



1	Time-Of-Flight monitoring reveals higher sediment redistribution rates related to burrowing animals
2	than previously assumed
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41 Abstract

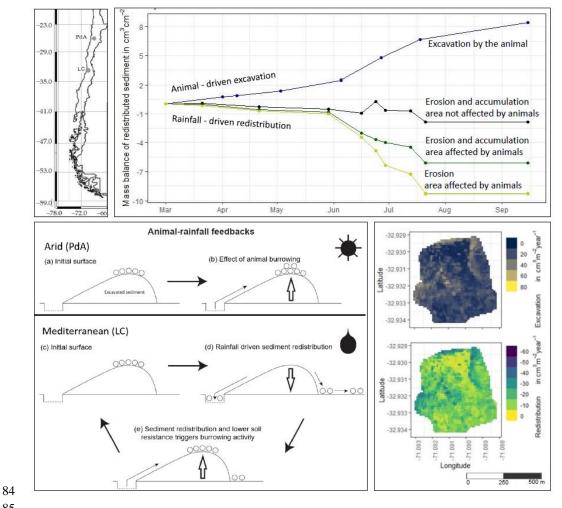
Burrowing animals influence surface microtopography and hillslope sediment redistribution, but changes often remain undetected due to a lack of autonomous high resolution field monitoring techniques. In this study we present a new approach to quantify microtopographic variations and surface changes caused by burrowing animals and rainfall-driven erosional processes applied to remote field plots in arid and mediterranean Chile. We compared the mass balance of redistributed sediment within plot areas affected and not affected by burrowing animals, quantified the cumulative sediment redistribution caused by animals and rainfall, and upscaled the results to the hillslope scale. The new instrument showed a very good detection accuracy. The cumulative sediment redistribution within areas affected by burrowing animals was higher (-10.44 cm³ cm⁻² year ¹) in the mediterranean than the arid climate zone (-1.41 cm³ cm⁻² year⁻¹). Daily sediment redistribution during rainfall within areas affected by burrowing animals were up to 350% / 40% higher in the mediterranean / arid zone compared to the unaffected areas, and much higher than previously reported in studies not based on continuous microtopographic monitoring. Furthermore, 38% of the sediment eroding from the burrows accumulated within the burrow entrance while 62% was incorporated into overall hillslope sediment flux. The cumulative sediment excavation by the animals was 14.62 cm³ cm⁻² year⁻¹ in the mediterranean and 16.41 cm³ cm⁻² year-1 in the arid climate zone. Our findings can be implemented into long-term soil erosion models that rely on soil processes but do not yet include animal-induced surface processes on microtopographical scales in their algorithms. Keywords: Biogeomorphology, bioturbation, sediment transport, burrowing animals, rainfall, Time-of-Flight camera, Chile





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83 **Graphical abstract**







86 1. Introduction

87 Animal burrowing activity affects surface microtopography (Reichman and Seabloom, 2002; Kinlaw 88 and Grasmueck, 2012), surface roughness (Yair, 1995; Jones et al., 2010; Hancock and Lowry, 2021) and soil 89 physical properties (Ridd, 1996; Yair, 1995; Hall et al., 1999; Reichman and Seabloom, 2002; Hancock and 90 Lowry, 2021; Coombes, 2016; Larsen et al., 2021). Previous studies estimated both positive as well as 91 negative impacts of burrowing animals on sediment redistribution rates. The results were obtained by applying 92 tests under laboratory conditions using rainfall simulators, conducting several field campaigns weeks to months 93 apart, or by measuring the volume of excavated or eroded sediment in the field using methods such as erosion 94 pins, splash boards, or simple rulers (Imeson and Kwaad, 1976; Reichman and Seabloom, 2002; Wei et al., 95 2007; Le Hir et al., 2007; Li et al., 2018; Li et al., 2019c; Li et al., 2019b; Voiculescu et al., 2019; Chen et al., 96 2021; Übernickel et al., 2021b; Li et al., 2019a). Although burrowing animals are generally seen as ecosystem 97 engineers (Gabet et al., 2003; Wilkinson et al., 2009), their role in soil erosion, in general, and for numerical 98 soil erosion models, in particular, is, to date, limited to predictions of the burrow locations and particle mixing 99 at these locations (Black and Montgomery, 1991; Meysman et al., 2003; Yoo et al., 2005; Schiffers et al., 100 2011). The complex interaction of sediment excavation and accumulation and erosion processes at the burrow 101 and hillslope scales are not yet included in the modelling, as for this, a suitable method capable of measuring 102 all occurred redistribution processes is needed.

103 The reason for this knowledge gap is that previous studies have not provided data on low magnitude 104 but frequently occurring sediment redistribution due to the specific limitations of their approaches. Field 105 experiments with, for example, rainfall simulators can unveil processes but cannot cover the time-dependant 106 natural dynamics of sediment redistribution. For data samplings that used methods such as erosion pins or 107 splash boards, the sites had to be revisited each time and the data were thus obtained only sporadically 108 (Imeson and Kwaad, 1976; Hazelhoff et al., 1981; Richards and Humphreys, 2010). Similarly, estimations of 109 the excavated sediment volume are currently limited to one-time measurements or studies conducted several 110 months apart (Black and Montgomery, 1991; Hall et al., 1999; Yoo et al., 2005). We expect that non-111 continuously conducted measurements do not include all frequently occurring excavation and erosion 112 processes. For this, a spatio-temporally high-resolution and continuous monitoring of sediment redistribution 113 is needed.

114 High-resolution, ground-based imaging sensing techniques might overcome such aforementioned 115 problems. Terrestrial laser scanner systems have shown to be a suitable tool for estimation of sediment 116 redistribution and erosion processes (Nasermoaddeli and Pasche, 2008; Afana et al., 2010; Eltner et al., 117 2016b; Eltner et al., 2016a; Longoni et al., 2016). However, they are expensive and labour-intensive and, thus, 118 the study sites had to be personally revisited for each measurement. A continuous, autonomous monitoring of 119 many mound areas in parallel is thus not possible. However, Time-of-Flight (ToF) technology offers new 120 possibilities for a high-resolution monitoring of sediment redistribution (Eitel et al., 2011; Hänsel et al., 2016) 121 but a cost-effective field monitoring device is still missing.

122 In our study, we developed, tested and applied a cost-effective Time-Of-flight camera to autonomously 123 monitor the rainfall-driven and animal-driven sediment redistribution in areas affected by burrowing animals 124 with high temporal (four times a day) and spatial (6 mm) resolution. For this, we equipped several plots in 125 remote study sites of Chile in the arid and mediterranean climate zone. We selected these sites in order to 126 analyse sediment redistribution by burrowing activity of vertebrates under different rainfall regimes and as 127 these sites were particularly shown to be strongly affected by burrowing activity (Grigusova et al., 2021). Then,





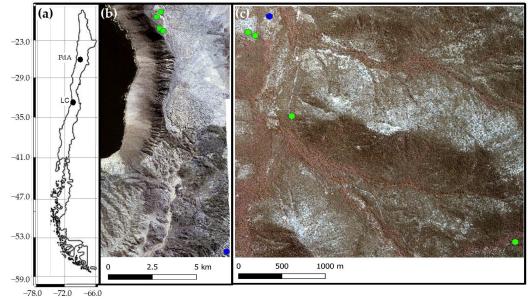
128 we quantified the daily sediment redistribution within areas affected and not affected by burrowing animals.
129 We analysed the impacts of animal burrowing activity and rainfall on the sediment redistribution and quantified
130 the volume of sediment which is additionally incorporated to the hillslope sediment flux due to presence of
131 burrows. Finally, we estimated sediment redistribution on a burrow scale and upscaled sediment redistribution
132 rates to the entire hillslopes.

133

134 2. Study sites

135 Our study sites were located in the Chilean Coastal Cordillera in two climate zones (Fig. 1): in the National 136 Park Pan de Azúcar (further as Pan de Azúcar or PdA) and the National Park La Campana (further as La 137 Campana or LC). The Las Lomitas site in PdA is located in the arid climate zone of the Atacama Desert with a 138 precipitation rate of 12 mm year⁻¹, and it has a mean annual temperature of 16.8 °C (Übernickel et al., 2021a). 139 Here, the vegetation cover is below 5%, and it is dominated by small desert shrubs, several species of cacti 140 (Eulychnia breviflora, Copiapoa atacamensis) and biocrusts (Lehnert et al., 2018). LC is located in the 141 mediterranean climate zone with a precipitation rate of 367 mm year-1 and a mean annual temperature of 142 14.1 °C (Übernickel et al., 2021a). LC is dominated by an evergreen sclerophyllous forest with endemic palm 143 trees, Jubaea chilensis. Both research sites have a granitic rock base, and the dominating soil texture is sandy 144 loam (Bernhard et al., 2018). In PdA, the study setup consisted of one north-facing and one south-facing 145 hillslope. The hillslope inclinations were $\sim 20^{\circ}$, and a climate station was located ~ 15 km from the camera sites. 146 In LC, the setup consisted of two north-facing and one south-facing hillslopes. The hillslope inclinations were 147 ~25°, and a climate station was located ~250 m from the south-facing hillslope (Übernickel et al., 2021a). 148

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Figure 1. Location of the cameras and climate stations on which this study was based. Black points show the location of the research sites in Chile. The green points represent the camera plots, and the blue points the

153 climate stations: (a) Location of study sites in Chile: PdA stands for Pan de Azúcar, LC for La Campana; (b)





154 Study setup in Pan de Azúcar; (c) Study setup in LC. The background images in (b) and (c) are orthophotos

- $155 \qquad \text{created from WorldView-2 data from 19 July 2019. For exact latitude and longitude see Table A2.}$
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157 3. Methodology

158 3.1 Time-of-Flight (ToF) principle

A Time-of-Flight-based camera illuminates an object with a light source, usually in a non-visible spectrum, such as near-infrared, for a precise length of time. The here employed cameras were pulse-based, meaning the light pulse was first emitted by the camera, then reflected from the surface, and finally measured by the camera using two temporary windows. The first temporary window measures the incoming reflected light while the light pulse is also still emitting from the camera. The second temporary window measures the incoming reflected light when no pulse is emitting from the camera. The distance from the camera to the object can then be calculated as follows:

166 $d = \frac{1}{2} * c * t * (\frac{g_1}{g_1 + g_2})$

(1)

167 In Eq. (1), d (m) is the distance from the camera to the object, c (m s⁻¹) is the speed of light (299,792,458 m s⁻¹), t (s) is the overall time of the illumination and measurement, g_1 is the ratio of the reflected photons to all 169 photons accumulated in the first window, and g_2 the ratio of the reflected photons to all photons accumulated 170 in the second window (Sarbolandi et al., 2018; Li, 2014).

171 The sensor in our camera came from Texas Instruments and the data scan contained information on 172 320 x 240 points. The camera field of view (FOV) and the spatial resolution of the scans depended on the 173 height of the camera above the surface. The distance was calculated for every point, and the object was saved 174 in binary format as a collection of 3D points with x-, y- and z-coordinates. The scans taken by the camera were 175 transformed from the binary format to a point cloud. Each point in the point cloud was assigned to an x-, y- and 176 z-coordinate. The coordinates were distributed within a three-dimensional Euclidian space, with the point at 177 the camera nadir being the point of origin. x- and y-coordinates describe the distance to the point of origin (m). 178 z-coordinate describes the distance (m) from the object to the camera. The lowest point of the scanned surface 179 thus has the highest z-coordinate value.

