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The perpetual fragility of creeping hillslopes

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9

Abstract

10

11 Soil-mantled hillslopes owe their smooth, convex shape to creep^{1,2}; the slow and persis-
12 tent, gravity-driven motion of grains on slopes below the angle of repose. Existing models
13 presume that soil creep occurs via mechanical displacement of grains by (bio)physical dis-
14 turbances^{3,4}. Recent simulations⁵, however, suggest that soil can creep without these
15 disturbances, due to internal relaxation dynamics characteristic of disordered and fragile
16 solids such as glass. Here we report experimental observations of creeping motion in an
17 undisturbed sandpile, at micron resolution over timescales of $10^0 - 10^6$ s, for a variety of nat-
18 ural and synthetic granular materials. We observe two behaviors typically associated with
19 creeping glass: strain occurs as localized and spatially-heterogeneous grain motions⁶; and
20 creep rates decay as a power-law function of time⁷. Further, creep can be accelerated or
21 suppressed by thermal cycles and shaking, respectively. Averaged strain profiles decay ex-
22 ponentially with depth, in agreement with field observations of creeping hillslope soils⁸⁻¹⁰.
23 Our findings demonstrate that soil is fragile in terms of sensitivity to disturbances, but
24 that creep dynamics are robust across grains and glasses. Mapping soil creep to the more
25 generic glass problem provides a new framework for modeling hillslope sediment transport,
and new insights on the nature of yield and failure.

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Keywords— geomorphology, granular physics, glassy dynamics, relaxation and rejuvenation, aging

28 Introduction

29 The shapes of hills encode a signature of tectonics, climate and life, through the influence of these processes on
30 sediment transport^{4,11–13}. Soil fails by landslides on the steepest slopes, leaving telltale scars on the landscape. Below
31 the angle of repose, however, soil-mantled hillslopes are characteristically smooth and convex^{4,13}. Although this soil
32 is considered a solid, it appears to flow over geologic time in a process called soil creep^{14,15}. What is the mechanism
33 for granular motion below the angle of repose? This has been speculated on for over 100 years^{1,2}. Modern treatments
34 trace their origin to Culling³, who envisioned that the net effect of environmental disturbances (biological, hydrological
35 and physical) acting on and within soil was to inject porosity, which facilitates particle motion. He also recognized
36 that porosity, and the associated particle activity, must diminish with depth. In the continuum limit Culling proposed
37 a diffusion-like relation between sediment flux and topographic gradient, that has been elaborated on by many authors
38 and implemented in virtually all landscape evolution models^{4,13,15–18}. Remarkably, the hypothesized grain motions
39 in Culling’s model have never been experimentally examined. More broadly, Culling’s mathematical formulation
40 corresponds to a physical picture of soil as a peculiar kind of “granular gas” (Supplementary Materials Section S1)
41 that is inconsistent with known granular mechanics. Researchers have begun to recognize the need to understand
42 grain-scale dynamics, in order to derive physically-informed models of soil mixing and transport on hillslopes^{19,20}.
43 While tracers have been used for over 60 years to measure coarse profiles of soil displacement on hillslopes¹⁴, the slow
44 and erratic nature of creep has prevented direct observation of grain motions in the field. The canonical hillslope
45 laboratory experiment of Roering and colleagues²¹ showed how acoustic noise can induce grain motion below the
46 angle of repose; however, our reanalysis indicates that grains were actually fluidized into inertial flows, rather than
47 sub-critical creep (Fig. S1).

