig. 2. Estimated 95 % confidence intervals for the predictors used in the models, where (A) for total epilithic abundance and, (B) for species richness within the epilithic community.

Table 2
Fixed Effect Estimates from the Mixed-Effects Models for the land snail abundance, land snail species richness and *Xerocrassa montserratensis* abundance. The table presents the slop estimates, associated standard errors (SE), and p-values for each variable.

Fixed effect	Lad snail abundance			Lad snail richness			*X. montserratensis* abundance		
	Estimate	SE	p-value	Estimate	SE	p-value	Estimate	SE	p-value
Intercept	2.89	0.27	<0.001	0.98	0.14	<0.001	1.42	0.18	<0.001
Wild boar activity	−0.40	0.27	0.17	−0.16	0.18	0.37	−0.30	0.22	0.17
Orientation	−0.06	0.12	0.66	0.07	0.08	0.39	−0.27	0.11	0.02
Slope	−0.06	0.15	0.72	−0.06	0.1	0.56	−0.24	0.13	0.05
Conglomerate coverage	0.08	0.17	0.64	0.005	0.10	0.99	0.11	0.09	0.23
Large pebble coverage	0.33	0.13	0.02	0.09	0.08	0.29	0.14	0.14	0.33
Vegetation abundance	0.25	0.15	0.11	0.15	0.09	0.09	−0.22	0.13	0.08

4. Discussion

This study provides valuable insights into the habitat preferences of xerophilous land snails and epilithic communities in Mediterranean rock outcrops. By examining a range of environmental factors related to habitat characteristics, this research advances understanding of the mechanisms driving species abundance and distribution in these challenging environments. The findings emphasize the role of substrate composition as a key determinant of both epilithic and land snail communities. However, despite some limitations, such as the small number of rock outcrop sites and the temporal mismatch between epilithic and land snail data collection, our results offer relevant findings for conservation and habitat management in these fragile and unique environments. Although our sampling focused on visual searches in rocky habitats with minimal soil and litter, this approach is appropriate for saxicolous and medium-sized species. Micro-snails typically associated with humus or leaf litter are unlikely to occur in these outcrops due to the absence of such substrates, which explains their absence in our dataset. Furthermore, relationships between epilithic cover and snail communities are considered exploratory due to the temporal mismatch

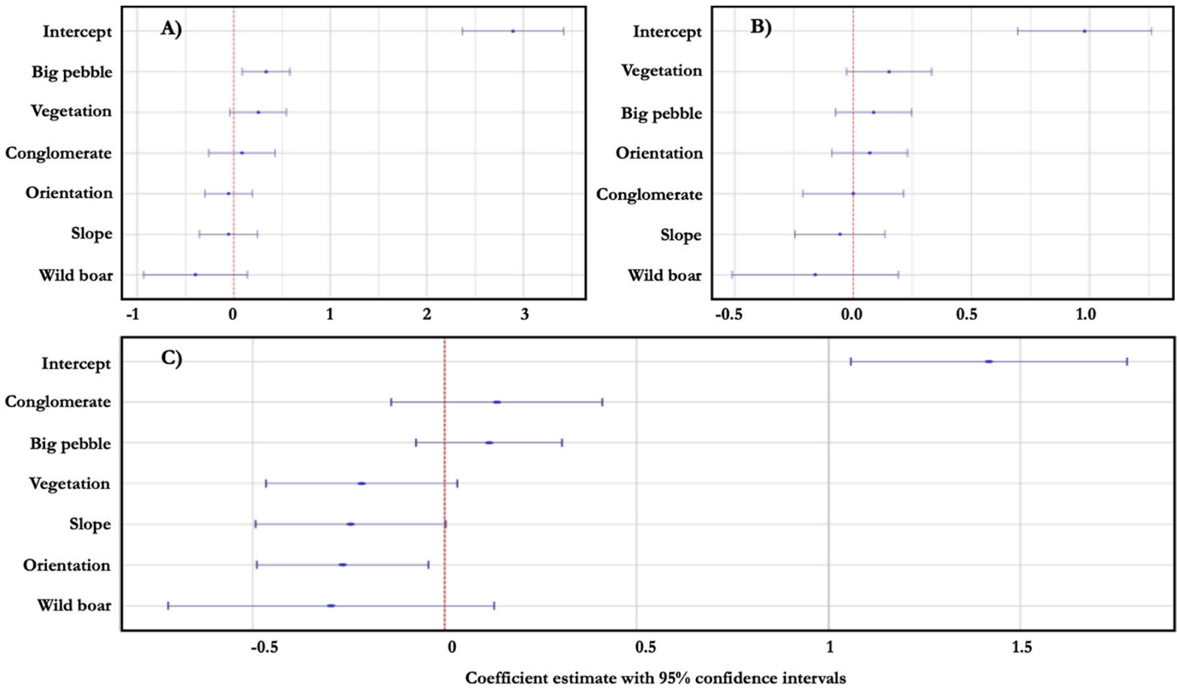

Fig. 3. Estimated model 95 % confidence intervals for the predictors used in the models, where (A) for land snail total abundance, (B) species richness in the study area, and (c) *Xerocrassa montserratensis* abundance.

