Transient dwarfism of soil fauna during the Paleocene–Eocene Thermal Maximum

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Soil organisms, as recorded by trace fossils in paleosols of the Willwood Formation, Wyoming, show significant body-size reductions and increased abundances during the Paleocene–Eocene Thermal Maximum (PETM). Paleobotanical, paleopedologic, and oxygen isotope studies indicate high temperatures during the PETM and sharp declines in precipitation compared with late Paleocene estimates. Insect and oligochaete burrows increase in abundance during the PETM, suggesting longer periods of soil development and improved drainage conditions. Crayfish burrows and molluscan body fossils, abundant below and above the PETM interval, are significantly less abundant during the PETM, likely because of drier floodplain conditions and lower water tables. Burrow diameters of the most abundant ichnofossils are 30–46% smaller within the PETM interval. As burrow size is a proxy for body size, significant reductions in burrow diameter suggest that their tracemakers were smaller bodied. Smaller body sizes may have resulted from higher subsurface temperatures, lower soil moisture conditions, or nutritionally deficient vegetation in the high-CO_2 atmosphere inferred for the PETM. Smaller soil fauna co-occur with dwarf mammal taxa during the PETM; thus, a common forcing mechanism may have selected for small size in both above- and below-ground terrestrial communities. We predict that soil fauna have already shown reductions in size over the last 150 years of increased atmospheric CO_2 and surface temperatures or that they will exhibit this pattern over the next century. We retrodict also that soil fauna across the Permian-Triassic and Triassic-Jurassic boundary events show significant size decreases because of similar forcing mechanisms driven by rapid global warming.

climate change | evolution | extinction | ichnofossils | paleosols

The impacts of recent climate change on soil biotic communities are poorly understood, although extremely important, because the soil fauna promotes and regulates such vital ecosystem functions as organic matter decomposition and mineralization, nutrient cycling, and pedoturbation (1). Global surface temperatures are expected to increase 1.8–4.0 °C by the end of the 21st century in response to higher atmospheric concentrations of anthropogenic CO_2 and other greenhouse gases (2). Most experimental work has focused on the effects of elevated temperatures and pCO_2 on plants and soil microbial communities (3). The response of temporary to permanent soil meso- and macrofaunas to climate change is virtually unknown. This lack of understanding is significant because of their often important role as keystone species and ecosystem engineers, modulating the flux of resources to other organisms by physically modifying the soil environment, promoting soil structure development, and suppressing soil-borne diseases and pests (4).

Ancient soils (paleosols) formed during the Paleocene–Eocene Thermal Maximum (PETM), a short-lived episode of severe global warming, are preserved in the Willwood Formation, Bighorn Basin, Wyoming, and contain a diverse and abundant assemblage of trace fossils (ichnofossils) produced by burrowing soil fauna (5) (Fig. 1). The PETM is one of the best analogs for modern global warming because both share similar magnitudes and rates of pCO_2 and temperature increases (6). The PETM is recorded worldwide in ≈55.8 Ma continental and marine deposits by a negative 2–6‰ carbon isotope excursion (CIE) in carbonate and organic carbon sources that persisted for ≈100 kyr (7, 8). In the Bighorn Basin, paleoflora leaf-margin analyses (9) and oxygen isotope studies (10) suggest mean annual temperatures approaching 26 °C during the PETM—a 3–7 °C increase from latest Paleocene estimates. In addition, a nearly 40% decline in mean annual precipitation is suggested in the Bighorn Basin by leaf-area analyses (9) and mineral weathering indices (11). Significant changes in marine and continental biotic communities are reported for the PETM, including significant test-size reductions and mass extinctions of benthic foraminifera (12, 13) and a dramatic turnover in fossil mammal faunas in North America (14). The CIE and global warming likely resulted from a large release of ^{13}C-depleted carbon to the atmosphere (15), although there is no consensus on the carbon source (16, 17).

In this study, we evaluate the net effects of increased temperatures and atmospheric CO_2 on meso- and macroscale soil biotic communities as recorded by their ichnofossils in the Willwood Formation before, during, and after the PETM. Ichnofossils—burrows, nests, tracks, trails, and borings—record the approximate body size and habitat preferences of tracemaking organisms, as well as their behavioral responses to physical, chemical, and biological conditions in ancient environments (18). Trace fossils in marine settings during episodes of environmental stress and mass extinction events show significant decreases in diversity, burrowing density, burrow size, tiering, and depth of bioturbation (19). Terrestrial invertebrates, in particular, are sensitive to changes in soil moisture and temperature because they must avoid desiccation and overheating, extreme moisture highs and lows, excess CO_2, and hypoxia (20). Abundant ichnofossils in the Willwood Formation and the well-documented stratigraphic position of the CIE in the Bighorn Basin provide an opportunity to test how soil biota responded to global warming during the PETM or whether they were buffered from higher thermal regimens and CO_2 concentrations by their subsurface soil environment.