48 Creep has also been recognized in the context of dense granular flows. These flows have been modeled with a local
49 ‘ $\mu(I)$ rheology’ where the effective friction (μ) is a function of a dimensionless shear rate called the inertial number,
50 $I \equiv \dot{\epsilon}d/\sqrt{P/\rho}$, where $\dot{\epsilon}$ is shear rate, d is grain size, P is confining pressure and ρ is density²². Inertial flows transition
51 at depth to a slow creep regime, characterized by intermittent and apparently random particle motions^{23,24} and
52 exponential velocity profiles^{25,26}. Recent experiments and simulations suggest the transition to creep occurs below
53 $I \sim 10^{-5}$ (refs.^{5,26,27}). The local $\mu(I)$ rheology predicts that grains should be static below yield, and therefore
54 cannot describe the creep regime²⁶. To account for creep, nonlocal models have been proposed in which fluidized
55 motions from the inertial regime diffuse downward into the bulk²⁸. However, recent experiments have revealed creep
56 in the absence of a flowing layer^{29,30}. Observations in a progressively tilted sandbox showed that, on approach to
57 the angle of repose, sporadic and localized grain motions became more frequent and eventually linked up to affect
58 yield²⁹. Granular simulations have reproduced these behaviors without any imposed disturbances⁵. The addition of
59 low-amplitude ($\ll d$), random perturbations accelerated simulated creep rates, but did not qualitatively change the
60 dynamics^{5,31}; however, the spectrum of disturbances explored in these models is quite limited.

61 Creep in amorphous solids, such as glass, is associated with sub-yield plastic deformation in response to an
62 applied stress⁶. A unifying characteristic of amorphous solids is that they are fragile: any particle configuration is
63 metastable, and very small perturbations can lead to structural rearrangements^{27,32}. These creep motions are manifest
64 as spatially heterogeneous, mesoscopic (length $\gg d$) zones of strain⁶. In glasses, relaxation by plastic rearrangements
65 leads to aging; rigidity increases with time, leading to a slow down in creep rates. This decline in plasticity can
66 be reversed by rejuvenation, typically by changing temperature³³. There is emerging evidence that granular creep
67 shares deep similarities with glasses^{5,27}, and theorists have proposed that mechanical noise in granular systems may
68 modulate creep in an analogous manner to thermal fluctuations in glasses^{7,34}. No experiments, however, have been
69 conducted to test these ideas. In this study we examine creep dynamics of an undisturbed sub-critical sandpile,
70 probing grain motions through time using an optical technique that allows us to observe exceedingly slow strain
71 rates. Creep behavior in the sandpile exhibits all of the hallmarks of relaxation in glassy materials. We also explore
72 how disturbances can enhance or reverse aging, completing the picture of soil creep as relaxation and rejuvenation of a
73 fragile solid and illustrating that in the natural environment, hillslopes are made perpetually fragile by environmental
74 perturbations. Comparisons of experimental creep profiles with data from natural hillslopes indicate that laboratory
75 observations are generalizable.

Undisturbed creep results

Our first objective is to demonstrate the existence of creep in a minimally-disturbed model hillslope. Based on previous work^{5,23,25,26,29}, we expect creep rates to be exceedingly slow ($\leq 10^{-6} m/s$) which makes typical particle tracking methods impractical. Instead, we measure grain motions via spatially-resolved Diffusing Wave Spectroscopy (DWS)³⁵, which determines strain associated with changes in the granular structure that occur on the order of the optical wavelength ($10^{-6} m$) (see Methods). Our experimental system consists of a granular heap initially prepared (time $t = 0$) just below the angle of repose, that is confined in an acrylic cell (Fig. 1) sitting on a vibration-isolating optical table (see Methods, Fig. S2). Most experiments used glass beads with ideal optical properties; however, natural sand, and a mixture of equal parts sand and kaolinite powder, were also tested (Fig. S3).

The first important result is that creep occurred for all experiments and granular materials, and it persisted over all observed timescales ($10^0 - 10^6$ s M1-4). Initial creep velocities ($t = 0$) were on the order of nm/s (cm/year) i.e., comparable to measured rates of hillslope soil creep in the field (see below) – and we confirmed that inertial numbers for undisturbed creep were all below yield ($I < 10^{-5}$) (Figs. S4, S5). All experiments exhibited glass-like ‘spatially-heterogeneous dynamics’⁶, manifest as discrete, mesoscopic ($\gg d$) zones of strain that occurred throughout the system (Fig. 1c). At early times, these deformation zones were relatively larger and more concentrated near the sandpile surface. At later times these zones became smaller and occur less frequently, with lower spatial density. Cumulative strain ϵ resulting from this deformation diminished with depth beneath the surface because of increasing confining pressure, which restricts dilation that is often associated with grain rearrangement^{23,29} (Fig. 4b). We also observed sensitivity to the preparation protocol, a ubiquitous phenomenon in fragile solids³⁶. For example: the region of intense and persistent deformation seen near the pile apex (Figs. 1; 3 M1) always occurred at the location where avalanches had formed when the sand was first poured.