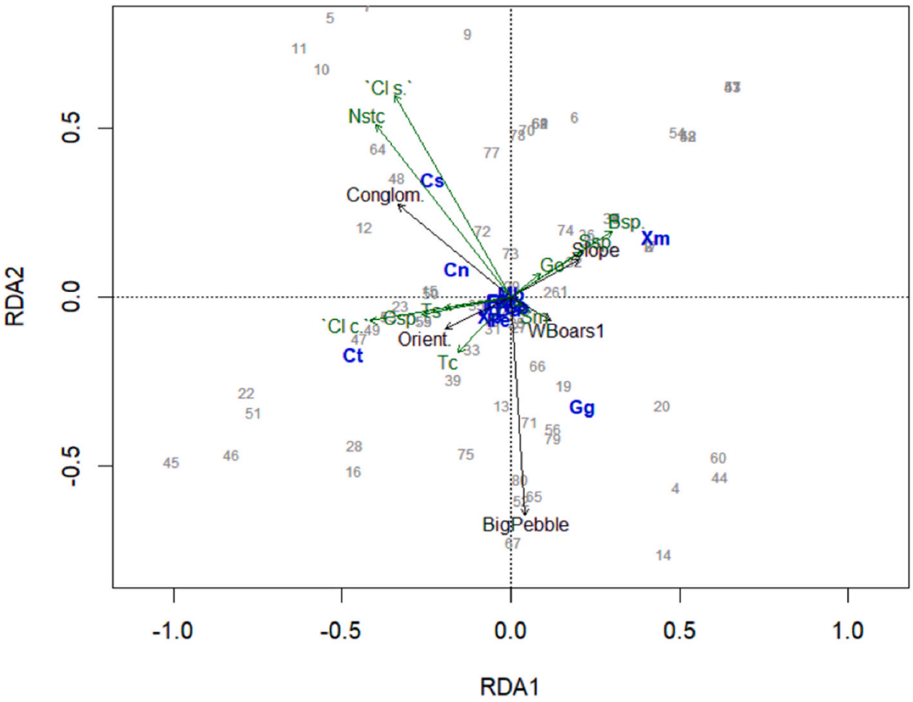

Fig. 4. Partial redundancy analysis (RDA) plot displaying abbreviated names for both species and environmental variables. Land snail species are shown in bold blue (where, Xm corresponds to *Xerocrassa montserratensis*; Gg = *Granopupa granum*, Cs= *Chondrina soleri*, Cn = *Cepaea nemoralis*, Ct = *Chondrina tenuimarginata*). Lichen, cyanophyte, and bryophyte species are in dark green (Bsp = *Bryum* sp., Ssp = *Squamarina* sp., Go = *Grimmia orbicularis*, Cl c = *Cladonia* group *convoluta*, Cl s = *Cladonia* group *subrangiformis*, Csp = *Collema* sp., Tc = *Trichostomum crispulum*, Ts = *Tortella squarrosa*, Nstc = *Nostoc sp.*). Abiotic variables are in black (Conglom = conglomerate coverage, BigPebble = Large pebble cover, WBoars = wild boars damage, Orient = sub-plot orientation, and Slope = sub-plot slope). Sampling 10x10 sub-plots are indicated in grey. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

between datasets and should not be interpreted as causal.

Our results suggest that epilithic abundance tends to increase with higher conglomerate coverage and the presence of sand, clay, and small pebbles. These patterns align with previous studies, indicating that specific epilithic species thrive in rocky substrates due to their ability to tolerate harsh conditions and rely on stable microclimates (Cannon et al., 2020). The presence of moss species like *T. squarrosa*, which prospers in stabilized gravel and sandy substrates (Köckinger and

Hedenäs, 2023), further supports the idea that epilithics are well-adapted to substrate variations.

Epilithic abundance, influenced by conglomerate coverage and fine substrates, aligns with the habitat preferences of certain species present in the area. For example, *Collema* sp. thrives on rocks (Cannon et al., 2020), so increased conglomerate coverage naturally promotes its presence. Similarly, moss species like *T. squarrosa*, which grow in moist, stabilized gravel or sand (Köckinger and Hedenäs, 2023), benefit from higher sand, clay and small pebble coverage, which also supports species with similar ecological requirements. Notably, conglomerate coverage appeared to influence not only epilithic abundance but also species richness, suggesting that substrate diversity enhances community complexity by providing a range of microhabitats suited to different epilithic species. This underscores the potential role of substrate heterogeneity in maintaining biodiversity in xerophilic environments (Spitale and Nascimbene, 2012).