Geologic Setting. The alluvial Paleogene Willwood Formation is an up to 1400-m-thick succession of mudstone and sandstone interpreted as distal- and proximal-overbank alluvial deposits and trunk-channel deposits, all modified by varying degrees of pedogenesis (21). At Polecat Bench, northwest of Powell, Wyoming, a stratigraphic interval ≈40 m thick was deposited during the PETM (Fig. 2). Changes in the sedimentology, paleosol morphology, and geochemistry within this interval suggest that the Willwood floodplain experienced significantly improved

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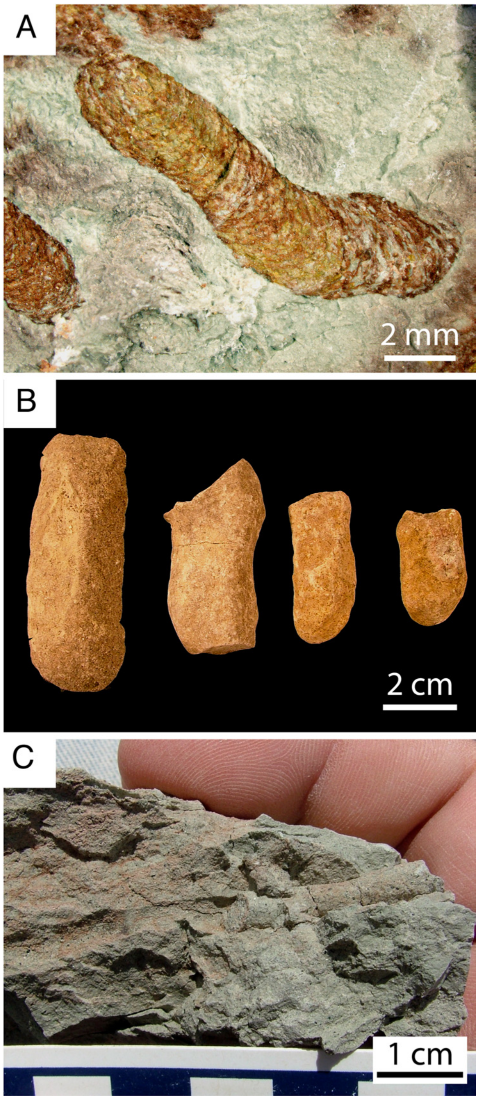

Fig. 1. Trace fossils in paleosols and alluvial deposits of the Willwood Formation at Polecat Bench, Wyoming. (*A*) *Naktodemasis bowni* is interpreted as the backfilled locomotion traces of burrowing insects such as cicada nymphs, cydnids, and beetle larvae. (*B*) *Cylindricum* isp. and (*C*) *Planolites* isp. are similar to simple burrows constructed on modern floodplains by extant burrowing soil fauna, such as beetles, bees, spiders, wasps, and ants (see Supporting Information).

drainage during the PETM (11, 22, 23). The PETM interval is characterized by a series of thick, mudrock-dominated, predominantly red cumulic paleosols with pervasive mottles and abundant rhizoliths and burrows. Pedogenic carbonate nodules as well as carbonate-filled rhizoliths and burrows increase significantly within the PETM interval, particularly in red paleosol horizons. The first appearances in the Bighorn Basin of such mammal taxa as artiodactyls, perissodactyls, primates, and hyaenodontids mark the transition from the Paleocene Clarkforkian (Cf) to the Eocene Wasatchian (Wa) North American land mammal faunas. The Wa-0 fauna is coincident with the main body of the PETM and is characterized by dwarf mammal species 50–60% smaller than preceding Clarkforkian or later Wasatchian congeners (24). Fossil plant localities in the Willwood Formation suggest a rapid northward expansion of the subtropical flora during the PETM (9). In addition, the abundance and morphological diversity of insect feeding damage on fossil leaves in this formation is highest during the PETM and suggests increased and more specialized insect herbivory (25).

Results

Seven ichnofossil morphotypes representing soil biota—*Naktodemasis bowni*, *Cylindricum* ichnospecies (isp.), *Planolites* isp., *Camborygma litonomos*, *Steinichnus* isp., *Edaphichnium lumbricatum*, and cocoon traces—are present throughout the measured section [see *SI Text* and Table S1]. Relative abundances of *N. bowni*, *Cylindricum* isp., *E. lumbricatum*, and *Steinichnus* isp. increase within the PETM interval, especially in red, yellow-brown, and purple paleosols and when compared with paleosols of similar maturity outside the PETM interval (Fig. 2). Of these, significant increases in abundance are indicated for *N. bowni* ($H_{1,73} = 9.82, P < 0.002$) and *Steinichnus* isp. ($H_{1,24} = 4.70, P < 0.030$) within the PETM interval. *Camborygma litonomos* and *Planolites* isp. decrease in abundance within the PETM interval, although only *C. litonomos* is significantly less abundant ($H_{1,21} = 5.27, P < 0.022$). Decreased abundance of *C. litonomos* in red paleosols within the PETM interval is particularly striking because their profusion in similar Willwood deposits outside the PETM interval creates a distinctly prismatic rock fabric (23). Cocoon traces are a minor constituent throughout the measured section. Molluscan body fossils, both gastropods and bivalves, are common to abundant in avulsion deposits and weakly developed paleosols outside the PETM interval, but are less common through much of the PETM interval at Polecat Bench.

