Received: 28 June 2024 | Revised: 24 September 2024 | Accepted: 27 September 2024

DOI: 10.1002/esp.6008

RESEARCH ARTICLE

ESPL WILEY

The geomorphic work of the European mole (*Talpa europaea*): Long-term monitoring of molehills using structure-from-motion photogrammetry

Timothy Baxter[1] | Sam Woor[2,3] | Martin Coombes[4] | Heather Viles[4]

[1]Department of Geography, University of California, Santa Barbara, Santa Barbara, California, USA

[2]Department of Geoscience, University of the Fraser Valley, Abbotsford, Canada

[3]Department of Earth, Ocean and Atmospheric Sciences, University of British Columbia, Vancouver, Canada

[4]School of Geography and the Environment, University of Oxford, Oxford, UK

Correspondence
Timothy Baxter, Department of Geography, University of California, Santa Barbara, Santa Barbara, California, USA.
Email: timothybaxter@ucsb.edu

Funding information
Engineering and Physical Sciences Research Council; UKRI, Grant/Award Number: EP/L016036/1

Abstract

Moles—small insectivorous mammals of the family Talpidae—are widespread across the Northern Hemisphere. These subterranean mammals are easily detected through the mounds, or molehills, they construct as surface bioproducts of tunnel systems excavated underground. The dense aggregation of these bioconstructions in a range of environments (e.g., floodplains, woodland, coastal dunes and upland regions) indicates that moles may play an important role in sediment systems. However, compared with other fossorial mammals (e.g., gophers and rabbits), the impact of moles as direct and indirect biogeomorphic agents is poorly understood. Furthermore, little is known about how molehills develop and degrade over time or how long they persist as landscape features. By examining molehills created by the European mole (*Talpa europaea*) over 4 months on a floodplain in Oxfordshire, UK, we provide a quantitative assessment of how these landforms evolve over time and space. Through the creation of high-resolution digital elevation models (DEMs) using structure-from-motion (SfM) photogrammetry, we derive a variety of metrics describing molehill morphology and produce a detailed record of how molehills change at weekly time intervals. In addition, measurements of molehill volume are used to estimate the excavation rate of moles over a month. Findings show that (i) molehills are dynamic landforms that change in size and shape in response to phases of construction, collapse, erosion and rebuilding; (ii) rates of degradation are influenced by soil characteristics and seasonal weather conditions; (iii) molehills can persist as landscape features for several months; and (iv) moles are capable of moving a substantial volume of sediment in highly active areas (3.89 m^3 ha^{-1} $month^{-1}$). Future work is now needed to determine the geomorphic impact of *T. europaea* over larger spatial scales (e.g., river catchments) and longer timescales (e.g., years–decades) to determine its importance in relation to other bioturbators and within the wider sediment system.

KEYWORDS
bioconstruction, bioturbation, ecosystem engineering, fossorial, mole, photogrammetry, sediment system, zoogeomorphology

1 | INTRODUCTION

Organisms play a fundamental role in the global sediment system as drivers of erosion, transport and deposition in terrestrial, fluvial and oceanic environments (Viles, 2020). This includes fossorial and semi-fossorial animals that have developed digging behaviours as key adaptive strategies for living underground (Butler, 1995; Corenblit et al., 2021). Mammalian examples include rabbits (e.g., Rutin, 1992), badgers (e.g., Coombes & Viles, 2015), wombats (e.g., Borchard & Eldridge, 2011), mole-rats (e.g., Davies & Jarvis, 1986), mice (e.g., Eriksson & Eldridge, 2014) and gophers (e.g., Winchell et al., 2016). However, fossorial behaviour is not limited to mammals, with many species of fish (e.g., Bhatt et al., 2009), molluscs (e.g., Sassa et al., 2011), birds (e.g., Germain et al., 2022), reptiles (e.g., Kinlaw & Grasmueck, 2012) and insects (e.g., Bétard, 2021; de Freitas et al., 2021; Viles et al., 2021) also known to burrow. Although individually small in size, at a population scale, fossorial animals can collectively move large volumes of sediment (Haussmann, 2017). Pocket gophers (*Thomomys bottae*), for example, have an estimated bioturbation rate of up to 28.5 t ha^{-1} $year^{-1}$ in highly active areas (Cox, 1990).

Burrowing animals directly influence geomorphic processes through the bioturbation of surface and subsurface sediment, resulting in the formation of spoil heaps and other distinctive landforms, such as burrows and tunnels (Butler, 1995; Whitesides et al., 2022). In certain environments susceptible to erosion, such as unstable cliffs, hillslopes, river banks and sand dunes, the creation of subterranean features can also facilitate slope failure and other mass wasting events (Rutin, 1992; Sanders et al., 2021). Indirectly, burrowing activity can affect soil characteristics (e.g., texture, infiltration capacity, chemical composition and nutrient availability) and vegetation cover, resulting in secondary impacts on surface runoff and erosion (Abaturov, 1968, 1972).

Despite impacting the global sediment system in nearly every environment around the world (Kinlaw, 1999; Teal et al., 2008; Übernickel et al., 2021; Whitford & Kay, 1999), the role of fossorial animals is poorly understood, monitored and quantified compared with other agents of sediment movement. A lack of research in this area has previously been attributed to assumptions about the scale, importance and number of species undertaking geomorphic work being minimal (Rice, 2021). Practical challenges associated with measuring and observing processes that occur quickly, stochastically or episodically also likely compound these assumptions.

1.1 | The European mole

Often considered a pest by farmers and gardeners for damaging crops and drainage systems (Atkinson, Macdonald, & Johnson, 1994; Baker & Macdonald, 2015; Quy & Poole, 2004), the European mole (*Talpa europaea*) is a small insectivorous mammal uniquely adapted for subterranean life (Figure 1). Adult moles vary in size (5–20 cm long) and bodyweight (70–130 g), although males are typically larger than females (Atkinson, 2013). The range of the European mole stretches across Europe, from northern Spain to western Russia, with most observations recorded in Britain (i.e., England, Wales and Scotland) and the Netherlands (Figure 2). In Britain, the European mole is found in a variety of habitats (e.g., woodland, arable land, pasture, meadows, gardens, parkland and sand dunes), ranging in elevation from coastal environments to mountainous regions (Davies, 1966; Macdonald et al., 1997; Mellanby, 1966; Milner & Ball, 1970), and has an estimated population of around 41 million individuals (Mathews et al., 2018). Throughout Europe, estimates of mole density generally range between one and 10 per hectare (Bolton, 1969; Funmilayo, 1977; Goszczyński, 1983; Grulich, 1959; Harris et al., 1995; Larkin, 1948; Mellanby, 1966) and rarely exceed 20 per hectare (Quy & Poole, 2004), although figures as high as 45 per hectare have been reported (Ford, 1935b; Haeck, 1969; Mellanby, 1971).

The European mole has developed numerous adaptations for living a solitary life underground, including large and powerful forelimbs relative to its body size that allow it to construct networks of tunnels in which it hunts for prey (Arlton, 1936; Catania, 2000; Glosmann et al., 2008). Typically located within 1 m of the ground surface, mole tunnels can extend several hundred metres in length (Haeck, 1969), with moles reportedly capable of excavating up to 30 m per day (Godfrey, 1955; Godfrey & Crowcroft, 1960; Skoczeń, 1958). The distribution of moles and the extent of their home ranges depends on a variety of factors, including food supply (Edwards et al., 2001; Funmilayo, 1977; Macdonald et al., 1997; Mellanby, 1966, 1967), soil characteristics (i.e., stoniness, acidity, humidity; Corbet & Southern, 1977; Milner & Ball, 1970; Saey et al., 2014), climate (Mellanby, 1966, 1967; Nesterkova, 2014) and changes in seasonal weather conditions (Haeck, 1969; Imeson, 1976), human activity (e.g., ploughing, management strategies; Ennik, 1967; Haeck, 1969; Schaefer, 1981), land use (Edwards et al., 2001; Fellowes et al., 2020; Smith, 2013), proximity to water sources (Funmilayo, 1977; Imeson, 1976; Wijnhoven et al., 2006) and levels of pollution (Nesterkova, 2014) as well as the frequency and magnitude of disturbance events, such as floods (Mikuś, 2020; Mikus & Uchman, 2013).

FIGURE 1 The European mole (*Talpa europaea*, Michael David Hill/CC BY-SA 3.0.) and molehills in Sheringham Park, Norfolk, UK, photographed by the authors in November 2023. Standard card (8.56 × 5.40 cm) shown for scale. [Color figure can be viewed at wileyonlinelibrary.com]

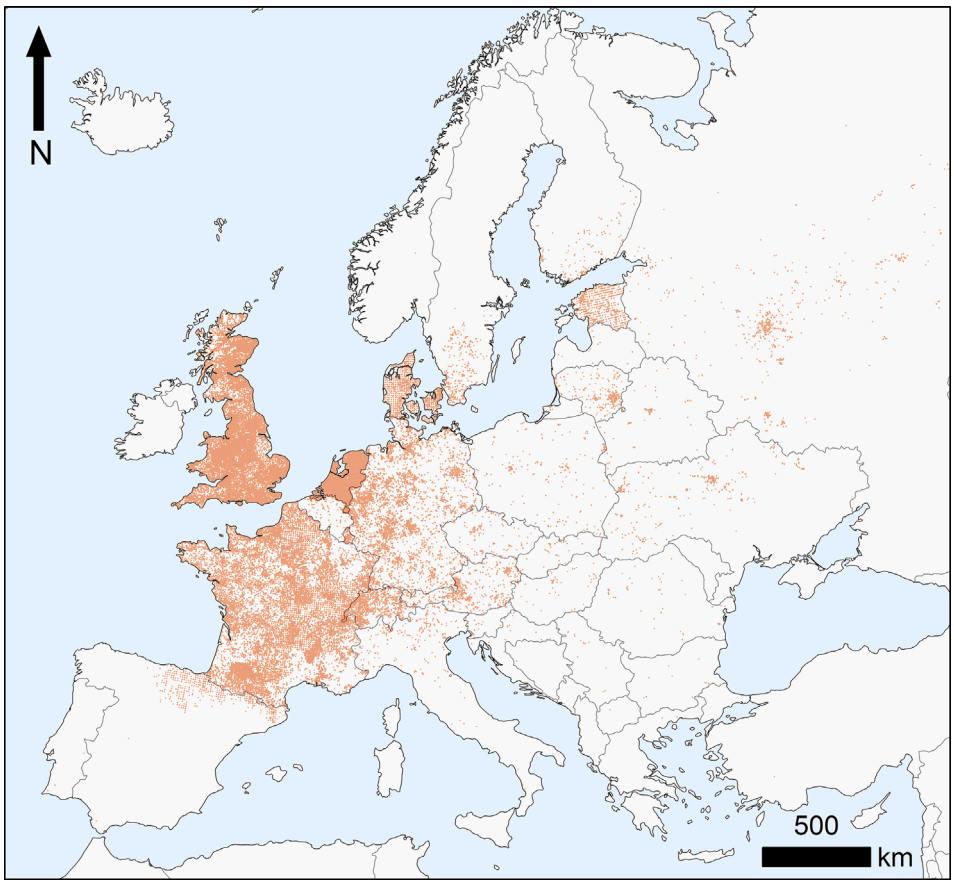

FIGURE 2 Recorded observations of the European mole (*Talpa europaea*) between 1900 and 2023 (GBIF.org [09 November 2023] GBIF occurrence download https://doi.org/10.15468/dl.brfumb). [Color figure can be viewed at wileyonlinelibrary.com]

In Britain, estimates of the home range of moles vary between 300 and 3000 m^2 (Gorman & Stone, 1990; Macdonald et al., 1997; Stone & Gorman, 1985).

1.2 | The European mole as an ecosystem engineer

Compared with other fossorial mammals of a similar size, such as gophers (e.g., Anzah & Butler, 2017; Winchell et al., 2016) and mole-rats (e.g., Davies & Jarvis, 1986; Jarvis & Sale, 1971), the geomorphic impact of the European mole has been relatively understudied. *Talpa* spp. are, however, recognised as important ecosystem engineers due to their effects on local-scale soil conditions and ground cover disturbance (Bliss et al., 2006; Katzerke et al., 2010; Streitberger et al., 2014; Streitberger & Fartmann, 2013). Surface and subsurface features created by the European mole provide favourable conditions for the colonisation and establishment of diverse communities of plants and animals (Seifan et al., 2010). For instance, the tunnelling activity of moles has been shown to increase earthworm density (Schaefer & Sadlier, 1981) and provide underground shelter for various species of anthropods, gastropods, amphibians and other small mammals (Napierala et al., 2016; Stepanova et al., 2021). Near the surface, burrowing moles uproot and damage plants (Voronov, 1967) and influence the physical and chemical properties of soil (Platt et al., 2016; Watt, 1974). Small-scale disturbances have been shown to impact the porosity and permeability of soil (Abaturov, 1968; Mellanby, 1971; Schaefer & Sadlier, 1981) as well as its aeration (Olszewski & Skoczeń, 1965), humidity and moisture content (Goszczyńska & Goszczyński, 1977; Schaefer & Sadlier, 1981; Schiffers et al., 2010; Skoczeń et al., 1976), grain size distribution (Imeson & Kwaad, 1976), chemical composition (Ramzaev & Barkovsky, 2018; Wijnhoven et al., 2006), nutrient availability (Canals & Sebastia, 2000; Seifan et al., 2010), humus content and microbiology (Abaturov, 1972; Stepanova et al., 2021; Voronov, 1967). Furthermore, by forming raised mounds of bare soil (i.e., molehills), moles create physicochemically distinct microhabitats (Huntley & Reichman, 1994) that differ in light exposure (Canals & Sebastìa, 2000; Seifan et al., 2010), wind exposure (Voronov, 1967), shelter (Dennis & Sparks, 2005), temperature (Dennis, 2004; Goszczyńska & Goszczyński, 1977; Seifan et al., 2010) and disturbance (Parish & Turkington, 1989b) compared with the surrounding area.

The combined effects of moles on soil properties, microtopography and near-surface microclimates generate sites for seed germination and a variety of regeneration niches for both new and established plants (Milton et al., 1997; Parish & Turkington, 1989b; Voronov, 1967; Watt, 1974), including native and non-native pioneer species that use molehills as gateways for colonisation (Davies, 1966; Hole, 1981; Kiełtyk & Mirek, 2015). In doing so, moles impact the composition (Davies, 1966; Jalloq, 1975; Parish & Turkington, 1989a; Watt, 1974), diversity (Canals & Sebastìa, 2000; Milton et al., 1997; Seifan et al., 2010), biomass (Goszczyńska & Goszczyński, 1977) and spatio-temporal dynamics (Canals & Sebastià, 2002; Schiffers et al., 2010) of plants. The unique environmental conditions on molehills are also known to attract and benefit a variety of animals, including those of conservation concern (Streitberger & Fartmann, 2013). This includes ants (Bliss et al., 2003; Bliss et al., 2006; Katzerke et al., 2010; King, 1977; Mellanby, 1971; Voronov, 1967) and butterflies (Dennis, 2004; Dennis & Sparks, 2005; Streitberger et al., 2014; Streitberger & Fartmann, 2013, 2015) that use molehills for nest-building and oviposition, respectively, resulting in indirect geomorphological and ecological impacts.