Land snail abundance showed a tendency to correlated with large pebbles coverage, a substrate feature that retains moisture and provide shelter, both critical for snail survival in arid environments (Baskin et al., 2007; Dvoǿáková and Horsák, 2012; Spitale and Nascimbene, 2012). The separation of large pebbles from the conglomerate matrix may further enhances these microhabitats, creating conditions favourable for snails.

Overall, the link between epilithic and snail abundance was weak, and any patterns should be considered exploratory. For example, *X. montserratensis* showed a weak association with slope and wild boar activity in the RDA analysis, suggesting that these factors may contribute to habitat heterogeneity rather than exerting a strong filtering effect. Slope influences microclimatic conditions such as moisture retention and temperature fluctuations, which are important for gastropods in arid environments (Kemencei et al., 2014). While wild boar activity, although often disruptive, may create microhabitats through soil disturbance, increasing heterogeneity in vegetation and substrate composition (Barrios-Garcia and Ballari, 2012). However, the GLMM results did not identify wild boar activity as a significant predictor of *X. montserratensis* abundance, indicating that its influence is likely indirect or confounded with other unmeasured factors. Similarly, epilithic species such as *Bryum sp.*, *Squamarina sp.* and *G. orbicularis* appear to share similar microhabitat preferences with *X. montserratensis*. *G. granum* also shows some preference for larger pebbles, suggesting it may benefit from similar microhabitat conditions. Although RDA suggested these associations, they were not confirmed by GLMM, reflecting the distinct nature of the two approaches: RDA captures multivariate gradients in community composition, whereas GLMM tests individual predictors for a single species. Therefore, these patterns should be considered exploratory rather than causal.

Conversely, *C. tenuimarginata* and *C. soleri* seems to prefer stable microhabitats with less slope and the absence of wild boar activity. These habitats are also characterised by higher conglomerate coverage and specific orientations. *Chondrina* species are typically associated with rocks and walls, particularly limestone substrates (Somoza-Valdeolmillos et al., 2022). *C. tenuimarginata* is frequently found in open rocky areas with vertical walls (Bros, 2000), which aligns with the observed association with conglomerate coverage. These species also show a preference for certain epilithic taxa, such as *Nostoc sp.*, *Collema sp*. and *Cladonia* species, suggesting a shared affinity for specific microhabitats with snails. *C. nemoralis*, a widely distributed species across Europe (Welter-Schultes, 2012), however, appears in this study to be linked with *Chondrina sp*. species adapted to xerophilic open rock environments.

While environmental variables play a role in shaping these communities, other unmeasured factors may also be influential. Historical processes, interspecific interactions, and climate change could all be significant drivers of species distribution in Mediterranean rock outcrops (Cameron et al., 1980; Magnin et al., 1995). The drought conditions during the study period likely affected both epilithic and snail communities (Essa et al., 2023), potentially introducing bias into the results. Future research should explore the impact of extreme climatic events on these fragile ecosystems and explore microclimatic conditions, soil chemistry, and biotic interactions in greater detail.

Another point to consider is the lack of a clear relationship between epilithic and snail abundances. The ecology of land snails, particularly their feeding preferences and habitat selection, remains largely unstudied (Cook, 2001; Grime and Blythe, 1969). Both land snails and epilithic organisms are valuable bioindicators of ecosystem health (Gerlach et al., 2013; Gheoca et al., 2021; Halleraker et al., 1998; Puig-Gironès and Real, 2018), and any significant habitat changes, whether due to human activity or climate change, could have profound consequences for these vulnerable species (Lydeard et al., 2004; Nicolai and Ansart, 2017). Conservation efforts should focus on preserving the structural diversity of rock outcrop habitats, particularly the varied substrates that support both snail and epilithic communities.

This study represents one of the first efforts to explore biotic and abiotic interactions in Mediterranean rock outcrops. Our results emphasize the role of substrate composition and microhabitat heterogeneity as key factors influencing epilithic and snail communities, although the ecological link between these two groups remains weak and should be interpreted cautiously. The relatively low explanatory power of the models reflects the complexity of these ecosystems and the influence of unmeasured factors, underscoring the need for further research. Although our findings provide limited evidence for direct management actions, they align with previous studies highlighting the vulnerability of rock outcrop habitats to multiple pressures. Foot traffic and domestic animal movement can cause erosion and homogenization of microhabitats, reducing essential substrate diversity for both snails and epilithic (Spitale and Nascimbene, 2012). Establishing designated pathways and restricting access to key areas may help preserve habitat integrity. Educational programs for park visitors, highlighting the ecological value of these habitats, could further reduce human impact.

Forest encroachment into rock habitats should also be monitored, as afforestation, reduces the availability of open spaces for xerophilous species like *X. montserratensis* and *C. soleri* (Santos et al., 2012). These species depend on microclimatic conditions provided by open rocky habitats, and fragmentation could lead to biodiversity loss through extinction debt (Cameron et al., 1980). Forest management should therefore include measures to maintain open rock outcrops. Wild boar activity showed only weak and inconsistent associations in our analyses, but previous research indicates that their foraging behavior can damage microhabitats by uprooting bulbous plants and disturbing substrates (Barrios-Garcia and Ballari, 2012; Kemencei et al., 2014). Monitoring their impact and considering population control in sensitive areas may be necessary.

