Review 1 Emmanuel Gabet

The authors clearly did a lot of work both in terms of field measurements and modeling. The results and the framing of the manuscript of the manuscript, however, left me feeling a bit underwhelmed.

Dear Emmanuel Gabet,
Thank you very much for your reviews. We find your comments helpful and integrated your suggestions into the manuscript. Please find our response below.

We understand that you question the novelty of our study, and have re-phrased our manuscript so that it is hopefully clearer what the main contributions of this manuscript to the discipline is.

The framing of the project felt a bit misleading. In the introduction, the authors argue that few models have accounted for bioturbation and that, when they have, the effects of bioturbation are 'hard-coded' into them. First, this is not accurate, and I provide examples of models where the effects of bioturbation are emergent properties. Second, the model presented by the authors has several instances where processes related to bioturbation are hard coded into the model and do not arise naturally from more fundamental processes like competition, access to resources, compaction, etc. Therefore, I would recommend that the authors become more familiar with other models that have incorporated bioturbation and, also, not oversell their own model.

To our knowledge, earlier studies observed the statistical relationship between bioturbation and sediment redistribution in the field. Equations were developed describing the impact of bioturbation on sediment redistribution, often also in dependence on surrounding vegetation, topography or burrow structure. Lastly, earlier studies integrated this equation into a long-term landscape evolution model. These models were not validated against ground-truth data.
Our approach differed in several ways: We estimated the impact of bioturbation on soil properties and topography. We predicted the locations of burrows within the hillslope catchment. Then, we changed the model spatial parameter values (soil properties, topography) accordingly at each of the burrow locations. We specifically did not create an equation describing the relationship between bioturbation and rainfall-driven sediment redistribution, but instead used the established model algorithms to redistribute sediment.
The advantage and novelty of our approach is no bias regarding increase or decrease of sediment redistribution during the modelling as we solely changed the model parameter values, usage of machine learning for the spatial parametrisation of the model, validation of our model, and daily temporal and 0.5 m spatial resolution.

Table A4. Review of studies which integrated any kind of bioturbation into models. Previous models integrated either benthic, invertebrate or single species of vertebrate bioturbators. Models applied either described the vertical soil mixing or long-term landscape evolution models. None of the previous studies included vertebrate burrows of bioturbators into an erosion model which would be capable to capture the daily redistribution processes.

References	Bioturbators	Integrated processes	Targeted process	Model
Francois et al. 1997, Francois et al. 2002, Kadko and Heath 1984, Croix et al. 2002 and several others	Various benthic bioturbators	Equations describing soil mixing within a floodplain	Vertical soil mixing within a floodplain	Mathematical equations
Orvain et al. 2006, Román – Sánchez et al. 2019, Orvain 2005, Orvain 2003, Sanford 2008 and several others	Various invertebrates	Equations describing vertical soil mixing	Influence of vertical soil mixing on lateral redistribution	Mathematical equations
Gabet 2000	Pocket gophers	Equation describing diffusion caused by gopher bioturbation	Relief changes over 40 000 years, lateral redistribution	Landscape evolution
Gabet et al. 2014	Pocket gophers	Equations describing sediment accumulation caused by gophers	Relocation of sediment to create Mima mounds	Landscape evolution
Temme and Vanwalleghem 2016	Not specified invertebrates	Bioturbation causes soil mixing between model layers. Mixing is proportional to depth in the profile, soil thickness, and soil carbon content, and layer distance	Soil and landscape evolution	Landscape evolution
Vanwalleghem et al. 2013				Landscape evolution
Yoo and Mudd 2008		Bioturbation is considered as the cause of colluvial transport. Colluvial fluxes are calculated as a function of soil thickness and slope gradient on sloping grounds		Landscape evolution
Pelletier et al. 2013		Vertical soil mixing. Rate increases linearly with aboveground biomass.	creep including abiotic and bioturbation-driven transport	Landscape evolution

Van der Meij et al.2020		Vertical soil mixing. Rate depends on vegetation type.	Soil and landscape evolution	Landscape evolution
Our model	Vertebrates	The model includes burrow structure, adjusted soil properties and adjusted vegetation cover. Burrow distribution determined by machine learning.	Daily lateral sediment redistribution	Daily erosion model

“In the introduction, the authors argue that few models have accounted for bioturbation and that, when they have, the effects of bioturbation are 'hard-coded' into them. First, this is not accurate.”