Information on the time-dependent dynamics of creeping motion in the pile is encoded in the correlation function G of the speckle patterns (see Methods). In the experiments reported here, G decayed monotonically with lag time τ ; this decay was most rapid at early times t indicating fast grain motions, and slowed through time (Fig. 2). Normalizing the lag time of each correlation by the e-folding time, we find that the curves $G(\tau/\tau_e)$ collapse onto a single exponential master curve (Fig. 2) consistent with previous observations of granular creep²³ and molecular dynamics simulations of glass³⁷. The growth of the relaxation timescale τ_e increased as a power-law function of time (Fig. 2). Such power-law ‘aging’ is a classical behavior of creeping glass and other amorphous solids⁷. Our interpretation is that the initially loose sandpile has many ‘soft spots’³² associated with low packing density and/or frictional contacts, and that strain relaxes these soft spots, redistributing stress within the system, leading to an overall slowing down of creep with time⁷.

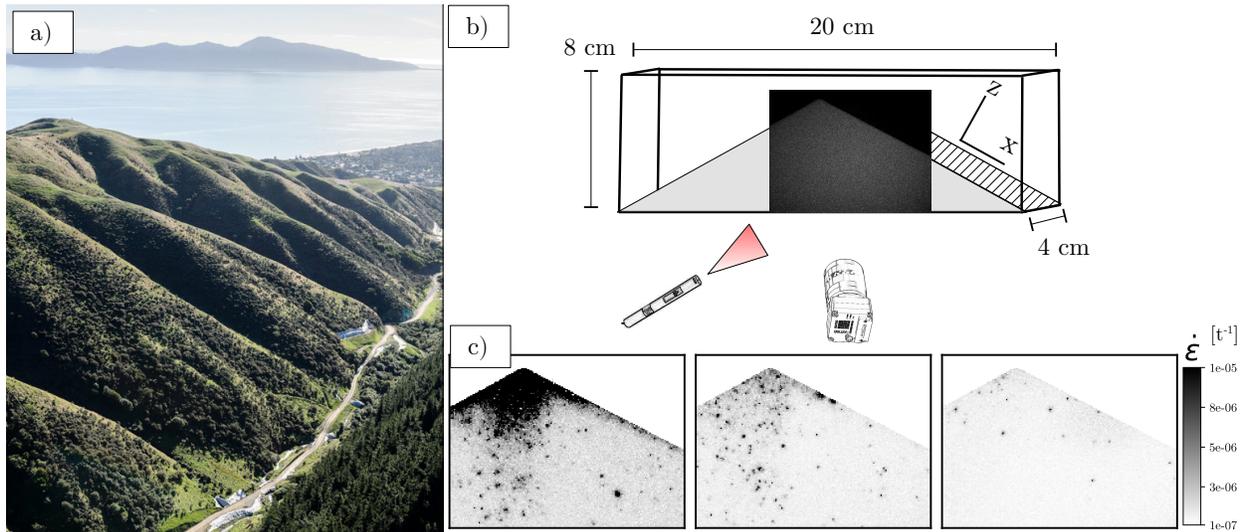


Figure 1: Experimental setup and phenomenology. a) Soil-mantled hillslope in the Te Puka Valley, New Zealand (PC: Waka Tokahi, NZ Transport Agency). b) Experimental DWS setup. c) Spatially-resolved maps of creep rates at three times ($t = 1, t = 16$ and $t = 1024$ s) since building the pile.