Lastly, climate change and extreme events such as droughts pose additional risks to xerophilous species (Essa et al., 2023). Long-term monitoring programs, such as the one implemented in this study (Puig-Gironès and Real, 2018), are essential for detecting trends and informing adaptive management. Furthermore, recent genetic evidence identifying four distinct evolutionary units within *X. montserratensis* (Català et al., 2021) reinforces the need to integrate genetic diversity into future conservation planning.

CRediT authorship contribution statement

Paula Gavarró: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Vicenç Bros:** Writing – review & editing, Writing – original draft, Validation, Methodology, Investigation. **Llorenç Sáez:** Writing – review & editing, Writing – original draft, Validation, Supervision, Methodology, Investigation, Data curation, Conceptualization. **Xavier Santos:** Writing – review & editing, Writing – original draft, Validation, Supervision, Conceptualization. **Joan Real:** Writing – review & editing, Funding acquisition. **Daniel Pons:** Writing –

review & editing, Funding acquisition. **Roger Puig-Gironès:** Writing – review & editing, Writing – original draft, Validation, Supervision, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

Funding statement

This work has been carried out through the Biodiversity Monitoring Centre of Mediterranean Mountains (CMBMM) thanks to a convention of Diputació de Barcelona and Universitat de Barcelona (Exp. 2021/0016157).

Declaration of competing interest

Acknowledgements

So, we are grateful to Joana Barber, Angel Miño and David Carrera for their support. We would also like to thank Agents Rurals de la Generalitat de Catalunya for the drone images caption.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.actao.2025.104153.

Data availability

Data will be made available on request.

References

Abeli, T., Vamosi, J.C., Orsenigo, S., 2018. The importance of marginal population hotspots of cold-adapted species for research on climate change and conservation. J. Biogeogr. 45, 977–985. https://doi.org/10.1111/jbi.13196.

Adamo, P., Violante, P., 2000. Weathering of rocks and neogenesis of minerals associated with lichen activity. Appl. Clay Sci. 16, 229–256. https://doi.org/10.1016/S0169-1317(99)00056-3.

Altonaga, K., Puente, A.I., Martínez-Ortí, A., Prieto, C.E., Gómez-Moliner, B.J., 2011. *Xerocrassa montserratensis* (hidalgo, 1870). In: Verdú, J.R., Numa, C., Galante, E. (Eds.), Atlas Y Libro Rojo De Los Invertebrados Amenazados De España (Especies Vulnerables), vol. II. Dirección General de Medio Natural y Política Forestal, Ministerio de Medio Ambiente, Medio Rural y Marino, Madrid, pp. 971–974.

Anderson, D.C., Harper, K.T., Holmgren, R.C., 1982. Factors influencing development of cryptogramic soil crusts in Utah deserts. J. Range Manag. 35, 180. https://doi.org/10.2307/3898386.

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecol. 26 (1), 32–46. https://doi.org/10.1111/j.1442-9993.2001.01070 x.

Anglès i Vila, M., Maestro i Maideu, E., 2012. Els conglomerats de Sant Llorenç del Munt (Eocè mitjà-superior). Butlletí de la Institució Catalana d'Història Natural 76, 71–82.

Astor, T., 2014. What do Snails do in Ecosystems? It is a Matter of Traits. Swedish University of Agricultural Sciences, Uppsala. Doctoral thesis.

Autumn, K., Barcenas-Peña, A., Kish-Levine, S., Huang, J.-P., Lumbsch, H.T., 2020. Repeated colonization between arid and seasonal wet habitats, frequent transition among substrate preferences, and chemical diversity in Western Australian Xanthoparmelia lichens. Front. Ecol. Evol. 8. https://doi.org/10.3389/fevo.2020.00129.

Baroudi, F., Al Alam, J., Fajloun, Z., Millet, M., 2020. Snail as sentinel organism for monitoring the environmental pollution; a review. Ecol. Indic. 113, 106240. https://doi.org/10.1016/j.ecolind.2020.106240.

Barrios-Garcia, M.N., Ballari, S.A., 2012. Impact of wild boar (*Sus scrofa*) in its introduced and native range: a review. Biol. Invasions 14, 2283–2300. https://doi.org/10.1007/s10530-012-0229-6.

Baskin, J.M., Baskin, C.C., Lawless, P.J., 2007. Calcareous rock outcrop vegetation of eastern North America (exclusive of the Nashville Basin), with particular reference to use of the term "cedar glades". Bot. Rev. 73. https://doi.org/10.1663/0006-8101(2007)73[303:crovoe]2.0.co;2.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Software 67. https://doi.org/10.18637/jss.v067.i01.

Baur, B., 1988. Population regulation in the land snail *Arianta arbustorum*: density effects on adult size, clutch size and incidence of egg cannibalism. Oecologia 77, 390–394. https://doi.org/10.1007/BF00378049.