1.3 | The European mole as a geomorphic agent

While relatively few studies have directly investigated the role of moles as geomorphic agents, they have been shown to alter microtopography (Hole, 1981; Mellanby, 1971), excavate considerable volumes of sediment (Abaturov, 1972; Goszczyńska & Goszczyński, 1977; Grulich, 1958, 1959; Skoczeń, 1958; Wijnhoven et al., 2006), contribute to the downhill movement of sediment in mountainous regions (Imeson, 1976; Imeson & Kwaad, 1976; Jonca, 1964, 1972; Tansley & Adamson, 1925) and modify riverbank morphology (Bylak & Kukula, 2020; Mellanby, 1971; Mikuś, 2020; Mikus & Uchman, 2013; Schaefer & Sadlier, 1981; Turcek, 1956) and the internal structure of man-made levees (Chlaib et al., 2014). Mole tunnels, for example, are thought to act as a conduit for river water during flood events, thereby promoting the formation of lateral branching channels, progressive bank erosion and increased sediment supply (Bylak & Kukula, 2020; Mikus & Uchman, 2013). In addition, several studies have commented on the ability of moles to indirectly facilitate biogeomorphological activity through the creation of landforms (i.e., tunnels and molehills) that support other bioturbators, such as ants (Katzerke et al., 2010; Voronov, 1967), earthworms (Gabet et al., 2003; Mellanby, 1971; Schaefer & Sadlier, 1981) and small fossorial mammals (Hole, 1981; Stepanova et al., 2021), and the loosening of soil that promotes further displacement by larger animals, such as grazing livestock (Ennik, 1967; Goszczyńska & Goszczyński, 1977; Kiełtyk & Mirek, 2015; Ramzaev & Barkovsky, 2018; Turcek, 1965).

Molehills represent the most easily identifiable geomorphic impact of the European mole (Figure 1). Moles construct these conical landforms from the loose sediment excavated from tunnels. As such, they can be used to estimate how much sediment moles displace over time at a given location to better quantify their role as local and regional scale agents of sediment mobility. Previous estimates of excavation rates vary greatly (between 1 and 150 m^3 ha^{-1} $year^{-1}$; e.g., Abaturov, 1972; Imeson, 1976; Jonca, 1964; Wijnhoven et al., 2006) and are often difficult to compare because of differences in the design (i.e., time and spatial monitoring scale and method), local conditions (i.e., soil type and climate), reported metrics (i.e., volume vs. mass) and research focus of different studies. As for the landforms themselves, molehills have received little attention in terms of their longevity (i.e., the length of time a molehill has positive relief compared with its surroundings) and evolution over time, although it has been noted that rainfall and freeze–thaw processes can significantly alter their morphology (Imeson, 1976; Imeson & Kwaad, 1976; Jonca, 1972). Typical dimensions of molehills reported in the literature are 10–50 cm in diameter and 10–30 cm in height (Jonca, 1972; Skoczeń, 1958). Occasionally, however, moles will construct larger mounds (50–150 cm in diameter, 30–100 cm in height), known as 'fortresses', in areas prone to flooding and/or in thin soils (Grulich, 1958; Napierala et al., 2016; Olszewski & Skoczeń, 1965). These rare bioconstructions (less than 5% of moles construct fortresses) usually contain breeding nests, indicating they may provide above-ground refuge for young moles during flood events (Atkinson, 2013; Baker & Macdonald, 2015).

Although the dimensions of molehills have been reported in a variety of different environments (e.g., woodland, grassland, arable land and uplands), few studies have provided quantitative measurements of molehills at fine spatial (i.e., mm) and long temporal (i.e., weeks-to-months) scales. The generally small size of molehills and rapidity at which they can change create challenges for monitoring their evolution over time. For instance, only the largest mounds are visible in most widely available satellite imagery (although see Koshkina et al., 2019 and Lopucki et al., 2022). Recent advances in techniques, such as structure-from-motion (SfM) photogrammetry, have enabled researchers to undertake detailed mapping and quantification of small-scale geomorphic landforms and features using relatively inexpensive and portable equipment, for example, a digital camera and ground control points (Baxter et al., 2023; Mol & Clarke, 2019; Verma & Bourke, 2019). Such techniques offer a novel approach to capturing often subtle changes in individual molehills at small spatial scales (mm), allowing for a more nuanced understanding of how molehills develop and change over time.

In this study, we present 4 months of data obtained by monitoring the morphological changes in molehills constructed by *T. europaea* on a floodplain in Oxfordshire, UK. Through the creation of high-resolution digital elevation models (DEMs) using SfM photogrammetry, we derive a variety of metrics describing molehill morphology and produce a detailed record of how molehills change at weekly time intervals. In addition, measurements of molehill volume are used to estimate the excavation rate of moles at the study site over the course of a month. Findings show that (i) molehills are dynamic landforms that can persist in the landscape for several months, (ii) there are seasonal patterns (autumn–winter) to their morphology and degradation and (iii) the cumulative impact of mole burrowing is likely to be highly significant for localised soil bioturbation and sediment transport on floodplains. We hope that this case study serves as a useful starting point for future work on this geomorphologically important, yet commonly overlooked, animal.

2 | METHODOLOGY AND METHODS

2.1 | Regional setting

The European mole has been studied in Oxfordshire, UK, for over 100 years (e.g., Allroggen et al., 2019; Atkinson & MacDonald, 1994; Atkinson, Macdonald, & Johnson, 1994; Baker et al., 2015; Baker & Macdonald, 2015; Ford, 1935a, 1935b; Larkin, 1948; Macdonald et al., 1997). This includes several studies that have reported and/or investigated mole activity in University Parks (e.g., Atkinson & MacDonald, 1994; Macdonald et al., 1997; Viles, 2016), a public park (~0.3 km^2) located northeast of Oxford city centre, England, UK (Figure 3a). Located on the floodplain of the River Cherwell, the park is owned and managed by the University of Oxford and is open to the public nearly every day of the year. The park consists of landscape features typical of managed parkland, including lawns, meadows, sports fields, gardens, flower beds, wooded walkways, clusters of trees and a pond.

University Parks was selected as the study site as it is home to a visible mole population, with molehills a common site in the Parks' meadows and along the banks of the River Cherwell. Previous estimates suggest University Parks supports a mole population between 15 and 40 individuals (~6.7 moles per hectare), with adult males and females weighing on average 75.4 ± 5.1 and 68.0 ± 5.1 g, respectively (Macdonald et al., 1997). It is the policy of the park managers that moles are not exterminated and are only subject to management plans

FIGURE 3 (a) Location of University Parks in relation to the River Cherwell, Oxford city centre and buildings associated with the University of Oxford (purple) including those located in the science area; (b) the study site (orange circle) and an adjacent field where the number of molehills were counted over a 1-month period (yellow rectangle; Google Earth Pro, 14/05/2023, University Parks, South Parks Road, Oxford, UK. 51°45′44″ N, 1°15′02″ W, eye alt 791 ft); (c) molehills in the wider vicinity of the study site, with the white wooden posts demarcating the area used for the molehill count and excavation rate estimates; (d) molehill 'scars' (i.e. small areas of bare soil) clearly visible in historic satellite imagery of the study site taken during a drought period in 2009 (Google Earth Pro, 29/05/2009, University Parks, South Parks Road, Oxford, UK. 51°45′40″ N, 1°15′02.88″ W, eye alt 791 ft. © 2024 Infoterra Ltd & Bluesky). [Color figure can be viewed at wileyonlinelibrary.com]

when they encroach onto sports pitches. Images available on Google Earth show that molehills are widely distributed in areas of the Parks not used for sport and away from public footpaths (Figure 3b,d). A considerable amount of scarring (circular patches of disturbed grass) as a result of previous mole burrowing is also visible in areas with extant mole activity.

Meteorological data from the Radcliffe Meteorological Station (located within 1 km from the study site) was used to provide environmental context to the observations and measurements of molehill morphology throughout the study period. Over the current standard 30-year average period (1991–2020), the mean temperature in Oxford was 11.0°C (mean daily maximum 15.0°C, mean daily minimum 7.1°C). January is the coldest month of the year on average (mean temperature 5.2°C), while July is the warmest (mean temperature 18.1°C). The annual precipitation is 682 mm, falling on average 118 days per year. The driest period of the year is late winter to early spring, and the wettest period is autumn; however, there is significant annual variability. On average, there are 34 days of frost per year.

The underlying geology of University Parks is mudstone (Oxford Clay Formation and West Walton Formation). Superficial deposits are primarily dominated by sand and gravel (Summertown-Radley and Northmoor deposits) and by free draining, lime-rich loamy soils. Towards the northeast of the park, alluvium and clayey soils with a high groundwater table become more dominant close to the banks of the River Cherwell.

2.2 | Site selection

Within a grassy field bordering the River Cherwell to the east of University Parks (51°45′44″ N, 1°15′03″ W, Figure 3), we used observations and SfM photogrammetry to monitor how molehills developed and changed over time. Specifically, we monitored how molehills within a circular area approximately 4 m in diameter and 12.5 m^2 in area changed over a 121-day period between 28 September 2022 and 27 January 2023.

The study site was chosen because of the abundance of mole activity in the surrounding area over both space and time, as evidenced by on-site observations and historical satellite imagery (Figure 3d). Its proximity (<30 m) to the University Parks Offices also meant that staff working at the park could easily check on the experiment to ensure that it had not been damaged because of vandalism or adverse weather, as had previously occurred during a preliminary experiment established at a different location. The 4-month study period allowed us to monitor how molehills developed and/or changed over different seasons (i.e., late summer to mid-winter) and weather conditions during a time of year when moles are known to be active (Allroggen et al., 2019; Baker et al., 2016).

Within the study site, we initially identified six newly formed (<2 days old) molehills to monitor (hereafter referred to as MA, MB, MC, ME, MF and MH). Within a week, however, two more molehills appeared (MD and MG); as such, we monitored eight molehills in total. The study site was fenced off at the beginning of the experiment to reduce the risk of animals (e.g., dogs and foxes) and members of the public disturbing the molehills.

2.3 | Morphology from digital elevation models

Over the 121-day monitoring period, SfM photogrammetry was used to record the surface topography of the eight molehills every 4–14 days, apart from the last measurement, which was recorded 42 days after the previous measurement. In total, the topography of each molehill was recorded 12 times (see Figures 4 and 5 for the exact dates of data collection). Unfortunately, due to poor light conditions on 16 December 2022, it was not possible to create an accurate DEM of MC. As such, the topography of this molehill was recorded 11 times, rather than 12.

Following a similar method outlined by Verma and Bourke (2019), three 12-bit coded markers and a scale bar downloaded from Agisoft Metashape (MS, v1.6.5) software were attached to control targets made of treated, weather-resistant cedar. To protect against deformation during humid conditions, the control targets were laminated and covered in textured plastic tape to completely seal them against moisture. To aid precision, the coded markers were placed on the control targets in the exact position they were displayed in the graphics editor on MS (Laburda et al., 2021). A digital vernier calliper with 0.01 mm accuracy was then used to measure the spacing of the coded markers and confirm they were uniformly positioned on each of the control targets (Table 1). A control target was then fixed at a constant distance of 45 cm from the centre of each molehill for the entire monitoring period to allow for the accurate scaling of DEMs using a local reference system. Coded scale bars (2 × 5 cm, with 0.01 mm accuracy) attached to each of the control targets were used as independent check points to calculate the horizontal and vertical error of the DEMs and assess the overall quality of the resulting models (Cullen et al., 2018; Verma & Bourke, 2019).

TABLE 1 Local coordinates for each vertex of the coded control targets.

Coded marker	X (m)	Y (m)	Z (m)
Marker 1	0	0	0
Marker 2	0.0858	0	0
Marker 3	0.1254	0.0915	0

For each measurement, a Sony Alpha a6600 APS-C Mirrorless Camera with an E 20 mm F2.8 lens and an effective resolution of 24.2 megapixels (Mpx) was used to capture 13 photographs of each molehill: 12 overlapping photographs were taken at equally spaced ordinal points (i.e., North, North–North-East, North-East, East–North-East, East) around the perimeter of each molehill, with an additional photograph taken from directly above to record the plan view. Photographs were angled towards the centre of each molehill (approx. 60° angle) and were taken at ~50 cm from the surface. Measurements were taken during overcast conditions to prevent uneven lighting and extreme contrast on the molehills.

Using Darktable v4.0, the raw images were checked to ensure they were well exposed and no photometric correction was required before conversion to 24-bit uncompressed tiff format (Baxter et al., 2023; Verma & Bourke, 2019). Image quality (Q) was then assessed in MS using the Estimate Image Quality tool; all images had Q values >0.7 (Cullen et al., 2018). In total, 1222 images were evaluated. Dense point clouds with approximately 7 million points were then generated for each molehill ($n = 8$) for every measurement period ($n = 12$; for MC, $n = 11$) in MS using uniform processing parameters (Table S1) carefully selected according to previous works that have analysed small-scale geomorphological features using SfM photogrammetry (e.g., Laburda et al., 2021; Verma & Bourke, 2019). The dense point clouds were then exported to CloudCompare (CC) v2.11.3 and used to generate DEMs with a ground sampling distance (GSD) of 1 mm/pix using the Rasterize tool, resulting in the creation of 95 topographic models. Differences in molehill topography from one timestep to another were then determined by analysing and comparing the DEMs using the Raster Calculator tool in ArcMap v10.8 to create DEMs of difference (DoDs; Cullen et al., 2018; Williams, 2012).

Throughout the study, the accuracy and comparability of the models was enhanced by guaranteeing the following: (i) all photographs were taken by the same person with the same camera and lens; (ii) each molehill was fitted with an identical reference control target; (iii) every photograph was taken in diffuse lighting conditions; (iv) each measurement involved recording 13 images with 95%–100% overlap that simultaneously contained all three coded markers and a reference scale bar; (iv) the images were processed using uniform parameters in MS and CC (Laburda et al., 2021). For each model, the root-mean-square error (RMSE) was calculated for the reference control points and check points (Table S2). For the control points, the mean $RMSE_{xy}$ value of all the models was 0.25 ± 0.09 mm, while $RMSE_z$ was 0.18 ± 0.06 mm. For the check points, the mean $RMSE_{xy}$ value was 0.29 ± 0.10 mm, while $RMSE_z$ was 0.23 ± 0.09 mm. In addition, the minimum level of detection (LoD) was determined to estimate the propagated error of the calculated DoDs for each molehill (Williams, 2012). Across all the molehills, the mean LoD was 0.34 mm, with a maximum LoD of 0.70 mm (Table S2).