Of the trace and body fossils observed, *N. bowni*, *Cylindricum* isp., and *Planolites* isp. are present in large enough numbers that changes in burrow diameter with respect to stratigraphic position of the PETM can be evaluated confidently (Fig. 3, Table S2). Mean diameters of *N. bowni*, *Cylindricum* isp., and *Planolites* isp. constructed during the PETM are significantly smaller than those above and below the PETM interval (Table 1*A*). It should be noted, however, that there is a documented positive relationship between burrow size and grain size of host deposits for some Willwood trace fossils (26), such that larger-diameter burrows are associated generally with coarser-grained deposits (sandstones), although they are otherwise morphologically identical to smaller-diameter burrows in fine-grained deposits (mudrocks). Given the lithologic shift to mudrock-dominated paleosols within the PETM interval (22, 11), ichnofossil diameters were evaluated with respect not only to stratigraphic position (PETM vs. non-PETM) but also to the grain size of the host depositional units and potential combined effects (Table S3). The combined effects of stratigraphic position and host-deposit grain size are nonsignificant for all three morphotypes, and indicate that the significant reductions in burrow sizes are not caused by changes in the ratio of fine- to coarse-grained deposits within the PETM interval (Fig. 4).

An additional concern is that mean size changes within the PETM interval are not truly indicative of a decrease in diameter sizes but instead are recording a decrease in size variance; in other words, means are smaller within the PETM because the largest burrow sizes are not present. When evaluated as subsets of all of the burrows measured, however, the largest and smallest *Naktodemasis bowni* and *Cylindricum* isp. specimens are significantly smaller within the PETM interval (Table 1*B*). Similar analyses of *Planolites* isp. also showed smaller burrow diameters within the PETM, although nonsignificantly so. These analyses indicate that mean diameter decreases within the PETM interval are directional (27) and not artifacts of decreased size variance.

Discussion

The Willwood trace-fossil record supports recent studies suggesting a widespread biologic response to the PETM (24, 25) and drier floodplain conditions within the Bighorn Basin (11, 22, 23).