180

181 3.2 Data processing

182 The distortion caused by the hillslope and the camera angle was corrected for each point cloud as 183 follows: 184 $z_{car} = z_{uncar} - \tan(\alpha + \beta) * distance(v_1 - v_1)$ (2)

- 184 $z_{cor} = z_{uncor} tan(\alpha + \beta) * distance(y_1 y_i)$ (2)185In Eq. (2), z_{cor} is the corrected distance (m) between the camera and surface (m), z_{uncor} is the uncorrected *z*-186coordinate (m), α is the tilt angle of the camera (°), β is the surface inclination (°), and y_i is the distance of the187point to the point of origin at the camera nadir (m). The most frequent errors were identified and treated as188follows. Due to the ambient light reaching the camera sensor, the *z*-coordinate values of some of the points189were incorrect (scattering error). To remove this error, a threshold value was calculated for each point cloud:
- 190 $\Omega = mean_{zcor-coordinates} \pm sd_{zcor-coordinates}$. (3) 191 In Eq. (3), Ω is the threshold value, mean_{zcor-coordinate} is the average value, and sd_{zcor-coordinate} is the standard 192 deviation of the corrected *z*-coordinates (m). Then all points with a *z*-coordinate above and below this value 193 were deleted. Point clouds with more than 50% of points above the threshold value Ω were also not considered 194 for further processing. A drift error occurred when the *z*-coordinate values of around one-third of the point





195 clouds decreased by several centimetres from one point cloud to another. Here, the average z-coordinate of 196 ten point clouds before and after the drift were calculated, and the difference was added to z-coordinates of 197 the points affected by the drift. The corrected height values were then transformed into a digital surface model 198 (DSM).

199

200 3.3 Accuracy of the ToF cameras

201 The accuracy of the ToF camera was tested under laboratory conditions by recreating similar surface 202 conditions as in the field (sloping surface, covered by sediment). An artificial mound using sediment extracted 203 from a riverbank in central Germany was used, mimicking a mound created by a burrowing animal. During the 204 test, the camera was installed 100 cm above the surface. The camera FOV was 3 m² and the scan spatial 205 resolution was 6 mm. The surface was scanned twice by the ToF camera. Then 100 - 450 cm³ of sediment 206 was manually extracted from the mound. The volume of the extracted sediment was measured by a measuring 207 cup. After extraction, the surface was again scanned twice by the camera. The experiment was repeated 45 208 times with varying amounts of extracted sediment. The scans were transformed to point clouds in VoxelViewer-209 0.9.10, and the point clouds were corrected according to Eq. (2) and (3). The z-coordinates of the two point 210 clouds before and two point clouds after the extraction were averaged. The point clouds were then transformed 211 into DSMs, and the differences between the time steps were calculated. A scan was taken of a smooth surface, 212 and the standard deviation of its z-coordinates was calculated and saved as a threshold value. Solely, the 213 differences between the DSMs below this threshold (0.2 cm) were considered in the calculation of the detected 214 sediment extraction. The detected extracted sediment volume was then calculated for each experiment as 215 follows:

216 $Vol_{detected} = \sum_{p}^{1} (DSM_{before} - DSM_{after}) * res^{2}$,

In Eq. (4), Voldetected is the volume of the extracted sediment as detected by the camera (cm³), p is the number of pixels, DSM_{before} (cm) is the DSM calculated from the scan taken before the extraction, DSM_{after} (cm) is the DSM calculated from the scan taken after the extraction, res (cm) is the resolution of the scan, which was 0.6 cm. To evaluate the camera's accuracy, the measured volume of the extracted sediment was compared to the volume detected by the camera. The camera's accuracy was estimated between the detected volume and measured volume as follows:

223 $MAE = \sum_{1}^{n} \frac{(Vol_{detected} - Vol_{measured})}{area}$

(5)

(4)

In Eq. (5), MAE (cm³/cm²) is the mean absolute error, n is the number of scans, Vol_{measured} (cm³) is the volume of the extracted sediment measured by the measuring cup, and the area is the total surface area monitored by the camera (cm²).

227

228 3.4 Installation of the cameras in the field

We installed 8 custom-tailored ToF-based cameras on 4 hillslopes in two climate zones in areas including visible signs of bioturbation activity (burrows) and areas without visible signs of bioturbation (Fig. 2). The cameras were installed in LC on the north-facing upper hillslope (LC-NU), north-facing lower hillslope (LC-NL), south-facing upper hillslope (LC-SU) and the south-facing lower hillslope (LC-SL); in PdA on the northfacing upper hillslope (PdA-NU), north-facing lower hillslope (PdA-NL), south-facing upper hillslope (PdA-SU) and south-facing lower hillslope (PdA-SL). The custom-tailored cameras were installed during a field campaign in March 2019, the monitoring took place for seven months, and the data were collected in October 2019. The





236 construction consisted of a 3D ToF-based sensor from Texas Instruments (Li, 2014), a RasperryPi single board 237 computer (SBC), a timer, a 12 V 12 Ah battery and three 20 W solar panels for unattended operation (Fig. 1). 238 Solar panels were located at the camera pole and were recharging the battery via a charge controller. The 239 camera was located approximately one meter above the surface, facing the surface with a tilt angle of 10 240 degrees. The timer was set to close the electric circuit 4 times a day: at 1 a.m., 5 a.m., 8 a.m. and 10 p.m. At 241 these times, the camera and the computer were turned on for 15 minutes. The camera turned on and took five 242 scans delayed one second from each other and sent them to the SBC. Each camera had its own WiFi (Wireless 243 Fidelity) and the data could be read from the SBC via Secure Shell (SSH).

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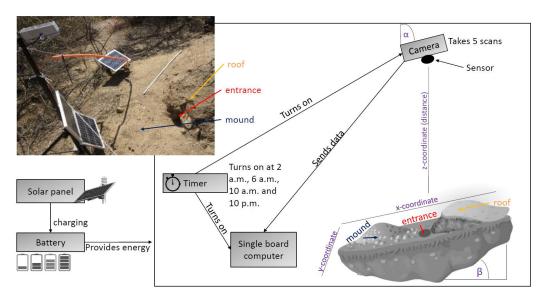




Figure 2. Scheme and photo example of a Time-of-Flight-based camera installation in the field. The photo example is from upper north-facing hillslope in La Campana. Black boxes describe single installation parts. Purple descriptions are the variables needed for the correction of the scans. Roof, entrance and mound describe areas affected by the burrowing animal. The *x*-, *y*- and *z*-coordinates are 3D coordinates identifying the position of each point in space, where the *x*-coordinate is the length, *y*-coordinate is the width and the *z*coordinate is the distance between the camera sensor and the surface. α is the inclination of the camera, and β is the surface inclination.

253

3.5 Delineation of the Area Affected and Non-Affected by Burrowing Animals in the Camera's Field ofView

The surface area scanned by the cameras was divided by a delineation scheme into areas affected (A) and not (directly) affected (N) by burrowing animals. The affected areas included three sub-areas: (i) mound (M), (ii) entrance (E) and (iii) burrow roof (R). "Mound" describes the sediment excavated by the animal while digging the burrow. "Entrance" describes the entry to the animal burrow up to the depth possible to obtain via the camera. "Burrow roof" describes the part of the sediment above and uphill the burrow entrance (Bancroft et al., 2004). During the burrow's creation, sediment was not only excavated but also pushed aside and uphill the entrance, which created the burrow's roof. We assume that this elevated microtopographical feature then





forms an obstacle for sediment transported from uphill, which leads to its accumulation in this area. The remaining surface within the camera's FOV was classified as not affected (N) by the burrowing animal during the creation of its burrow.

266 For the delineation, we used the DSM calculated from the point cloud, and a slope layer calculated 267 from the DSM (Horn, 1981). Entrance was assigned to an area determined by a search algorithm starting at 268 the lowest point of the DSM (pixel with the highest z-coordinate value). We increased the circular buffer around 269 the starting point by one pixel until the average depth of the new buffer points was not higher than the height 270 of the camera above the surface, or until the slope of at least 50% of the new buffer points was not 0. Then, 271 we masked all pixels within the buffer with a depth lower than the average depth of the points within the buffer, 272 which had a slope that was 0. The remaining pixels belonged to the entrance area. Then, the surface scan 273 was divided into an uphill and downhill part with regards to the entrance position. Both the uphill and the 274 downhill parts were subdivided into 16 squares.

275 To delineate the mound in the downhill part, we first identified the highest points (pixel with the lowest 276 z-coordinate value) within all 16 squares. We then calculated the distance of these maxima to the entrance, 277 and the pixel located nearest to the entrance was identified as the highest point of the mound (i.e., seed point). 278 Consecutively, we increased the circular buffer around the seed point by one pixel until the average depth of 279 the new buffer points was not lower than the height of the camera above the surface, or until the slope of at 280 least 50% of the new buffer points was not 0. Then, we masked all pixels within the buffer with a depth higher 281 than the average depth of the points within the buffer, which had a slope that was 0. The remaining pixels were 282 classified as mound area. To delineate burrow roof, we used the same approach as for the delineation of 283 mound and applied it on the uphill part of the surface scan. All pixels that were not classified during the entire 284 delineation process were treated as areas not affected by animals. The position and the boundaries of 285 entrance, mound and burrow roof were validated visually (Fig. 3 and A1). 286

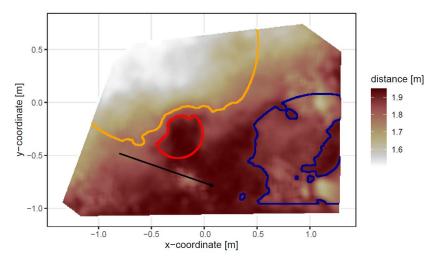


Figure 3. Corrected digital surface model of the camera on the upper north-facing hillslope in La Campana with delineated areas. The point of origin of the coordinate system is at the camera nadir. Distance refers to the distance between surface and camera. The red line delineates the burrow entrance, blue the mound and





orange the burrow roof. The area which was outside of any delineated area was classified as not affected by animal burrowing activity. The arrow indicates a downhill direction of the hillslope.

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294 **3.6 Calculation of daily sediment mass balance budget**

The volume of the redistributed sediment was calculated daily and was then cumulated from the first day of monitoring. For the calculation of the daily sediment redistribution, the change in the surface level detected by the camera was calculated first. For each day, the scans from the day before and after the respective day were averaged and subtracted. As described in Section 2.2., all values with a difference below and above the threshold value of 0.2 cm were set to 0. The redistributed sediment volume was then calculated from the surface change for each pixel as follows:

301 $Vol_{redistributed} = (S_b - S_a) * res^2$

(6)

 $302 \qquad \text{In Eq. (6), Vol_{redistributed} (cm^3 \text{ pixel}^{-1}) is the volume of the calculated redistributed sediment, S_b (cm) the scan$

before, S_a (cm) the scan after the rainfall event and *res* is the spatial resolution (cm). Using the daily volume of the redistributed sediment per pixel, we calculated the daily mass balance budget by summing the volume

305 of sediment eroding or accumulating within each delineated area.

