



The geomorphology of burrowing bioturbation in the Central French Pyrenees

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Abstract. Burrowing mammals can alter mountain hillslopes by excavating subsurface voids, producing mounds of loose sediment, and creating local weaknesses in banks and slopes. Their geomorphic role remains poorly documented in alpine and subalpine catchments, where steep slopes, shallow soils, seasonal snowmelt, and grazing can rapidly rework small disturbances. We quantified the geomorphic imprint of marmots, voles, and moles in the eastern Bastan catchment, Central French Pyrenees, using field surveys, burrow and mound measurements, and soil analyses. We recorded 439 vole burrow entrances, 131 marmot burrow entrances, and 357 molehills. Vole activity was especially associated with gully banks, where 274 entrances were counted along 50 surveyed gully segments and local densities reached 3 entrances m^{-1} . Marmot burrows were less frequent but larger: 42 measured internal voids had a mean volume of $4.68 \times 10^{-2} \text{ m}^3$ and a total measured volume of 1.97 m^3 . Marmot mounds averaged $1.95 \times 10^{-2} \text{ m}^3$, whereas molehills were smaller ($5.26 \times 10^{-3} \text{ m}^3$) but more numerous. Soil pH and median grain size did not differ significantly between mounds and adjacent soil. The clearest soil-property effect was the higher bulk density of marmot mounds relative to adjacent soil, suggesting post-excavation compaction. Overall, burrowing mammals in the Bastan create a visible microtopographic and subsurface signature: molehills roughen fine-grained grassland surfaces, marmot burrows generate large local voids and mounds, and vole galleries are concentrated in gully banks where they may favour bank collapse and gully widening.

1 Introduction

Bioturbation, here defined as the physical relocation of sediment by organisms, is a recognised driver of soil production and sediment redistribution on hillslopes (Gabet et al., 2003). Despite this, the zoogeomorphological role of burrowing mammals remains underrepresented in geomorphology (Butler, 1995): ecological studies record changes to soil chemistry, structure and vegetation caused by fossorial species (Zhang et al., 2003; Whitesides, 2015; Ballová et al., 2019), while geomorphological work shows that burrow networks and mound production can alter local erosion and sediment budgets (Borghi et al., 1990; Hall et al., 1999; Germain et al., 2021; Reichman and Seabloom, 2002). Integrating these perspectives is essential to evaluate how animal activity contributes to landscape change.



Mountain environments are particularly sensitive to bioturbation because soils are shallow, slopes are steep and hillslopes are prone to rapid response following disturbance (Blanpied et al., 2020; Party et al., 2016; Bekaert, 2022). The eastern part of the Bastan catchment in the Central French Pyrenees provides a compact, representative setting for this work: it hosts extensive subalpine grasslands and concentrated burrowing by Alpine marmots, multiple vole taxa and moles (including recent records of *Talpa aquitania* in the region; Nicolas et al., 2021), so that species-specific patterns of excavation and mound persistence can be observed across contrasting substrates and aspects.

This paper quantifies the geomorphic footprint of those burrowing mammals in the Bastan catchment. Specifically, we (i) map and describe the surface and subsurface features produced by marmots, voles and moles; (ii) estimate soil displacement; and (iii) test for direct alteration of selected soil properties.

2 Materials and methods

2.1 Study area

Fieldwork was conducted in the easternmost part of the Bastan catchment (42.90° N, 0.14° E), upstream of Barèges in the central French Pyrenees (Hautes-Pyrénées, Occitania). The broader Bastan catchment ranges from 658 m a.s.l. at the confluence with the Gave de Pau to 3091 m a.s.l. at the peak of Néouvielle (Blanpied et al., 2020). Sampling focused on a compact high-mountain sector between approximately 1850 and 2025 m a.s.l., where accessible slopes include grasslands, gully banks, boulder-rich areas, and exposed soil. The area lies near the transition between the granitic Néouvielle massif on the north-facing slopes and the schistose Tourmalet massif to the south. Soils are thin and heterogeneous, including lithosols and rankosols on ridges and brunisols and alocrisols on mid-slopes (Party et al., 2016). Vegetation consists mainly of subalpine and alpine grasslands used for summer grazing. These open habitats are intensively modified by burrowing mammals and are prone to erosion, bank collapse, and shallow landsliding (Bekaert, 2022).