2.4 | Molehill morphological metrics

Various morphological characteristics were measured for each molehill over time using the DEMs derived from SfM photogrammetry (Table 2). Details of these metrics and how they were calculated are

TABLE 2 The morphological metrics calculated from structure-from-motion (SfM)-derived digital elevation models (DEMs) used to characterise how molehill morphology changed over time throughout the study period.

Characteristic	Abbreviation	Units	Description
Maximum height	h_{max}	cm	The highest point of the molehill
Mean height	h_{avg}	cm	Average height of all pixels in the molehill
Perimeter	P	cm	Length of perimeter around the base of the molehill
2D planar area	A_{plan}	cm^2	Total planimetric footprint of the molehill
3D surface area	S_m	cm^2	Total surface area of the 3D molehill
Volume	V_m	cm^3	Total volume of sediment comprising the molehill
Arc-chord ratio	ACR	-	A measure of rugosity or surface roughness of the molehill. Calculated by taking the ratio of contoured area to the area of a plane of best fit.
Reock degree of compactness	R	-	A measure of compactness or roundness. Calculated by taking the ratio of A_{plan} to the area of the minimum bounding circle (A_{MBC}) that encloses it.
Polsby–Popper score	PP	-	An additional measure of compactness or roundness. Calculated by taking the ratio of A_{plan} to the area of a circle with the same perimeter (P_{plan}).
Hemi-sphericity	HS	-	How closely the morphology of a molehill resembles a perfect hemisphere, calculated by taking the ratio of the surface area of the molehill to the surface area of an idealised hemisphere of equal volume.

provided in greater detail in Data S3. Size measurements (i.e., height, perimeter, surface area and volume) are reported in centimetres (i.e., cm, cm^2, cm^3) to aid comparability with other studies that have reported values of animal spoil heaps. The generation of high-resolution DEMs allowed for qualitative interpretations of the potential processes driving morphological changes in the molehills throughout the study period.

2.5 | Regression analysis

Linear regression was used to investigate how the measured morphological metrics changed over time for each of the studied molehills. Given that some of the molehills experienced phases of construction/re-building during the first 1–2 weeks of monitoring, regression analysis was conducted using measurements taken (i) across the entire study period and (ii) with the first measurement removed, as this provides a better characterisation of morphological changes due to degradational processes.

While recognising the limitations of conducting regression analysis with a small sample size ($n = 8$), we also used power law regression to explore the relationships between morphological metrics averaged across the study period. Regression has been used in previous studies to quantitively relate the morphological characteristics of biogeomorphic features to other phenomena of interest, such as the dimensions of signal crayfish burrows and riverbank erosion (Sanders et al., 2021) as well as the surface area and volume of badger setts (Coombes & Viles, 2015). In the case of the studied molehills, power law regression was used to test whether simple morphological metrics (i.e., mean molehill height and perimeter) could be used to predict sediment volume. SfM photogrammetry provides high-resolution measurements of total volume that do not rely on assumptions about molehills fitting idealised three-dimensional shapes (e.g., elliptic paraboloids), as has been employed in previous studies (e.g., Bliss et al., 2006; Katzerke et al., 2010). Such relationships may, therefore, permit the quick and accurate estimation of sediment movement due to mole activity using simple metrics measured in the field.

2.6 | Molehill count and estimates of sediment production rate

In a 2680 m^2 field adjacent to the main study site (demarcated by white posts at each corner; Figure 3b–d), the number of molehills that formed over a one-month period was also recorded. On 2 February 2023, all the molehills in this field were levelled as a consequence of the grass being mown. The number of newly formed molehills that emerged in this field over a 32-day period was then counted on 5 March 2023. This count was used to generate an estimate of sediment production per hectare, using the average volume of the molehills for which the SfM-derived DEMs were available.

3 | RESULTS

3.1 | Morphological change over time

3.1.1 | Volume

During the first 2 weeks of monitoring, the majority of the molehills increased in volume (Figure 4). MB, for example, increased by 4111 cm^3 (95%) in the first 2 weeks. The two newly constructed molehills—MD and MG—had the greatest percentage increase in volume during this time period, increasing by 378% (675 cm^3) and 826% (1169 cm^3), respectively. In contrast, MA, MC and MF decreased in volume by 3% (60 cm^3), 16% (56 cm^3) and 22% (623 cm^3), respectively. After this initial phase of change, molehill volume generally decreased with time or remained relatively constant. There were, however, a few exceptions to this trend: after initially decreasing in volume, MF increased by 172 cm^3 (8%) between 13 and 21 October 2022. The volume of several molehills (i.e., MA, MD, ME, MG and MH) also increased substantially between 2 and 16 December 2022, before decreasing until the end of the monitoring period. Regression analysis indicated that, across the entire study period, molehill volume significantly decreased with time for MA, MC, MF and MH ($R^2 \geq 0.364$, $p < 0.05$ in all cases). In contrast, no overall trend was found for MB, MD, ME or MG (Table S5).

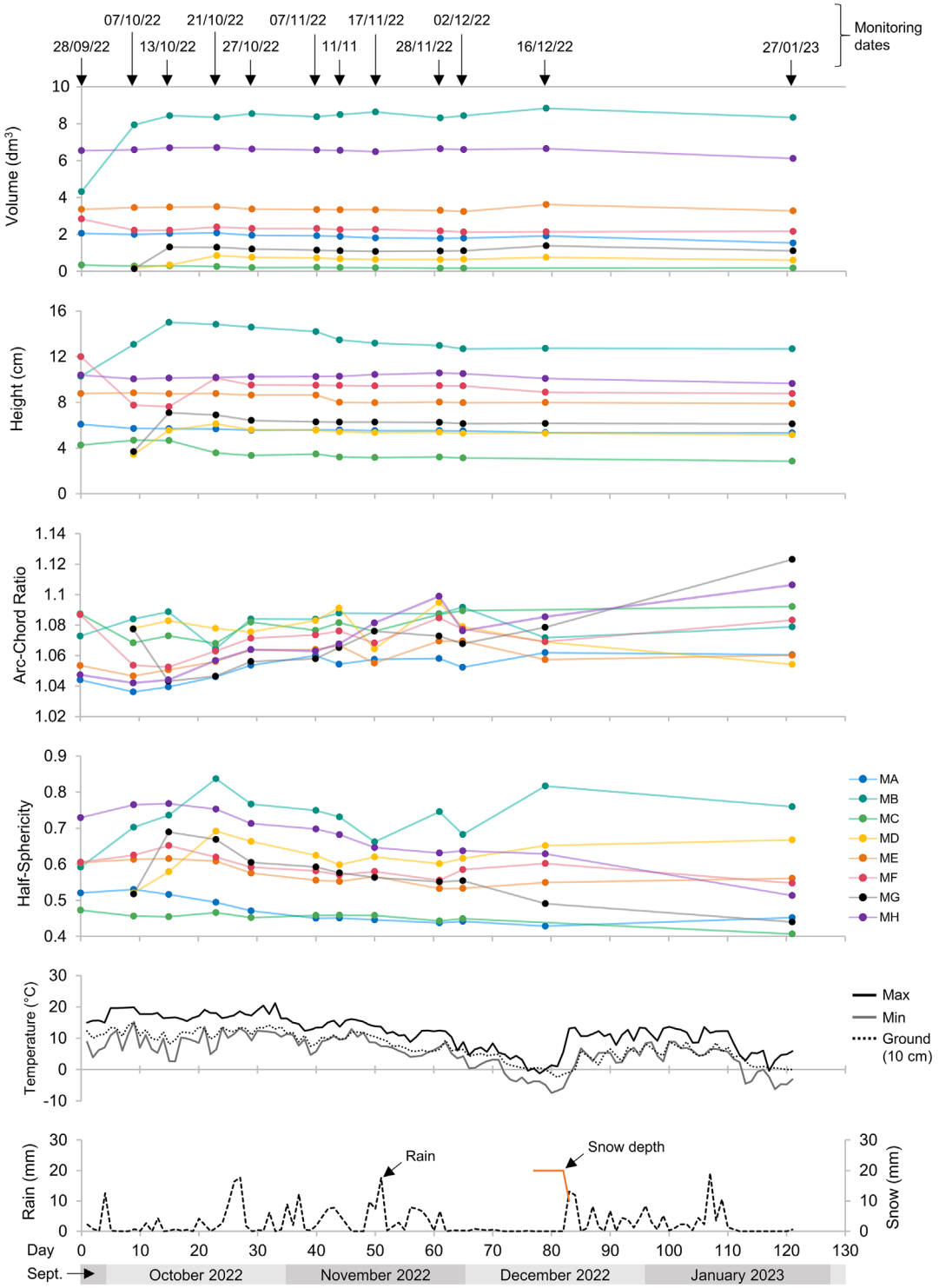

FIGURE 4 Changes to key morphological metrics for each molehill over the monitoring period between 27 September 2022 and 27 January 2023: molehill volume (dm^3, first row); height (cm, second row); arc-chord ratio rugosity (third row); half-sphericity (fourth row). Temperature (°C, fifth row) and precipitation (mm, sixth row) records obtained from the Radcliffe Observatory Meteorological Station are also shown. [Color figure can be viewed at wileyonlinelibrary.com]

Over the monitoring period, MF experienced the greatest (absolute) decrease in volume (i.e., 711 cm^3, 25%), while MB experienced the greatest (absolute) increase in volume (4516 cm^3, 105%). MB experienced the greatest rate of increase in volume for a molehill after it was initially formed (402 cm^3/day), while MF experienced the greatest rate of decrease in volume (69 cm^3/day). MB had the greatest maximum volume at 8837 cm^3 (16 September 2022), and MC had the smallest at 342 cm^3 (28 September 2022). The mean maximum volume (± SD) of the molehills was 3334 ± 2988 cm^3 (Table 3).

3.1.2 | Height

Substantial changes in height were recorded for several molehills during the first 2 weeks of monitoring (Figure 4). While MF decreased by 4.4 cm (36%), MB, MD and MG increased by 4.5 cm (46%), 2.7 cm (78%) and 3.2 cm (87%), respectively. In contrast, changes in height for MA, ME, MC and MH were comparatively small over the same time period (i.e., less than 10%). In general, molehill height steadily decreased 15 days after the start of the experiment,

TABLE 3 Key morphological metrics recorded for each molehill during the monitoring period. This includes the greatest rate of increase (+) and decrease (−) in molehill height and volume after the initial phase of construction. Values in bold denote the highest values of a variable measured over the study period.

	Height				Perimeter		Surface area		Volume			
			Greatest rate of change (cm/day)								Greatest rate of change (cm^3/day)	
	Max. (cm)	Mean (cm)	+	−	Max. (cm)	Mean (cm)	Max. (cm^2)	Mean (cm^2)	Max. (cm^3)	Mean (cm^3)	+	−
MA	6.1	5.6	<0.1	<0.1	100.4	91.7	670	624	2089	1903	8.6	23.2
MB	**15.0**	**13.3**	0.3	0.2	**131.0**	**125.1**	**1259**	**1151**	**8837**	**8085**	**401.8**	29.4
MC	4.7	3.6	<0.1	0.1	43.6	36.5	140	104	342	228	94.7	10.7
MD	6.1	5.3	0.4	0.1	54.0	48.4	236	192	853	621	63.6	16.3
ME	8.8	8.4	<0.1	0.2	108.2	104.7	888	821	3618	3385	10.8	23.0
MF	12.0	9.3	0.3	**0.5**	89.2	83.9	604	539	2845	2291	21.4	**69.2**
MG	7.1	6.1	**0.6**	0.1	77.2	65.1	422	322	1382	1093	194.8	15.9
MH	10.6	10.2	<0.1	<0.1	122.6	121.7	1164	1149	6714	6567	15.9	14.4
Mean	8.8	7.8	-	-	90.8	85.7	673	626	3335	3098	-	-

although there were some notable exceptions: the height of MF increased by 2.5 cm (33%) between the 13 and 21 October 2022 (Days 15–23) before steadily decreasing (Figure 5), whereas small increases in height were recorded for MH between 7 October 2022 and 28 November 2022 (Days 9–61). Regression analysis indicated that for the majority of the molehills (i.e., MA, MB, MC, MD, ME and MG), height significantly decreased over time ($R^2 \geq 0.462$, $p < 0.05$ in all cases) between the second and final measurement periods (Table S6).

The highest recorded molehill was MB on 13 October 2022 at 15.0 cm. MB also had the greatest height averaged over the monitoring period at 13.3 cm. The greatest rate of increase in height was recorded for MG (0.6 cm/day) between 7 and 13 October 2022, whereas the greatest rate of decrease in height was recorded for MF (0.5 cm/day) between 28 September and 7 October 2022. Overall, the average maximum height of the molehills was 8.8 ± 3.5 cm (Table 3).

In general, changes in mean height ($h_{avg.}$) followed a similar pattern to peak height throughout the monitoring period. However, noticeable increases in $h_{avg.}$ were observed for several molehills between 2 and 16 December 2022. In contrast, the peak height of the molehills remained relatively stable during the same time period (Figure 4).

3.1.3 | Surface area and perimeter

As with volume and height, the surface area and perimeter of the molehills changed substantially following their initial formation. During the first 2 weeks of monitoring, MB, MD and MG increased in perimeter by 9.9 cm (9%), 22.7 cm (73%) and 40.6 cm (147%), respectively, and in surface area by 231 cm^2 (25%), 154 cm^2 (198%) and 295 cm^2 (469%), respectively. In contrast, MF decreased in perimeter and surface area by 0.7 cm (8%) and 95 cm^2 (16%) over the same time period. Following this initial phase of change, the surface area and perimeter of the molehills remained relatively constant with a few notable exceptions: increases in surface area and perimeter were recorded for MA, MD, ME and MG on 16 December 2022; the surface area and perimeter of MC decreased relatively consistently throughout monitoring; and MB experienced greater variability between measurement periods compared with the other molehills. Across the entire study period, regression analysis indicated a significant negative relationship between surface area and time for two molehills—MA (F (1, 10) = 15.96, R^2 = 0.615, p-value = 0.0025) and MC (F (1, 10) = 0.12.64, R^2 = 0.584, p-value = 0.0062). In contrast, no significant relationship was found for MB, MD, ME, MF, MG and MH (Table S7). Over the study period, the average perimeter and surface area of the molehills were 85.7 ± 3.1 cm and 626 ± 382 cm^2, respectively (Table 3). MB had the greatest mean perimeter (125.1 cm) and surface area (1151 cm^2), as well as the greatest maximum perimeter (131.0 cm) and surface area (1259 cm^2). MG had the greatest range in perimeter (46.9 cm) and surface area (359 cm^2).

3.1.4 | Compactness and roundness

In general, relatively high (i.e., >0.5) Polsby–Popper (PP) and Reock (R) scores were recorded for each molehill throughout the monitoring period. Regression analysis indicated that, for most molehills (i.e., MB, MD, ME, MF and MG), PP and R scores did not significantly change over time (Tables S8 and S9). However, significant relationships were found for MA, MC and MG. Furthermore, the strength of these relationships (i.e., R^2 values) increased when the first measurement was removed from the analysis. On average, the 2D planar area of the molehills had PP and R scores of 0.94 and 0.72, respectively. MH had the greatest average PP (0.976) and R (0.824) scores, whereas MC had the smallest (PP = 0.904; R = 0.574).