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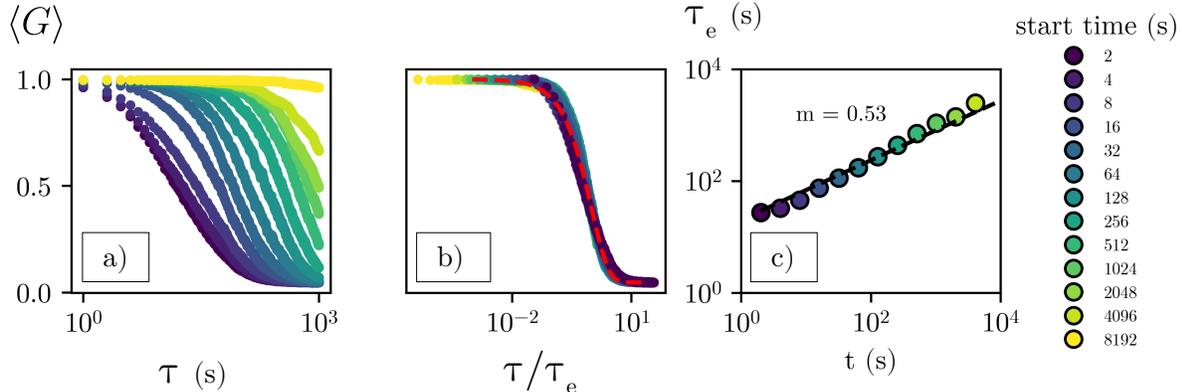


Figure 2: Glassy relaxation in an undisturbed granular heap. a) Spatially-averaged correlation function for 13 start times. b) Data are reasonably collapsed by τ_e ; red dotted line indicates exponential decay. c) Growth of the relaxation timescale; slope determined from least-squares regression of $t = t_0 \tau_e^m$, where $m = 0.53$.

109 The role of mechanical disturbances

110 In the above description, granular creep progressively slows down. In this picture of relaxation, creep rates should
 111 tend asymptotically toward zero with time. Not all of our experiments, however, exhibited this behavior. Humidity
 112 fluctuations occurred for some runs, producing a complex response in terms of creep dynamics – notably at late
 113 start times (Fig. S8). Data indicate that some reversible (elastic) strain occurred in these runs — perhaps due
 114 to nanoscale capillary bridges or other tribological effects^{38,39}. Similar behavior has been seen for weakly heated
 115 granular materials^{35,40}, suggesting that some kinds of disturbance may reverse relaxation and reactivate creep.

116 Natural hillslopes appear to creep indefinitely, and they are perpetually disturbed: bombarded by seismic waves,
 117 thermal cycles, wetting and drying, and bioturbation^{8–10,16,41,42}. We posit that the same relaxation processes observed
 118 in our experiments also play out in natural soils, but that some environmental disturbances rejuvenate soil creep.
 119 Inspired by previous work^{35,40} we examine heating as a method for creep rejuvenation in our experiments (see
 120 Methods). Thermal loading may be considered a proxy for shrink-swell and freeze-thaw cycles that occur in natural
 121 soils^{8–10,42} (see Methods). The sandpile was first allowed to relax for 10^4 s before applying disturbances. At the
 122 instant heat was turned on, an increase in strain rate $\dot{\epsilon}$ was observed as most of the pile began to creep faster (Fig. 3).
 123 This was likely due to thermo-mechanical stresses created by volumetric expansion of the grains⁴⁰, though expansion
 124 of the apparatus walls may have also played a role. Interestingly, the spatially-averaged strain rate $\langle \dot{\epsilon} \rangle$ (see Methods)
 125 increased by more than ten times, reaching the same value observed at $t = 0$; i.e., just after preparation of the
 126 sandpile. Correlation functions also appeared similar to those observed at $t = 0$ (Fig. S10). This demonstrates that a
 127 few seconds of heating was able to reverse 10^4 s of aging. Once heat was switched off, $\langle \dot{\epsilon} \rangle$ dropped immediately, then
 128 slowly decayed toward the pre-heating value (Fig. 3a). Repeated cycles of heating and cooling produced concurrent
 129 cycles of rejuvenation and relaxation, respectively; the overall effect was to sustain an approximately constant average
 130 creep rate, that did not decay with time (Fig. S11). The ability of thermal cycling to sustain enhanced creep rates
 131 has intriguing implications for natural hillslope soils.