2.2 Field methods

Fieldwork was conducted from 1 to 15 July 2024. The eastern part of the catchment was selected because it contains the main accessible geomorphic and ecological settings where burrowing activity was expected: grassland slopes, gully banks, rock outcrops, boulder-rich areas, and moister fine-grained patches.

2.2.1 Plot surveys

Field data were collected as 50 numbered 10 × 10 m plot records. Of these, 47 had complete polygon geometries and were used for DEM-based topographic extraction; the remaining three retained valid field counts but incomplete polygon information. Plots were positioned along walking transects within the sampling area. Transects were generally walked downslope from high points so that plots captured variation in slope angle, elevation, vegetation, exposure, and substrate, rather than only locations with obvious burrowing activity. The four corners of each plot were georeferenced using a Garmin Etrex 30 handheld GNSS



where possible. Within each plot, visible burrow entrances and mounds were counted and assigned to marmot, vole, or mole based on entrance size, mound morphology, and associated field observations. Additional plot-level observations included vegetation cover, rock cover, rock outcrops, soil depth, and slope angle.

Soil samples were collected from the centre of each plot to characterise the local soil matrix. Where mounds were present, paired samples were collected from the mound and from adjacent undisturbed soil within the same plot. These paired samples were used to test whether mound material differed from the surrounding soil matrix.

2.2.2 Gully transects

Gully banks were surveyed along 50 transect segments in order to document burrows in locations where bank collapse and sediment remobilisation are most likely. Most segments were 10 m long; where long sections without burrows occurred, start and end points were recorded at the boundaries of those sections and a new segment was started where burrows reappeared. For this reason, gully results are reported both as total counts and as burrow densities per metre. At the start and end of each segment, GNSS coordinates were recorded. Along each segment, burrows in the gully banks were counted, their likely animal origin was noted, and bank characteristics such as overhangs, collapses, exposed bedrock, debris, and nearby shallow landslides were described and photographed.

2.2.3 Estimation of excavated soil quantity

For measurable burrows and mounds, width, height, and length were recorded together with an approximate shape class. Volumes were then estimated using the geometric equations in Table 1. These values are approximate because both burrows and mounds are commonly irregular. For fresh, uncompacted mounds, the entire mound was also measured by scooping the material into a 650 ml measuring cup and recording the number of full scoops plus the remaining volume. Volume measurements were made where features were measurable, both inside plots and at additional field-observation points. They therefore represent feature-scale excavation estimates and should not be interpreted as annual turnover rates.

Table 1. Equations used to estimate burrow and mound volumes from field measurements.

Feature	Shape	Volume equation
Burrow	Ellipsoid	$V = \frac{4}{3}\pi abc$
Burrow	Cylinder	$V = \pi r^2 h$
Mound	Cone	$V = \frac{1}{3}\pi r^2 h$
Mound	Wedge	$V = \frac{1}{2}lwh$
Mound	Truncated cone	$V = \frac{1}{3}\pi h(r_1^2 + r_1 r_2 + r_2^2)$
Mound	Dome-like pile	$V = \frac{2}{3}\pi r^2 h$

For ellipsoids, a , b , and c are semi-axes. For cylindrical and conical forms, r is radius and h is height or length, depending on feature orientation.