Beyer, W.N., Saari, D.M., 1977. Effect of tree species on the distribution of slugs. J. Anim. Ecol. 46, 697. https://doi.org/10.2307/3635.

Blondel, J., Aronson, J., Bodiou, J.-Y., Boeuf, G., 2010. The Mediterranean Region: Biological Diversity in Space and Time. Oxford University Press, Oxford.

Brodo, I.M., 1973. Substrate ecology. In: Ahmadjian, V., Hale, M.E. (Eds.), The Lichens. Academic Press, U.S, pp. 401–441. https://doi.org/10.1016/B978-0-12-044950-7.50017-9.

Bros, V., 2000. Els mol·luscs gasteròpodes (Mollusca, Gasteropoda) del massís de Sant Llorenç del Munt i la serra de l'Obac. V Trobada d'Estudiosos de Sant Llorenç del Munt i l'Obac 29, 87–95. https://doi.org/10.5281/zenodo.6199541.

Bros, V., 2008. *Xerocrassa montserratensis* (Hidalgo, 1870). In: ICHN (Ed.), Invertebrats Que Requereixen Mesures De Conservació a Catalunya, 63. Institució Catalana d'Història Natural, Barcelona, p. 61. https://doi.org/10.13140/RG.2.2.28713.26728.

Bros, V., 2011. Composició de la comunitat de mol·luscs de les codines en el Parc Natural de Sant Llorenç del Munt i l'Obac, i l'impacte del trepig i l'erosió en el Montcau. VII Monografies de Sant Llorenç del Munt i l'Obac 7, 43–52. https://doi.org/10.5281/zenodo.6162548.

Bros, V., Llobet, T., 2011. Flora i Fauna Del Parc Natural De Sant Llorenç Del Munt I L'Obac. BRAU edicions, Barcelona.

Cameron, R.A.D., 1970. The effect of temperature on the activity of three species of Helicid snail (Mollusca: gastropoda). J. Zool. 162, 303–315. https://doi.org/10.1111/j.1469-7998.1970.tb01267.x.

Cameron, R.A.D., Down, K., Pannet, D.J., 1980. Historical and environmental influences on hedgerow snail faunas. Biol. J. Linn. Soc. 13, 75–87. https://doi.org/10.1111/j.1095-8312.1980.tb00071.x.

Cannon, P., Otálora, M., Košuthová, A., Wedin, M., Aptroot, A., Coppins, B., Simkin, J., 2020. Peltigerales: collemataceae. Revisions of British and Irish Lichens 2. https://doi.org/10.3929/ethz-b-000450927. British Lichen Society, Zurich.

Casas, C., Brugués, M., Cros, R.M., Sérgio, C., 2020. Handbook of Mosses of the Iberian Peninsula and the Balearic Islands. Institut d'Estudis Catalans, Barcelona.

Català, C., Bros, V., Castelltort, X., Santos, X., Pascual, M., 2021. Deep genetic structure at a small spatial scale in the endangered land snail *Xerocrassa montserratensis*. Sci. Rep. 11, 8855. https://doi.org/10.1038/s41598-021-87741-7.

Cook, A., 2001. Behavioural ecology: on doing the right thing, in the right place at the right time. In: Barker, G.M. (Ed.), The Biology of Terrestrial Molluscs, 487. CABI publishing, New York, p. 447. https://doi.org/10.1079/9780851993188.0447.

Corlett, R.T., Tomlinson, K.W., 2020. Climate change and edaphic specialists: irresistible force meets immovable object? Trends Ecol. Evol. 35, 367–376. https://doi.org/10.1016/j.tree.2019.12.007.

Darnajoux, R., Zhang, X., Mcrose, D.L., Miadlikowska, J., Lutzoni, F., Kraepiel, A.M.L., Bellenger, J., 2017. Biological nitrogen fixation by alternative nitrogenases in boreal cyanolichens: importance of molybdenum availability and implications for current biological nitrogen fixation estimates. New Phytol. 213, 680–689. https://doi.org/10.1111/nph.14166.

De Oliveira, T., Hättenschwiler, S., Handa, I.T., 2010. Snail and millipede complementarity in decomposing Mediterranean forest leaf litter mixtures. Funct. Ecol. 24, 937–946. https://doi.org/10.1111/j.1365-2435.2010.01694.x.

Dong, X., Martin, J., Cohen, M., Tu, T., 2023. Bedrock mediates responses of ecosystem productivity to climate variability. Commun. Earth Environ. 4. https://doi.org/10.1038/s43247-023-00773-x.

Dvořáková, J., Horsák, M., 2012. Variation of snail assemblages in hay meadows: disentangling the predictive power of abiotic environment and vegetation. Malacologia 55, 151–162. https://doi.org/10.4002/040.055.0110.