306

307 3.7 Calculation of animal-caused and rainfall-caused sediment redistribution

308 The animal-caused sediment redistribution occurred when the animal actively reworked sediment 309 within its burrow. Under the assumption that the burrows are actively used by the animals, we defined four 310 cases when the sediment was redistributed due to the burrowing activity. For this, we pairwise compared the 311 DSMs of each scan with the scan saved before. The four cases were: (i) as the animal excavates sediment 312 from the entrance, the depth of the entrance must increase in the second scan; (ii) as the excavated sediment 313 accumulates on the mound, the height of the mound must increase in the second scan; (iii) as the burrowing 314 might lead to an expansion or a collapse of the burrow roof, an increase or decrease of the burrow roof must 315 occur between the scans; (iv) as the animal only digs within his burrow, no changes must occur between the 316 two scans within the area not affected by the animal. The animal-caused redistribution was then calculated for 317 these days as the volume of sediment redistributed within mound and burrow roof. The entrance was ignored 318 in the calculation. As the sediment excavated from the entrance accumulated on the mound and the sediment 319 accumulated within entrance collapsed from the burrow roof, by including the entrance in the calculation, these 320 sediment volumes would be counted twice.

321 The rainfall-caused sediment redistribution was calculated as follows: From the data from the climate 322 stations (Übernickel et al., 2021a), we calculated the daily precipitation in mm. The sediment redistribution 323 recorded immediately and within five scans before and after a rainfall event is defined to be the result of the 324 rainfall event. The five-scan buffer is necessary as the climate stations are located up to a 15 km distance from 325 the cameras (Fig. 1). We calculated the rainfall-caused sediment redistribution within (i) areas affected by the 326 burrowing animal (i.e., entrance, mound and burrow roof) and (ii) within areas not affected by the burrowing 327 animal. To estimate the sediment volume which accumulated within the entrance, we also calculated the 328 volume of redistributed sediment solely (iii) within the mound and burrow roof. From this volume, we subtracted 329 the volume redistributed within all affected areas. We did not directly calculate the accumulation rate within the 330 entrance as the cameras did not provide data on the complete underground burrow structure.

331

332 3.8 Hillslope-wide upscaling of redistributed sediment





333	Hillslope-wide upscaling of the results generated in this study was performed by utilising a previous
334	estimation of vertebrate burrow density (Grigusova et al., 2021). In this study, the density of burrows created
335	by vertebrate burrowing animals, which we interpreted as vertebrate burrow density (number of burrows per
336	100 m ²), was measured in situ within eighty 100 m ² plots and then upscaled to the same hillslopes on which
337	the cameras were located by applying machine-learning methods, using the UAV-data as predictors. Hence,
338	the modelled burrows in the previous study were in fact areas affected by burrowing animals in this study.
339	From the camera data, we calculated the average cumulative volume of redistributed sediment after
340	a period of one year within affected (Volaffected (cm ³ cm ⁻² year ⁻¹)) and non-affected (Volnot affected (cm ³ cm ⁻² year ⁻¹))
341	¹)) areas and the average sediment volume redistributed (excavated) by the animal (Vol _{exc} (cm ³ cm ⁻² year ⁻¹)),
342	separately for each site. Additionally, we estimated the volume of sediment that was additionally redistributed
343	during rainfall events due to the presence of the burrow (Vol _{add} (cm ³ cm ⁻² year ⁻¹)). Vol _{add} was calculated as the
344	difference in the redistributed sediment volume between affected and non-affected areas according to Eq. (7).
345	$Vol_{add} = \frac{(M_{affected} - M_{unaffected})}{7} * 12 \qquad , \tag{7}$
346	We then upscaled the Vol _{affected} (cm ³ cm ⁻² year ⁻¹), Vol _{exc} (cm ³ cm ⁻² year ⁻¹)) and Vol _{add} (cm ³ cm ⁻² year ⁻¹)
347	1)) to the hillslope using the same approach: First, we calculated the average volume of the redistributed
348	sediment per burrow (Vol _{per burrow} [cm ³ burrow ⁻¹ year ⁻¹]):
349	$Vol_{per \ burrow} = \frac{(Area_{burrow} * Vol)}{7} * 12 $ (8)
350	In Eq. (8), Areaburrow (cm ²) is the average size of the burrows that are monitored by the cameras; Vol is Volaffected
351	(cm ³ cm ⁻² year ⁻¹), Volexc (cm ³ cm ⁻² year ⁻¹) or Voladd (cm ³ cm ⁻² year ⁻¹). Using the hillslope-wide predicted
352	vertebrate burrow densities (Dens $_{burrow}$ (number of burrows 100 m $^{-2}$)) from Grigusova et al. 2021, we estimated
353	the volume of redistributed sediment for each pixel of the raster layers (Volper pixel (cm ³ m ⁻² year ⁻¹)) according
354	to Eq. (9):
355	$Vol_{per \ pixel} = \frac{Vol_{per \ burrow^*} \ Dens_{burrow}}{7} * 12 \tag{9}$
356	The average hillslope-wide volume of redistributed sediment (Volhillslope-wide (m ³ ha ⁻¹ year ⁻¹)) was then
357	estimated as follows:
358	$Vol_{hillslope-wide} = \frac{\sum_{1}^{m} Vol_{per pixel}}{7} * 12 * 0.001 \qquad , \tag{10}$
359	In Eq (10), m is the number of pixels.
360	
361	4. Results
362	4.1 Camera accuracy
363	The accuracy between the measured extracted sediment volume and sediment volume calculated
364	from the camera scans was very high (MAE = $0.023 \text{ cm}^3 \text{ cm}^{-2}$, $R^2 = 0.77$, Fig. 4). The accuracy between the
365	calculated and measured extracted sediment was higher when the two scans taken before as well as after the
366	extraction of the sediment were averaged and the sediment volume was estimated using these averaged
367	scans. When calculating the redistributed sediment from solely one scan before and after extraction, the
368	accuracy slightly decreased (MAE = 0.081 cm ³ cm ⁻² , R^2 = 0.64). The cameras tended to overestimate the
369	volume of redistributed sediment.





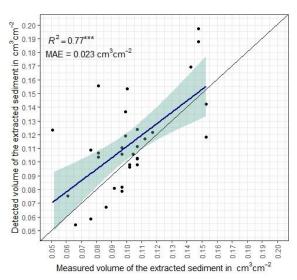




Figure 4. Estimation of Time-of-Flight camera accuracy based on averaging two surface scans before and after the sediment extraction under controlled conditions. The *x*-axis shows the exact sediment volume measured with a cup. The *y*-axis represents the volume of the sediment calculated from the camera scans (according to Equation (4)). The blue line is the linear regression calculated from the measured and detected volume. The green shadow shows the confidence interval of 95% for the linear regression slope. ****p* ≤ 0.001. MAE is the mean absolute error, and *R*² the coefficient of determination.

377

378 4.2 Data quantity and quality

Six out of eight custom-tailored cameras collected data over the seven-month period (Table A2). One camera collected data for a period of three months and one camera stopped working a few days after installation. The quantity of usable point clouds taken at 1 a.m., 5 a.m. and 10 p.m. was higher than of point clouds taken at 8 a.m. Approximately 20% of points was removed from the point clouds before final analysis due to the high scattering at the point cloud corners. After data filtering (see Section 3.2.), 1326 scans were usable and for 86% of the days, at least one usable scan was available. The usable scans were distributed continuously within the monitoring period.

In LC, the areas affected by the burrowing animal always consisted of an entrance, mound and burrow roof. In PdA, there was no burrow roof on the upper hillslopes. Burrows without a burrow roof were located on shallower parts of the hillslopes (up to an inclination of 5°), and the angle of the burrow entrance to the ground was ~90°. Burrows with a burrow roof were located on steeper parts of the hillslopes (with an inclination above 5°), and the angle of the burrow entrance to the ground was ~45°.

391

392 4.3 Mass balance of redistributed sediment

The cameras detected (i) sediment redistribution directly following rainfall events and (ii) due to the burrowing activity in times without rainfall (Fig. 5 and 6). In all cases, areas affected by burrowing activity (entrance, burrow roof and mound) exhibited higher sediment redistribution rates than areas not affected by burrowing. In addition, the volume of redistributed sediment by animal activity was higher after a rainfall event





397 occurred. After rainfall events, sediment eroded especially at the boundaries of the burrow roof and mound. 398 Sediment eroded from the burrow roof accumulated within the burrow entrance or was redistributed to the 399 mound (Fig. 7). We can also identify detected sediment accumulation on the upper parts of the burrow roof. 400 After the burrowing activity, sediment was excavated from the entrance and cameras detected accumulation 401 on the mound and within the burrow roof. The sediment accumulation and erosion within the area not affected 402 by the animal was evenly distributed around the burrow (Fig. 7).

403 In the following, the dynamics are exemplarily explained for four cameras. Animal burrowing activity 404 was detected seven times by the camera LC NU (Fig. 5a, A2a and A3a) during the monitoring period, by an 405 increase in sediment volume in the area delineated as mound. Simultaneously, the burrow entrance showed 406 signs of modification and sediment accumulation, but these changes were less clear. Overall, the volume of 407 the excavated soil varied. From April until June, up to 0.5 cm³ cm⁻² of sediment was excavated by the animal 408 and accumulated on the mound. From June until September, animal burrowing activity was detected at four 409 time slots (5 June 2019, 9 June 2019, 1 July 2019 and 18 August 2019) and sediment volume of up to 2 cm³ 410 cm-2 accumulated each time on the mound, burrow roof and within the entrance. During the rainfall events of 411 up to 20 mm day-1 on 16 June 2019, 27 mm day-1 on 29 June 2019 and 7 mm day-1 on 13 July 2019, sediment 412 volume of up to 4 cm³ cm⁻² eroded, especially from the burrow roof and the mound while a sediment volume 413 of up to 1 cm³ cm⁻² accumulated within the entrance during each rainfall event.

414 Camera LC-SL (Fig. 5b and A3b) showed burrowing activities eight times and sediment volumes of up 415 to 3 cm³ cm⁻² accumulated within the entrance and burrow roof. The camera detected sediment erosion of up 416 to 2 cm³ cm⁻² after a rainfall event of 27 mm day⁻¹ on 27 July 2019. On the south-upper hillslope, the camera 417 detected animal burrowing activity six times, with a sediment accumulation of up to 3 cm³ cm⁻² (Fig. A2 and 418 A3).