3.1.5 | Hemi-sphericity

Apart from MC, the HS scores of the molehills increased during the first 1–3 weeks of monitoring. MB, MD, MF and MG experienced

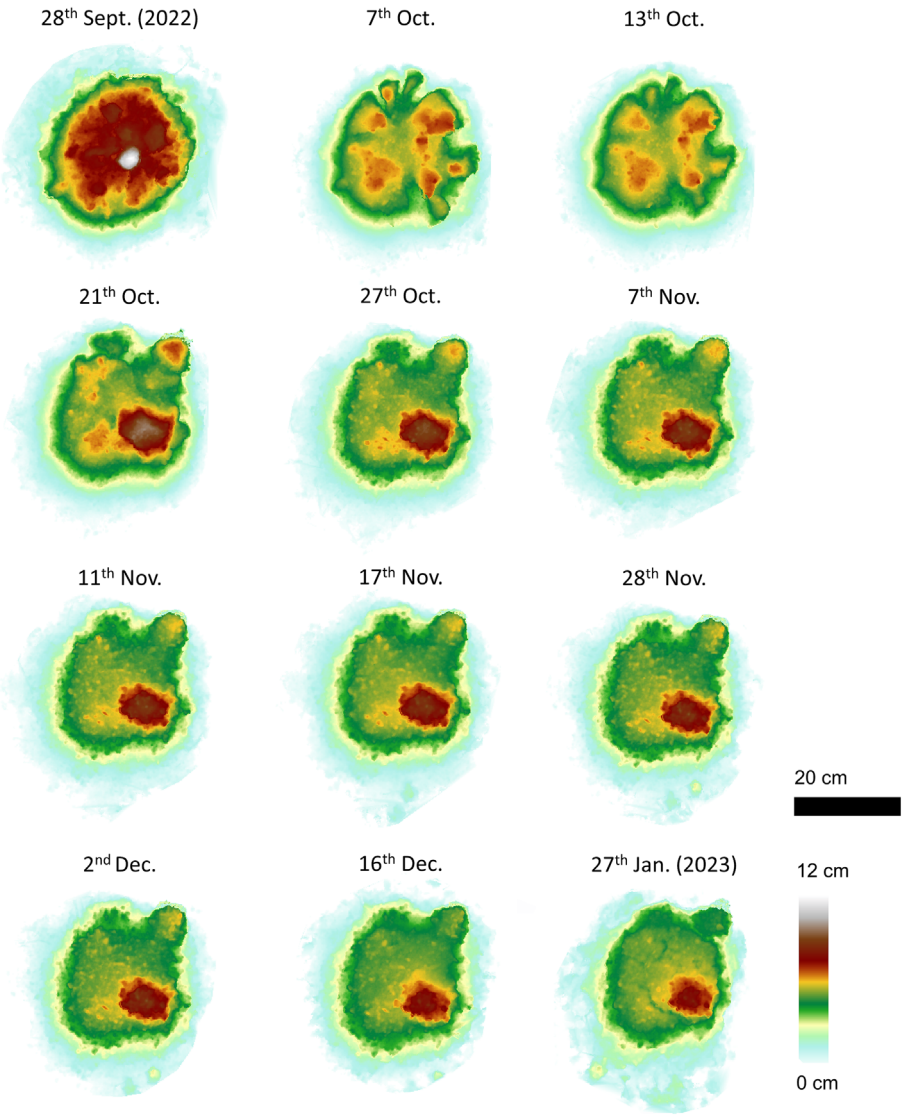

FIGURE 5 Digital elevation models (DEMs) of molehill MF over the entire study period. Distinct phases of collapse and rebuilding are discernible between 28 September and 7 October, and 13 and 21 October, respectively. [Color figure can be viewed at wileyonlinelibrary.com]

the greatest changes in HS during this period, increasing by 0.245 (41%), 0.171 (33%), 0.046 (7%) and 0.172 (33%), respectively. After this initial phase, the HS scores of the molehills generally decreased over time, although noticeable increases were recorded for several molehills (i.e., MB, MD, ME and MF) between 28 November and 16 December 2022. Across the entire study period, regression analysis indicated that for the majority of the molehills (MA, MC, ME, MF, MG and MH), HS scores significantly decreased over time ($R^2 \geq 0.493$, $p < 0.05$ in all cases; Table S10). Larger molehills (i.e., MB and MH) typically had higher HS scores than smaller molehills; MD was an exception to this trend given that it had the third highest mean HS score but the second smallest mean volume. Across the entire study period, the mean HS score for the molehills was 0.586. MB had the greatest average HS score (0.732), while MC had the smallest (0.453).

3.1.6 | ACR rugosity

In general, arc-chord ratio (ACR) rugosity decreased between the first and second measurement periods before increasing with time (Figure 4). For instance, the mean ACR rugosity of MA, MC, MF, MG and MH initially decreased by 1.9% between measurements one and two before increasing by 4.2% by the end of the monitoring period. Regression analysis indicated that ACR rugosity significantly increased over time for MA, MC, MF, MG and MH ($R^2 \geq 0.561$, $p < 0.01$ in all cases) between the second and last monitoring period. In contrast, no overall trends in ACR rugosity were observed for MB, MD and ME (Table S11).

3.2 | Morphometric regression analysis

The morphological metrics that yielded the strongest relationships with mean molehill volume were perimeter and height (Figure 6). The resulting power law regressions indicated significant relationships between mean perimeter and volume ($F = (1, 6) = 206.09$, $R^2 = 0.97$, $p < 0.001$) and mean height and volume ($F = (1, 6) = 51.85$, $R^2 = 0.90$, $p < 0.001$). Conducting a multiple power law regression incorporating both mean molehill perimeter and height as independent variables yields an even greater R^2 value of 0.99 ($F = (2, 5) = 448.29$, $p < 0.01$ for both x variables) and a lower standard error describing the variance in the regression relationship relative to the single-variable regressions (Table 4).

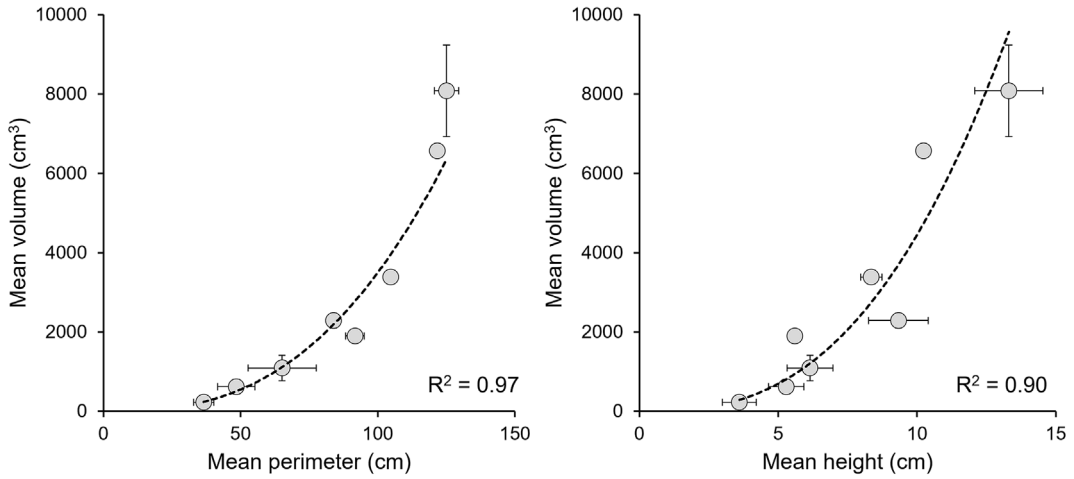

FIGURE 6 Power law regression models of the relationship between mean molehill perimeter (left) and height (right) versus mean molehill volume for the eight studied molehills throughout the study period. Error bars for all the recorded values ($n = 95$) are plotted as 1 standard deviation around the mean values. Regression equations and standard errors are given in Table 4.

TABLE 4 Parameters of the single variable regression relationships between mean molehill perimeter (P) and height (H), as well as multiple variable regression relationship incorporating both P and H, and mean molehill volume (V_m).

Regression equation	R^2	Standard error	*p* value
Single variable regression			
$V_m = 0.0035P^{2.66}$	0.97	0.22	<0.001
$V_m = 2.12H^{2.68}$	0.90	0.42	<0.001
Multiple variable regression			
$V_m = 0.034P^{1.86}H^{0.94}$	0.99	0.11	<0.01

3.3 | Morphological features

Throughout the study period, distinct morphological features were observed on several molehills. This includes protrusions and depressions of sediment that formed on the molehills as they experienced intermittent phases of construction, collapse, erosion and/or rebuilding. The development and transformation of these features was analysed by comparing DEMs of the molehills over time (e.g., Figure 5).

During the initial phase of construction, columns of sediment developed at the peaks of several molehills. This includes, for example, a column of sediment 6 cm high and 2.5 cm in diameter that formed at the centre of MF (Figure 5). In general, these unstable features collapsed within a week of forming (Figures 5 and 7a). However, in some instances, protrusions of sediment were re-established during subsequent phases of rebuilding. MF, for example, increased in height by 2.5 cm due to rebuilding between 13 and 21 October 2022, 2 weeks after its initial collapse (Figure 7c). Worm casts, small heaps of sediment ejected from the digestive tracts of earthworms, mainly *Aporrectodea* and *Lumbricus* species, also formed on several molehills during the later stages of the study, causing localised changes in molehill morphology (Figure S4). The largest worm cast formed on MH between 27 October and 2 December 2022 and was approximately 4 cm high and 3.5 cm in diameter (Figure 7d).

Circular depressions formed at the centre of two molehills during monitoring. This includes a hole 2.5 cm deep and 2.5–3 cm in diameter that formed on ME between 27 October and 7 November 2022. On MB, a central depression formed on two separate occasions: first between 27 October and 7 November 2022 (2.5 cm deep, ~3 cm in diameter) and second between 28 November and 2 December 2022 (3 cm deep, ~3 cm in diameter). It is worth noting that the second of these depressions was caused by a large stone (3 × 2 × 1.5 cm) being displaced downslope of the molehill towards its edge (Figure 7b).

Towards the end of the monitoring period, substantial cracks formed on several molehills (e.g., Ma, MB, MD and MH). These cracks generally started to form during the beginning of the 2022/23 winter (i.e., between 11 November and 16 December 2022) and were most pronounced in January 2023 towards the end of the study (Figure 7f). At this time, several molehills developed a 'plateau-like' morphology, with relatively flat tops and steep sides (Figure 7e).

3.4 | Estimating sediment production

Over a 1-month period between 2 February 2023 and 5 March 2023, 313 molehills were recorded in a 2680 m^2 field adjacent to the main study site, following the levelling of all molehills in the area due to mowing. This is equivalent to 11.68 molehills per 100 m^2. While recognising the limitations of extrapolating results over different spatial and temporal scales, we provide coarse estimates of percentage cover and excavation rate by treating the eight molehills modelled using SfM photogrammetry as representative examples of molehills in the entire field. Such extrapolations are commonly applied in studies of bioturbation given the challenges of monitoring small and stochastic features over large spatial and temporal scales (e.g., Coombes & Viles, 2015).

Given the average surface area of the eight molehills (626 ± 382 cm^2), we estimate molehills covered approximately 19.59 ± 11.96 m^2 (i.e., 0.73%) of the field over a 1-month period. Given the average volume derived from SfM photogrammetry of the studied molehills (3334 ± 2988 cm^3), we estimate the moles moved

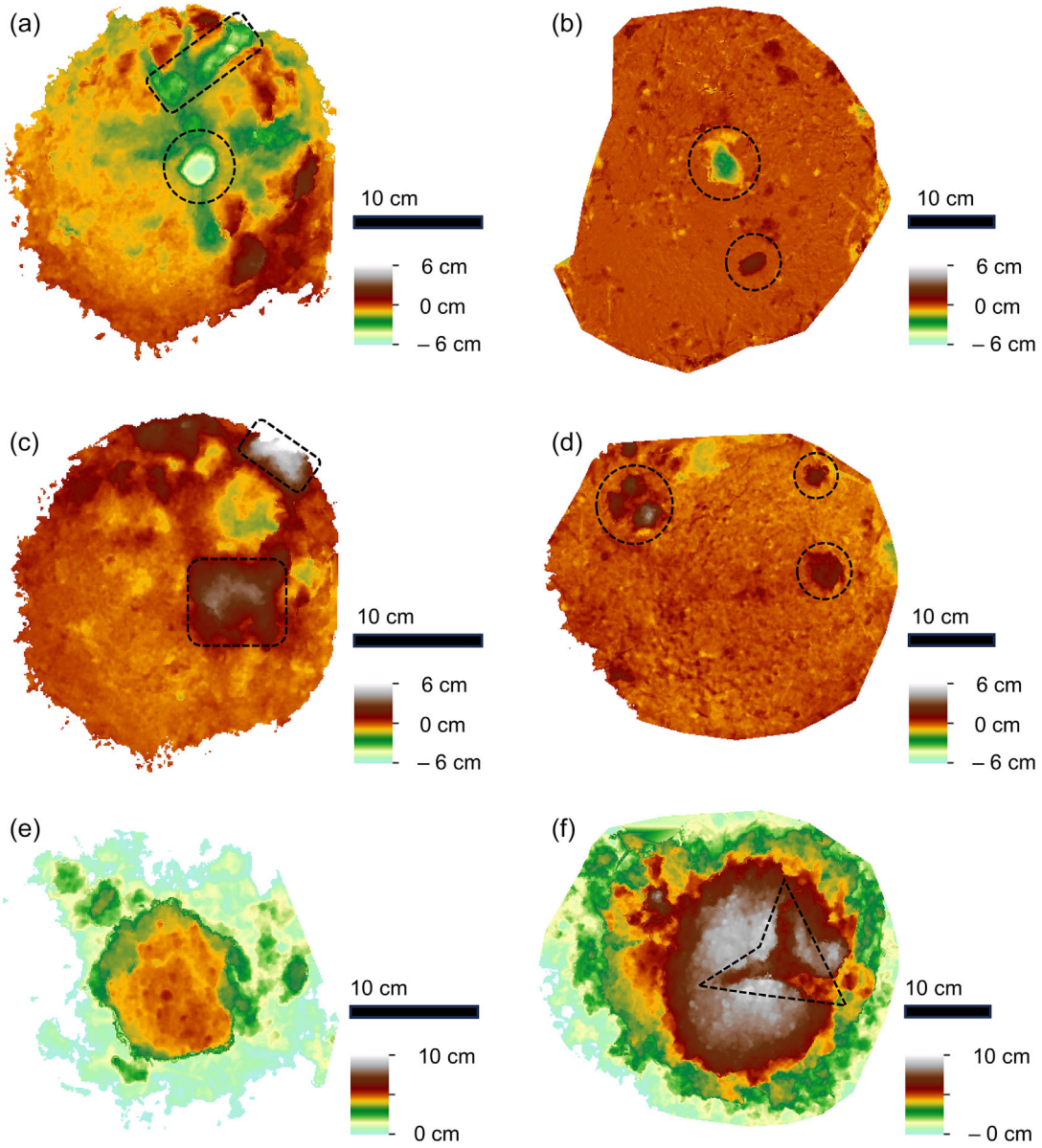

FIGURE 7 The development and transformation of key morphological features shown by comparing digital elevation models (DEMs) of molehills over time (a to d), and static models of molehills with distinct morphologies (e and f): (a) MF, areas of significant collapse, including a central column of soil 6 cm in height, observed between 29 September and 7 October 2022; (b) MB, the formation of a central depression caused by the downslope movement of a large stone observed between 28 November and 2 December 2022; (c) MF, areas of substantial rebuilding observed between 13 and 21 October 2022; (d) MH, the formation of wormcasts observed between 27 October and 2 December 2022; (e) a plateau-like morphology (e.g., relatively flat with step sides) formed on the surface of MG observed on 27 January 2023; (f) cracks that developed on the surface of MH observed on 27 January 2023. [Color figure can be viewed at wileyonlinelibrary.com]

approximately 1.042 ± 0.936 m^3 of soil in the field. This corresponds to an excavation rate of 3.89 m^3 ha^{-1} $month^{-1}$, which, extrapolated over 12 months, corresponds to 46.68 m^3 ha^{-1} $year^{-1}$ assuming a constant rate of burrowing activity.