Essa, Y.H., Hirschi, M., Thiery, W., El-Kenawy, A.M., Yang, C., 2023. Drought characteristics in Mediterranean under future climate change. npj Clim. Atmos. Sci. 6, 133. https://doi.org/10.1038/s41612-023-00458-4.

Fitzsimons, J.A., Michael, D.R., 2017. Rocky outcrops: a hard road in the conservation of critical habitats. Biol. Conserv. 211, 36–44. https://doi.org/10.1016/j.biocon.2016.11.019.

Franklin, J., Serra-Díaz, J., Syphard, A., Regan, H., 2016. Global change and terrestrial plant community dynamics. Proc. Natl. Acad. Sci. 113, 3725–3734. https://doi.org/10.1073/pnas.1519911113.

Fröberg, L., Baur, A., Baur, B., 1993. Differential herbivore damage to calcicolous lichens by snails. Lichenologist 25, 83–95. https://doi.org/10.1006/lich.1993.1015.

Fröoberg, L., Stoll, P., Baur, A., Baur, B., 2011. Snail herbivory decreases cyanobacterial abundance and lichen diversity along cracks of limestone pavements. Ecosphere 2, 1–43. https://doi.org/10.1890/ES10-00197.1.

García, M.B., Domingo, D., Pizarro, M., Font, X., Gómez, D., Ehrlén, J., 2020. Rocky habitats as microclimatic refuges for biodiversity. A close-up thermal approach. Environ. Exp. Bot. 170, 103886. https://doi.org/10.1016/j.envexpbot.2019.103886.

Gerlach, J., Samways, M., Pryke, J., 2013. Terrestrial invertebrates as bioindicators: an overview of available taxonomic groups. J. Insect Conserv. 17, 831–850. https://doi.org/10.1007/s10841-013-9565-9.

Gheoca, V., Benedek, A.M., Schneider, E., 2021. Exploring land snails' response to habitat characteristics and their potential as bioindicators of riparian forest quality. Ecol. Indic. 132, 108289. https://doi.org/10.1016/j.ecolind.2021.108289.

Grime, J.P., Blythe, G.M., 1969. An investigation of the relationships between snails and vegetation at the Winnats Pass. J. Ecol. 57, 45–66. https://doi.org/10.2307/2258207.

Grube, M., Berg, G., 2009. Microbial consortia of bacteria and fungi with focus on the lichen symbiosis. Fungal Biology Reviews 23, 72–85. https://doi.org/10.1016/j.fbr.2009.10.001.

Halleraker, J.H., Reimann, C., De Caritat, P., Finne, T.E., Kashulina, G., Niskaavaara, H., Bogatyrev, I., 1998. Reliability of moss (*Hylocomium splendens* and *Pleurozium schreberi*) as a bioindicator of atmospheric chemistry in the Barents region: interspecies and field duplicate variability. Sci. Total Environ. 218, 123–139. https://doi.org/10.1016/S0048-9697(98)00205-8.

Hodgetts, N.G., Söderström, L., Blockeel, T.L., Caspari, S., Ignatov, M.S., Konstantinova, N.A., Lockhart, N., Papp, B., Schröck, C., Sim-Sim, M., Bell, D., Bell, N.E., Blom, H.H., et al., 2020. An annotated checklist of bryophytes of Europe, Macaronesia and Cyprus. J. Bryolog. 42, 1–116. https://doi.org/10.1080/03736687.2019.1694329.

Hoffmann, M.H., Meng, S., Kosachev, P.A., Terechina, T.A., Silanteva, M.M., 2011. Land snail faunas along an environmental gradient in the Altai Mountains (Russia). J. Molluscan Stud. 77, 76–86. https://doi.org/10.1093/mollus/eyq039.

Hotopp, K.P., 2002. Land snails and soil calcium in central Appalachian mountain forest. Southeast. Nat. 1, 27–44. https://doi.org/10.1656/1528-7092(2002)001[0027:LSASCI]2.0.CO;2.

Johnson, M.S., 2011. Effects of contrasting habitats and weather on abundance of the land snail Theba pisana (O.F. Muller, 1774): a 34-year study. J. Molluscan Stud. 77, 218–225. https://doi.org/10.1093/mollus/eyr006.

Kemencei, Z., Farkas, R., Páll-Gergely, B., Vilisics, F., Nagy, A., Hornung, E., Sólymos, P., 2014. Microhabitat associations of land snails in forested dolinas: implications for coarse filter conservation. Community Ecol. 15, 180–186. https://doi.org/10.1556/ComEc.15.2014.2.6.

Köckinger, H., Hedenäs, L., 2023. The supposedly well-known carbonate indicator Tortella tortuosa (Pottiaceae, Bryophyta) split into eight species in Europe. Lindbergia 2023, 1. https://doi.org/10.25227/linbg.24903.

Labaune, C., Magnin, F., 2001. Land snail communities in Mediterranean upland grasslands: the relative importance of four sets of environmental and spatial variables. J. Molluscan Stud. 67, 463–474. https://doi.org/10.1093/mollus/67.4.463.