2.3 Soil properties and statistical analysis

- 75 Bulk density was determined by oven-drying soil cores of 235 ml at 105 °C for 24 h and dividing dry mass by core volume. Grain size distribution was measured by dry sieving with mesh sizes of 2 mm, 500 μm , 250 μm , and 63 μm , separating particles into pebbles (>2 mm), coarse sand (2–0.5 mm), medium sand (0.5–0.25 mm), fine sand (0.25–0.063 mm), and a silt plus clay fraction (<0.063 mm). All samples were weighed before and after sieving; mass loss was less than 1 %. Soil pH was measured in the field by mixing a soil-water suspension and inserting an electronic pH meter once the mixture had stabilised.
- 80 Paired t -tests were used to compare mound material with adjacent soil from the same plot. These tests were conducted for all paired mound samples and separately for marmot mounds and molehills. Vole mounds were too rare for a species-specific paired comparison. Reported p values in the manuscript are based on cleaned paired data in which placeholder values were treated as missing values.

3 Results

85 3.1 Geomorphological signature

- Marmot burrows were the largest excavated features observed in the study area. Entrances were usually rounded to slightly oval, with a typical diameter of about 18 cm, but the internal configuration varied from shallow entrances to multi-chambered systems several decimetres to metres deep. Collapsed burrows exposed subsurface corridors and voids (Fig. 1e), showing that marmot excavation can remove support from below the grass-covered surface. Many entrances occurred beneath boulders or at
- 90 rock outcrops (Fig. 1c), where rock fragments appeared to stabilise the entrance. Associated mounds varied from loose, fresh, dome-like deposits to elongated ridges and compacted, eroded remnants (Fig. 1a–d). Some mounds contained fine material and coarse clasts of more than 1 kg, whereas others were organic-rich or had been reduced to scattered coarse fragments. Older mounds were sometimes colonised by *Urtica dioica*. Marmot burrows were spatially clustered in colonies, producing strong local disturbance rather than a uniform catchment-wide pattern.
- 95 Mole activity was expressed mainly as clusters of molehills (Fig. 1k). These clusters occurred on flat to gently sloping fine-grained soils with few surface clasts. Individual molehills were typically around 30 cm in diameter, although their preservation varied. Fresh mounds were loose and unvegetated (Fig. 1g), while older or trampled mounds were compacted, flattened, or partly vegetated (Fig. 1j). The geomorphic effect of moles was therefore concentrated in small activity zones where many mounds created a rough, hummocky microtopography.
- 100 Vole burrows were smaller and less conspicuous, usually 3–4 cm in diameter and generally lacking associated mounds (Fig. 1f). Despite this small size, vole activity was widespread and especially visible in exposed or weak substrates, including gully banks, trail edges, collapsed marmot burrows, and a shallow landslide scar. Grazing trails often led to burrow entrances (Fig. 1h). In gullies, some burrows crossed between adjacent channels (Fig. 1i), whereas others ran parallel to gully walls and exposed segments of underground galleries (Fig. 1l). Overhanging banks commonly began or ended at vole entrances,



105 suggesting that vole galleries can locally weaken gully banks and may contribute to bank collapse or gully widening. The main surface and subsurface features observed during fieldwork are summarised schematically in Fig. 2.

3.2 Burrow abundance and excavated soil volume

Burrowing features were abundant but strongly species-dependent in their spatial expression (Table 2). Voles were the most numerous, with 439 recorded entrances in the study area. Of these, 274 were counted along gully banks, representing more than 60 % of all recorded vole entrances. Mean gully-bank density was $0.52 \text{ entrances m}^{-1}$, but the median was zero because many surveyed segments contained no vole burrows; the highest local density was $3 \text{ entrances m}^{-1}$. Within the plots, 151 vole entrances occurred in 24 of the 50 plot records. Moles produced 357 recorded molehills, of which 326 were located in 14 plot records. Most molehills were grouped in four activity zones, where the mean density was $0.34 \text{ molehills m}^{-2}$. Marmots accounted for 131 recorded burrow entrances, with 22 entrances inside plot records and 5 along gully banks. The largest mapped colony contained 41 entrances, including a dense subcluster of 19 entrances.