132 Tapping of grains may induce surface flows on heaps, but also leads to compaction of the bulk^{43,44}. Tapping may
 133 mimic some effects of seismic shaking of hillslopes⁴¹. We allowed an initial pile to relax for 10^4 s, then tapped the
 134 pile with a metronome at 1 Hz (see Methods). Taps initially excited grains throughout the pile. As time progressed,
 135 however, a thin and fast-moving surface layer developed a sharp boundary at its base, below which the bulk grain
 136 motions slowed dramatically and became very intermittent (Fig. 3). The development of these two regimes is similar
 137 to the creep-flow transition observed in experiments²³ and simulations⁵ of heap flows above the angle of repose (Fig.
 138 S12). There was an overall trend of decreasing $\langle \dot{\epsilon} \rangle$ with increasing number of taps (Fig. 3). We conclude that
 139 vibrations fluidized surface grains but drove compaction in the bulk⁴⁴, leading to more rapid relaxation (compared to
 140 the undisturbed case) as the pile evolved toward a denser, lower-energy state (Fig. S13). We interpret the boundary
 141 between fast and slow regions as a yield surface²⁹. These findings may have relevance for landslide development from
 142 earthquakes. In particular, while vibrations in our experiments excited surficial flow, the underlying bulk became
 143 more rigid and less susceptible to future fluidization.

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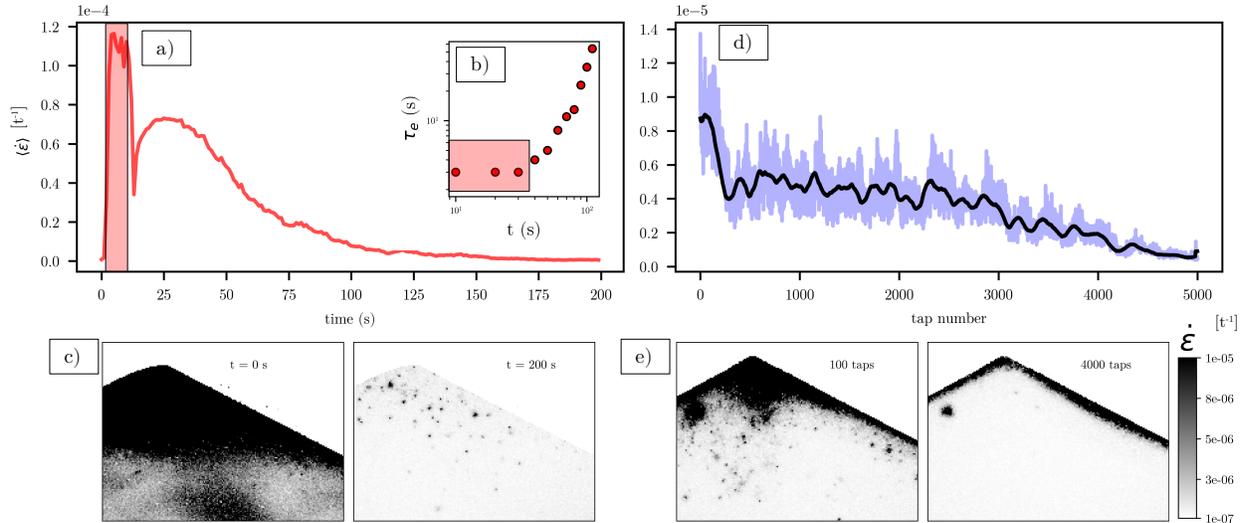


Figure 3: Mechanical perturbations drive rejuvenation and aging. a) Spatially-averaged strain rate including 10 s of heating applied (red rectangle) and relaxation after removal of the heat source. b) Relaxation timescale τ_e during and following heat response (Fig. S10). c) Spatial maps of strain rate during and following heat pulse. d) Time series of spatially-averaged strain rate (blue line). Black line indicates moving-window average (100 taps). e) Spatial maps of strain rate determined over one tap cycle (tap number indicated in figure). Note that after many taps, creep is mostly confined to a thin, localized layer at surface.