4 | DISCUSSION

4.1 | Molehill development and degradation

After 4 months of monitoring, we observed significant changes in molehill morphology. While most molehills emerged as broadly semi-spherical domes of sediment, intermittent phases of construction, collapse, erosion and/or rebuilding repeatedly modified the mounds, causing measurable changes in height, surface area and volume and the formation of distinct morphological features over relatively short periods of time. This includes small-scale topographic features observed in previous studies such as freestanding columns of sediment (Skoczeń, 1958), central depressions and pedestals of soil protected by overlying stones (Imeson & Kwaad, 1976), as well as other biogeomorphic features (e.g., wormcasts) superimposed on the mounds. Although the molehills generally decreased in size throughout the entire study period, transitory increases in molehill height and volume were observed, particularly within the first couple of weeks of monitoring. This includes, for example, the newly-formed molehills (MD and MG) that increased in volume by 90%–830% in less than a week.

During relatively dry weather at the beginning of the monitoring period (i.e., early October 2024; Figure 4), aeolian processes and gravitational forces likely facilitated the initial erosion of fine-grained sediment, causing relatively steady decreases in molehill height. This was occasionally punctuated by more significant lowering due to the collapse of unstable columns of sediment. Increases in height and volume were also observed as moles continually reworked the mounds and added sediment over a three-week period. Heavy rain in late October and mid-November likely accelerated the displacement of fine- and medium-sized material through splash erosion and run-off (Imeson & Kwaad, 1976). While this generally enhanced lowering at the centre of the mounds, surface area and mean height (i.e., averaged over the entire surface) remained relatively constant—and in some cases increased—as material moved downslope towards the edges of the molehills. Increasing accumulation at the base of the molehills generally caused the mounds to flatten and widen over time and decrease in hemi-sphericity. However, this trend was not universal, with some molehills progressively decreasing in surface area (e.g., MF, MA and MC), potentially as a result of material being transported away from the edge of the mounds by wind and surface runoff.

Increases in molehill rugosity are likely explained by the selective removal of fine-grained sediment and the subsequent exposure of larger, gravel-sized material. This assertion is supported by qualitative observations of molehill stoniness increasing throughout the monitoring period (Figure S4). As the molehills became stonier, the downslope transport of material likely decreased, causing erosion rates at the edges of the mounds to increase in response to recession and vertical lowering and eventually approach those at the centre (Imeson & Kwaad, 1976). Overall, however, increasing stoniness likely contributed to reduced rates of lowering with time as the larger, residual material formed a protective cover on the surface of the molehills. In several cases, this led to the development of stones supported by pedestals of sediment several centimetres high that were shielded from erosion. This finding supports similar observations of stones and organic detritus (e.g., tree leaves) protecting molehills and other bioconstructions, such as badger mounds, from erosion (e.g., Coombes & Viles, 2015; Imeson, 1976; Imeson & Kwaad, 1976; Jonca, 1972) and highlights the importance of both sedimentary characteristics and erosional processes as factors controlling rates of molehill degradation.

During cold weather towards the end of the experiment (i.e., mid-December and January; Figure 4), frost action likely resulted in the upward displacement of the molehills, causing cracks and voids to form on the surfaces. This was followed by a period of thawing that likely contributed to the removal of coarse material that had been uplifted because of frost heave. During this period, several molehills developed plateau-like appearances as unconsolidated material detached from the slopes of the mounds. This observation supports similar reports of molehills developing a fungiform or tower-like appearance after freezing events in mountainous regions of central Europe (e.g., Jonca, 1972). Therefore, as in previous studies (e.g., Imeson, 1976; Imeson & Kwaad, 1976), we find there is a seasonal pattern to molehill erosion in temperate climates, with finer material removed during relatively warm weather in association with deflation and rainfall and coarser material removed during the colder winter months.

In addition to abiotic surface processes, earthworms were found to modify molehill morphology through the construction of wormcasts. These biogeomorphic features caused localised increases in molehill volume and lasted for several weeks once formed. This observation builds on previous reports of trampling livestock (Ennik, 1967; Goszczyńska & Goszczyński, 1977; Ramzaev & Barkovsky, 2018; Turcek, 1965) and nest-building ants (Bliss et al., 2003; Bliss et al., 2006; Katzerke et al., 2010; King, 1977; Mellanby, 1971; Voronov, 1967) influencing molehill morphology. When considered together, these findings indicate that, under certain conditions, molehills may be considered as composite biogeomorphological landforms. Given that earthworms are a major food source for the European mole, wormcasts superimposed on molehills may also represent a novel example of a landform constructed because of a unique predator–prey relationship (Germain et al., 2022; Mathers et al., 2019). The ecology of biogeomorphological interactions (i.e., how predation, competition and facilitation influence biogeomorphological processes) represents an important, but as of yet, relatively understudied field of research that warrants future attention (Coombes, 2016). This could include, for instance, investigating the direct and indirect effects of organisms on local-scale sediment movement through interactions between fossorial animals and other biogeomorphic agents. For example, Germain et al. (2022) recently studied the combined geomorphic impact of foxes (*Vulpes vulpes*) and bank swallows (*Riparia riparia*), which the foxes prey upon. They found that foxes accentuate the cliff erosion performed by bank swallows by digging pits to reach the birds' underground burrows and feed on their chicks. In the case of molehills, our results show that following their formation, subsequent modification and decay is at least partly influenced by earthworms, the main prey organism of moles. Such intra-species influences on biogeomorphic processes warrant much more attention but could include, for example, the destruction of prairie dog (*Cynomys gunnisoni*) burrows and 'villages' by the American badger (*Taxidea taxus*), a fossorial predator.

4.2 | Molehill morphology and longevity

The morphological characteristics (i.e., height, volume, surface area) of the molehills monitored in this study broadly correspond to those previously reported in grassland and pasture environments in mainland Europe (e.g., Bliss et al., 2006; Katzerke et al., 2010; Kiełtyk & Mirek, 2015; Ramzaev & Barkovsky, 2018; Skoczeń, 1958; Wijnhoven et al., 2006; Table 5). They were, however, noticeably smaller than those previously recorded in woodland (e.g., Abaturov, 1968; Dennis, 2004; Imeson, 1976) and upland environments (e.g., Jonca, 1972; Milton et al., 1997), as well as mole fortresses and nests that are typically an order of magnitude larger than regular molehills (e.g., Grulich, 1958; Napierala et al., 2016; Olszewski & Skoczeń, 1965).

After 4 months of monitoring, the studied molehills were still recognisable. This observation supports previous reports of molehills persisting in the landscape for several years in some instances (e.g., Imeson, 1976; King, 1977) and opposes the widely held assumption that molehills are predominantly short-lived, ephemeral landforms (Wijnhoven et al., 2006). Once fully formed, we recorded a mean monthly (i.e., 31 days) downwearing rate of 0.4 cm in molehill height. This is lower than rates reported by Wijnhoven et al. (2006) for molehills on a floodplain in the Netherlands, who estimated weekly lowering of 0.43 cm (equivalent to ~1.9 cm per month), as well as Jonca (1972), who suggested that molehills may lose between 30%

TABLE 5 Characteristics of mounds formed by *T. europaea*. Range and/or mean values are reported; in instances where both are provided, the mean value is shown in closed brackets (). Dashes (-) indicate where no data were available. The table also indicates where the availability of data is unknown (Unk.) due to problems accessing the primary source material and/or an English translation. Details of the study site and location for each reference are reported in Table S12.

		Molehill morphology					Excavation rate		Density	
Reference	Year	Height (cm)	Diameter (cm)	Surface area (cm^2)	Volume (dm^3)	Mass (kg)	(m^3 ha^{-1} yr^{-1})	(kg m^{-2} yr^{-1})	No. per 100 m^2	% cover
This study	2023	2.9–15.0 (8.8 ± 3.5)	-	60–1260 (630 ± 380)	0.34–8.84 (3.33 ± 2.99)	-	46.68 [3.89][a]	-	11.68[a]	0.73[a]
Ramzaev and Barkovsky	2018	-	18–45 (32)	254–1590 (804)[b]	-	8.1 DW	-	3.3–6.6 DW	19–41	3.4
Napierala et al.	2016	100[c]	100–150[c]	7854–17671[b, c]	-	-	-	-	-	-
De Reu et al.	2016	-	-	-	-	-	-	-	15.7	-
Kiełtyk and Mirek	2015	-	20–26	314–531[b]	-	-	-	-	56–76	15–17.5
Katzerke et al.	2010	9.3[d]	-	30–244 (71 ± 38)[b, d]	0.05–82.47[d] (4.02 ± 11.46)	-	-	-	15.83[d]	0.78[d]
Rastvorova	2007	-	-	-	-	-	30	-	>100	-
Bliss et al.	2006	7.0–36.0[d] (23.3 ± 11.1)	18.0–77.5[d] (41.7 ± 19.7)	254–4717 (1366)[b, d]	1.1–82.5[d] (23.9 ± 26.8)	-	-	-	-	-
Wijnhoven et al.	2006	6.7 ± 3.2	-	-	-	0.95 ± 0.63 DW	3.66 [i]	0.11–2.03 (0.44) DW	<12.09	-
Dennis	2004	-	50.1 ± 1.3	1971[b]	-	-	-	-	-	1.54
Canals and Sebastià	2002	-	-	1900 ± 300	-	-	-	-	-	3.0–6.6 [max = 30]
Edwards et al.	2001	-	-	1400	-	-	-	-	-	3.2
Milton et al.	1997	-	-	1800 ± 3100	-	-	-	-	<1.09	<0.21
Skoczeń et al.	1983	Unk.	Unk.	Unk.	Unk.	Unk.	Unk.	Unk.	Unk.	20[j]
Goszczyńska and Goszczyński	19771977	-	10–45	79–1590[b]	1.0–2.8[e]	-	21	3.2 DW	-	16.6
Funmilayo	1977	-	-	-	-	-	-	-	2.92–14.55	
Skoczen et al.	1976	-	-	-	-	-	-	2.5–6.3 FW [f]	41.0–210.6	4.3–11.2
Imeson and Kwaad	1976	-	-	190–2420[e, g]	0.72–11.66[e, g]	2–5 FW	19.40[g]	2.0 FW [g]	16.2–68.2[g]	0.02–2.90 (0.48)[g]
Abaturov	1972	-	-	-	-	-	3.25–15.50 [i]	0.35–1.69 DW [h]	-	-
Jonca	1972	20–30	10–60	79–2827[b]	-	4.2 FW	0.83–2.50 [i]	0.30–0.33 FW [a]	14–100	-
Haeck	1969	-	-	250	-	-	-	-	2.5[e]	-
Abaturov	1968	6.3 ± 0.2–8.1 ± 0.4	-	469 ± 45–513 ± 29	2.03 ± 0.16–3.47 ± 0.24	2.31 ± 0.16–3.96 ± 0.33 DW	-	1.18 DW	-	36

TABLE 5 (Continued)

Reference	Year	Molehill morphology					Excavation rate		Density	
		Height (cm)	Diameter (cm)	Surface area (cm^2)	Volume (dm^3)	Mass (kg)	(m^3 ha^{-1} yr^{-1})	(kg m^{-2} yr^{-1})	No. per 100 m^2	% cover
Ennik	1967	-	-	-	-	-	-	-	0.8–15.5 (7.8)	-
Turcek	1965	-	-	-	-	-	10[k]	-	<0.2[k]	-
Olszewski and Skoczeń	1965	20–40[c]	30–110[c]	707–9503[b, c]	-	-	-	-	-	-
Jonca	1964	Unk.	Unk.	Unk.	Unk.	Unk.	150 [f, k]	Unk.	Unk.	Unk.
Grulich	1959	Unk.	Unk.	1000–1200 [l]	Unk.	Unk.	40 [m]	6.0–6.5 FW [k, m]	73.8 [m]	7 [m]
Skoczeń	1958	13–15	15–50	177–1963[b]	-	1.5–7.5 FW	-	-	-	-
Grulich	1958	40–50[c]	150[c]	17 671[b, c]	-	≥250 FW [c]	≥34.5	≥5.5 FW	70–200	7–20 [max = 50]

Abbreviations: Measured weight: DW, dry weight; FW, fresh weight.
[a]Estimated over a 1-month period.
[b]Estimated from the reported diameter assuming a perfectly circular base.
[c]Includes molehill fortresses and/or nest chambers.
[d]Includes molehills colonised by ants.
[e]Estimated from graphs.
[f]Time period not reported.
[g]Includes mounds created by moles (*T. europaea)* and voles (*Microtus arvalis*).
[h]Up to 14.52 kg m^{-2} yr^{-1} reported but data incomplete.
[i]Data reported in Übernickel et al. (2021).
[j]Data reported in Kiełtyk and Mirek (2015).
[k]Data reported in Jonca (1972).
[l]Data reported in Haeck (1969).
[m]Data reported in Skoczeń et al. (1976).

and 70% of their mass within 2–3 days due to thermal degradation (freeze–thaw), gravitational erosion and aeolian processes in upland regions of Poland. In contrast, the downwearing rates measured in this study are greater than those reported by Imeson and Kwaad (1976), who observed monthly lowering between 0.07 and 0.27 cm over a 15-month period for molehills on a forested hillslope in Luxembourg. In this instance, contrasting downwearing rates may be explained by differences in tree canopy cover and the density of fallen tree litter, which are both thought to reduce the effects of splash erosion on underlying molehills (Imeson & Kwaad, 1976).