Table 2. Abundance of visible burrowing features by species and survey context. Plot occurrence is based on the 50 numbered $10 \times 10 \text{ m}$ plot records. Gully density values are reported for vole burrows because gully segments were not always exactly 10 m long.

Species	Feature counted	Study-area total	Plot total	Occupied plots	Max. plot count	Gully observations
Marmot	Burrow entrance	131	22	8/50 (16%)	8	5 entrances
Mole	Molehill	357	326	14/50 (28%)	56	0
Vole	Burrow entrance	439	151	24/50 (48%)	22	274 entrances; mean 0.52 m^{-1} ; max. 3 m^{-1}

Study-area totals include plot records, gully-bank observations, and additional mapped burrowing features. For moles, the study-area total refers to mapped molehills; the 14 plot occurrences are concentrated in high-density activity zones.

Volume estimates show that the three taxa differ in the size and measurability of their geomorphic features (Table 3). Marmot burrows were the largest measurable subsurface features: 42 measured burrow voids had a mean internal volume of $4.68 \times 10^{-2} \text{ m}^3$ and a total measured volume of 1.97 m^3 . Marmot mounds averaged $1.95 \times 10^{-2} \text{ m}^3$ and summed to 0.95 m^3 across 49 measured mound observations. Molehills were smaller, with a mean volume of $5.26 \times 10^{-3} \text{ m}^3$, but their high number resulted in an estimated total molehill volume of 1.88 m^3 when scaled to the 357 mapped molehills. Vole excavation volume could not be quantified reliably because the burrows were narrow, tortuous, and generally lacked measurable mounds. Using measured bulk densities to convert mound volumes to dry mass gives an estimated $2.72 \times 10^3 \text{ kg}$ of excavated material when scaled molehill volume is included. This value should be interpreted as an approximate mass of visible or inferred mound material, not as an annual sediment flux.

3.3 Soil properties

Mound effects on soil properties were limited and species-dependent (Table 4). Soil pH, median grain size (d_{50}), and grain-size spread did not differ significantly between mound material and adjacent soil. Bulk density was significantly higher in marmot mounds than in adjacent soil (1.13 versus 0.69 g cm^{-3} , $p = 0.0369$), whereas molehills showed no bulk-density difference. The



Figure 1. Field observations showing the direct geomorphological imprint of burrowing bioturbation. (a) Large marmot mound in front of a burrow entrance (volume more than 75 L), containing a mix of fine material and clasts up to over 1 kg; (b) elongated marmot mound with mixed materials and dark, organic-rich soil; (c) flattened marmot mound with burrow excavated beneath a boulder; (d) marmot burrow beneath nettle vegetation, where the mound has largely disappeared and only coarse fragments remain; (e) collapsed marmot burrow, revealing a tunnel approximately 3 m long; (f) vole burrow entrance located at the edge of a walking trail; (g) fresh molehill; (h) vole grazing trail showing disturbed vegetation and terminating in a burrow entrance; (i) vole activity along blind-gully banks, with a perpendicular burrow connecting two parallel gullies; (j) older, compacted molehill; (k) cluster of molehills; (l) vole burrow in a gully bank, oriented parallel to the gully and exposing part of the gallery.