145 Comparison with field observations

146 Field measurements of soil creep on hillslopes are quite coarse compared to our experiments. Nonetheless, profiles of
 147 displacement, measured over decades by buried tracers in so-called ‘Young pits’ (Fig. 4a), provide a long-time average
 148 of soil motion at discrete depths z . Horizontal velocity profiles ($u(z)$) measured from a variety of environments are
 149 typically exponential-like^{14,45,46}, though quantitative comparisons among field sites have not been made. Here we
 150 examine previously published field data from Young pits at four sites around the world, where creep was reportedly
 151 driven by different forcings^{8–10,42}. We confirm that all field data have $I \ll 10^{-5}$, i.e., they are in the granular creep
 152 regime. All velocity profiles are reasonably well described by an exponential function $u/u_0 = e^{-z/\lambda}$, where u_0 is the
 153 surface velocity and λ is a decay length determined from data fitting (Figs. 4c, S6). The latter two parameters must
 154 be related to site-specific soil characteristics and environmental disturbance regimes, but exploring this is beyond the
 155 scope of this paper. For these hillslopes $u_0 \sim 10^{-9}$ m/s (Figs. 4c, S6), comparable to our measured experimental
 156 creep rates for the initially loose and heated grains.

157 We compare our undisturbed creep experiments to field data, by first generating depth (z) profiles of downslope
 158 (x)-averaged cumulative strain through time from the surface to 1-cm below (Fig. 4b). Our experiments permit
 159 determination of strain rate rather than velocity (see Supplementary Materials Section S5); however, the normalized
 160 strain rate profile $\dot{\epsilon}/\dot{\epsilon}_0 = e^{-z/\lambda}$ is essentially equivalent to a normalized velocity profile. We see that our experimental
 161 data fall on top of the field profiles (see Fig. S3 for experiments with other materials). It is important to note, however,
 162 that while exponential profiles have been reported for granular creep in many experiments^{23,25,26}, an exponential
 163 profile is not diagnostic of creep. Inertial flows may also exhibit exponential velocity profiles^{22,28}. Also, creep in
 164 highly heterogeneous soils, or soils with macro-scale disturbances such as tree throw⁴⁷, can exhibit erratic velocity
 165 profiles that are not well fit by an exponential.

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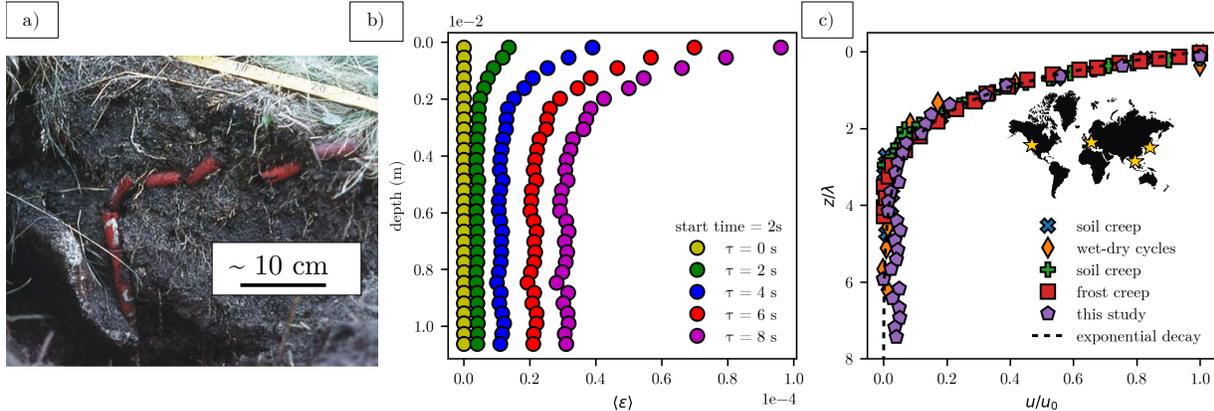


Figure 4: Depth-averaged strain profiles from the lab and field. a) Excavated Young Pit indicating the displacement of tracer pegs over a 17-year interval (PC Alfred Jahn). b) Depth and horizontally-averaged cumulative strain profiles at three lag times, measured in an undisturbed creep experiment. Profiles start at 2048 s after deposition. c) Compilation of soil deformation data from four studies and field environments - originally compiled by Roering⁴⁶. Freeze-thaw cycles near Strasbourg, France⁸, wet-dry cycles in Kuala Lumpur, Malaysia⁴², freeze-thaw cycles in the Japanese Alps⁹, wet-dry cycle in Stanford, California¹⁰. Data are fit by an exponential decay, the parameters of which are then used to reasonably collapse the data (Fig. S6)