Assuming a constant rate of lowering, we estimate that the molehills recorded in this study may have persisted in the landscape for 250–2927 days (0.7–8 years) if left undisturbed. In reality, erosion rates likely change over time in response to changing seasons and weather, vegetation cover and stochastic disturbance events caused by human activity and larger animals that were deliberately excluded from this experiment. As observed towards the end of the monitoring period, extreme weather events (e.g., frost, but also rainstorms, floods, drought, etc.) and changes in molehill stoniness may enhance or retard overall rates of breakdown. More broadly, the longevity of molehills likely depends on a variety of factors relating to the local environment, climatic conditions and how they are managed. This includes slope gradient (Coombes & Viles, 2015; Imeson, 1976; Imeson & Kwaad, 1976; Jonca, 1972; Tansley & Adamson, 1925), soil characteristics (Imeson, 1976; Milner & Ball, 1970), vegetation cover (Edwards et al., 2001), the amount and character of surface water flow (Imeson & Kwaad, 1976; Jonca, 1972) and the frequency and magnitude of disturbance events linked to human activity, wildlife and extreme weather (Atkinson, Macdonald, & Johnson, 1994; Ennik, 1967; Goszczyńska & Goszczyński, 1977; Jonca, 1972; Wijnhoven et al., 2006).

4.3 | Excavation rate

The results of this study indicate that moles are capable of moving substantial volumes of sediment locally. For a floodplain in Oxfordshire, UK, we estimate that moles can excavate up to 3.89 m^3 ha^{-1} $month^{-1}$ of sediment. This is comparable to monthly excavation rates reported by Goszczyńska and Goszczyński (1977) for meadows in Poland (0.56–3.25 m^3 ha^{-1} $month^{-1}$) as well as yearly excavation rates reported by Wijnhoven et al. (2006) for a floodplain in the Netherlands (3.66 m^3 ha^{-1} $year^{-1}$) and Abaturov (1972) for forests in Russia (3.25–15.50 m^3 ha^{-1} $year^{-1}$; Table 5). As we monitored molehill development during a time of year when moles are known to be active and in response to a specific disturbance event (the levelling of previous molehills by mowing), the yearly excavation rate for moles in University Parks is likely to be lower than our estimate of 46.68 m^3 ha^{-1} $year^{-1}$. Nevertheless, given the density of molehills in certain areas of the park (>11 per 100 m^2) and its location on a relatively flat floodplain, moles have the potential to be major drivers of sediment movement in this environment. Importantly, our results suggest that moles move significantly more sediment than other fossorial mammals of a similar size, such as the European rabbit (*Oryctolagus cuniculus*) and European badger (*Meles meles*), which are reported to excavate up to 3.28 and 0.03 m^3 ha^{-1} $year^{-1}$, respectively (Coombes & Viles, 2015; James et al., 2011). In order to better characterise the excavation rates of European moles and reduce the uncertainties associated with extrapolating results (as reflected by the relatively high errors reported in this study), we suggest that future studies should collect high-resolution morphometric data from a larger sample of molehills (i.e., $n > 8$) in a variety of environmental contexts.

4.4 | Ecological implications

Although the ecological impacts of the studied molehills were not directly investigated, molehill 'scars' (i.e., remnant patches of disturbed soil as a result of previous mole burrowing) were qualitatively observed to support different plant communities compared with surrounding, undisturbed areas in University Parks. This finding supports similar reports of mole activity influencing vegetation cover through direct and indirect impacts on soil characteristics, microtopography and local-scale microclimates (Bliss et al., 2006; Katzerke et al., 2010; Streitberger et al., 2014; Streitberger & Fartmann, 2013). Changes in plant communities caused by the construction and degradation of molehills and other biogeomorphic features also likely influence local-scale run-off, erosion and deposition. However, the importance of these secondary geomorphic impacts on landscape evolution and ecosystem dynamics has rarely been studied (although see Imeson & Kwaad, 1976) and therefore warrants future research attention.

4.5 | Future work

Compared with formational processes, the preservation, re-engineering and degradation of biogeomorphological features have received limited research attention (Jones, 2012). Through the long-term, repeated monitoring of molehills at high resolution, this study provides foundational evidence that contributes to an improved understanding of the geomorphic contribution of animals to landscape evolution. By combining methods and understanding in biogeomorphology and ecology, future research should explore in greater detail the persistence and degradation of biogenic landforms, as well as the long-term geomorphological and ecological consequences of their formation and decay. This could include, for example, investigating the wider, landscape-scale impacts of spoil heaps as they undergo repeated phases of construction, abandonment, degradation and reworking. A better understanding of the degradational processes acting on biogenic landforms in the present could also aid interpretations of their preserved signatures in the sedimentary stratigraphic record for studying biogeomorphic processes over geological timescales (e.g., Marchetti et al., 2024).

As demonstrated in this study, SfM photogrammetry can be used as an effective tool to investigate the geomorphic evolution of biogenic landforms. SfM photogrammetry allowed for the detection of mm-scale changes in molehill morphology (the highest resolution measurements of these features to date), enabling a more nuanced understanding of how these landforms develop and degrade over time. As such, SfM photogrammetry should be recognised as a useful addition to the toolbox of methods available to researchers investigating dynamic changes in small-scale bioconstructions over time and space. Future research should establish the benefits of using SfM photogrammetry in combination with remote sensing (Koshkina et al., 2019; Lopucki et al., 2022), unmanned aerial vehicles (UAVs; De Reu

et al., 2016; Trachet et al., 2017), infrared thermography (Viles, 2016), ground penetrating radar (Allroggen et al., 2019; Chlaib et al., 2014; Saey et al., 2014) and ecological modelling (Coombes & Viles, 2015), as well as more traditional methods that have been used to investigate the development and breakdown of sedimentary bio-constructions, such as grain size analysis, erosion pins and splash boards (Imeson & Kwaad, 1976). This will allow for a more holistic understanding of the geomorphic importance of moles and other bio-geomorphological agents over longer time periods and larger spatial scales. Recent technological advances that enable the rapid creation of DEMs at a (relatively) low cost, such as the integration of photo-grammetry/LiDAR capabilities into smartphones (e.g., iPhone Pro) and handheld tablets, may present new opportunities for applying SfM photogrammetry in the field, and the benefits and challenges of using these methods in geomorphological research should be explored further (Luetzenburg, 2022).

As demonstrated in this study, it may be possible to determine coarse estimates of molehill volume by taking simple measurements, such as molehill height and/or perimeter, that are easily recorded in the field using cheap and easy-to-use equipment (e.g., ruler, tape measure), and applying simple regression models if a sub-sample of local molehills have known sediment volumes (e.g., Figure 6, Table 4). However, it is important to note that the regression relationships between molehill perimeter and height and molehill volume presented in Table 4 are unlikely to be universal, given the variability of other factors influencing the construction and morphology of molehills. These factors likely include soil type, climate conditions, gradient and season (Jonca, 1972), as well as the age of the measured molehill given the change in the morphological variables measured over time. Future work could include the comparison of regression relationships for estimating spoil heap volume across different environmental contexts and comparing predicted values of molehill volume based on regression to high-resolution measurements based on SfM photogrammetry.

5 | CONCLUSION

This case study provides the first detailed monitoring of changing molehill morphology through time using high-resolution digital methods. Through the construction of DEMs at the millimetre scale, it demonstrates that molehills are dynamic landforms that vary in their morphology over temporal scales of weeks–months and small spatial scales (inter-molehill variability across centimetres–metres). This adds to the growing body of research utilising SfM photogrammetry methods to capture rapid, small-scale biogeomorphological processes that, collectively, can have large-scale implications for sediment movement and landscape change. Results show that molehills undergo significant morphological changes, with erosion occurring rapidly following initial construction and then more slowly as finer sediment becomes progressively less available, leaving behind an 'armour' of larger and more stable clastic material. In drier late summer months, these processes of erosion appear to be primarily driven by aeolian and gravitational processes as the unstable parts of molehills collapse. In wetter and colder winter months, erosion from rain splash and frost heave becomes more important. High-resolution DEMs generated using SfM photogrammetry also reveal the reworking of molehills by other biogeomorphological agents, such as earthworms.

Our quantitative estimates of erosion rates suggest that molehills in low-gradient, temperate floodplain settings can persist as landscape features for 0.7–8 years, although this does not account for rapid changes due to stochastic disturbance events. We also estimate that moles could be responsible for displacing up to 3.89 $m^3\ ha^{-1}\ month^{-1}$ of sediment in the study area, which is comparable to the findings of previous studies across Europe. If extrapolated to regional scales across the floodplains of river systems in western Europe, the European mole could, therefore, play an important role in sediment mobility and bioturbation. However, these estimates are subject to uncertainties relating to factors such as the time of year monitoring is undertaken, the size of the local mole population as well as local soil type. Avenues for future research include developing methods to measure the geomorphological impact of moles and other mound-building organisms (e.g., ants, badgers, termites) over longer time periods and at larger spatial scales, such as combining SfM photogrammetry techniques with UAV surveys or the development of simple regression models for estimating molehill volume based on their perimeter and height, as is demonstrated in this study. Given the spatially and temporally heterogeneous nature of mole activity, repeating the types of surveys conducted here between different environmental contexts is likely to be important in better constraining the bio-geomorphological role of the European mole at larger spatial scales.

AUTHOR CONTRIBUTIONS

Timothy Baxter and Sam Woor contributed to the conception and design of the study under the guidance of Martin Coombes and Heather Viles. Timothy Baxter and Sam Woor collected the data, conducted the analysis and drafted the initial manuscript. All authors reviewed and edited drafts of the manuscript.

ACKNOWLEDGEMENTS

This study was supported by the University of Oxford and funding from the Engineering and Physical Sciences Research Council (EPSRC) and UKRI as part of the Centre for Doctoral Training in Science and Engineering in Arts, Heritage and Archaeology (SEAHA) [grant number: EP/L016036/1]. The authors would like to thank Paul Hutchinson at Oxford University Parks for accommodating this study and his expert knowledge, Charlie Knight for providing climate data from the Radcliffe Meteorological Station and Emily Read for her valuable insights and support.

CONFLICT OF INTEREST STATEMENT

The authors declare that the research was conducted in the absence of any commercial or financial relationship that could be construed as a potential conflict of interest.

DATA AVAILABILITY STATEMENT

The datasets used and/or analysed during the study are available from the corresponding author on reasonable request.

ORCID

Sam Woor https://orcid.org/0000-0002-1411-8486

REFERENCES

Abaturov, B.D. (1968) vlijanie rojuscej dejatel'nosti krota eriKtsti krota (*Talpa europaea* L) na poevennyi pokrov i rastitel'nosti' v

sirokolistvenno-elovam lesu (Importance of the digging activity of the mole (*Talpa europaea* L on soil cover and vegetation in a broad-leafed pine forest). *Pedobiologia*, 8(1), 240–264. Available from: https://doi.org/10.1016/S0031-4056(23)00326-8

Abaturov, B.D. (1972) The role of burrowing animals in the transport of mineral substances in the soil. *Pedobiologia*, 12(4), 261–266. Available from: https://doi.org/10.1016/S0031-4056(23)02043-7

Allroggen, N., Booth, A.D., Baker, S., Ellwood, S.A. & Tronicke, J. (2019) High-resolution imaging and monitoring of animal tunnels using 3D ground-penetrating radar. *Near Surface Geophysics*, 17(3), 291–298. Available from: https://doi.org/10.1002/nsg.12039

Anzah, F. & Butler, D.R. (2017) Revisiting an early classic on gopher bioturbation and geomorphology. *Progress in Physical Geography: Earth and Environment*, 41(4), 513–517. Available from: https://doi.org/10.1177/0309133317720836

Arlton, A.V. (1936) An ecological study of the mole. *Journal of Mammalogy*, 17(4), 349–371. Available from: https://doi.org/10.2307/1374401

Atkinson, R.P.D. (2013) *Moles*. Stansted, Essex, UK: Whittet Books.

Atkinson, R.P.D. & MacDonald, D.W. (1994) Can repellents function as a non-lethal means of controlling moles (*Talpa europaea*)? *Journal of Applied Ecology*, 31(4), 731–736. Available from: https://doi.org/10.2307/2404163

Atkinson, R.P.D., Macdonald, D.W. & Johnson, P.J. (1994) The status of the European mole *Talpa europaea* L. as an agricultural pest and its management. *Mammal Review*, 24(2), 73–90. Available from: https://doi.org/10.1111/j.1365-2907.1994.tb00136.x

Baker, S.E., Ellwood, S.A., Johnson, P.J. & Macdonald, D.W. (2016) Moles and mole control on British farms, amenities and gardens after strychnine withdrawal. *Animals*, 6(6), 39. Available from: https://doi.org/10.3390/ani6060039

Baker, S.E. & Macdonald, D.W. (2015) Moles on farmland: making mountains out of molehills? In: Macdonald, D.W. & Feber, R.E. (Eds.) *Wildlife conservation on farmland. Volume 2, conflict in the countryside*. Oxford: Oxford University Press. https://doi.org/10.1093/acprof:oso/9780198745501.003.0012

Baker, S.E., Shaw, R.F., Atkinson, R.P.D., West, P. & Macdonald, D.W. (2015) Potential welfare impacts of killtrapping European moles (*Talpa europaea*) using scissor traps and Duffus traps: a post-mortem examination study. *Animal Welfare*, 24(1), 1–14. Available from: https://doi.org/10.7120/09627286.24.1.001

Baxter, T., Coombes, M. & Viles, H. (2023) Intertidal biodiversity and physical habitat complexity on historic masonry walls: a comparison with modern concrete infrastructure and natural rocky cliffs. *Marine Pollution Bulletin*, 188, 114617. Available from: https://doi.org/10.1016/j.marpolbul.2023.114617

Bétard, F. (2021) Insects as zoogeomorphic agents: an extended review. *Earth Surface Processes and Landforms*, 46(1), 89–109. Available from: https://doi.org/10.1002/esp.4944

Bhatt, N.Y., Patel, S.J., Patel, D.A. & Patel, H.P. (2009) Burrowing activities of goby fish in the recent intertidal mud flats along the Navinal coast, Kachchh, Western India. *Journal of the Geological Society of India*, 74(4), 515–530. Available from: https://doi.org/10.1007/s12594-009-0159-9

Bliss, P., Katzerke, A., Moritz, R.F.A. & Neumann, P. (2003) Ecosystem engineering by moles (*Talpa europaea*) facilitates nest founding by mound-building ants (*Formica exsecta*). In: Stadler, J., Hensen, I., Klotz, S. & Feldmann, H. (Eds.) *Biodiversity – from patterns to processes*. Halle, Germany: Verhandlungen der Gesellschat für Ökologie.