Le Gall, M., Tooker, J.F., 2017. Developing ecologically based pest management programs for terrestrial molluscs in field and forage crops. J. Pest Sci. 90 (3), 825–838. https://doi.org/10.1007/s10340-017-0858-8.

Legendre, P., Legendre, L., 2012. Numerical Ecology, third ed. Elsevier, Amsterdam.

Lüdecke, D., Ben-Shachar, M., Patil, I., Waggoner, P., Makowski, D., 2021. Performance: an R package for assessment, comparison and testing of statistical models. J. Open Source Softw. 6, 3139. https://doi.org/10.21105/joss.03139.

Lydeard, C., Cowie, R.H., Ponder, W.F., Bogan, A.E., Bouchet, P., Clark, S.A., Cummings, K.S., Frest, T.J., Gargominy, O., Herbert, D.G., Hershler, R., Perez, K.E., Roth, B., Seddon, M., Strong, E.E., Thompson, F.G., 2004. The global decline of nonmarine mollusks. Bioscience 54, 321–330. https://doi.org/10.1641/0006-3568(2004)054[0321:TGDONM]2.0.CO;2.

Magnin, F., Tatoni, T., Roche, P., Baudry, J., 1995. Gastropod communities, vegetation dynamics and landscape changes along an old-field succession in Provence, France. Landsc. Urban Plann. 31, 249–257. https://doi.org/10.1016/0169-2046(94)01049-E.

Mänd, R., Tilgar, V., Leivits, A., 2000. Calcium, snails, and birds: a case study. Web Ecol. 1, 63–69. https://doi.org/10.5194/we-1-63-2000.

Mantel, N., 1967. The detection of disease clustering and a generalized regression approach. Cancer Res. 27, 209–220.

Martin, K., Sommer, M., 2004. Relationships between land snail assemblage patterns and soil properties in temperate-humid forest ecosystems. J. Biogeogr. 31, 531–545. http://www.jstor.org/stable/3554706.

Martínez-Ortí, A., 2011. *Xerocrassa montserratensis*. The IUCN red list of threatened species: e.T22254A9368348. https://doi.org/10.2305/IUCN.UK.2011-1.RLTS.T22254A9368348.en.

Martinez-Ortí, A., Bros, V., 2017. Taxonomic clarification of three taxa of Iberian geomitrids, *Helix montserratensis* Hidalgo, 1870 and subspecies (Gastropoda, Pulmonata), based on morpho-anatomical data. Anim. Biodivers. Conserv. 40, 247–267. https://doi.org/10.32800/abc.2017.40.0247.

Mazzoleni, S., Di Pasquale, G., Mulligan, M., Di Martino, P., Rego, F., 2004. Recent Dynamics of the Mediterranean Vegetation and Landscape. John Wiley & Sons, UK. https://doi.org/10.1002/0470093714.

Michael, D., Cunningham, R., Lindenmayer, D., 2008. A forgotten habitat? Granite inselbergs conserve reptile diversity in fragmented agricultural landscapes. J. Appl. Ecol. 45, 1742–1752. https://doi.org/10.1111/j.1365-2664.2008.01567.x.

Moreno-Rueda, G., 2007. Refuge selection by two sympatric species of arid-dwelling land snails: different adaptive strategies to achieve the same objective. J. Arid Environ. 68, 588–598. https://doi.org/10.1016/j.jaridenv.2006.08.004.

Moreno-Rueda, G., 2014. Distribution of arid-dwelling land snails according to dryness. J. Arid Environ. 103, 80–84. https://doi.org/10.1016/j.jaridenv.2014.01.006.

Nekola, J.C., 1999. Terrestrial gastropod richness of carbonate cliff and associated habitats in the great lakes region of North America. Malacologia 41, 231–252.

Nekola, J.C., 2010. Acidophilic terrestrial gastropod communities of North America. J. Molluscan Stud. 76, 144–156. https://doi.org/10.1093/mollus/eyp053.

Nica, D.V., Bordean, D.M., Borozan, A.B., Gergen, I., Bura, M., Banatean-Dunea, I., 2013. Use of land snails (Pulmonata) for monitoring copper pollution in terrestrial ecosystems. In: Whitacre, D.M. (Ed.), Reviews of Environmental Contamination and Toxicology, 137, 225. Springer, Berlin, p. 95. https://doi.org/10.1007/978-1-4614-6470-9_4.

Nicolai, A., Ansart, A., 2017. Conservation at a slow pace: terrestrial gastropods facing fast-changing climate. Conservation Physiology 5. https://doi.org/10.1093/conphys/cox007 cox007.

Okansen, J., Simpson, G.L., Blanchet, F.G., et al., 2024. Vegan: Community Ecology Package (R package version 2.6-6.1). https://CRAN.R-project.org/package=vegan.

Örstan, A., Pearce, T., 2006. Terrestrial gastropoda. In: Sturm, C.F., Pearce, T.A., Valdés, Á. (Eds.), The Mollusks: a Guide to Their Study, Collection, and Preservation. American Malacological Society, Los Angeles, pp. 262–285.