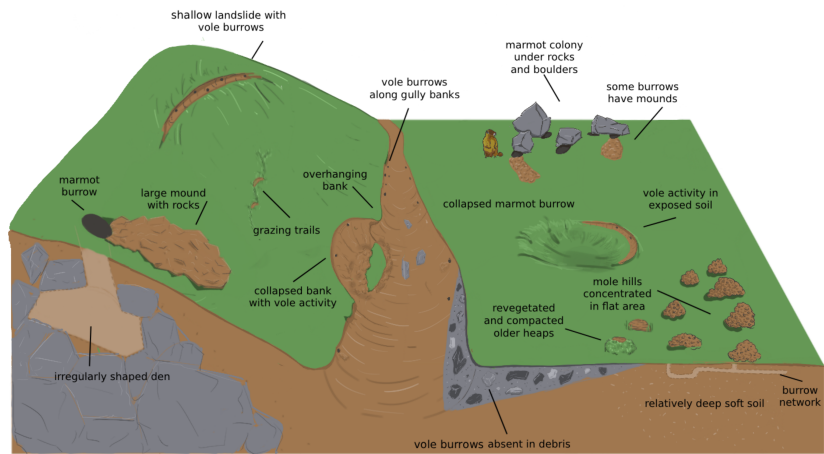


Figure 2. Schematic overview of the main geomorphological features produced by burrowing mammals in the study area, including mounds, entrances, subsurface voids, macropores, overhanging gully banks, and collapsed structures.

Table 3. Estimated mound and burrow volumes.

Species	Feature	<i>n</i>	Mean volume (m ³)	Total volume (m ³)
Marmot	Mound	49	1.95×10^{-2}	0.953
Marmot	Internal burrow void	42	4.68×10^{-2}	1.967
Mole	Molehills	14	5.26×10^{-3}	1.879 ^a
Vole	Burrow	–	–	–

^a Scaled estimate for all 357 mapped molehills. The directly measured molehill volume was 0.0737 m³. Vole burrow volume was not estimated because measurable mounds were generally absent and tunnel geometry was too tortuous.

coarse sand fraction was notably smaller in marmot mounds compared to control samples ($p=0.01$), whereas it was significantly higher in molehills. These opposing trends cancelled each other out, when the data for mole and marmot mounds were pooled, resulting in no overall significant difference in coarse sand content between mounds and control samples. A very strong effect ($p<0.001$) was recorded in the fraction of fine sand for mole hills, as they consistently contained less fine sand than their immediate surroundings (Fig. 3).

3.4 Geomorphological signature

3.4.1 Observed signature

Burrowing mammals produce a distinct set of surface and subsurface features in the Bastan catchment (Fig. 2): dense mole activity zones of small mounds and rough surface microtopography, large and often clast-rich marmot mounds and burrows with complex subterranean chambers, and widespread but subtle vole burrows concentrated on gully banks and exposed soils. The



Table 4. Paired comparisons between mound material and adjacent soil. Values are mean mound value / mean adjacent-soil value, followed by the paired t-test p value. Significant results ($p < 0.05$) are shown in bold.

Variable	All paired samples	Marmot	Mole
Bulk density (g cm^{-3})	0.90 / 0.77, $p = 0.0935$	1.13 / 0.69 , $p = 0.0369$	0.80 / 0.81, $p = 0.9201$
pH	6.64 / 6.51, $p = 0.3098$	6.67 / 6.46, $p = 0.3710$	6.53 / 6.49, $p = 0.7983$
d50 (mm)	0.13 / 0.23, $p = 0.1055$	0.15 / 0.38, $p = 0.1466$	0.12 / 0.14, $p = 0.1799$
Particle-size σ	0.93 / 0.95, $p = 0.0967$	0.94 / 0.96, $p = 0.2543$	0.94 / 0.95, $p = 0.4210$
Pebbles (%)	32.77 / 38.39 , $p = 0.0305$	33.42 / 44.33, $p = 0.0632$	33.11 / 34.67, $p = 0.4564$
Coarse sand (%)	32.84 / 32.06, $p = 0.6959$	32.42 / 23.25 , $p = 0.0106$	33.00 / 37.89 , $p = 0.0142$
Medium sand (%)	12.10 / 10.19 , $p = 0.0149$	11.67 / 8.67, $p = 0.0511$	12.11 / 11.17, $p = 0.2689$
Fine sand (%)	13.03 / 9.19 , $p = 0.0008$	13.67 / 10.58, $p = 0.1076$	12.44 / 8.17 , $p = 0.0059$
Silt + clay (%)	9.10 / 10.03, $p = 0.5043$	8.92 / 13.00, $p = 0.1642$	9.00 / 7.94, $p = 0.4601$

All paired samples include all paired mound-adjacent samples after placeholder values were treated as missing. Vole mounds were too rare for a separate paired test.