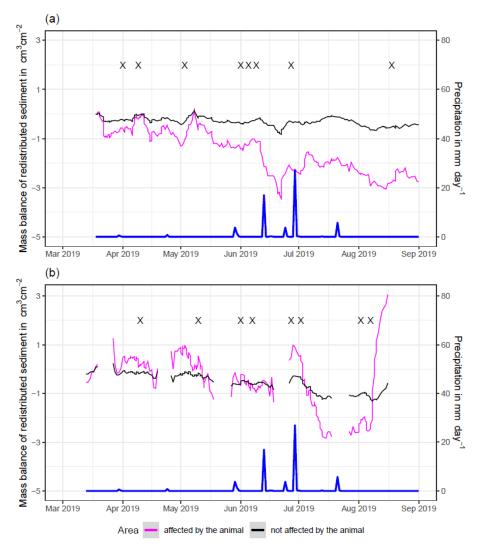
In contrast, camera PdA-NU pointed to animal burrowing activity up to 15 times where up to 1 cm³ cm⁻
² of sediment volume was redistributed from the entrance to the mound (Fig. 6a, A2e and A3e). At the end of
June on 27 June 2019, a rainfall event of 1.5 mm day⁻¹ occurred and up to 2 cm³ cm⁻² of sediment eroded
from the burrow roof and accumulated within the burrow entrance. We observed increased sediment
redistribution by the animal after the rainfall events.

424 Camera PdA-SL evenly revealed animal burrowing activity up to 15 times (Fig. 6b, A2f and A3f). The
425 burrowing had a strong effect on the sediment redistribution. The rainfall event of 1.5 mm day⁻¹ on 27 June
426 2019 did not cause any detectable surface change.

427









430 Figure 5. Examples of mass balance of redistributed sediment in mediterranean La Campana for areas 431 affected and not affected by burrowing animals: (a) The record of the camera on the upper north-facing hillslope 432 showed that larger rainfall events cause a negative sediment balance (sediment loss), followed by a phase of 433 positive sediment mass balance after approximately 3 days due to the fact of sediment excavation; (b) The 434 record of the camera on the lower south-facing hillslope showed a similar pattern to the camera on the upper 435 north-facing hillslope, but the phase of positive mass balance was delayed in comparison. The blue line is the 436 daily precipitation in mm day-1, and "X" marks the days at which animal burrowing activity was detected. Mass 437 balances for all cameras are displayed in Fig. A2 and A3.





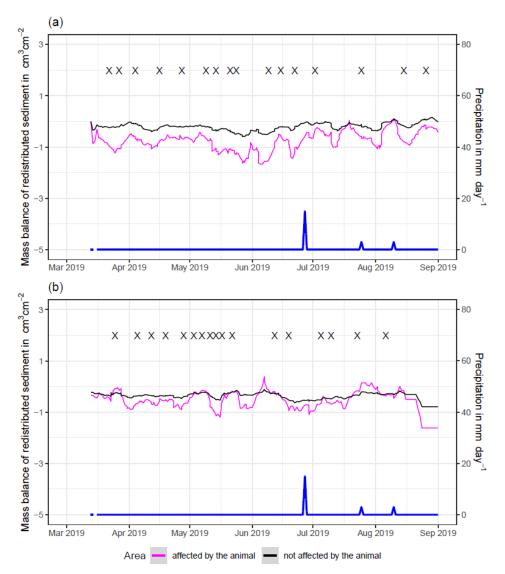
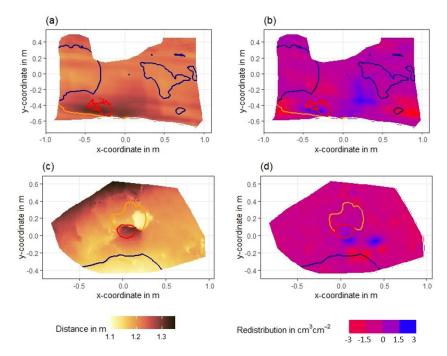


Figure 6. Examples of mass balance of redistributed sediment in the arid Pan de Azúcar for areas affected and not affected by burrowing animals: (**a**) The record of the camera on the upper north-facing hillslope showed that animal sediment excavation had a larger impact on the mass balance than rainfall events; (**b**) The record of the camera on the lower south-facing hillslope showed a similar pattern to the camera on the upper northfacing hillslope. The blue line is the daily precipitation in mm day⁻¹, and "X" marks the days at which animal burrowing activity was detected. Mass balances for all cameras are displayed in Fig. A2 and A3.







446

447 Figure 7. Examples of surface scans showing the digital surface model (DSM) before a rainfall event (a, c) at 448 two camera locations in La Campana, and the calculated volume of redistributed sediment (b, d) after the 449 rainfall event: (a) DSM of a scan from the camera on the upper north-facing hillslope in La Campana; (b) 450 Detected sediment redistribution (cm³ cm⁻²) on the upper north-facing hillslope in La Campana after a rainfall 451 event of 17.2 mm day⁻¹; (c) DSM of a scan from the camera on the upper south-facing hillslope in La Campana; 452 (d) Detected sediment redistribution (cm³ cm⁻²) on the upper south-facing hillslope after a rainfall event of 17.2 453 mm day-1. Red is the outline of the burrow entrance. Green is the outline of mound. Orange is the outline of 454 the burrow roof. The area which is not outlined is the area not directly affected by animal burrowing activity. 455 Redistribution is the volume of the redistributed sediment, either accumulated (positive value) or eroded 456 (negative value) per cm³ cm⁻². After the rainfall events, sediment mostly accumulated within the burrow 457 entrance or near mounds and eroded from burrow roofs and mounds.

458

459 4.4 Cumulative volume of redistributed sediment

460 The analysis of cumulative volume of the redistributed sediment caused by burrowing animal activity
461 and rainfall over the monitored period of seven months for all eight cameras showed a heterogeneous pattern
462 (Fig. 8 and A4, Tables A3 and A4).

In LC, the cumulative volume of the sediment excavated by the animal within the burrow roof and mound increased continuously (Fig. 8). Especially between the rainfall events from June until August, a cumulative volume of on average 6.5 cm³ cm⁻² was excavated by the animal. We calculated that, on average, 8.53 cm³ cm⁻² cumulatively eroded from the burrow roof and mound; while 2.44 cm³ cm⁻² sediment volume accumulated within the entrance (Fig. 8). These results indicate that 28% of sediment eroding from the burrow roof accumulated within the entrance, while over 62% of sediment eroded downhill. Averaged over all camera

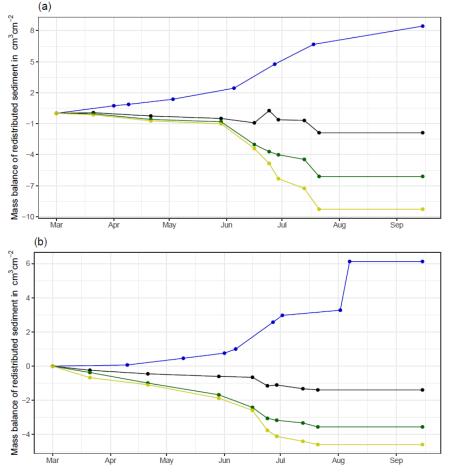




scans, 338% more sediment was redistributed by rain within the affected area compared to the non-affectedarea (Fig. 9).

In PdA, cameras continuously detected animal burrowing activity and excavation of the sediment (Fig. A4). The volume of the detected excavated sediment increased steadily within all cameras. The cumulative sediment accumulation surpasses the sediment eroded due to the rainfall. The volume of the sediment eroded within the affected areas was 40% higher than within the non-affected areas (Fig. 9). The results show that approximately 50% of the eroded sediment accumulated within the entrance.

476



477 Redistribution - By animal within R, M - By rainfall within UN - By rainfall within R, M, E - By rainfall within R, M

478 Figure 8. Examples of the cumulative volume of redistributed sediment within affected and non-affected areas

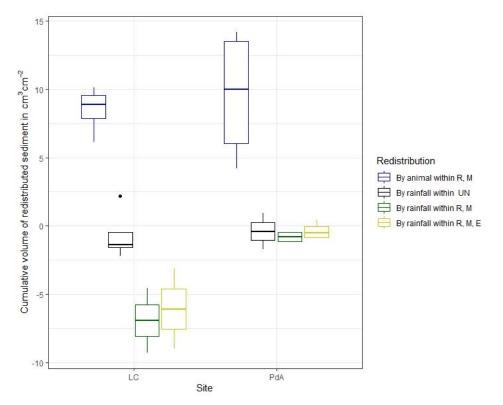
479 caused by animal burrowing activity or rainfall in mediterranean La Campana: (a) Upper north-facing hillslope;

480 (b) Lower south-facing hillslope. Positive values indicate sediment accumulation. Negative values indicate

sediment erosion. E is the burrow entrance; M is the mound; R is burrow roof; UN is the area not directlyaffected by the animal burrowing activity. Cumulative volumes for all cameras are in Fig. A4.







484

Figure 9. Cumulative volume of the redistributed sediment for all cameras. Positive values indicate sediment accumulation. Negative values indicate sediment erosion. Whiskers indicate the median of sediment redistribution. E is the burrow entrance; M the mound; R is the burrow roof; UN is area not affected by the animal burrowing activity; LC stands for National Park La Campana in the mediterranean climate zone; PdA stands for National Park PdA in the arid climate zone.

490

491 **4.5 Hillslope wide excavation and redistribution**

492Grigusova et al. (2021) showed that the density of vertebrate burrows was between 6 and 12 per 100493m² in LC and between 0 and12 per 100 m² in Pan de Azúcar. The volume of the sediment excavated by the494animal and redistributed during rainfall events varied between sites and across the hillslopes (Fig. 10, A5 and495A6; Tables A3 and A4).

496The volume of the sediment excavated by the animal per burrow was lower in LC (1226.61 cm³ burrow-4971 year-1) than in PdA (1498.66 cm³ burrow-1 year-1) (Fig. 9, Table 1). However, on the hillslope scale, a higher498total area-wide volume of excavations was calculated for LC compared to PdA (0.67 m³ ha-1 year+1 vs. 0.18 m³499ha-1 year-1), due to the higher burrow density in LC.

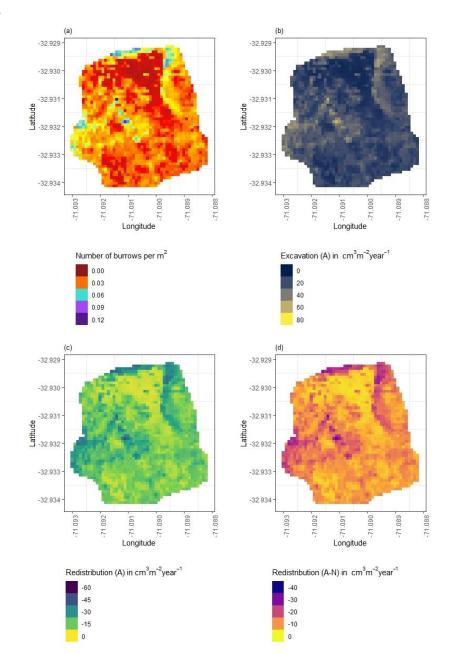
500The volume of the sediment redistributed within the area affected by burrowing activity during rainfall501events on the hillslope scale was higher in LC (-0.48 m³ ha⁻¹ year⁻¹) than in PdA (-0.05 m³ ha⁻¹ year⁻¹) (Table5021). The volume additionally redistributed sediment due to the presence of the burrows was well higher in LC503than in PdA (Fig. 10, A5 and A6).