Discussion and outlook

167

168 By probing a seemingly static sandpile with speckle imaging, our experiments have revealed a seething and ceaseless
 169 creeping motion — even in the near absence of mechanical disturbances. These motions are strikingly similar to
 170 recent observations of creep in a heap of Brownian (micron-scale) particles⁴⁸, even though our sand grains are non-
 171 Brownian. Further, we have shown how granular creep rates can be tuned by imposing external disturbances that
 172 are geophysically relevant. Our experiments reveal deep similarities in how grains and glasses creep, and provide
 173 compelling evidence that mechanical disturbances in granular systems play a role akin to thermal fluctuations in
 174 glasses^{7,27,34}.

175 Intriguingly, even though the mechanics of grain motion are fundamentally different from Culling’s model, our
 176 final result provides a kind of confirmation of his physical intuition³. In particular: heterogeneity in granular structure
 177 leads to seemingly random grain motions that decrease with depth; and mechanical disturbances can introduce new
 178 stresses and/or porosity that facilitate motion. Creep motions are consistent with granular self diffusion⁴⁹; however,
 179 this does not imply that there is any Culling-like diffusion relation between flux and slope. Moreover, Culling and
 180 subsequent hillslope researchers did not anticipate persistent creep even in the (near) absence of disturbance. How
 181 do we understand the similarity in creep rates and profiles between our undisturbed and initially loose sandpile,
 182 and natural (disturbed) hillslope soils? Our new view separates creep into a generic relaxation process whose rate
 183 depends on granular friction/cohesion and structure, and diverse rejuvenation processes associated with environmental
 184 disturbances. We speculate that the primary role of biophysical disturbance in natural hillslopes is to maintain soil in
 185 a loose and fragile state, where relaxation rates are high. Other types of disturbance, however, can have the opposite
 186 effect; shaking can lead to compaction and enhanced aging, depressing bulk creep rates even as surface motions are
 187 enhanced.

188 Although soil is sensitive to disturbances, geologic history, and boundary effects^{5,27}, qualitative creep dynamics
 189 are robust across materials and environments. Future granular simulations could be used to reveal how disturbances
 190 influence the contact forces and/or structure that ultimately drive creep. Experiments could examine the consequences
 191 of cohesion/adhesion, surface charge, moisture, bioturbation and other effects on creep dynamics. Resolving these
 192 factors will allow derivation of a coarse-grained creep rheology model, whose kinematics and scales are determined by
 193 physically-meaningful parameters. Our results indicate that elastoplastic models developed to describe the rheology
 194 of amorphous solids⁷ — that can explicitly incorporate mesoscopic scales of grain rearrangements, and rejuvenation
 195 by mechanical noise — may be good candidates. An improved model of soil creep is not only useful for predicting
 196 hillslope sediment transport; it will also help us to better understand how creeping soil accelerates to the yield point,
 197 which leads to catastrophic landslides⁵.

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297 **Methods and protocols**

298 **Measuring grain motion**

299 The principle of DWS is that highly coherent light illuminates our granular heap, where photons scatter and interfere,
 300 which produces a random ‘speckle pattern’ that is collected with a CCD camera (Fig. 1, Supplementary Material
 301 S3). As grains slowly creep past one another, they change the photon trajectories and render new speckle patterns.
 302 We achieve spatially-resolved measurements by partitioning images into a grid with cells (metapixels) of size l^* , the
 303 mean free path of photons within the material. This quantity is around $l^* \approx 3d$ for the granular materials used (see
 304 Methods). Fluctuations in the speckle pattern between a start time t and a lag time τ within each metapixel are
 305 quantified via the normalized correlation function, $G(t, \tau)$ (Fig. 2)³⁵. Global dynamics across the whole sandpile
 306 are measured by averaging G for each metapixel, signified as $\langle G \rangle$. This allows determination of the first important
 307 quantity for assessing glassy dynamics: the relaxation time τ_e , determined as the time at which $\langle G \rangle = 1/e$ (Fig.
 308 2). For most experiments we used monodisperse glass beads (Cerroglass), of diameter $d_s = 100\mu\text{m}$ and density $\rho =$
 309 2.6 g/cc , to build the sandpile. This material was chosen because its scattering properties are well understood and
 310 it is standard in DWS experiments. From the correlation function G , we can apply optical theory³⁵ to determine
 311 the second important quantity for examining glassy dynamics: ϵ , the strain that occurs within a volume set by l^*
 312 (see Supplemental Materials Section S3). Whereas DWS can still be used to examine relative grain motions for the
 313 sand and clay mixtures we used, use of more complex materials precludes us from calculating l^* and hence from
 314 determining absolute strain ϵ (Supplementary Material S5).