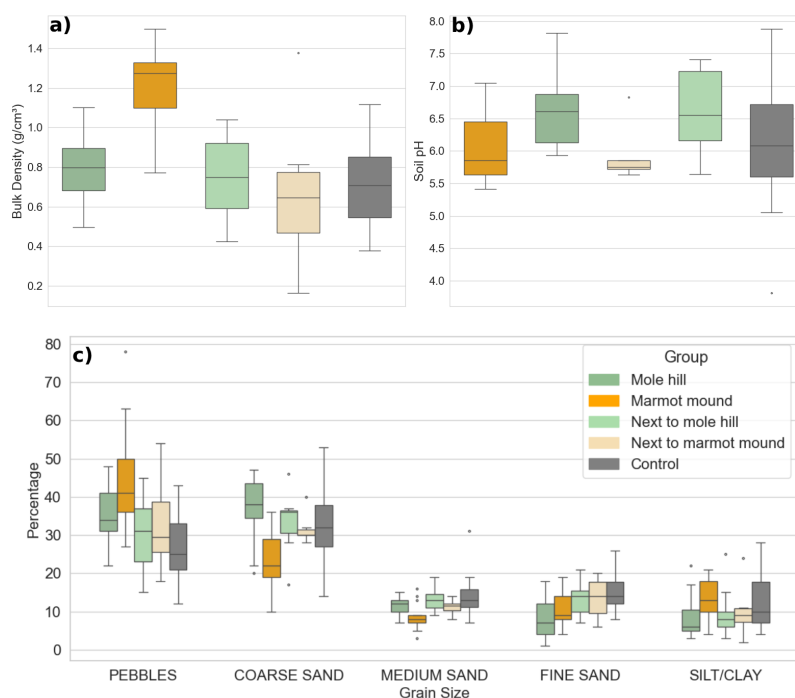


Figure 3. Boxplots of selected soil properties comparing samples from molehills and marmot mounds with samples taken adjacent to these features and from control plots without visible burrowing bioturbation. (a) Bulk density, showing the highest values in marmot mounds; (b) soil pH, showing no clear separation among sample groups; (c) grain-size distribution, showing species-dependent differences in some fractions but no uniform textural shift caused by mound formation.



zone of bioturbation corresponds with a major sediment source area at the catchment scale (Frankl et al., 2025), suggesting that bioturbation may aggravate land degradation processes. Where present, collapsed burrows, overhanging banks and unvegetated soil deposits indicate interaction with other geomorphic processes, including gully erosion, trampling and shallow landsliding. These species-dependent signatures control the spatial distribution of loose sediment and macropore networks at the hillslope scale.

3.4.2 Surface roughness and sediment availability

High mound density, as observed in mole activity zones, increases surface roughness and thereby perturbs overland flow, promoting local retention and micro-deposition while simultaneously increasing the supply of erodible, unvegetated material (Cavalli et al., 2013; Trevisani et al., 2012; Chen et al., 2021). Thus, burrow fields can act as temporary sediment sinks under low transport capacity but become episodic sediment sources during high-intensity melt or rainfall events, amplifying sediment pulses downslope. Marmot mounds, although more sparsely distributed, also contribute to sediment availability, as several mounds showed preferential removal of fine material, leaving coarse debris exposed at the surface.