504The hillslope-wide redistribution rates increased with burrow density, which, as stated in Grigusova et505al. (2021), largely depends on vegetation distribution and topography. In LC, more sediment was excavated in





506 parts of the hillslope with a vegetation cover of over 50% m⁻² (~0.60 m³ ha⁻¹ year⁻¹) than in non-vegetated 507 parts of the hillslope (~0.2 m³ ha⁻¹ year⁻¹). However, dense vegetation covers over 80% m⁻² reduced volume 508 of redistributed sediment due to the animals' burrowing activity (Fig. A5, A7c and A7d). More sediment was 509 redistributed in the middle and upper parts of the hillslope (Fig. A5, A7a and A7b). In PdA, the volume of 510 sediment redistributed by the burrowing animals increased with vegetation cover and elevation (Fig. A6 and 511 A8).







514 Figure 10. Example of the hillslope-wide volume of redistributed sediment for a time period of one year on the 515 south-facing hillslope in La Campana: (a) Density of burrows as estimated by Grigusova et al. (2021); (b) 516 Volume of the sediment excavated by the animals; (c) Volume of the sediment redistributed during rainfall 517 events within affected areas; (d) Volume of additionally redistributed sediment during rainfall events due to the 518 presence of the burrows. The values were calculated per burrow as stated in Section 3.7. by subtracting the 519 sediment volume redistributed within animal-affected areas from the sediment volume redistributed within non-520 affected area and then upscaled. The letters in brackets indicate if the upscaling was conducted using data 521 from affected or non-affected areas by burrowing animals. "A" stands for affected area. By "A-N", the 522 redistribution calculated from non-affected areas was subtracted from the redistribution calculated within 523 affected areas to obtain the additional volume of redistributed sediment due to the burrows' presence. 524

Table 1. Summary of the volume of redistributed sediment according to site, area, and disturbance type. Vol_{exc} describes the volume of the sediment excavated by the animals. Vol_{affected} describes the volume of the sediment redistributed during rainfall events within affected areas. Vol_{add} describes the volume of additionally redistributed sediment during rainfall events due to the presence of the burrows. The values were calculated per burrow, as stated in Section 3.7., by subtracting the sediment volume redistributed within animal-affected areas from the sediment volume redistributed within non-affected areas and then upscaled.

Variable		Volume of redistributed sediment				
Disturbance	Area	LC	Pan de Azúcar			
Vol _{exc}	Affected area	14.62 cm ³ cm ⁻² year ⁻¹	16.41 cm ³ cm ⁻² year ⁻¹			
	Per burrow	1226.61 cm ³ burrow ⁻¹ year ⁻¹	1498.66 cm ³ burrow ⁻¹ year ⁻¹			
	Hillslope-wide	0.67 m ³ ha ⁻¹ year ⁻¹	0.18 m³ ha ⁻¹ year ⁻¹			
Volaffected	Affected area	-10.44 cm ³ cm ⁻² year ⁻¹	-1.41 cm ³ cm ⁻² year ⁻¹			
	Per burrow	-876.38 cm ³ burrow ⁻¹ year ⁻¹	-126.36 cm ³ burrow ⁻¹ year ⁻¹			
	Hillslope-wide	-0.48 m³ ha-1 year-1	-0.05 m ³ ha ⁻¹ year ⁻¹			
Vol _{add}	Affected area	-7.37 cm ³ cm ⁻² year ⁻¹	-1.18 cm ³ cm ⁻² year ⁻¹			
	Per burrow	-619.2 cm ³ burrow ⁻¹ year ⁻¹	-48.36 cm ³ burrow ⁻¹ year ⁻¹			
	Hillslope-wide	-0.34 m ³ ha ⁻¹ year ⁻¹	-0.02 m ³ ha ⁻¹ year ⁻¹			

531

532

533 5. Discussion

534 Our results showed that the new ToF device is a suitable tool for high-resolution, autonomous 535 monitoring of surface changes, applicable also in remote areas. The ability of a continuous observation of 536 sediment redistribution over a longer time during our study provided new insights into the importance of 537 burrowing animals for sediment redistribution. Our research reveals that the presence of vertebrate burrows 538 increases hillslope sediment redistribution rates much more than previously assumed (up to 208%). We 539 showed that the quantity of animal-related sediment redistribution, however, varied on rainfall occurrence, with 540 an increase in sediment redistribution between 40% in the arid research area and 338% percent in the 541 mediterranean research area.

542

543 5.1 Suitability of the ToF method for surface monitoring





544 The here proposed monitoring technique enables an automatic monitoring of surface changes on a 545 microtopographic scale, and its measurement continuity allows for the analysis of ongoing 546 biogeomorphological processes in high temporal resolution.

547 Our ToF device stands in contrast to earlier studies that used laser scanning technology to monitor 548 microtopographic changes, with regard to the costs, measurement frequency and sampling autonomity (Table 549 A5).

550 Previous authors mainly applied expensive laser scanning for the estimation of sediment redistribution, 551 and the research sites had to be personally revisited for each of the measurements (Nasermoaddeli and 552 Pasche, 2008; Eltner et al., 2016b; Eltner et al., 2016a; Hänsel et al., 2016). In contrast to other laser scanning 553 methods (Table A5), our approach is instrumentally much more cost-effective and, thus, easier to apply and 554 more available also for smaller case studies with multiple objects to be observed at the same time. The cost 555 for the laser scanners and needed equipment used in previous studies varied between USD 4500 and up to 556 USD 240,000 (Nasermoaddeli and Pasche, 2008; Morris et al., 2011) (Table A5). In comparison, the cost of 557 our ToF system comprises only USD 900, which is a 5-240 times lower price.

In terms of data quality, our ToF device is more precise or comparable to those employed in other studies. The accuracy of the camera ($R^2 = 0.77$) was in the range of previous studies ($R^2 = 0.26-0.83$ (Eitel et al., 2011), Table A5). The horizontal point spacing of our cameras was 0.32 cm, and the maximum number of points per cm² was 8.5. These values are similar to previous studies in which the used devices had a horizontal point spacing in the range of 0.25–0.57 cm (Kaiser et al., 2014; Nasermoaddeli and Pasche, 2008)) (Table A5), and the maximum number of points per cm² in a range of 1 point–25 points cm⁻² (Eitel et al., 2011; Longoni et al., 2016) (Table A5).

565 Our cameras tended to slightly overestimate or underestimate the volume of redistributed sediment. 566 This error occurs when the pulse reflects from several vertical objects such as walls or, in our case, branches 567 or stones and then enters the camera sensor. This phenomenon was also observed in previous studies 568 applying laser scanners and is inevitable if the goal is to study surface changes under natural field conditions 569 (Kukko and Hyyppä, 2009; Ashcroft et al., 2014). During operation of the cameras, we learnt that our newly 570 developed instruments are particularly capable of delivering usable scans at night. This is likely due to the 571 strong scattered sunlight reaching the camera sensor during the day, blurring the data (Li, 2014). Thus, we 572 recommend focusing on nocturnal operation to prevent light contamination from the surroundings.

573 We could thus prove that the ToF cameras are a suitable and cost-effective method for a continuous 574 monitoring of sediment redistribution at a microtopographic scale without the need of expensive laser scanning 575 campaigns.

576

577 5.2. Sediment Redistribution

578 Our research reveals that the presence of vertebrate burrows generally increases hillslope sediment 579 redistribution. We show, however, that the ratio between the sediment redistribution caused by rainfall in the 580 areas affected and not affected by burrowing animals varies between the climate zones. The sediment 581 redistribution in the affected areas was 40% higher in the arid research site, and in the mediterranean research 582 site, it was 338% higher when compared to the areas not affected by burrowing animals (Fig. 9, Tables A3 and 583 A4).

584 By monitoring microtopographical changes in a high spatio-temporal resolution, we found that the 585 occurrence of larger rainfall events played a two-fold, accelerating role in influencing sediment redistribution





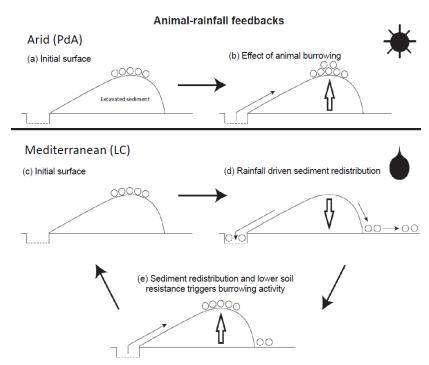
586 (Fig. A3 and A4). Firstly, rainfall-runoff eroded burrow material causing increased sediment loss. Ultimately, 587 after the rainfall, the cameras detected animal burrowing activity. The rainfall triggered the burrowing activity 588 which was likely related to a lower burrowing resistance of the soil due to the increased soil moisture (Rutin, 589 1996; Romañach et al., 2005; Herbst and Bennett, 2006). This double feedback led to frequently occurring but 590 small redistribution rates. However, cumulatively, this mechanism increased downhill sediment fluxes. Previous 591 studies most likely missed this low magnitude but frequent surface processes and, thus, did not estimate the full volume of redistributed sediment due to the fact of their sporadically taken measurements. To quantify all 592 593 occurred sediment redistribution processes, a continuous frequent surface monitoring, like the here presented, 594 is needed.

595 In contrast to our result, the maximum increase in the sediment volume redistributed during rainfall 596 events measured in the areas affected by burrowing animals when compared to not affected areas was 208% 597 ((Imeson and Kwaad, 1976) Table A6). Our results, however, indicate an increase of up to 338% (Table 9). 598 This means, that the contribution of animals' (vertebrates') burrowing activity in the mediterranean climate 599 appear larger than previously observed by using field methods such as erosion pins or splash traps (-3 -600 208%, (Imeson and Kwaad, 1976; Hazelhoff et al., 1981; Black and Montgomery, 1991), Table A6). In contrast, 601 in arid PdA, our study found a much smaller increase (40%, Fig. 9) in the sediment volume redistributed during 602 rainfall events measured in the areas affected by burrowing animals when compared to not affected areas. 603 This is lower than previously estimated (125%, (Black and Montgomery, 1991), Table A6). However, solely 604 one rainfall event above 0.2 mm day-1 occurred during our monitoring period. Hence, we conclude that the 605 contribution of burrowing activity of animals to hillslope sediment transport is much larger in areas with frequent 606 rainfall events than previously thought, while it has been realistically estimated by previous studies for areas 607 with rare rainfall events (Table A6).

608 Overall, our study revealed a strong impact of animal excavation processes on sediment redistribution 609 in the mediterranean climate zone (0.67 m³ ha⁻¹ year⁻¹), which were more in a range of excavated volume 610 observed in previous studies by bears and porcupines (0.49 m³ ha⁻¹ year⁻¹, (Hall et al., 1999), Table A8) than 611 rodents (0.02 m³ ha⁻¹ year⁻¹, (Hall et al., 1999)). The estimated sediment excavation in the arid climate zone 612 (0.18 m³ ha⁻¹ year⁻¹, Fig. A4, Table A8) was in the order of magnitude of previous studies (0.05–0.2 m³ ha⁻¹ 613 year-1, (Black and Montgomery, 1991; Yoo et al., 2005), Table A8). Our results thus suggest that animal 614 burrowing activity is an important part of the environmental mechanisms leading to increased sediment fluxes 615 in wetter (as a consequence of animal-triggered excavation and rainfall-triggered erosion) and drier (as a 616 consequence of animal-triggered excavation) regions (Fig. 11).