315 **Experimental procedures**

316 Our experimental system is not meant to be a scaled model of a hillslope, either in a geometric or dynamic sense.
 317 Rather, it is designed to optimize the direct observation of grain motions, in order to understand the granular physics
 318 of creep that are relevant for soil motion at the pedon scale in nature. Reported experiments were conducted in
 319 relatively constant ambient temperature ($21\text{C} \pm 0.2$) and relative humidity ($23.8\% \pm 0.3$) conditions (Fig. S7).
 320 The heap was prepared by allowing a fixed volume/flow rate of granular material (well within the continuous-flow
 321 regime²²) to flow out of a funnel, at a fixed height 8 cm above the center of the cell bottom. Results are reported
 322 for glass beads, unless otherwise stated. Our ‘undisturbed’ experiments consisted of allowing the initial pile to relax
 323 under gravity, with no imposed external disturbances. We note, however, that small-scale ambient fluctuations in
 324 temperature and relative humidity did occur (Fig. S7). We conducted a ‘short’ duration experiment at a frame rate
 325 of $f = 1\text{Hz}$ for 10^4 seconds (2.8 hours) immediately following preparation, and a ‘long’ duration experiment with
 326 $f = 0.2\text{Hz}$ for 10^6 seconds (11 days). Image collection began at the start of emptying the funnel, while analysis
 327 of creep dynamics reported here started as the last grain entered the system and avalanching ceased ($t = 0$) —
 328 making the initial condition a sandpile prepared just below the angle of repose (Fig. 1). We computed both the
 329 instantaneous strain rate determined from successive image pairs through time, $\dot{\epsilon}(\tau = 1\text{s}) = \epsilon(t)f$ (e.g., Fig. 1),
 330 and the temporal evolution of the relaxation timescale τ_e sampled from different start times t , for each metapixel
 331 in an image. From these we generated ensemble-average values for each image, $\langle \dot{\epsilon} \rangle$ and $\langle \tau_e \rangle$, that characterized the
 332 spatially-averaged dynamics of the sandpile through time (Figs. 1, 2, 3). From instantaneous strain values we also
 333 computed surface-normal (z) profiles of downslope (x)-averaged strain (Figs. S4, S5); this allowed us to generate
 334 depth profiles of cumulative strain through time, for comparison to field data (Fig. 4).

335 Disturbance protocols

336 For experiments with disturbance, a pile prepared following the protocol above was allowed to relax for 10^4 s before
337 disturbances began. Heating of glass beads produces a small but measurable volume expansion⁴⁰ (coefficient of
338 thermal expansion $\sim 10^{-6} K^{-1}$) that is reversed as grains cool. At $t = 0$ heat was applied to the side of the cell for
339 10 s by a heat gun, producing a measured sidewall temperature of 50C (Fig. S9). After 10 s the heating element
340 was removed, while the creep response was documented for another 200 s (Fig. 3). For tapping experiments, discrete
341 taps were delivered to the pile using a metronome (double pendulum) that rests on a platform attached to the cell
342 (Fig. S9). At $t = 0$ we initiated a series of 5000 taps delivered at a rate of 1 Hz, and recorded images at the same
343 rate — but phase-lagged from the taps — for the 5000-s duration (Figs. 3, S9).

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347 contributed to interpretation and writing.

348 **Competing interest statement:** The authors declare no competing interests.

349 **Additional information:** Extended data figures and methods are included in Supplementary Materials.

350 **Data availability statement:** Data will be deposited in the publicly shared repository figshare, and all code used
351 to analyze these data will be publicly available on github.