We agree that the term ‘hard-coded’ can be misleading. We have rewritten the section of the introduction, and deleted the term.

Lines 141 – 162: Most landscape models do not yet implement impacts of bioturbators on water and sediment fluxes (Brosens et al., 2020; Anderson et al., 2019; Braun et al., 2016; Cohen et al., 2015; Cohen et al., 2010; Carretier et al., 2014; Welivitiya et al., 2019). There are numerous models describing benthic soil mixing (Francois et al. 1997, Francois et al. 2002, Kadko and Heath 1984, Croix et al. 2002), biodiffusion caused by all invertebrate bioturbators (Maysman et al. 2005, Rakotomalala et al. 2015, Morris et al. 2006) or vertical soil mixing and lateral sediment redistribution caused by single invertebrate species (Orvain et al. 2006, Román – Sánchez et al. 2019, Orvain 2005, Orvain 2003, Sanford 2008). However, there are also models which described the impact of bioturbation on sediment redistribution by the vertebrate animal species: such as the impact of pocket gophers on non-linear hillslope diffusion (Gabet 2000) or on the creation of Mima mounds (Gabet et al. 2014). Several models include soil vertical mixing caused by bioturbation and its effect on landscape evolution on a millennial scale. This rather large spatio-temporal scale however means an omission of the natural variability in burrow sizes and densities, climate zones and seasonality. In these models, soil erosion is proportionally increasing with increasing bioturbation, vertical soil mixing rates are uniform, and bioturbation is positively linked with vegetation cover (Temme and Vanwalleghem, 2016; Vanwalleghem et al., 2013; Yoo and Mudd, 2008; Pelletier et al., 2013). None of the previous studies included vertebrate bioturbator burrows of various sizes and spatial distribution by adjusting the soil properties and topography into a raster-based area-wide soil erosion model. This approach would enable to understand impact of all vertebrate bioturbators by considering the spatial distribution and variable impacts of bioturbator burrows on sediment redistribution.

“Second, the model presented by the authors has several instances where processes related to bioturbation are hard coded into the model and do not arise naturally from more fundamental processes like competition, access to resources, compaction”

We do not directly include processes like competition, access to resources or compaction. However, we indirectly do consider variable habitat preferences of bioturbators.

We predicted the locations of burrows into the hillslope catchment by applying machine learning techniques in combination with remotely sensed data (retrieved from WorldView-2 satellite) as predictors. Specifically, we used all spectral bands ranging from 400 nm until 1080 nm (blue, green, yellow, red, red edge and near infrared) as predictors, as well as vegetation indices NDVI.

This method is based on the reflectance and emission of light from Earth‘s surface which can be directly related to physiological, morphological and structural composition of plants (Jetz et al., 2016). Several studies have proven a significant correlation between species richness and spectral indices capturing the greenness and chlorophyll content (Glenn et al., 2008), or leaf area (Cantiago et al., 2015). Various machine learning techniques were applied using satellite data as predictors to estimate species richness (Heumann et al., 2011; Baldeck et al., 2015; Akbari and Kalbi, 2017) or for analysis of fine plant traits and phenology (Mascaro et al., 2014; Fassnacht et al., 2014; Keshtkar et al., 2017).

We therefore argue that our machine learning model was capable to draw a link between the burrow distribution and preferred bioturbator’ habitats while accounting the spectral information as a proxy for the habitat traits such as access to resources or competition. Please see Grigusova et al., xxx for more information.

„Not oversell their own model.”