618

619 Figure 11. Scheme of the animal-driven and rainfall-driven sediment redistribution processes in both climate 620 zones: (a) Describes the initial surface of the burrow before a start of a redistribution process and (b) the 621 animal excavation process in the arid zone. Here, due to sporadically occurring rainfall events, sediment 622 redistribution is mostly controlled by the animal burrowing activity; (c) Describes the initial burrow surface in 623 the mediterranean climate zone. (d) the process of sediment redistribution during a rainfall event and (e) the 624 following animal burrowing activity. The burrowing is triggered by decreased soil resistance due to the 625 increased soil moisture after rainfall as well as by sediment accumulation within the burrow's entrance. The 626 burrowing activity leads to a new supply of sediment being excavated to the surface. In the mediterranean 627 climate zone, the sediment redistribution is controlled by both animal burrowing activity and rainfall. The 628 alternating excavation and erosion process ultimately lead to an increase in redistribution rates.

629

630 Magnitudes of sediment volume redistributed within areas affected by burrowing animals similar to our 631 results were previously obtained solely in studies applying rainfall simulator. These studies estimated an 632 increase in the volume of sediment redistributed during rainfall events, measured in the areas affected by 633 burrowing animals when compared to not affected areas, to be between 205% and 473% (Li et al., 2018; Chen 634 et al., 2021), Table A6). However, a rainfall simulator can only provide data on surface processes within a plot 635 of a few m² in size and under ideal laboratory conditions while ignoring the uphill microtopography, vegetation 636 cover and distribution (Iserloh et al., 2013) which were shown to reduce erosion rates. More importantly, the 637 rainfall intensity on hillslopes decreases with (i) the angle of incidence of the rain, (ii) the inclination of the 638 surface and iii) the relative orientation of the sloping surface to the rain vector (Sharon, 1980). When simulating 639 a rainfall event with the same rainfall volume as in the field, the rain is induced directly over the treated surface 640 and has thus a higher velocity which leads to an increased splash erosion than under natural conditions (Iserloh





et al., 2013). We thus propose that the rainfall experiments overestimate the erosion rate while the correcterosion rate can be measured solely under field conditions.

643 Cumulative sediment redistribution within burrow roof, mound and entrance was, on average, 28% 644 lower than cumulative sediment redistribution only within the mound and the burrow roof (Fig. 9 and A4). These 645 results suggest that 28% of the eroded sediment from animal mounds and burrow roofs is re-accumulated 646 within the burrow entrance during rainfall-runoff events, and the remaining 62% is incorporated into overall 647 hillslope sediment flux. Our numbers contrast with previous studies, which quantified that about 58% of the 648 sediment excavated by animals will accumulate back in the burrow entrance and only 42% is incorporated to 649 downhill sediment flux (Andersen, 1987; Reichman and Seabloom, 2002). Hence, our results indicate not only 650 higher redistribution rates within areas affected by the burrowing animals but also point to much higher supply 651 of sediment to the downhill sediment flux as previously thought.

652 On the hillslope scale, the contrast between our estimated volume of redistributed sediment during 653 rainfall events within areas affected by burrowing animals (from -0.67 until -1.18 cm³ cm⁻² year⁻¹) and the 654 previous studies was even higher than on the burrow scale (from -0.183 until -1.56 cm³ cm⁻² year-1, (Imeson 655 and Kwaad, 1976; Li et al., 2018), Table A7). This was well pronounced when estimating the hillslope-wide 656 volume of the sediment excavated by the animals (from 0.18 cm³ cm⁻² year⁻¹ until 0.67 cm³ cm⁻² year⁻¹ 657 according to our study, and from 0.05 cm³ cm⁻² year⁻¹ until 0.49 cm³ cm⁻² year⁻¹ according to previous studies, 658 (Black and Montgomery, 1991; Hall et al., 1999), Table A8). The previous studies estimated the area-wide 659 excavated soil volume solely once or twice a year. We propose that these measurements only describe the 660 current burrow distribution, however, cannot consider the continuous excavation and erosion dynamics.

661 Our study offers new insights previously undescribed in literature. Our cost-effective ToF device 662 provides data on surface changes in a high spatio-temporal resolution. The high temporal resolution could 663 unravel ongoing low magnitude but frequent excavation and erosion processes. High spatial resolution enabled 664 us to estimate the exact volume of sediment fluxes from the burrows downhill. Our results indicate that the 665 contribution of burrowing animals on the burrow as well as on the hillslope scale was much higher than 666 previously assumed. In our future research, we intend to include our findings into long-term soil erosion models 667 that rely on soil processes but do not yet include animal-induced surface processes on microtopographical 668 scales in their algorithms.

669

670 6. Conclusion

671 Our study provides new insights on the impacts of burrowing animals on hillslope sediment fluxes. The 672 continuous high-resolution monitoring enables to study the surface processes in detail and the high temporal 673 data availability revealed higher redistribution rates within areas affected by burrowing animals than previously 674 assumed. We discovered an alteration between sediment excavation by the animal and sediment erosion 675 during rainfall events which unveil a continuous sediment contribution of burrowing animals to hillslope 676 sediment flux. Although we concentrated on the impacts of burrowing animals on sediment redistribution, the 677 applicability of the cameras is not limited to our research topic. Other possible applications could, for example, 678 be a study of surface roughness, impacts of dead wood on erosion, biomass changes throughout the year or 679 decomposition processes.

680

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- 689 Author contribution: JB, AL and SA planned the campaign; PG and SA performed the measurements; PG
- $690 \qquad \text{analysed the data and wrote the manuscript draft; AL, JB, NF, RB, KÜ, LP, CR, DK and PP reviewed and edited}$
- 691 the manuscript.
- 692 Code/Data availability: Code and all raw data can be provided by the corresponding author upon request.
- 693
- 694

695 Appendices

696 Table A1. List of abbreviations

α [°]	Tilt angle of the camera
b [°]	Surface inclination
Ω	Threshold value for the scan scattering error
Α	Affected area
Affected area	Area directly affected by the burrowing animal
Area _{burrow}	mean in the field measured size of the burrows which are monitored
Area	total surface area monitored by the camera
BD	Bulk density
c [m/s]	Speed of light
D	Distance from the camera to the object
Dens _{burrow}	Burrow density
DSM	Digital surface model
DSM _{after}	DSM calculated from the scan taken after the extraction
DSM _{before}	DSM calculated from the scan taken before the extraction
Entrance	entrance to the animal burrow
g [-]	ratio [-] of the reflected photons to all photons
LC	National Park LC
LC-NL	Camera in LC on the lower north-facing hillslope
LC-NU	Camera in LC on the upper north-facing hillslope
LC-SL	Camera in LC on the lower south-facing hillslope
LC-SU	Camera in LC on the upper south-facing hillslope
MAE	Mean absolute error
MAP [°]	Mean annual precipitation
m.a.s.l.	Meters above sea level
MAT	Mean annual temperature
mClay [%]	Mean content of clay
mean _{z-coordinate}	Mean value of the z-coordinates





Mound	the sediment excavated by the animal while digging the burrow
mSand [%]	Mean content of sand
mSilt [%]	Mean content of silt
Ν	Number of scans
Ν	Not affected area
Not affected area	Area not directly affected by the burrowing animal
PdA	National Park Pan de Azúcar
PdA-NL	Camera in PdA on the lower north-facing hillslope
PdA-NU	Camera in PdA on the upper north-facing hillslope
PdA-SL	Camera in PdA on the lower south-facing hillslope
PdA-SU	Camera in PdA on the upper south-facing hillslope
Res	resolution
Roof	sediment pushed aside and uphill the entrance during burrow creation
Sa	scan after the rainfall event
Sb	scan before the rainfall event
SBC	Single board computer
sd _{z-coordinate}	standard deviation of the z-coordinates
SSH	Secure shell
t [s]	Overall time of camera illumination
TOC [%]	Total organic carbon
ТоҒ	Time-of-Flight
Volaffected	volume of redistributed sediment within affected area
Vol _{detected}	volume of the extracted sediment as detected by the camera
Voladd	difference in redistributed sediment volume between affected and not
	affected areas
Vol _{exc}	Volume of the sediment excavated by the animal
Vol _{hillslope-wide}	Hillslope-wide volume of redistributed sediment
Vol _{measured}	volume of the extracted sediment measured by the measuring cup
Vol _{per burrow}	Volume of redistributed sediment per burrow
Vol _{per pixel}	Volume of redistributed sediment per pixel
Volredistributed	volume of the calculated redistributed sediment
Vol _{not affected}	volume of redistributed sediment within not affected area
y i	distance of the point to the point of origin at the camera nadir
Z _{cor}	Corrected z-coordinate
Zuncor	Uncorrected z-coordinate

698 Table A2. Number of usable scans for each camera

Camera	Latitude	Longitud	Number of	Percentage of usable scans	Time
		е	scans	taken at 1am / 5am / 8am / 10pm	period
PdA-NU	-25.98131	-70.6166	238	29 / 27 / 20 / 24	18.318.9.





PdA-NL	-25.98277	-70.61278	52	24 / 0 / 40 / 36	27.331.5
PdA-SU	-25.97477	-70.61641	351	30 / 26 / 32 / 11	16.319.9.
PdA-SL	-25.97177	-70.61409	167	48 / 38 / 7 / 8	16.319.9.
LC-NU	-32.95230	-71.06231	215	37 / 20 / 8 / 33	9.39.9.
LC-NL	-32.93928	-71.08613	3	-	6.312.9
LC-SU	-32.93078	-71.09066	160	22 / 28 / 26 / 25	28.322.5
LC-SL	-32.93110	-71.08987	167	27 / 25 / 22 / 26	16.319.9.
					-

699

700 Table A3. Summary of the volume of redistributed sediment, according to area and disturbance type. Volexc

701 describes volume of the sediment excavated by the animals. Vol_{affected} describes volume of the sediment

702 redistributed during rainfall events within affected areas. Voladd describes the difference in redistributed

703 sediment volume within affected and not affected area during rainfall.