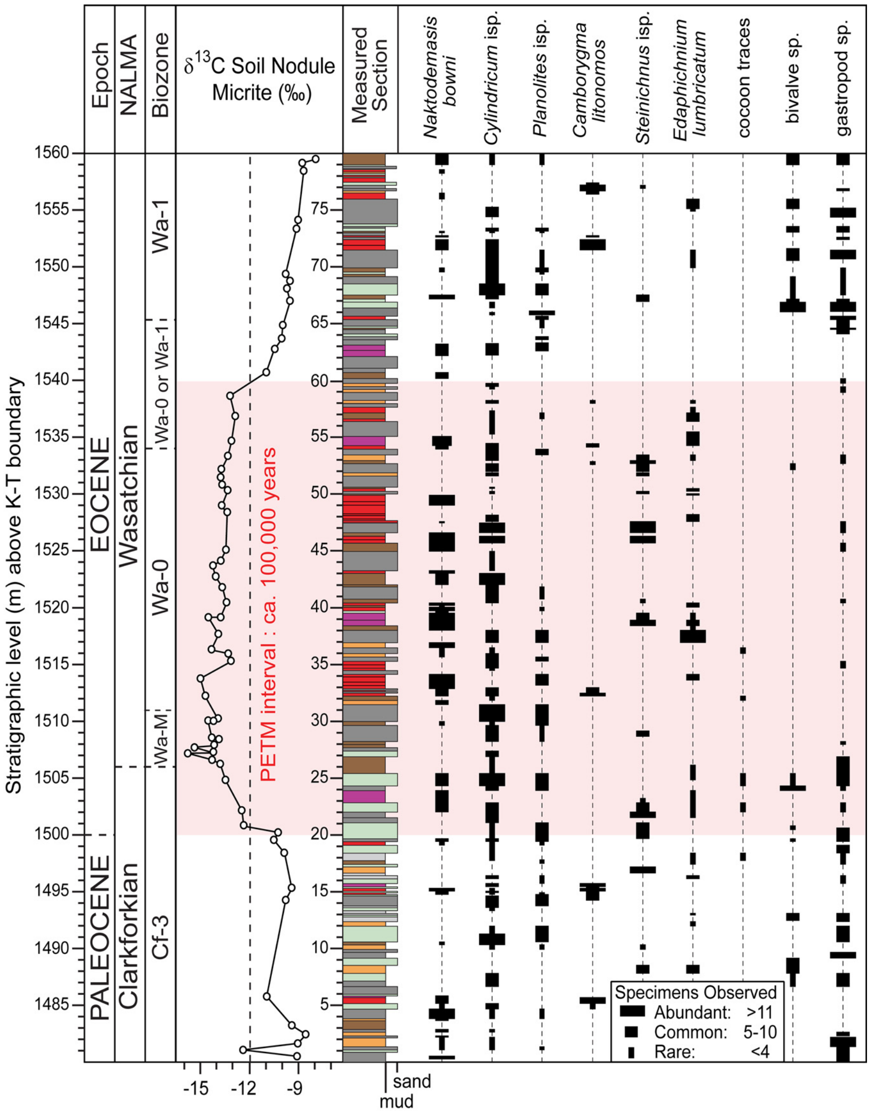

Fig. 2. Composite measured section showing δ^{13}C chemostratigraphy and PETM interval (shaded area) (45), North American Land Mammal Age (NALMA) biozones (8), meter levels, and relative abundances of trace fossils and molluscan body fossils at Polecat Bench, Wyoming, examined as part of this study.

The greater abundance of probable insect and oligochaete trace fossils (Table S1) within mature paleosols of the PETM interval suggests that these organisms responded positively to better drainage conditions and longer periods of landscape stability. The majority of soil biota live within the upper part of the vadose zone (28), and increased soil drainage or lower water tables would promote pedogenesis and bioturbation by these organisms. Likewise, significant decreases in *Camborygma litonomos* within the PETM interval suggest that water tables were at depths beyond the burrowing ability of local crayfish populations at that time (23). Extant freshwater crayfish that construct burrows identical to *C. litonomos* live mostly in open waters, but burrow to reproduce or escape desiccation in areas with fluctuating water tables (29). Crayfish require standing water for respiration and were probably restricted to stream channels and other such aquatic habitats when floodplain drainage improved during the PETM. Increasingly abundant *C. litonomos* toward the top of the PETM interval likely signal a return to wetter floodplain conditions. Molluscan body fossils follow much the same pattern; predominantly drier floodplain conditions would influence bivalves in particular because these are fully aquatic organisms.

Burrow size for many organisms is correlated generally with tracemaker body size (30); therefore, significant reductions in burrow diameters during the PETM suggest that their tracemakers were smaller bodied. Regardless of the taxonomic identities of the individual tracemakers, our data show a negative response in burrow size during the PETM. These changes may record the replacement of larger pre-PETM soil biota, with smaller immigrant taxa better adapted to warmer or drier soil conditions. Alternatively, burrow-size reductions may suggest that soil fauna endemic to the Bighorn Basin experienced a transient period of phyletic dwarfism in response to the PETM. Reduced tracemaker body sizes of ≈30–46% within the PETM interval (Table S3) parallel previously documented size reductions in Wa-0 mammal faunas (24) and suggest a common forcing mechanism, or that a combination of causes promoted dwarfism in both above- and below-ground biotic communities.

Higher temperatures, drier climate conditions, and elevated atmospheric CO_2 levels inferred for the PETM may have had impacts on such ontogenetic processes as growth rates and development times in soil biota, as well as the nutritional value of their food sources—all of which govern adult body size within