We toned the relevant sections in the manuscript down, and tried to be more precise about our approach:

Lines 173 – 184: In this study, we include vertebrate bioturbator burrows into a semi-empirical soil erosion model (DMMF) at a daily temporal and 0.5 m spatial resolution. For this, we predict the distribution of burrows by applying machine learning techniques in combination with using remotely sensed data as predictors. Then, we adjust soil properties, topography and vegetation properties at predicted burrow locations based on field and laboratory measurements. We validate the model using field sediment fences. We run the model for a time period of 6 years, once with and without burrow adjustments. We estimate the impact of bioturbator burrows on sediment redistribution (including accumulation, erosion, and excavation), and surface runoff within four sites along the Chilean climate gradient. Lastly, we analyse how the impact of bioturbation on sediment redistribution depends on the burrow structure, climate, topography, and adjacent vegetation. Our study shows the importance of including bioturbation into erosion modelling, and describes the interplay between bioturbation, environmental parameters such as… and sediment redistribution.

The main conclusions seem to be that (1) bioturbation increases rates of sediment redistribution, (2) that the rate of sediment transport by bioturbation increases with slope, and (3) models that incorporate bioturbation will yield better results than models that don't when applied to landscapes where bioturbation is an important process. First, conclusions (1) and (2) are not novel - both of these have been know for a long time and have already been demonstrated in previous studies. Second, conclusion (3) seems trivial - of course models that incorporate the main sediment transport processes will be more accurate than those that don't. I would encourage the authors, therefore, to identify what is truly new and unique about their study.

Based on the fact that all earlier studies did not validate the model output, it is very good news for the earlier studies listed in Table A4 that our study found similar tendencies in sediment redistribution. Please note that the results of our study go beyond the general points stated above, and clarify many processes in much more detail:

(1) Bioturbation increases rates of sediment redistribution.

a) Burrowing animals' population dynamics, and animal behaviour differ in between climatic zones, and so does hillslope sediment transport. First research gap we close in this study, is that we compare the impact of bioturbation on sediment redistribution along the climate gradient:

Lines 507-508: The impact of burrows on sediment redistribution was significant in arid PdA, semi-arid SG and Mediterranean LC.

b) We, for the first time, provide exact numbers regarding the summed impact of all present bioturbators present within the hillslope catchment on sediment redistribution.

Lines 508-511: Burrows increased sediment redistribution by 137.8 % ±16.4 % in arid PdA (3.53 kg ha^{-1} $year^{-1}$ vs. 48.79 kg ha^{-1} $year^{-1}$), by 6.5 % ±0.7 % in semi-arid SG (129.16 kg ha^{-1} $year^{-1}$ vs. 122.05 kg ha^{-1} $year^{-1}$) and by 15.6 % ±0.3 % in Mediterranean LC (4602.69 kg ha^{-1} $year^{-1}$ vs. 3980.96 kg ha^{-1} $year^{-1}$).

c) We differentiate between sediment erosion and sediment accumulation, while previous studies talk about sediment redistribution generally.

Lines 512-518: Overall, bioturbation increased sediment accumulation in the arid zone (as the magnitude of the sediment excavation by the animal exceeded sediment erosion which occurs during rainfall events), but increased sediment erosion in semi-arid and Mediterranean climate (where animal burrowing activity and rainfall is present). The largest impact was found under Mediterranean conditions. We found no significant effect on redistribution in the humid zone (Figure 7).

d) We compare results at a spatial resolution of hillslope catchments as well as of a single burrow, while previous studies concentrated on single burrows, catchments or climate zones separately:

e) Additionally, we for the first time, take sediment redistribution by burrowing animals during burrow excavation into account (burrow creation, maintenance, movement of sediment to the surface) as described in Grigusova et. al. 2022 and upscale in into the hillslope catchment:

Lines 561-570: The density of burrows was the highest in arid PdA, then Mediterranean LC, semi-arid SG and the lowest in humid NA. Burrows were mostly distributed within groups of several burrows in Mediterranean LC and semi-arid SG, while they were more evenly distributed in arid PdA and humid NA. The burrows were of largest size in Mediterranean LC, followed by arid PdA, semi-arid SG and humid NA. Similarly, the highest volume of excavated sediment at the beginning of the modelling period was in Mediterranean LC and arid PdA. The volume of excavated sediment during the burrow reconstruction after rainfall events was the highest in humid NA, followed by Mediterranean LC, semi-arid SG and arid PdA. The fraction of sediment excavated by the animal to the amount of sediment redistributed during rainfall events was 128 % in PdA, 24 % in SG, 33.5 % in LC and 5.6 % in NA.