Disturbance	Area	PdA	LC
Vol _{exc}	Affected area	16.41 cm ³ cm ⁻² year ⁻¹	14.62 cm ³ cm ⁻² year ⁻¹
	Per burrow	1498.66 cm ³ burrow ⁻¹ year ⁻¹	1226.61 cm ³ burrow ⁻¹ year ⁻¹
	Hillslope-	0.18 m³ ha-1 year1	0.67 m ³ ha ⁻¹ year ⁻¹
	wide		
Volaffected	Affected area	-1.97 cm ³ cm ⁻² year ⁻¹	-10.44 cm ³ cm ⁻² year ⁻¹
	Per burrow	-126.36 cm ³ burrow ⁻¹ year ⁻¹	-876.38 cm ³ burrow ⁻¹ year ⁻¹
	Hillslope-	-0.05 m³ ha-1 year-1	-0.48 m³ ha-1 year-1
	wide		
Voladd	Affected area	-1.18 cm ³ cm ⁻² year ⁻¹	-7.37 cm ³ cm ⁻² year ⁻¹
	Per burrow	-48.36 cm ³ burrow ⁻¹ year ⁻¹	-619.2 cm ³ burrow ⁻¹ year ⁻¹
	Hillslope-	-0.02 m³ ha-1 year-1	-0.34 m³ ha¹ year¹
	wide		

704

705

Table A4. Summary of the mass of redistributed sediment in Pan de Azúcar, according to area and disturbance
 type. Vol_{exc} describes volume of the sediment excavated by the animals. Vol_{affected} describes volume of the

sediment redistributed during rainfall events within affected areas. Vol_{add} describes the difference in

redistributed sediment volume within affected and not affected area during rainfall.

Disturbance	Area	PdA	LC
Vol _{exc}	Affected area	20.18 g cm ⁻² year ⁻¹	13.44 g cm ⁻² year ⁻¹
	Per burrow	1843.35 g burrow ⁻¹ year ⁻¹	1127.66 g burrow ⁻¹ year ⁻¹
	Hillslope-	246.17 kg ha-1 year-1	611.66 kg ha ⁻¹ year ⁻¹
	wide		
Volaffected	Affected area	-1.73 g cm ⁻² year ⁻¹	-9.6 g cm ⁻² year ⁻¹
	Per burrow	-155.42 g burrow-1 year-1	-806.26 g burrow-1 year-1
	Hillslope-	-56.23 kg ha ⁻¹ year ⁻¹	-436.97 kg ha ⁻¹ year ⁻¹
	wide		
Vol _{add}	Affected area	-1.45 g cm ⁻² year ⁻¹	-6.79 g cm ⁻² year ⁻¹





	Per burrow				-569.65 g burrow ⁻¹ year ⁻¹		
Hillslop wide)e-	-16.29 kg	ha ⁻¹ year ⁻¹	-308.5	i7 kg ha⁻¹ year⁻¹		
Table A5. Review of stu	idies wh				•		
Reference	K-	Error	Horizontal	Points per	Model	Price	
			point spacing	cm ⁻²			
Our results	0.77	0.15 cm	0.32 cm	8.5	Texas	900 \$	
					Instruments		
					OPT3101		
(Eitel et al., 2011)	0.23-	0.07 cm	NA	25	Leica	102 375	
	0.86				ScanStation 2		
(Eltner et al., 2013)	NA	0.4 cm	NA	6.4	Riegl LMS-	16 795	
					Z420i		
(Kaiser et al., 2014)	NA	NA	0.57 cm	NA	Riegl LMS-	16 795	
					Z420i		
(Longoni et al.,	NA	NA	NA	1	Riegl LMS-	16 795	
2016)					Z420i		
(Morris et al., 2011)	NA	0.5 cm	NA	NA	Maptek I-Site	240 000	
					4400LR		
(Nasermoaddeli and	NA	0.2 cm	0.25 cm	NA	Leica Cyrax	4500 \$	
Pasche, 2008)					HDS 2500		
(Thomsen et al.,	NA	NA	0.4 cm	NA	Leica	102 375	
2015)					ScanStation 2		

712

713 **Table A6.** Review of studies which estimated the sediment redistribution in areas affected and not affected

714 areas and the proposed impact.

Reference	Climate	Animals	Method	Monitoring	Frequenc	Affected	Not	impa
				period	у	areas	affected	ct
							areas	
Our	arid	vertebrat	scannin	7 months	Daily	1.97 cm ³	1.39 cm ³	+40
results		es	g			cm ⁻² year-	cm ⁻²	%
						1	year ^{_1}	
Our	mediterr	vertebrat	scannin	7 months	daily	10.44 cm ³	1.39 cm ³	+338
results	anean	es	g			cm ⁻² year-	cm ⁻²	%
						1	year-1	
(Imeson	continen	rodents	erosion	15 months	monthly	20 mm		NA
and	tal		pins					
Kwaad,								
1976)								





(Imeson	continen	rodents	splash	15 months	monthly	91.75g	94g	-3%
and	tal		boards			24.49 cm ⁻²		
Kwaad,						= 3.75 cm ³		
1976)						cm-2		
(Imeson	continen	rodents	rainfall	One-time	NA	0.2 g –	0.009 g –	+208
and	tal		simulati	measureme		0.73 g	0.23 g	%
Kwaad,			on (7.5	nt				
1976)			cm /					
			hour					
			intensity					
)					
(Imeson,	continen	vertebrat	rainfall	One-time	NA	0.18-0.3	0.146	+123
1977)	tal	es	simulati	measureme		100 J ⁻¹ m ⁻²	100 J ⁻¹ m	%
			on	nt		rain	-² rain	
(Hazelhoff	continen	earthwor	splash	12 months	monthly	NA	NA	+180
et al.,	tal	ms	traps					%
1981)								
(Black and	arid	pocket	erosion	10 months	2 months	NA	NA	+125
Montgome		gopher	pins					%
ry, 1991)								
(Hakonso	tempera	pocket	rainfall	2 years	2 – 3	2.4 – 8.7	4.4 – 15	-43%
n, 1999)	te	gophers	simulato		weeks	mg ha⁻¹	mg ha⁻¹	
			r (60 mm					
			/ hour)					
(Li et al.,	tempera	mole	rainfall	One time	15	22.1 g 115	-	+473
2018)	te	crickets	simulati	measureme	measure	cm ⁻² = 5.2	cm ⁻² =	%
			on (36	nt	ments	cm ³ cm ⁻²	1.09 cm ³	
			mm /				cm ⁻²	
<u> </u>			hour)	<u> </u>				170
(Li et al.,	tempera	mole	rainfall	One time	15	35.3 g	5 g 123	+473
2018)	te	crickets	simulati	measureme	measure	220.5 cm ⁻²		%
			on (36	nt	ments	$= 6.24 \text{ cm}^3$	1.09 cm ³	
			mm /			cm ⁻²	cm ⁻²	
(Char if	lah	a la iva	hour)	One time	2	0.00	0.00	.005
(Chen et	lab	chinese	rainfall	One-time	3	2,69 g cm ⁻	-	
al., 2021)		zocor	simulati		measure	² = 2.69	cm ⁻² =	%
			on (80	nt	ments	cm ³ cm ⁻²	0.88 cm ³	
			mm /				cm ⁻²	
			hour)					





- 717 Table A7. Review of studies which estimated the sediment redistribution in areas affected by burrowing
- 718 animals, average burrow density as found in the literature and area-wide yearly contribution of burrowing
- 719 animals to sediment redistribution.

Climate	Animals	Affected areas	Average	Average	Area-wide
			burrow	burrow size	redistribution
			density		
Arid	vertebrates	1.97 cm ³ cm ⁻²	0-12 10 m ⁻² = 0-	91.35 cm ²	1.18 cm ³ ha ⁻²
		year ⁻¹	1.2 m ⁻²		year-1
			(Grigusova et		
			al., 2021)		
mediterranean	vertebrates	10.44 cm ³ cm ⁻²	6-12 10 m ⁻² =	84.36 cm ²	0.67 m ³ ha ⁻¹
		year ⁻¹	$0.6 - 1.2 m^{-2}$		year ⁻¹
			(Grigusova et		
			al., 2021)		
Continental	rodents	91.75g 24.49	14 625 m ⁻² =	24.49 cm ²	0.183 m ³ ha ⁻¹
		cm ⁻² = 3.75 cm ³	0.02 m ⁻² (Pang	(Imeson and	year ⁻¹
		cm ⁻² (Imeson	and Guo, 2017)	Kwaad, 1976)	
		and Kwaad,			
		1976)			
Temperate	mole crickets	22.1 g 115 cm ⁻²	405 ha ⁻¹	115 cm ² (Li et	0.24 m ³ ha ⁻¹
		= 5.2 cm ³ cm ⁻²	(Castner and	al., 2018)	year ⁻¹
		(Li et al., 2018)	Fowler, 1984)		
Temperate	mole crickets	35.3 g 220.5	405 ha ⁻¹	220.5 cm ² (Li et	0.56 m ³ ha ⁻¹
		cm ⁻² = 6.24 cm ³	(Castner and	al., 2018)	year-1
		cm ⁻² (Li et al.,	Fowler, 1984)		
		2018)			
Lab	chinese zocor	2,69 g cm ⁻² =	94.69 2500m ⁻²	1256 cm ²	1.35 m ³ ha ⁻¹
		2.69 cm ³ cm ⁻²	= 0.04 m ⁻² =		year-1
		(Chen et al.,	400 ha ⁻¹		
		2021)			

720

721 **Table A8.** Review of studies which estimated the volume of sediment excavated by burrowing animals.

	Climate	Animals	Method	Monitoring period	Frequency	volume of the excavated
						sediment
Our results	arid	vertebrates	scanning	7 months	daily	0.18 m ³ ha ⁻¹ year ⁻¹
Our results	mediterranean	vertebrates	scanning	7 months	daily	0.67 m ³ ha ⁻¹ year ⁻¹





(Black	and	arid	porcupines	mound	3 years	yearly	0.2 m ³ ha ⁻¹
Montgomery	/ ,			volume			year ⁻¹
1991)							
(Black	and	arid	isopods	mound	3 years	yearly	0.11 m ³ ha ⁻¹
Montgomery	/,			volume			year ⁻¹
1991)							
(Black	and	arid	pocket	mound	2 years	3 model	0.05 – 0.11 m ³
Montgomery	/,		gopher	volume		runs	ha-1 year-1
1991)							
(Rutin, 1996)	subtropical	scorpions	mound	6 months	2-29 days	0.42 m ³ ha ⁻¹
				volume			year⁻¹
(Hall et al., 1	999)	alpine	rodents	mound	1 year	yearly	0.02 m ³ ha ⁻¹
				volume			year-1
(Hall et al., 1	999)	alpine	bears	mound	1 year	yearly	0.49 m ³ ha ⁻¹
				volume			year ⁻¹
(Yoo et al., 2	2005)	arid	pocket	mound	1 year	One model	0.1-0.2 m ³ ha ⁻
			gopher	volume		run	¹ year ⁻¹





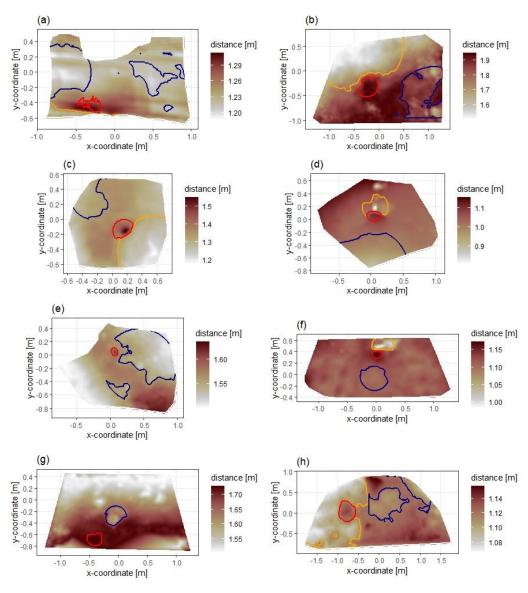


Figure A1. Delineation of the areas. The point of origin of the coordinate system is at the camera nadir. Depth is the distance between the surface and the camera. Red is the outline of the burrow entrance. Green is the outline of mound. Orange is the outline of burrow roof. Area which is not outlined is area not directly affected by the animal burrowing activity. Arrow indicates downhill direction of the hillslope. (a) LC-NU. (b) LC-NL (c) LC-SU. (d) LC-SL. (e) PdA-NU. (f) PdA-NL. (g) PdA-SU. (h) PdA-SL.