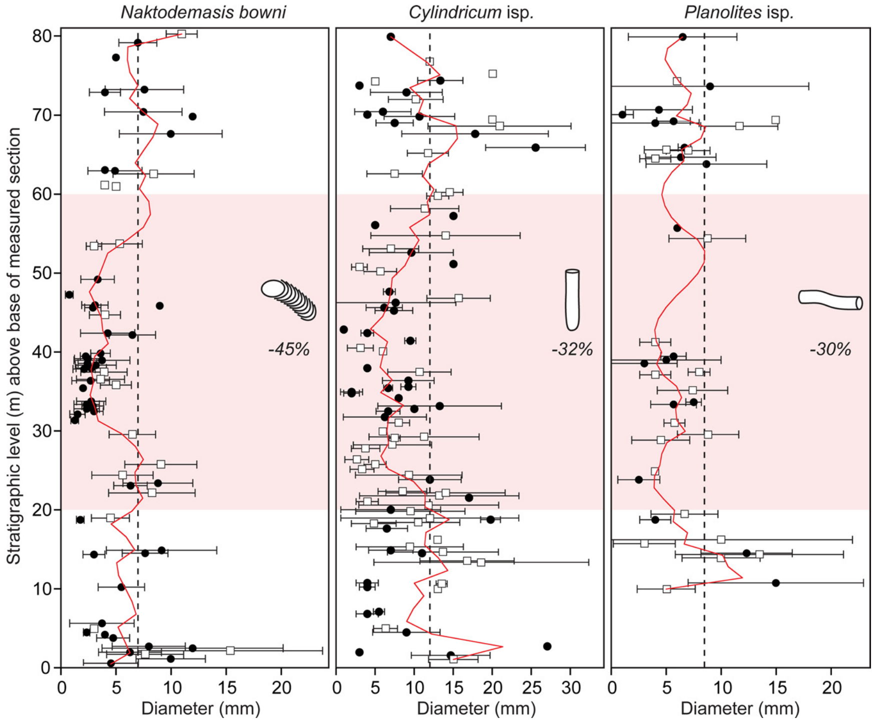

Fig. 3. Burrow diameter trends for *Naktodemasis bowni*, *Cylindricum* isp., and *Planolites* isp. showing percent changes of mean burrow size reductions within the PETM interval. Black circles represent mean burrow diameters from fine-grained deposits; open squares represent mean burrow diameters from coarse-grained deposits; and horizontal bars represent one standard error. Dashed vertical lines indicate mean of burrow diameters from below and above the PETM interval. Curves (red) were fitted by using a Stineman smoothing function of all data points for a given morphotype. Shaded area represents PETM interval.

a given species (31). Climate-induced, intraspecific changes in body size or increased sexual dimorphism have been reported in some extant species (32). In such diverse organisms as protists, plants, nematodes, mollusks, crustaceans, hemimetabolous and holometabolous insects, and ectothermic chordates, >83% of experimental studies demonstrate a significant inverse relationship between rearing temperature and adult body size (33). Higher temperatures may suppress adult body size by significantly increasing rates of ontogenic development and differentiation, decreasing maximum life spans, and increasing juvenile mortality (34). Little is known about how soil-moisture conditions influence invertebrate size, although smaller body size does correlate with drier soils in some species of dung beetle (35). The direct effects of elevated atmospheric CO_2 on soil invertebrates are likely to be negligible because pCO_2 concentrations are typically 10–50 times higher in soils than in the atmosphere (3). High pCO_2 effects on vegetation, however, must indirectly affect soil biota because plant tissues and photosynthates form the base of the soil food web (36). Studies show that elevated pCO_2 levels (twice current levels of ≈350 ppm by volume) increase photosynthesis, reduce nitrogen and Rubisco concentrations (an enzyme regulating carbon fixation), and substantially decrease the nutritional value of plant tissue resulting in slower growth rates, incomplete development, and increased mortality in some her-

Table 1. Trace fossil diameters in relation to the Paleocene–Eocene Thermal Maximum (PETM)*

	Naktodemasis bowni		*Cylindricum* isp.		*Planolites* isp.	
	F	*P* value	*F*	*P* value	*F*	*P* value
A	(*n* = 371)		(*n* = 309)		(*n* = 107)	
PETM (P)	71.53	<0.0001	23.19	<0.0001	6.33	<0.0130
Grain size (g)	34.86	<0.0001	1.23	NS	4.54	<0.0360
Interaction (P*g)	0	NS	2.27	NS	0.36	NS
B	(*n* = 75)		(*n* = 96)		(*n* = 41)	
Max. diameters	6.45	<0.0130	4.88	<0.0290	1.13	NS
Min. diameters	18.3	<0.0001	8.93	<0.0040	0.7	NS

α = 0.05 with 1 degree of freedom in all comparisons

*(A) Results of two-way ANOVAs evaluating trace-fossil diameters with respect to the PETM, grain size of host deposits, and the combination of these two factors. Effect of PETM (P: mean diameter of all burrows above and below the PETM interval compared with mean diameter of all like burrows within the PETM interval) is significant in all three ichnotaxa. While grain-size effects (g) vary between the trace fossil morphotypes, the interaction between PETM and grain-size (P*g) is consistently nonsignificant (NS), indicating that smaller burrow sizes are associated with stratigraphic position with respect to the PETM and not due to differences in host deposit lithologies. (B) results of one-way ANOVAs comparing only the maximum and minimum diameters of each trace-fossil type from within the PETM interval to those outside the interval to evaluate whether apparent size changes within PETM were due to decreased size variance. Max., maximum; Min., minimum.