3.4.3 Macroporosity and subsurface routing

Burrow systems and persistent biogenic macropores enhance preferential infiltration and can integrate into subsurface flow networks, facilitating rapid internal routing of water and potentially initiating internal erosion (piping) (Beven and Germann, 1982; Martinez-rica et al., 1991; Gabet et al., 2003; Verachtert et al., 2013). Such preferential conduits may remain active after colony abandonment and, under high inputs, reopen sealed entrances or canalise flow, increasing lateral connectivity and subsurface sediment export (Reichman and Seabloom, 2002; Germain et al., 2021).

3.4.4 Instability and geomorphic consequence

By removing support and reducing root reinforcement, dense burrow networks can locally weaken slope material and predispose sites to shallow landslides or bank collapse, especially where grazing or intense hydrological forcing occurs (Hall and Lamont, 2003; Thorn, 1978; Bekaert, 2022). Although rare, these failure events can mobilise large sediment volumes and thus have outsized effects on sediment budgets; quantifying their frequency and magnitude requires targeted monitoring or process-based modelling beyond the scope of this study.

3.5 Burrow density and quantification

The observed burrowing patterns reveal a clear functional partitioning among species, with distinct implications for sediment redistribution and surface modification. However, it is important to note that in this study, burrow density and geomorphic impact are inferred from visible entrances, mounds and surface disturbance. This approach underrepresents subsurface excavation that leaves little or no persistent surface signature. Voles contribute a widespread, high-frequency landscape footprint,



moles concentrate activity into discrete patches that generate the highest local disturbance intensity, and marmots produce large, long-lived excavations that are spatially restricted but high in per-burrow magnitude.

170 These patterns are explained by species ecology: voles reproduce rapidly, form dense, semi-fossorial colonies and readily exploit grazed pastures, producing many small entrances over wide areas (Martinez-rica et al., 1991; Germain, 2025; Wilske et al., 2015). Moles are strictly fossorial, highly territorial and continuously maintain tunnel networks, so they move large amounts of soil per individual but concentrate activity into discrete, high-density patches (Sondergaard, 2006; Baldwin, 2024; Pearce et al., 2025). Marmots are large, social and reuse complex burrow systems (fewer entrances per animal, larger per-
175 burrow excavation), so their impact is intense per site but spatially limited (Perrin et al., 1993; Haussmann, 2017).

In short: voles dominate the *landscape footprint* (frequency), moles dominate *local intensity* (peak density), and marmots dominate *per-burrow magnitude* (volume). These contrasts, consistent with previous field studies, explain why small, abundant species can drive broad-scale sediment perturbation while larger, social or strictly fossorial species produce powerful but spatially constrained geomorphic effects (Haussmann, 2017; Hall et al., 1999; Wijnhoven et al., 2007).

180 Comparisons with the literature indicate that the measured soil displacement reflects background, non-outbreak conditions rather than extreme irruption events: reported turnover rates during documented vole outbreaks or unusually dense marmot populations can be orders of magnitude higher than the routine rates observed here (e.g. Germain, 2025; Martinez-rica et al., 1991; Zimina, 1980). However, our estimates are broadly comparable to other field-scale, non-outbreak measurements (Hall et al., 1999; Gabet et al., 2003).

185 Methodological and post-depositional processes limit direct inference of annual turnover from surface measurements. Morphometric estimates of burrow volume typically exceed scooped/wet-mass measures, and measured mound volumes were often smaller than internal burrow volumes, implying loss by downslope transport, compaction, or reworking (cf. Germain et al., 2021; Wijnhoven et al., 2007). Vole excavation could not be reliably quantified with the available surface methods because their burrows are long, narrow and tortuous; hence cumulative vole subsurface turnover is likely underestimated despite
190 their high abundance. Finally, mound-persistence depends on local slope, vegetation and snowmelt timing, so single-campaign surveys capture a snapshot rather than an annual turnover rate.