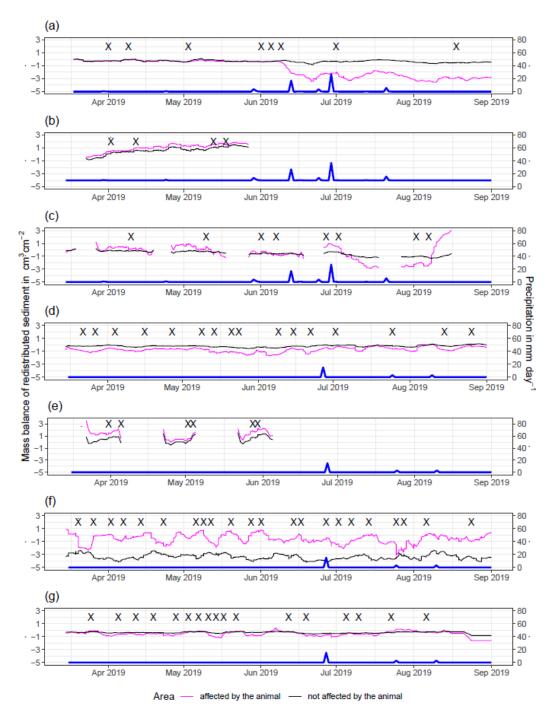
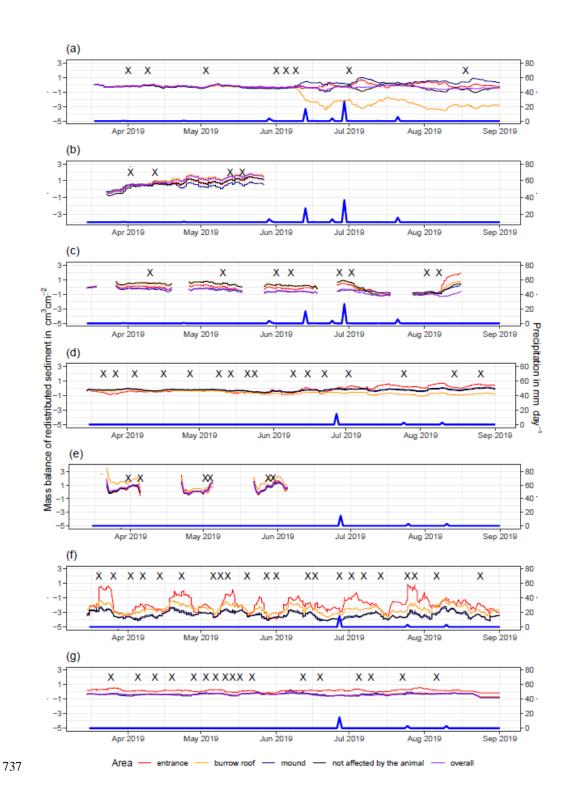


Figure A2. Sediment mass balance for the period of 7 months separately for areas affected and not affected
by burrowing animal as measured by the cameras. (a) LC-NU. (b) LC-SU. (c) LC-SL. (d) PdA-NU. (e) PdA-NL.
(f) PdA-SU. (g) PdA-SL. For abbreviations see Table A1.



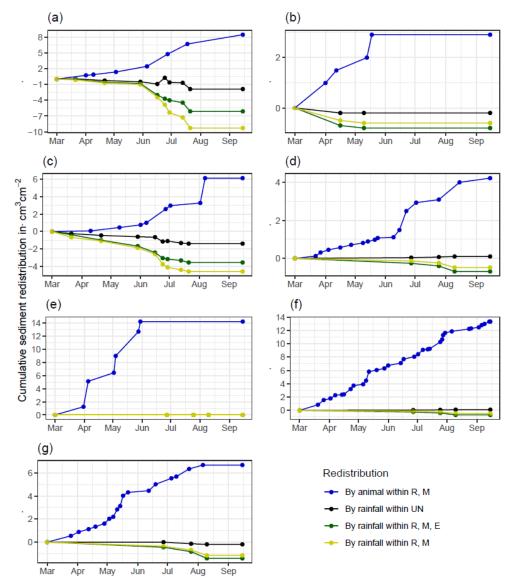








- 738 **Figure A3.** Sediment mass balance for the period of 7 months separately for all delineated areas as measured
- 739 by the cameras. (a) LC-NU. (b) LC-SU. (c) LC-SL. (d) PdA-NU. (e) PdA-NL. (f) PdA-SU. (g) PdA-SL. For
- 740 abbreviations see Table A1.
- 741

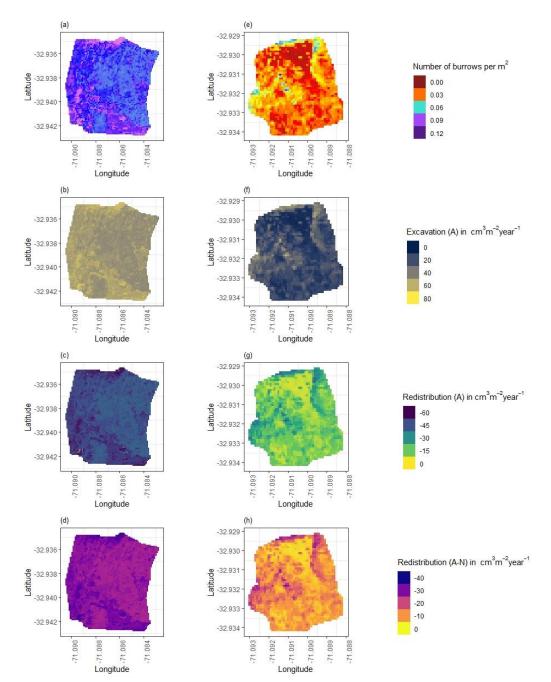


742

Figure A4. Cumulative volume of redistributed sediment for all cameras. Positive values indicate sediment
accumulation. Negative values indicate sediment erosion. Whiskers are the median sediment redistribution. E
is the burrow entrance. M is the mound. R is burrow roof. UN is area not directly affected by the animal
burrowing activity. LC is mediterranean climate zone. PdA is arid climate zone. (a) LC-NU. (b) LC-SU. (c) LCSL. (d) PdA-NU. (e) PdA-NL. (f) PdA-SU. (g) PdA-SL. For abbreviations see Table A1.









749 Figure A5. Hillslope-wide volume of redistributed sediment for a time period of one year in LC. (a-d) North-750 facing hillslope. (e-h) South-facing hillslope. (a) and (e) Density of burrows as estimated by Grigusova et al. 751 2021. (b) and (f) Volume of the sediment excavated by the animals. (c) and (g) Volume of the sediment 752 redistributed during rainfall events within affected areas. (d) and (h) Volume of additionally redistributed 753 sediment during rainfall events due to presence of the burrows. The values were calculated per burrow as 754 stated in section 3.7 by subtracting the sediment volume redistributed within animal affected area from the





- 755 sediment volume redistributed within not affected area and then upscaled. A stays for affected area, N stays
- 756 for not affected area by the burrowing animal.

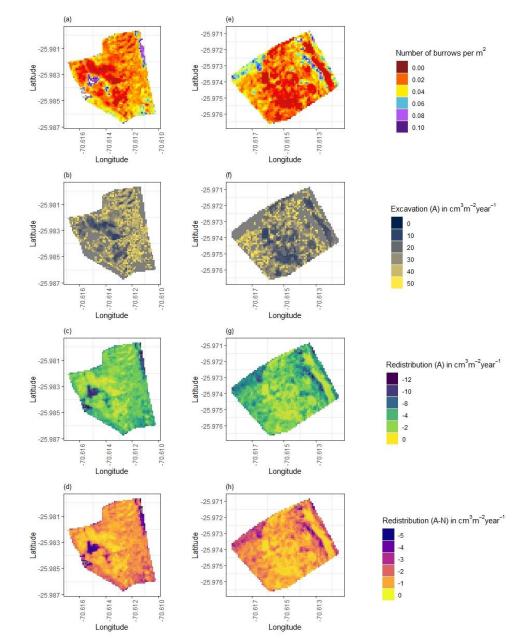




Figure A6. Hillslope-wide volume of redistributed sediment for a time period of one year in Pan de Azúcar. (ad) North-facing hillslope. (e-h) South-facing hillslope. (a) and (e) Density of burrows as estimated by Grigusova et al. 2021. (b) and (f) Volume of the sediment excavated by the animals. (c) and (g) Volume of the sediment redistributed during rainfall events within affected areas. (d) and (h) Volume of additionally redistributed sediment during rainfall events due to presence of the burrows. The values were calculated per burrow as

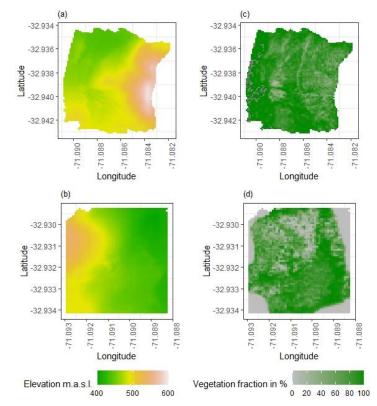




764 stated in section 3.7 by subtracting the sediment volume redistributed within animal affected area from the

- 765 sediment volume redistributed within not affected area and then upscaled. A stays for affected area, N stays
- 766 for not affected area by the burrowing animal.





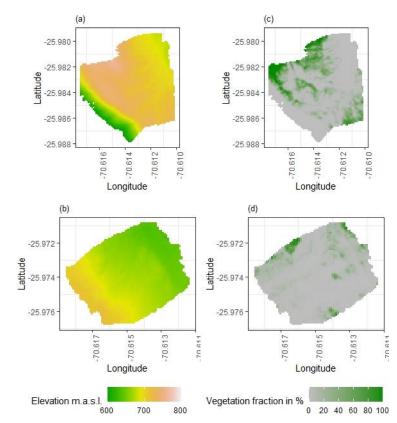
768

769 Figure A7. Digital surface model (a) and (b) and vegetation cover (c) and (d) of the hillslopes in LC. (a) and

770 (c) North-facing hillslope. (b) and (d) South-facing hillslope. m.a.s.l stands for meters above sea level.







772 Figure A8. Digital surface model (a) and (b) and vegetation cover (c) and (d) of the hillslopes in Pan de Azúcar.

773 (a) and (c) North-facing hillslope. (b) and (d) South-facing hillslope. m.a.s.l stands for meters above sea level.





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