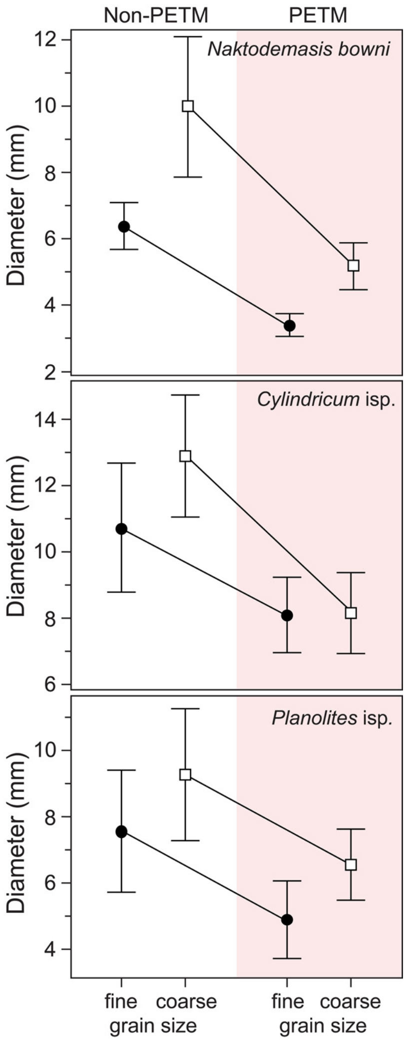

Fig. 4. Mean burrow diameters of *Naktodemasis bowni*, *Cylindricum* isp., and *Planolites* isp. from above and below the PETM (non-PETM) compared with those within the PETM interval and separated by grain-size of host deposit: fine-grained deposits (black circles) and coarse-grained deposits (open squares). Results of two-way ANOVA (Table 1) indicate that the burrow sizes are significantly smaller within the PETM interval regardless of host deposit grain size, with no interaction between stratigraphic position with respect to the PETM and grain size.

bivorous insects (37, 38). Smaller adult body size might be expected under these conditions; however, size differences are often less dramatic than those associated with reported temperature effects (38).

Our research suggests that soil organisms are not buffered from transient climate change and that their trace fossils, in the absence of body fossils, record the effects of such major climate perturbations as the PETM. Changes in animal body size may be a potentially powerful biomonitoring tool to gauge past, current, and future impacts of climate change on continental ecosystems. We predict that extant insects and other soil arthropods will respond or have responded in a manner similar to recent increases in greenhouse gases and surface temperatures. Well-documented and extensive museum insect collections—numbering in the tens of millions worldwide, with some dating back to preindustrial times—and specimens recovered from archaeological sites should be re-examined and compared with living specimens to look for changes in conspecific body size. Looking forward, it may be possible for ongoing and future insect monitoring programs that collect morphometric data to detect body-size changes through this century and to quantify potential climate-warming effects in living populations. Likewise, looking back into deep time, we retrodict that soil organisms living through such proposed hyperthermal events as the Permian–Triassic and Triassic–Jurassic mass extinctions (39, 40) will also show significantly decreased body sizes because of contributing factors similar to those that operated during the PETM.

Materials and Methods

We excavated and measured 54 stratigraphic sections from ≈20 m below to ≈20 m above the PETM interval as established by previous isotopic analyses of carbonate nodules (41) and mammalian biostratigraphic studies (42). Stratigraphic units were characterized in the field by color, grain size, sedimentary structures, mottle colors, nodule types and abundance, and slickensides. All units were measured with a Jacob staff and sighting level. We recorded the stratigraphic position, relative abundance, and diameters of trace fossils. Burrows were described according to their architectural and surficial burrow morphology and burrow fill (29). Burrow diameters and lengths were measured in the field and laboratory with a standard metric ruler. Trace fossil relative abundances were ranked as rare (fewer than four specimens), common (five to 10 specimens), or abundant ($>$11 specimens) based on the number of observed specimens of a given ichnotaxon within an ≈1-m-wide cross-section of each stratigraphic unit. Relative abundance differences from within and outside (below and above) the PETM interval were evaluated by using a nonparametric Kruskal-Wallis test (H). Changes in burrow diameters from within and outside the PETM interval were analyzed by two-way ANOVA ($\alpha = 0.05$) with interaction terms by using a generalized linear model after log transformation of the measurements to correct for positive skew. The maximum and minimum burrow diameter means of each morphotype were evaluated by ANOVA to determine whether apparent size changes were because of decreased size variance within the PETM interval. Kruskal-Wallis and ANOVA statistical tests were preformed by using Minitab Statistical Software (43). Curve fitting was accomplished by using KaleidaGraph (Synergy Software, Reading, PA) to apply a Stineman-interpolated smooth curve of the data points (44).