(2) Rate of sediment transport by bioturbation increases with slope.

We did not find out that the rate of sediment transport by bioturbation always increases with slope. Instead, we could show that there is a complex interaction of bioturbation, climate and spatial ecosystem complexity. This is illustrated in Fig. 10 and described in section 4.4.

Specifically, bioturbation increases erosion with increasing slope, but also enhances erosion with decreasing vegetation cover, increasing sink connectivity, and topography ruggedness as well as with decreasing soil wetness. Bioturbation enhances sediment accumulation with increasing surface roughness and soil wetness, as well as with increasing vegetation cover.

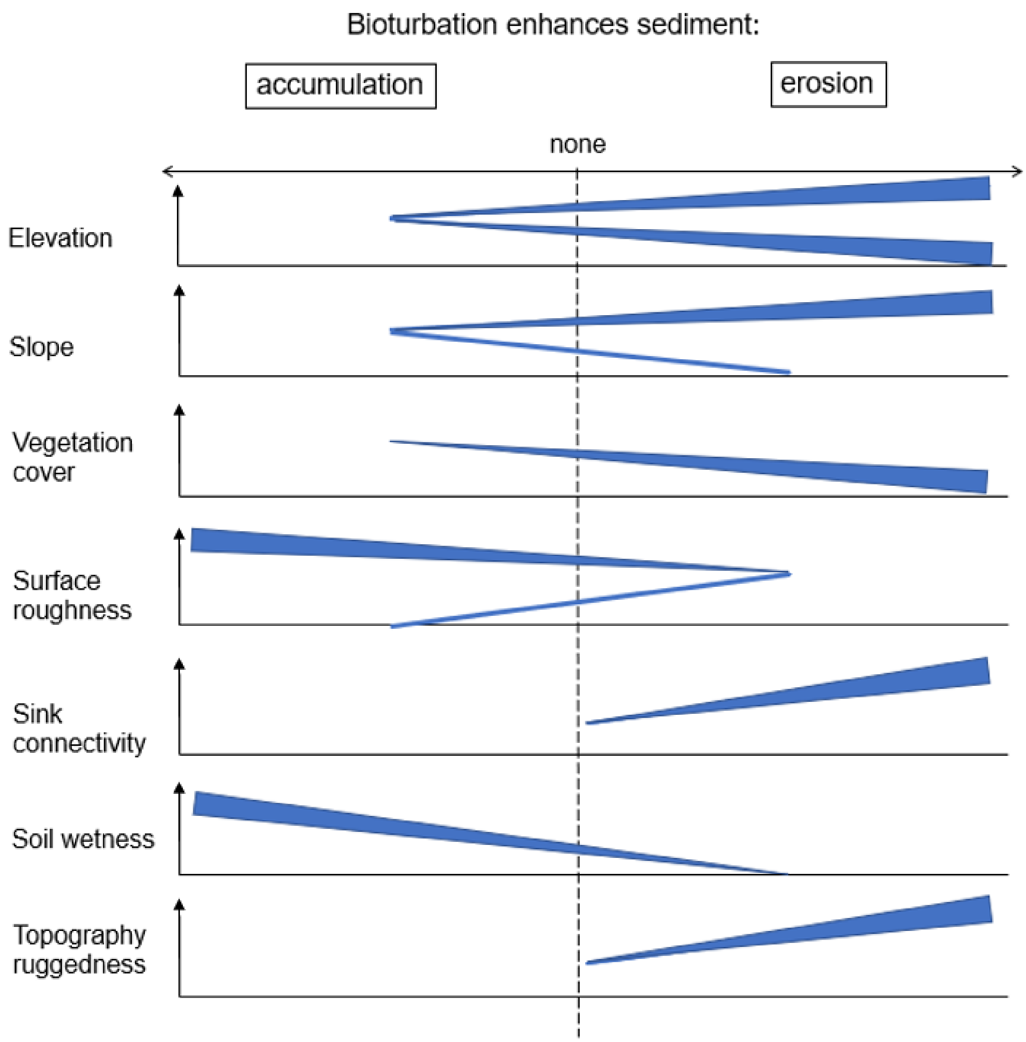

Figure 10. This figure is a conceptual summary of the detailed results from figures A3 – A8. Bioturbation increases erosion or accumulation depending on the values of environmental parameters. The dependencies are the same for all climate zones. The figure is the conceptual summary for all climate zones, therefore, there are no values stated on the x- and y-axes. The x-axis shows if bioturbation increases erosion or accumulation. The y-axis are environmental parameters. Line thicknesses indicate the magnitude of impact. Please note that bioturbation has no impact on sediment redistribution in regions with low sink connectivity and topographic ruggedness. The relationship between the values of environmental parameters and the impact of bioturbation is not linear: Bioturbation can have the same impact on sediment redistribution at high or low values of an environmental parameter, but a contrasting impact at middle values of this parameter (as in this case for elevation, slope or surface roughness).

(3) models that incorporate bioturbation will yield better results than models that don't. Seems trivial.

Of course, it is trivial that models which are better parameterized should give better results. However, to our knowledge (Table 4), this study is the first (or one of the first if we maybe missed a study during our review) that really include all burrows of vertebrate bioturbators into a soil erosion model. Our study thus shows the importance of the inclusion of bioturbation into the models.

Furthermore, to validate our model, we used a previously not applied method for model validations, by setting several sediment fences through out hillslope catchments and using the data of regularly collected sediment for ground truth validation. This approach was previously not applied as well: Previous authors defined an equation based on field experiments and then included it into the model with no further model validation which would be based on the redistribution data measured in situ in the same hillslope catchment for which the model was applied.

We rewrote parts of abstract and introduction regarding our novel findings as follows:

Abstract:

Animal burrowing activity is generally known to affects soil texture, bulk density, soil water content and the redistribution of sediments and nutrients. Nevertheless, our current understanding over the relevance of burrowing processes for shaping the earth surface in space and time is largely incomplete, mainly due to the limited availability of suitable monitoring and modelling tools. To address these knowledge deficits, we included bioturbation of vertebrates into a semi-empirical Morgan-Morgan-Finney soil erosion model in order to analyse the impact of bioturbation on sediment redistribution in high spatio-temporal resolution along a climate gradient of coastal Chile. For spatial model parameterization we predicted the distribution of burrows by machine learning techniques applied to remotely sensed data, and adjusted the parameter values of burrows based on field and laboratory data. We validated the model output using data from custom-tailored sediment fences. A specific analysis furthermore unveiled interrelations between bioturbation-moderated sediment redistribution and other co-founding factors such as burrow structure, climate, topography and vegetation. Our results showed that the consideration of bioturbation greatly increased the model performance. Model results generally revealed the overall importance of vertebrate bioturbators for both, sediment erosion and accumulation. However, the more extensive results showed contrasting effects of bioturbation on sediment redistribution in the arid, semi-arid, Mediterranean and humid climate zones. Increased sediment accumulation effects dominated in the arid zone while sediment erosion effect where found for the semi-arid and the Mediterranean zone. Impacts in the humid zone appeared neglectable. Modifications of the general findings where observed under varying co-founding factors. Bioturbation increased erosion with increasing slope, sink connectivity and topography ruggedness, decreasing vegetation cover and soil wetness. Sediment accumulation was supported by increasing surface roughness, soil wetness and vegetation cover. Altogether, our study found an increase of erosion due to bioturbation in the semi-arid and Mediterranean zone of up to 16 % which can lead to considerable changes in the shape of the landscape.

Introduction:

Lines 173 – 184: In this study, we include vertebrate bioturbator burrows into a semi-empirical soil erosion model (DMMF) at a daily temporal and 0.5 m spatial resolution. For this, we predict the distribution of burrows by applying machine learning technique and using remotely sensed data as predictors. Then, we adjusted soil properties, topography and vegetation properties at predicted burrow locations based on field and laboratory measurements. We validated the model in the field by collecting sediment in sediment fences. We ran the model for a time period of 6 years, once with and without burrow adjustments. We estimate the impact of bioturbator burrows on sediment redistribution (including accumulation, erosion, and excavation), and surface runoff along within four sites along Chilean climate gradient. Lastly, we analyse how the impact of bioturbation on sediment redistribution depends on the burrow structure, climate, topography, and surrounding vegetation. Our study shows the importance of including bioturbation into erosion modelling and the interplay between bioturbation, environmental parameters and sediment redistribution.