Taken together, the counts and volume estimates imply that routine bioturbation in the Bastan catchment produces measurable background sediment turnover and alters sediment availability and surface roughness, but that extreme geomorphic impacts are episodic and tied to outbreaks or rare failure events. Quantifying the contribution of burrowers to catchment sediment budgets therefore requires (i) method-consistent estimates of both subsurface and surface volumes, (ii) repeated surveys
195 to capture temporal variability (outbreaks, snowmelt), and (iii) process modelling or targeted monitoring to resolve the role of post-depositional transport and collapse in converting excavated soil into catchment sediment flux.



3.6 Soil properties

3.6.1 Bulk density

200 Contrary to previous observations that burrow mounds generally have lower bulk density than surrounding soils (Zaitlin and Hayashi, 2012; Reichman and Seabloom, 2002), marmot mounds in this study exhibited significantly higher values. This may result from surface compaction by the animals themselves, trampling by livestock, or consolidation under snow cover. The absence of roots within mounds likely reduced macroporosity relative to the adjacent grass-covered soil, further increasing density. In contrast, mole mounds showed no consistent difference in bulk density, suggesting that their smaller volume and
205 limited surface exposure reduce compaction and post-depositional modification. These patterns indicate that the mechanical and ecological context of mound formation, rather than excavation alone, controls resulting soil structure in alpine terrain.

3.6.2 Grain-size distribution

Differences in grain-size fractions between mound and control samples were minor and inconsistent, indicating no systematic textural shift associated with excavation. Marmot mounds showed a modest reduction in the coarse-sand fraction relative to
210 adjacent matrix, whereas mole mounds were richer in coarse sand and depleted in fine sand. The marmot pattern is unlikely to reflect an inability to move coarse particles (marmots can displace clasts over 1 kg); instead it is plausibly caused by within-mound sorting during excavation or by post-depositional loss/downslope redistribution of heavy particles, as reported for alpine mounds elsewhere (Hall and Lamont, 2003; Kinlaw, 1999). The mole signal may reflect either selective handling or preferential erosion of fines after deposition. Vole mounds were too scarce for robust comparison, but the few examples comprised fine
215 material, consistent with other studies that report limited vole-driven grain-size change (Ma et al., 2021). Overall, in steep alpine terrain short-term transport and weathering commonly overprint any primary excavation signal.

4 Conclusions

Burrowing mammals create a clear geomorphic imprint in the eastern Bastan catchment. Voles were the most abundant burrowers and were strongly concentrated along gully banks, where their galleries can contribute to overhanging banks and local
220 collapse. Moles produced dense clusters of small mounds that roughen fine-grained grassland surfaces. Marmots produced fewer but much larger burrows and mounds, including collapsed voids and clast-rich excavated material.

Measured excavation volumes confirm this contrast. Marmot burrows had the largest feature-scale volumes, while molehills were smaller but numerous enough to represent a comparable visible mound volume when scaled to all mapped molehills. Vole excavation could not be measured volumetrically, but the high number of entrances in gully banks makes them geomorphically
225 relevant through bank weakening rather than through measurable mound production.

Soil-property changes were limited. Soil pH and median grain size did not differ significantly between mound and adjacent soil, and grain-size fractions showed inconsistent species-dependent patterns. Marmot mounds were significantly denser than adjacent soil, probably because older mounds are compacted and contain fewer roots. Overall, the main geomorphic role of



230 burrowing mammals in the Bastan is physical: they create surface roughness, expose loose sediment, form subsurface voids and macropores, and locally weaken gully banks and slopes.

Data availability. The cleaned datasets and scripts used to reproduce the main values reported in this paper are available at <https://github.com/mvancappellen/pyrenees-bioturbation-data>.

235 *Author contributions.* MVC, SA, BD, and AF designed the field campaign. MVC, SA, and AF collected the field data. MVC and SA conducted the laboratory analyses. MVC processed the data, prepared the figures, and wrote the first draft of the manuscript. ML, BD, SA, and AF contributed to interpretation and manuscript revision. AF and SA supervised the research.

Competing interests. The authors declare that they have no conflict of interest.



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