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1. Brussaard L (1997) Biodiversity and ecosystem functioning in soil. *Ambio* 26:563–570.
2. Intergovernmental Panel on Climate Change (2007) *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (Cambridge Univ Press, Cambridge, United Kingdom), p 996.
3. Kandeler E, et al. (1998) The response of soil microorganisms and roots to elevated CO_2 and temperature in a terrestrial model ecosystem. *Plant Soil* 202:251–262.
4. Wolters V, et al. (2000) Effects of global changes on above- and belowground biodiversity in terrestrial ecosystems: Implications for ecosystem functioning. *Bioscience* 50:1089–1098.
5. Bown TM, Kraus MJ (1983) Ichnofossils of the alluvial Willwood Formation (lower Eocene), Bighorn Basin, northwest Wyoming, USA. *Palaeogeogr Palaeoclimatol Palaeoecol* 43:95–128.
6. Zachos JC, et al. (2005) Rapid acidification of the ocean during the Paleocene-Eocene Thermal Maximum. *Science* 308:1611–1615.
7. Koch PL, Zachos JC, Gingerich PD (1992) Correlation between isotope records in marine and continental carbon reservoirs near the Paleocene/Eocene boundary. *Nature* 358:319–322.
8. Magioncalda R, Dupuis C, Smith T, Steurbaut E, Gingerich PD (2004) Paleocene-Eocene carbon isotope excursion in organic carbon and pedogenic carbonate: Direct comparison in a continental stratigraphic section. *Geology* 32:553–556.
9. Wing SL, et al. (2005) Transient floral change and rapid global warming at the Paleocene-Eocene boundary. *Science* 310:993–996.
10. Koch PL, et al. (2003) Carbon and oxygen isotope records from paleosols spanning the Paleocene-Eocene boundary, Bighorn Basin, Wyoming. *Causes and Consequences of Globally Warm Climates in the Early Paleogene*, eds Wing SL, Gingerich PD, Schmitz B, Thomas E (Geological Society of America, Special Paper 369, Boulder, Colorado), pp 49–64.