Not enough information was provided regarding the model. I understand that the model is described elsewhere, but individual manuscripts must stand on their own. For example, the authors report that, at some sites, including bioturbation in the model increases runoff rates but decreases in others; however, no explanation was provided describing why bioturbation would affect runoff rates and, without a description of how the model works, it's impossible for a reader to evaluate or even understand this result. I think that the most interesting result of this study is how well the modeled sediment flux matches the measured sediment flux, but without a good description of the model, that result was difficult to evaluate. Also, given the importance of that comparison, I would recommend putting Figure A3 into the main text.

We addressed points made in this paragraph as follows:

“Not enough information was provided regarding the model.”

We added paragraphs describing the model:

Lines 338 – 362: The model is a semi-empirical raster-based Morgan-Morgan Finney soil erosion model. During the model simulation, water and sediment are transferred from pixels located at higher elevations to pixels situated at lower elevations. This occurs in two stages: The first stage is the hydrological phase where the model calculates surface runoff which happens when the amount of surface water input exceeds the water-holding capacity. The amount of surface runoff is computed by taking the infiltration capacity of the surface, the volume of surface water input, and the fraction of the impervious area of a pixel into account. Infiltration capacity represents the maximum amount of surface water that can penetrate the subsurface layer. It is determined by the percentage of the impervious area and the available pore space.

The second stage is the sediment phase, where the model estimates the sediment budget for each particle size class, based on the surface conditions. The model calculates the detachment and deposition of sediments in a step-by-step process. The sources of sediments are detached particles from the pixel itself due to rainfall and surface runoff and delivered soil particles from higher elevation pixels. The detachment of soil particles by rainfall occurs when raindrops hit the ground with enough energy to detach soil particles from the surface. Rainfall has different impacts on areas with and without canopy cover, as canopy cover changes the kinetic energy of raindrops.

The amount of soil particles detached by raindrops is calculated based on the soil particle detachability, the percentage of each particle size class, the bare soil surface area, and the kinetic energy of effective rainfall. The amount of detached soil particles by surface runoff is calculated based on the soil particle detachability, the amount of runoff, the slope angle of the pixel, and the proportion of the bare surface area. The third source of sediment is from higher elevation pixels and is averaged by the surface area of the pixel.

Once sediments are delivered to the surface runoff, a portion of the suspended sediments settles to the bottom due to gravitational force. To calculate this settling, the model requires the flow velocity of the runoff and the settling velocity of each particle size class, which are influenced by the flow depth, slope angle of the pixel, and Manning's roughness coefficient (Choi et ail. 2019).

How bioturbation was included into the model is described in section 3.4.3.

"At some sites, including bioturbation in the model increases runoff rates but decreases in others; however, no explanation was provided describing why bioturbation would affect runoff rates."

As for the runoff rates, we hypothesize that it is not only the additional availability of sediment on the surface and the topography of the vicinity which controls the contribution of bioturbation to sediment surface runoff, but also the spatial distribution of animal burrows. In the semi-arid and Mediterranean zone, there are groups of several burrows located ultimately next to each other, compared to arid and humid zones with a more even burrow distribution. We interpret that due to grouping of burrows changing the topography and surface roughness, surface runoff might be redirected and centralized around these groups of burrows and thus increase the sediment erosion in the areas surrounding them. This mechanism could explain, why bioturbation promotes sediment erosion especially in the Mediterranean zone, as in this zone the precipitation rate is much higher than in the semi-arid zone.

We discuss this hypothesis in section 5.2 and show it in Figure 11 and A9

"I would recommend putting Figure A3 into the main text."

Finally, I would recommend cutting down on the number of figures. There were figures presented as results that were just a simple function of how the model was parameterized (eg., Fig. A5) or figures that didn't seem to be relevant (eg, Fig. A6).

We put Figure A3 into the main text. We cut figures A5 and A6.