Bliss, P., Katzerke, A. & Neumann, P. (2006) The role of molehills and grasses for filial nest founding in the wood ant *Formica exsecta* (Hymenoptera: Formicidae). *Sociobiology*, 47, 903–913.

Bolton, P.J. (1969) Studies in the general ecology, physiology and bioenergetics of woodland lumbricidae. In: *PhD thesis*. Durham: Department of Zoology. Durham University.

Borchard, P. & Eldridge, D.J. (2011) The geomorphic signature of bare-nosed wombats (*Vombatus ursinus*) and cattle (*Bos taurus*) in an agricultural riparian ecosystem. *Geomorphology*, 130(3-4), 365–373. Available from: https://doi.org/10.1016/j.geomorph.2011.04.021

Butler, D.R., 1995. *Zoogeomorphology: animals as geomorphic agents*. Cambridge University Press, Cambridge, UK, https://doi.org/10.1017/CBO9780511529900

Bylak, A. & Kukula, K. (2020) Geomorphological effects of animals in mountain streams: impact and role. *Science of the Total Environment*, 749, 141283. Available from: https://doi.org/10.1016/j.scitotenv.2020.141283

Canals, R.M. & Sebastìa, M.T. (2000) Soil nutrient fluxes and vegetation changes on molehills. *Journal of Vegetation Science*, 11(1), 23–30. Available from: https://doi.org/10.2307/3236771

Canals, R.M. & Sebastià, M.T. (2002) Heathland dynamics in biotically disturbed areas: on the role of some features enhancing heath success. *Acta Oecologica*, 23(5), 303–312. Available from: https://doi.org/10.1016/S1146-609X(02)01159-1

Catania, K.C. (2000) Epidermal sensory organs of moles, shrew-moles, and desmans: a study of the family Talpidae with comments on the function and evolution of Eimer's organ. *Brain, Behavior and Evolution*, 56(3), 146–174. Available from: https://doi.org/10.1159/000047201

Chlaib, H.K., Mahdi, H., Al-Shukri, H., Su, M.M., Catakli, A. & Abd, N. (2014) Using ground penetrating radar in levee assessment to detect small scale animal burrows. *Journal of Applied Geophysics*, 103, 121–131. Available from: https://doi.org/10.1016/j.jappgeo.2014.01.011

Coombes, M.A. (2016) Biogeomorphology: diverse, integrative and useful. *Earth Surface Processes and Landforms*, 41(15), 2296–2300. Available from: https://doi.org/10.1002/esp.4055

Coombes, M.A. & Viles, H.A. (2015) Population-level zoogeomorphology: the case of the Eurasian badger (*Meles meles* L.). *Physical Geography*, 36(3), 215–238. Available from: https://doi.org/10.1080/02723646.2015.1026170

Corbet, G.B. & Southern, H.N. (1977) *The handbook of British mammals*. Oxford, UK: Blackwell Scientific Publications Ltd.

Corenblit, D., Corbara, B. & Steiger, J. (2021) Biogeomorphological eco-evolutionary feedback between life and geomorphology: a theoretical framework using fossorial mammals. *The Science of Nature*, 108(6), 55. Available from: https://doi.org/10.1007/s00114-021-01760-y

Cox, G.W. (1990) Soil mining by pocket gophers along topographic gradients in a Mima moundfield. *Ecology*, 71(3), 837–843. Available from: https://doi.org/10.2307/1937355

Cullen, N.D., Verma, A.K. & Bourke, M.C. (2018) A comparison of structure from motion photogrammetry and the traversing micro-erosion meter for measuring erosion on shore platforms. *Earth Surface Processes and Dynamics*, 6(4), 1023–1039. Available from: https://doi.org/10.5194/esurf-6-1023-2018

Davies, H. (1966) Molehills and pasture reversion. *Grass and Forage Science*, 21(2), 148–149. Available from: https://doi.org/10.1111/j.1365-2494.1966.tb00463.x

Davies, K.C. & Jarvis, J.U. (1986) The burrow systems and burrowing dynamics of the mole-rats *Bathyergus suillus* and *Cryptomys hottentotus* in the fynbos of the south-western Cape, South Africa. *Journal of Zoology*, 209(1), 125–147. Available from: https://doi.org/10.1111/j.1469-7998.1986.tb03570.x

de Freitas, D.F., Ker, J.C., da Silva Filho, L.A., Pereira, T.T., de Souza, O.F. & Schaefer, C.E.G. (2021) Pedogeomorphology and paleoenvironmental implications of large termite mounds at the Brazilian semiarid landscape. *Geomorphology*, 387, 107762. Available from: https://doi.org/10.1016/j.geomorph.2021.107762

De Reu, J., Trachet, J., Laloo, P. & De Clercq, W. (2016) From low cost UAV survey to high resolution topographic data: developing our understanding of a medieval outport of Bruges. *Archaeological Prospection*, 23(4), 335–346. Available from: https://doi.org/10.1002/arp.1547

Dennis, R.L.H. (2004) Landform resources for territorial nettle-feeding Nymphalid butterflies: biases at different spatial scales. *Animal Biodiversity and Conservation*, 27, 37–45.

Dennis, R.L.H. & Sparks, T.H. (2005) Landscape resources for the territorial nymphalid butterfly *Inachis io*: microsite landform selection and behavioral responses to environmental conditions. *Journal of Insect*

Behavior, 18(5), 725–742. Available from: https://doi.org/10.1007/s/0905-05-7022-7

Edwards, G.R., Crawley, M.J. & Heard, M.S. (2001) Factors influencing molehill distribution in grassland: implications for controlling the damage caused by molehills. *Journal of Applied Ecology*, 36(3), 434–442. Available from: https://doi.org/10.1046/j.1365-2664.1999.00411.x

Ennik, G.C. (1967) Mole activity in relation to pasture management and nitrogen fertilization. *Netherlands Journal of Agricultural Science*, 15(3), 221–228. Available from: https://doi.org/10.18174/njas.v15i3.17440

Eriksson, B. & Eldridge, D.J. (2014) Surface destabilisation by the invasive burrowing engineer *Mus musculus* on a sub-Antarctic island. *Geomorphology*, 223, 61–66. Available from: https://doi.org/10.1016/j.geomorph.2014.06.026

Fellowes, M.D.E., Acquaah-Harrison, K., Angeoletto, F., Santos, J., da Silva Leandro, D., Rocha, E.A., et al. (2020) Map-a-mole: greenspace area influences the presence and abundance of the European mole *Talpa europaea* in urban habitats. *Animals (Basel)*, 10(6), 1097–1108. Available from: https://doi.org/10.3390/ani10061097

Ford, J. (1935a) The animal population of a meadow near Oxford. *Journal of Animal Ecology*, 4(2), 195–207. Available from: https://doi.org/10.2307/1009

Ford, J. (1935b) A preliminary investigation on the ecology of the common mole (*Talpa europea*). *Journal of Animal Ecology*, 4(1), 88–89. Available from: https://doi.org/10.2307/1216

Funmilayo, O. (1977) Distribution and abundance of moles (*Talpa europaea* L.) in relation to physical habitat and food supply. *Oecologia*, 30(3), 277–283. Available from: https://doi.org/10.1007/BF01833635

Gabet, E.J., Reichman, O.J. & Seabloom, E.W. (2003) The effects of bioturbation on soil processes and sediment transport. *Annual Review of Earth and Planetary Sciences*, 31(1), 249–273. Available from: https://doi.org/10.1146/annurev.earth.31.100901.141314

Germain, D., Luciano, J., Milot, J.-F. & Faghfouri, A. (2022) The predator-prey relationship from a zoogeomorphic perspective: a study of the red fox (*Vulpes vulpes*) and bank swallow (*Riparia riparia*) in eastern Canada. *Geomorphology*, 414, 108378. Available from: https://doi.org/10.1016/j.geomorph.2022.108378

Glosmann, M., Steiner, M., Peichl, L. & Ahnelt, P.K. (2008) Cone photoreceptors and potential UV vision in a subterranean insectivore, the European mole. *Journal of Vison*, 8(4), 23. Available from: https://doi.org/10.1167/8.4.23

Godfrey, G.K. (1955) A field study of the activity of the mole (*Talpa Europaea*). *Ecology*, 36(4), 678–685. Available from: https://doi.org/10.2307/1931306

Godfrey, G.K. & Crowcroft, P. (1960) *The life of the mole*. London: Museum Press.

Gorman, M.L. & Stone, R.D. (1990) *The natural history of moles*. Bromley, Kent, UK: Christopher Helm.

Goszczyńska, W. & Goszczyński, J. (1977) Effect of the burrowing activities of the common vole and the mole on the soil and vegetation of the biocenoses of cultivated fields. *Acta Theriologica*, 22, 181–190. Available from: https://doi.org/10.4098/AT.arch.77-12

Goszczyński, J. (1983) Digging activity and estimation of the population density of moles. *Acta Theriologica*, 28, 328–332. Available from: https://doi.org/10.4098/AT.arch.83-27

Grulich, I. (1958) Změny rostlinných společenstev na lukách vlivem rycí činnosti krtka obecného (*Talpa europaea*) v podmínkách jižní Moravy (Changes in plant communities in meadows due to the burrowing activity of the common mole (*Talpa europaea*) in the conditions of southern Moravia). *Preslia*, 30, 341–356.

Grulich, I. (1959) Vyznam ryci ćinnosti krtka obecneho (*Talpa europea*) v CSSR (The significance of the burrowing activity of the common mole (*Talpa europaea*) in Czechoslovakia). *Prace Brnenske zakladny CSAV (Proceedings of the Brno Base of the Czechoslovak Academy of Sciences)*, 31, 157–212.

Haeck, J. (1969) Colonization of the mole (*Talpa europaea* L.) in the Ijsselmeer polders. *Netherlands Journal of Zoology*, 19(2), 145–248. Available from: https://doi.org/10.1163/002829669X00107

Harris, S., Morris, P., Wray, S. & Yalden, D. (1995) *A review of British mammals: population estimates and conservation status of British mammals other than cetaceans*. Peterborough: JNCC.

Haussmann, N.S. (2017) Soil movement by burrowing mammals. *Progress in Physical Geography: Earth and Environment*, 41(1), 29–45. Available from: https://doi.org/10.1177/0309133316662569

Hole, F.D. (1981) Effects of animals on soil. *Geoderma*, 25(1-2), 75–112. Available from: https://doi.org/10.1016/0016-7061(81)90008-2

Huntley, N. & Reichman, O.J. (1994) Effects of subterranean mammalian herbivores on vegitation. *Journal of Mammalogy*, 75(4), 852–859. Available from: https://doi.org/10.2307/1382467

Imeson, A.C. (1976) Some effects of burrowing animals on slope processes in the Luxembourg Ardennes. Part 1 the excavation of animal mounds in experimental plots. *Geografiska Annaler. Series A, Physical Geography*, 58(1-2), 115–125. Available from: https://doi.org/10.1080/04353676.1976.11879929

Imeson, A.C. & Kwaad, F.J.P.M. (1976) Some effects of burrowing animals on slope processes in the Luxembourg Ardennes. Part 2 the erosion of animal mounds by splash under forest. *Geografiska Annaler. Series A, Physical Geography*, 58(4), 317–328. Available from: https://doi.org/10.1080/04353676.1976.11879941

Jalloq, M.C. (1975) The invasion of molehills by weeds as a possible factor in the degeneration of reseeded pasture. I. The buried viable seed population of molehills from four reseeded pastures in West Wales. *Journal of Applied Ecology*, 12(2), 643–657. Available from: https://doi.org/10.2307/2402180

James, A.I., Eldridge, D.J., Koen, T.B. & Moseby, K.E. (2011) Can the invasive European rabbit (*Oryctolagus cuniculus*) assume the soil engineering role of locally-extinct natives? *Biological Invasions*, 13(12), 3027–3038. Available from: https://doi.org/10.1007/s10530-011-9987-9

Jarvis, J.U.M. & Sale, J.B. (1971) Burrowing and burrow patterns of East African mole-rats Tachyoryctes, Heliophobius and Heterocephalus. *Journal of Zoology*, 163(4), 451–479. Available from: https://doi.org/10.1111/j.1469-7998.1971.tb04544.x

Jonca, E. (1964) Wpływ gryzoni i kietów na erozję gleb na Pogórzu Wałbrzyskim, Sudety Środkowe (The influence of rodents and kites on soil erosion in the Wałbrzych Foothills, Central Sudetes). *Czasopismo Geograficzne*, 35, 61–72.

Jonca, E. (1972) Winter denudation of molehills in mountainous areas. *Acta Theriologica*, 17, 407–412. Available from: https://doi.org/10.4098/AT.arch.72-31

Jones, C.G. (2012) Ecosystem engineers and geomorphological signatures in landscapes. *Geomorphology*, 157–158, 75–87. Available from: https://doi.org/10.1016/j.geomorph.2011.04.039

Katzerke, A., Bliss, P. & Moritz, R.F.A. (2010) Size matters: mole (*Talpa europaea*) hills and nest-site selection of the ant *Formica exsecta*. *Population Ecology*, 52(2), 271–277. Available from: https://doi.org/10.1007/s10144-009-0180-2

Kiełtyk, P. & Mirek, Z. (2015) Importance of molehill disturbances for invasion by *Bunias orientalis* in meadows and pastures. *Acta Oecologica*, 64, 29–34. Available from: https://doi.org/10.1016/j.actao.2015.02.007

King, T.J. (1977) The plant ecology of ant-hills in calcareous grasslands: I. Patterns of species in relation to ant-hills in Southern England. *Journal of Ecology*, 65(1), 235–256. Available from: https://doi.org/10.2307/2259077

Kinlaw, A. & Grasmueck, M. (2012) Evidence for and geomorphologic consequences of a reptilian ecosystem engineer: the burrowing cascade initiated by the Gopher Tortoise. *Geomorphology*, 157–158, 108–121. Available from: https://doi.org/10.1016/j.geomorph.2011.06.030

Kinlaw, A.L. (1999) A review of burrowing by semi-fossorial vertebrates in arid environments. *Journal of Arid Environments*, 41(2), 127–145. Available from: https://doi.org/10.1006/jare.1998.0476

Koshkina, A., Grigoryeva, I., Tokarsky, V., Urazaliyev, R., Kuemmerle, T., Hölzel, N., et al. (2019) Marmots from space: assessing population size and habitat use of a burrowing mammal using publicly available satellite images. *Remote Sensing in Ecology and Conservation*, 6(2), 153–167. Available from: https://doi.org/10.1002/rse2.138

Laburda, T., Krása, J., Zumr, D., Devátý, J., Vrána, M., Zambon, N., et al. (2021) SfM-MVS photogrammetry for splash erosion monitoring under natural rainfall. *Earth Surface Processes and Landforms*, 46(5), 1067–1082. Available from: https://doi.org/10.1002/esp.5087

Larkin, P.A., 1948. The ecology of mole (*Talpa europaea* L.) populations. PhD thesis. Department of Zoology. University of Oxford, Oxford.