11. Kraus MJ, Riggins S (2007) Transient drying during the Paleocene-Eocene Thermal Maximum (PETM): Analysis of paleosols in the Bighorn Basin, Wyoming. *Palaeogeogr Palaeoclimatol Palaeoecol* 245:444–461.
12. Thomas E (1998) Biogeography of the late Paleocene benthic foraminiferal extinction. *Late Paleocene-Early Eocene Climatic and Biotic Events in the Marine and Terrestrial Records*, eds Aubry MP, Lucas SG, Berggren WA (Columbia Univ Press, New York), pp 214–235.
13. Kaiho K (1998) Global climatic forcing of deep-sea benthic foraminiferal test size during the past 120 m.y. *Geology* 26:491–494.
14. Clyde WC, Gingerich PD (1998) Mammalian community response to the latest Paleocene thermal maximum: An isotaphonomic study in the northern Bighorn Basin, Wyoming. *Geology* 26:1011–1014.
15. Zachos JC, et al. (2003) A transient rise in tropical sea surface temperature during the Paleocene-Eocene Thermal Maximum. *Science* 302:1551–1554.
16. Dickens GR, O'Neil JR, Rea DK, Owen RM (1995) Dissociation of oceanic methane hydrate as a cause of the carbon isotope excursion at the end of the Paleocene. *Paleoceanography* 10:965–972.
17. Storey M, Duncan RA, Swisher CC (2007) Paleocene-Eocene thermal maximum and the opening of the northeast Atlantic. *Science* 316:587–589.
18. Miller W, III ed (2007) *Trace Fossils: Concepts, Problems, Prospects* (Elsevier, Amsterdam), 1st Ed, p 611.
19. Barras CG, Twitchett RJ (2007) Response of the marine infauna to Triassic-Jurassic environmental change: Ichnological data from southern England. *Palaeogeogr Palaeoclimatol Palaeoecol* 244:223–241.
20. Wallwork JA (1970) *Ecology of Soil Animals* (McGraw Hill, London), p 238.
21. Kraus MJ (2001) Sedimentology and depositional setting of the Willwood Formation in the Bighorn and Clarks Fork Basins. *Paleocene-Eocene Stratigraphy and Biotic Change in the Bighorn and Clarks Fork Basins, Wyoming*, ed Gingerich PD (University of Michigan Papers on Paleontology, 33, Ann Arbor, Michigan), pp 15–28.
22. Smith JJ, Hasiotis ST, Kraus MJ, Woody DT (2008) Relationship of floodplain ichnocoenoses to paleopedology, paleohydrology, and paleoclimate in the Willwood Formation, Wyoming, during the Paleocene-Eocene Thermal Maximum. *PALAIOS* 23:683–699.
23. Smith JJ, Hasiotis ST, Woody DT, Kraus MJ (2008) Paleoclimatic implications of crayfish-mediated prismatic structures in paleosols of the Paleogene Willwood Formation, Bighorn Basin, Wyoming, U.S.A. *J Sediment Res* 78:323–334.
24. Gingerich PD (2003) Mammalian responses to climate change at the Paleocene-Eocene boundary: Polecat Bench record in the northern Bighorn Basin, Wyoming. *Causes and Consequences of Globally Warm Climates in the Early Paleogene*, eds Wing SL, Gingerich PD, Schmitz B, Thomas E (Geological Society of America, Special Paper 369, Boulder, Colorado), pp 463–478.
25. Currano ED, et al. (2008) Sharply increased insect herbivory during the Paleocene-Eocene Thermal Maximum. *Proc Natl Acad Sci USA* 105:1960–1964.
26. Smith JJ, Hasiotis ST, Kraus MJ, Woody DT (2008) Naktodemasis bowni: New ichnogenus and ichnospecies for adhesive meniscate burrows (AMB), and paleoenvironmental implications, Paleogene Willwood Formation, Bighorn Basin, Wyoming. *J Paleontol* 82:267–278.
27. McShea DW (1994) Mechanisms of large-scale evolutionary trends. *Evolution* 48:1747–1763.
28. Frouz J, Ali A, Frouzova J, Lobinske RJ (2004) Horizontal and vertical distribution of soil macroarthropods along a spatio-temporal moisture gradient in subtropical Central Florida. *Environ Entomol* 33:1282–1295.
29. Hasiotis ST, Mitchell CE (1993) A comparison of crayfish burrow morphologies: Triassic and Holocene fossil, paleo- and neo-ichnological evidence, and the identification of their burrowing signatures. *Ichnos* 2:291–314.
30. Twitchett RJ (2007) The Lilliput effect in the aftermath of the end-Permian extinction event. *Palaeogeogr Palaeoclimatol Palaeoecol* 252:132–144.
31. Davidowitz G, D'Amico LJ, Nijhout HF (2004) The effects of environmental variation on a mechanism that controls insect body size. *Evol Ecol Res* 6:49–62.
32. Parmesan C (2006) Ecological and evolutionary responses to recent climate change. *Annu Rev Ecol Evol Syst* 37:637–669.
33. Atkinson D (1994) Temperature and organism size—a biological law for ectotherms. *Adv Ecol Res* 25:1–58.
34. Sibly RM, Atkinson D (1994) How rearing temperature affects optimal adult size in ectotherms. *Funct Ecol* 8:486–493.
35. Vessby K (2001) Habitat and weather affect reproduction and size of the dung beetle *Aphodius fossor. Ecol Entomol* 26:430–435.
36. Young IM, et al. (1998) The interaction of soil biota and soil structure under global change. *Glob Change Biol* 4:703–712.
37. Fajer ED, Bowers MD, Bazzaz FA (1989) The effects of enriched carbon dioxide atmospheres on plant-insect herbivore interactions. *Science* 243:1198–1200.
38. Brooks GL, Whittaker JB (1999) Responses of three generations of a xylem-feeding insect, *Neophilaenus lineatus* (Homoptera), to elevated CO_2. *Glob Change Biol* 5:395–401.
39. de Wit MJ, et al. (2002) Multiple organic carbon isotope reversals across the Permo-Triassic boundary of terrestrial Gondwana sequences: Clues to extinction patterns and delayed ecosystem recovery. *J Geol* 110:227–240.
40. Cleveland DM, Nordt LC, Dworkin SI, Atchley SC (2008) Pedogenic carbonate isotopes as evidence for extreme climatic events preceding the Triassic-Jurassic boundary: Implications for the biotic crisis? *Geol Soc Am Bull* 120:1408–1415.
41. Bowen GJ, et al. (2001) Refined isotope stratigraphy across the continental Paleocene-Eocene boundary on Polecat Bench in the northern Bighorn Basin. *Paleocene-Eocene Stratigraphic and Biotic Change in the Bighorn and Clarks Fork Basin, Wyoming*, ed Gingerich PD (University of Michigan Papers on Paleontology, 33. Ann Arbor, Michigan), pp 73–88.
42. Gingerich PD (2001) Biostratigraphy of the continental Paleocene-Eocene boundary interval on Polecat Bench in the northern Bighorn Basin. *Paleocene-Eocene Stratigraphic and Biotic Change in the Bighorn and Clarks Fork Basin, Wyoming*, ed Gingerich PD (University of Michigan Papers on Paleontology, 33, Ann Arbor, Michigan), pp 37–71.
43. Minitab Inc. (2003) MINITAB Statistical Software, Release 14 for Windows (Minitab Inc., State College, Pennsylvania).
44. Stineman RW (1980) A consistently well-behaved method of interpolation. *Creative Comput* 6:54–57.
45. Bains S, et al. (2003) Marine-terrestrial linkages at the Paleocene-Eocene boundary. *Causes and Consequences of Globally Warm Climates in the Early Paleogene*, eds Wing SL, Gingerich PD, Schmitz B, Thomas E (Geological Society of America, Special Paper 369, Boulder, Colorado), pp 1–9.