Panareda, J.M., Pintó, J., 1997. Sant Llorenç Del Munt. Visió Geogràfica. Eumo Editorial. Vic, Barcelona.

Puig-Gironès, R., Real, J., 2018. A comprehensive but practical methodology for selecting biological indicators for long-term monitoring. PLoS One 17, e0265246. https://doi.org/10.1371/journal.pone.0265246.

Puig-Gironès, R., Santos, X., Bros, V., 2023a. Long-interval effects of wildfires on the functional diversity of land snails. Sci. Total Environ. 876, 162677. https://doi.org/10.1016/j.scitotenv.2023.162677.

Puig-Gironès, R., Muriana, M., Real, J., Sabaté, S., 2023b. Unravelling the influence of annual weather conditions and Mediterranean habitat types on acorn production, availability and predation. For. Ecol. Manag. 543, 121149. https://doi.org/10.1016/j.foreco.2023.121149.

R Core Team, 2023. R: a Language and Environment for Statistical Computing (4.3.1). R Foundation for Statistical Computing. https://www.R-project.org/.

Raghoebarsing, A.A., Smolders, A.J.P., Schmid, M.C., et al., 2005. Methanotrophic symbionts provide carbon for photosynthesis in peat bogs. Nature 436, 1153–1156. https://doi.org/10.1038/nature03802.

Sáez, L., Aymeric, P., 2021. An Annotated Checklist of the Vascular Plants of Catalonia (Northeastern Iberian Peninsula). Kit-book Serveis Editorials, Barcelona.

Santos, X., Bros, V., Ros, E., 2012. Contrasting responses of two xerophilous land snails to fire and natural reforestation. Contrib. Zool. 81, 167–180. https://doi.org/10.1163/18759866-08103004.

Schneider, C.A., Rasband, W.S., Eliceiri, K.W., 2012. NIH Image to ImageJ: 25 years of image analysis. Nat. Methods 9, 671–675. https://doi.org/10.1038/nmeth.2089.

Shachak, M., Steinberger, Y., 1980. An algae – Desert snail food chain: energy flow and soil turnover. Oecologia 46, 402–411. https://doi.org/10.1007/BF00346271.

Soler Brugués, M., Bros, V., Ramos, S., Puig-Gironès, R., 2025. From fire to soil: the role of prescribed burns in land snail communities for improve conservation. Eur. J. Soil Biol. 126, 103749. https://doi.org/10.1016/j.ejsobi.2025.103749.

Somoza-Valdeolmillos, E., Gómez-Moliner, B.J., Caro, A., et al., 2022. Molecular phylogeny of the genus Chondrina (Gastropoda, Panpulmonata, Chondrinidae) in the Iberian Peninsula. Mol. Phylogenet. Evol. 172, 107480. https://doi.org/10.1016/j.ympev.2022.107480.

South, A., 1965. Biology and ecology of Agriolimax reticulatus (Müll.) and other slugs: spatial distribution. J. Anim. Ecol. 34, 403–417. https://doi.org/10.2307/2657.

Spitale, D., Nascimbene, J., 2012. Spatial structure, rock type, and local environmental conditions drive moss and lichen distribution on calcareous boulders. Ecol. Res. 27, 633–638. https://doi.org/10.1007/s11284-012-0935-7.

Thompson, J.D., 2020. Plant Evolution in the Mediterranean: Insights for Conservation. Oxford University Press, Oxford.

Verrecchia, E., Yair, A., Kidron, G.J., Verrecchia, K., 1995. Physical properties of the psammophile cryptogramic crust and their consequences to the water regime of sandy soils, north-western Negev Desert, Israel. J. Arid Environ. 29, 427–437. https://doi.org/10.1016/S0140-1963(95)80015-8.

Wang, D., Shen, Y., Li, Y., Huang, J., 2016. Rock outcrops redistribute organic carbon and nutrients to nearby soil patches in three karst ecosystems in SW China. PLoS One 11, e0160773. https://doi.org/10.1371/journal.pone.0160773.

Welter-Schultes, F., 2012. European Non-marine Molluscs, a Guide for Species Identification. Planet Poster Editions, Goettingen.

Wolters, V., Ekschmitt, K., 1997. Gastropods, isopods, diplopods, and chilopods: neglected groups of the decomposer food web. In: Benckiser, G. (Ed.), Fauna in Soil Ecosystems: Recycling Processes, Nutrient Fluxes, and Agricultural Production, 305. Marcel Dekker, Inc, New York, p. 265.

Zavala, L.M., Jordán, A., Bellinfante, N., Gil, J., 2010. Relationships between rock fragment cover and soil hydrological response in a Mediterranean environment. Soil Sci. Plant Nutr. 56, 95–104. https://doi.org/10.1111/j.1747-0765.2009.00429.x.

Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology with R. Springer, New York. https://doi.org/10.1007/978-0-387-87458-6.