Lopucki, R., Klich, D. & Kociuba, P. (2022) Detection of spatial avoidance between sousliks and moles by combining field observations, remote sensing and deep learning techniques. *Scientific Reports*, 12(1), 8264. Available from: https://doi.org/10.1038/s41598-022-12405-z

Luetzenburg, G. (2022) Investigating coastal change with smartphone LiDAR. *Nature Review Earth and Environment*, 3(2), 104. Available from: https://doi.org/10.1038/s43017-022-00265-0

Macdonald, D.W., Atkinson, R.P.D. & Blanchard, G. (1997) Spatial and temporal patterns in the activity of European moles. *Oecologia*, 109(1), 88–97. Available from: https://doi.org/10.1007/s004420050062

Marchetti, L., MacDougall, M.J., Buchwitz, M., Canoville, A., Herde, M., Kammerer, C.F., et al. (2024) Origin and early evolution of vertebrate burrowing behaviour. *Earth Science Reviews*, 250, 104702. Available from: https://doi.org/10.1016/j.earscirev.2024.104702

Mathers, K.L., Rice, S.P. & Wood, P.J. (2019) Predator, prey, and substrate interactions: the role of faunal activity and substrate characteristics. *Ecosphere*, 10(1), 1–18. Available from: https://doi.org/10.1002/ecs2.2545

Mathews, F., Kubasiewicz, L.M., Gurnell, J., Harrower, C.A., McDonald, R.A. & Shore, R.F. (2018) A review of the population and conservation status of British mammals. A report by the Mammal Society under contract to Natural England. In: *Natural Resources Wales and Scottish Natural Heritage*. Peterborough: Natural England ISBN 978-1-78354-494-3.

Mellanby, K. (1966) Mole activity in woodlands, fens and other habitats. *Journal of Zoology*, 149(1), 35–41. Available from: https://doi.org/10.1111/j.1469-7998.1966.tb02979.x

Mellanby, K. (1967) Food and activity in the mole *Talpa europaea*. *Nature*, 215(5106), 1128–1130. Available from: https://doi.org/10.1038/2151128a0

Mellanby, K. (1971) *The mole*. London: Collins.

Mikuś, P. (2020) Recent vertebrate and invertebrate burrows in lowland and mountain fluvial environments (SE Poland). *Water*, 12(12), 3413. Available from: https://doi.org/10.3390/w12123413

Mikus, P. & Uchman, A. (2013) The effect of water-level fluctuations on river bank fauna in the Dunajec river. *Biuletyn Państwowego Instytutu Geologicznego*, 454(454), 71–76. Available from: https://doi.org/10.5604/08676143.1114054

Milner, C. & Ball, D.F. (1970) Factors affecting the distribution of the mole (*Talpa europaea*) in Snowdonia (North Wales). *Journal of Zoology*, 162(1), 61–69. Available from: https://doi.org/10.1111/j.1469-7998.1970.tb01257.x

Milton, S.J., Dean, W.R.J. & Klotz, S. (1997) Effects of small-scale animal disturbances on plant assemblages of set-aside land in Central Germany. *Journal of Vegetation Science*, 8(1), 45–54. Available from: https://doi.org/10.2307/3237241

Mol, L. & Clarke, L. (2019) Integrating structure-from-motion photogrammetry into rock weathering field methodologies. *Earth Surface Processes and Landforms*, 44(13), 2671–2684. Available from: https://doi.org/10.1002/esp.4693

Napierala, A., Madra, A., Leszczynska-Deja, K., Gwiazdowicz, D.J., Goldyn, B. & Bloszyk, J. (2016) Community structure variability of Uropodina mites (Acari: Mesostigmata) in nests of the common mole, *Talpa europaea*, in Central Europe. *Experimental and Applied Acarology*, 68(4), 429–440. Available from: https://doi.org/10.1007/s10493-016-0017-6

Nesterkova, D.V. (2014) Distribution and abundance of European mole (*Talpa europaea* L.) in areas affected by two Ural copper smelters. *Russian Journal of Ecology*, 45(5), 429–436. Available from: https://doi.org/10.1134/S1067413614050129

Olszewski, J.L. & Skoczeń, S. (1965) The airing of burrows of the mole, *Talpa europaea* Linnaeus, 1758. *Acta Theriologica*, 10, 181–193. Available from: https://doi.org/10.4098/AT.arch.65-11

Parish, R. & Turkington, R. (1989a) The colonization of dung pats and molehills in permanent pastures. *Canadian Journal of Botany*, 68(8), 1706–1711. Available from: https://doi.org/10.1139/b90-219

Parish, R. & Turkington, R. (1989b) The influence of dung pats and molehills on pasture composition. *Canadian Journal of Botany*, 68(8), 1698–1705. Available from: https://doi.org/10.1139/b90-218

Platt, B.F., Kolb, D.J., Kunhardt, C.G., Milo, S.P. & New, L.G. (2016) Burrowing through the literature: the impact of soil-disturbing vertebrates on physical and chemical properties of soil. *Soil Science*, 181(3/4), 175–191. Available from: https://doi.org/10.1097/SS.0000000000000150

Quy, R. & Poole, D. (2004) *A review of methods used within the European Union to control the European Mole, Talpa Europaea*. London, UK: Department for Environment, Food and Rural Affairs (DEFRA).

Ramzaev, V. & Barkovsky, A. (2018) Vertical distribution of (137)Cs in grassland soils disturbed by moles (*Talpa europaea* L.). *Journal of Environmental Radioactivity*, 184-185, 101–108. Available from: https://doi.org/10.1016/j.jenvrad.2018.01.011

Rastvorova, O.G. (2007) The influence of vertebrates on the soil in the forest-steppe oak area "The Wood on Vorskle". *Russkiy Ornitologicheskiy Zh.*, 16, 819–827.

Rice, S.P. (2021) Why so skeptical? The role of animals in fluvial geomorphology. *WIREs Water*, 8(6), 1–11. Available from: https://doi.org/10.1002/wat2.1549

Rutin, J. (1992) Geomorphic activity of rabbits on a coastal sand dune, De Blink dunes, the Netherlands. *Earth Surface Processes and Landforms*, 17(1), 85–94. Available from: https://doi.org/10.1002/esp.3290170107

Saey, T., Van Meirvenne, M., De Pue, J., Van De Vijver, E. & Delefortrie, S. (2014) Reconstructing mole tunnels using frequency-domain ground penetrating radar. *Applied Soil Ecology*, 80, 77–83. Available from: https://doi.org/10.1016/j.apsoil.2014.03.019

Sanders, H., Rice, S.P. & Wood, P.J. (2021) Signal crayfish burrowing, bank retreat and sediment supply to rivers: a biophysical sediment budget. *Earth Surface Processes and Landforms*, 46(4), 837–852. Available from: https://doi.org/10.1002/esp.5070

Sassa, S., Watabe, Y., Yang, S. & Kuwae, T. (2011) Burrowing criteria and burrowing mode adjustment in bivalves to varying geoenvironmental conditions in intertidal flats and beaches. *PLoS ONE*, 6(9), e25041. Available from: https://doi.org/10.1371/journal.pone.0025041

Schaefer, V.H. (1981) A test of the possible reduction of the digging activity of moles in pastures by increasing soil nitrogen. *Acta Theriologica*, 26, 118–123. Available from: https://doi.org/10.4098/AT.arch.81-9

Schaefer, V.H. & Sadlier, M.F.S. (1981) Factors influencing molehill construction by the coast mole (*Scapanus orarius* True). *Mammalia*, 45, 31–38.

Schiffers, K., Tielbörger, K. & Jeltsch, F. (2010) Changing importance of environmental factors driving secondary succession on molehills. *Journal of Vegetation Science*, 21(3), 500–506. Available from: https://doi.org/10.1111/j.1654-1103.2009.01157.x

Seifan, M., Tielbörger, K., Schloz-Murer, D. & Seifan, T. (2010) Contribution of molehill disturbances to grassland community composition along a productivity gradient. *Acta Oecologica*, 36(6), 569–577. Available from: https://doi.org/10.1016/j.actao.2010.08.005

Skoczeń, S. (1958) Tunnel digging by the mole (*Talpa europaea* Linne). *Acta Theriologica*, 2, 235–249, tables 20-24. Available from: https://doi.org/10.4098/AT.arch.58-11

Skoczeń, S., Nagawiecka, H., Boron, K. & Galka, A. (1976) The influence of mole tunnels on soil moisture on pastures. *Acta Theriologica*, 21, 543–548. Available from: https://doi.org/10.4098/AT.arch.76-48

Skoczeń, S., Szot, T. & Dabrowska, L. (1983) The effect of the activity of the mole (Talpa europaea) on the floristic composition of the grassland swards of southern Poland. *Acta Agraria et Silvestria (Series Agraria)*, 22, 101–120.

Smith, M.C., 2013. The distribution of mole hills of the European mole (*Talpa europea*) in a sub-urban environment. Wild Warwickshire, Warwickshire, UK.

Stepanova, I., Andreychev, A., Kulakhmetov, R. & Lobachev, E. (2021) Commensals of underground mammals: European mole (*Talpa europaea*, Eulipotyphla, Talpidae) and the greater mole-rat (*Spalax microphthalmus*, Rodentia, Spalacidae). *Biodiversitas Journal of Biological Diversity*, 22(10), 4665–4670. Available from: https://doi.org/10.13057/biodiv/d221059

Stone, R.D. & Gorman, M.L. (1985) Social organization of the European mole (*Talpa europaea*) and the Pyrenean desman (*Galemys pyrenaicus*). *Mammal Review*, 15(1), 35–42. Available from: https://doi.org/10.1111/j.1365-2907.1985.tb00385.x

Streitberger, M. & Fartmann, T. (2013) Molehills as important larval habitats for the grizzled skipper, *Pyrgus malvae* (Lepidoptera: Hesperiidae), in calcareous grasslands. *European Journal of Entomology*, 110(4), 643–648. Available from: https://doi.org/10.14411/eje.2013.087

Streitberger, M. & Fartmann, T. (2015) Vegetation and climate determine ant-mound occupancy by a declining herbivorous insect in grasslands. *Acta Oecologica*, 68, 43–49. Available from: https://doi.org/10.1016/j.actao.2015.07.004

Streitberger, M., Rose, S., Hermann, G. & Fartmann, T. (2014) The role of a mound-building ecosystem engineer for a grassland butterfly. *Journal of Insect Conservation*, 18(4), 745–751. Available from: https://doi.org/10.1007/s10841-014-9670-4

Tansley, A.G. & Adamson, R.S. (1925) Studies of the vegetation of the English chalk: III. The chalk grasslands of Hampshire-Sussex border. *Journal of Ecology*, 13(2), 177–223. Available from: https://doi.org/10.2307/2255283

Teal, L.R., Bulling, M.T., Parker, E.R. & Solan, M. (2008) Global patterns of bioturbation intensity and mixed depth of marine soft sediments. *Aquatic Biology*, 2(3), 207–218. Available from: https://doi.org/10.3354/ab00052

Trachet, J., Poulain, M., Delefortrie, S., Van Meirvenne, M. & De Clercq, W. (2017) Making a mountain out of a molehill? A low-cost and time-efficient molehill survey of the lost medieval harbor site of Monnikerede, Belgium. *Journal of Field Archaeology*, 42(6), 503–513. Available from: https://doi.org/10.1080/00934690.2017.1383106

Turcek, F.J. (1956) On the digging habits of some fossorial mammals on the Danube-dam in Southern Slovakia. *Saugtk*, 4, 61–63.

Turcek, F.J. (1965) The role of animals in baring and soil erosion on karst-lands. *Acta Theriologica*, 11, 203–215.

Übernickel, K., Pizarro-Araya, J., Bhagavathula, S., Paulino, L. & Ehlers, T.A. (2021) Reviews and syntheses: composition and characteristics of burrowing animals along a climate and ecological gradient, Chile. *Biogeosciences*, 18(20), 5573–5594. Available from: https://doi.org/10.5194/bg-18-5573-2021

Verma, A.K. & Bourke, M.C. (2019) A method based on structure-from-motion photogrammetry to generate sub-millimetre-resolution digital elevation models for investigating rock breakdown features. *Earth Surface Dynamics*, 7(1), 45–66. Available from: https://doi.org/10.5194/esurf-7-45-2019

Viles, H. (2016) Technology and geomorphology: are improvements in data collection techniques transforming geomorphic science? *Geomorphology*, 270, 121–133. Available from: https://doi.org/10.1016/j.geomorph.2016.07.011

Viles, H. (2020) Biogeomorphology: past, present and future. *Geomorphology*, 366, 106809. Available from: https://doi.org/10.1016/j.geomorph.2019.06.022

Viles, H.A., Goudie, A.S. & Goudie, A.M. (2021) Ants as geomorphological agents: a global assessment. *Earth-Science Reviews*, 213, 103469. Available from: https://doi.org/10.1016/j.earscirev.2020.103469

Voronov, V.N.P. (1967) Über die Wühltätigkeit des Maulwurfes (*Talpa europaea* L.). *Pedobiologia*, 8(1), 122–147. Available from: https://doi.org/10.1016/S0031-4056(23)00313-X

Watt, A.S. (1974) Senescence and rejuvenation in ungrazed chalk grassland (Grassland B) in Breckland: the significance of litter and of moles. *Journal of Applied Ecology*, 11(3), 1157–1171. Available from: https://doi.org/10.2307/2401770

Whitesides, C.J., Tsikalas, S.G., Butler, D.R. & Wamsley, J.M. (2022) The geomorphic impacts of animal burrowing and denning. *Treatise on Geomorphology*, 3, 89–102. Available from: https://doi.org/10.1016/B978-0-12-818234-5.00009-2

Whitford, W.G. & Kay, F.R. (1999) Biopedturbation by mammals in deserts: a review. *Journal of Arid Environments*, 41(2), 203–230. Available from: https://doi.org/10.1006/jare.1998.0482

Wijnhoven, S., Thonon, I., Velde, G.V.D., Leuven, R., Zorn, M., Eijsackers, H., et al. (2006) The impact of bioturbation by small mammals on heavy metal redistribution in an embanked floodplain of the river Rhine. *Water, Air, and Soil Pollution*, 177(1-4), 183–210. Available from: https://doi.org/10.1007/s11270-006-9148-4

Williams, R. (2012) DEMs of difference. *Geomorphological Techniques*, 2, 1–17.

Winchell, E.W., Anderson, R.S., Lombardi, E.M. & Doak, D.F. (2016) Gophers as geomorphic agents in the Colorado Front Range subalpine zone. *Geomorphology*, 264, 41–51. Available from: https://doi.org/10.1016/j.geomorph.2016.04.003

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Baxter, T., Woor, S., Coombes, M. & Viles, H. (2024) The geomorphic work of the European mole (*Talpa europaea*): Long-term monitoring of molehills using structure-from-motion photogrammetry. *Earth Surface Processes and Landforms*, 49(15), 4991–5011. Available from: https://doi.org/10.1002/esp.6008