feather rachises create less turbulent flow (12), which is an effect hypothesized to explain a lower observed drag coefficient than predicted from streamlined penguin body shape alone (14). They also facilitate reduction of intraplumage air (15). Most of the insulating properties of extant penguin contour feathers derive from their plumulaceous afterfeathers (16), which are not preserved or not present in *Inkayacu*.

Inkayacu shows that the large, subround melanosomes of extant penguin feathers were absent early in penguin evolution. At minimum, an increase in melanosome size and a decrease in their aspect ratio occurred after the early Eocene divergence of the clade that includes *Inkayacu* (Fig. 4, Clade X) and before the origin of extant penguins (Spheniscidae) by the late Miocene (5). The specific proportions of extant penguin melanosomes, the packing of these melanosomes into clusters within the barbs and rachis (10), and yellow, pterin-like pigmentation (17) are so far only known in the penguin crown clade.

Shifts in penguin plumage coloration indicated by the fossil may be linked to differences in ecology, thermoregulatory demands (18), or the more recent, predominantly Neogene, diversification of their primary mammalian predators (19, 20). However, they do not explain the aberrant melanosome morphology associated with extant penguin brown-black color. Indeed, rather than selection for color, these changes may represent an unanticipated response to the hydrodynamic

demands of underwater propulsion. Low aspect ratio, large size, and clustered melanosome distribution (10) may affect melanin packing and feather material properties. Melanin confers resistance to fracture (6, 21, 22), which is important to materials like feathers subjected to cyclical loading (22). Selective pressures for the color and material properties of penguin feathers could thus have led to nanoscale changes in melanosome morphology.

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Effects of Rapid Global Warming at the Paleocene-Eocene Boundary on Neotropical Vegetation

Carlos Jaramillo,[1]* Diana Ochoa,[1,2] Lineth Contreras,[3,1,4] Mark Pagani,[5] Humberto Carvajal-Ortiz,[6,1] Lisa M. Pratt,[6] Srinath Krishnan,[5] Agustin Cardona,[1] Millerlandy Romero,[1] Luis Quiroz,[1,7] Guillermo Rodriguez,[3,8] Milton J. Rueda,[9,3] Felipe de la Parra,[3] Sara Morón,[1,10] Walton Green,[1] German Bayona,[11,1] Camilo Montes,[1,11] Oscar Quintero,[12] Rafael Ramirez,[13] Germán Mora,[14] Stefan Schouten,[15] Hermann Bermudez,[16] Rosa Navarrete,[17] Francisco Parra,[18] Mauricio Alvarán,[16] Jose Osorno,[19] James L. Crowley,[20] Victor Valencia,[21] Jeff Vervoort[22]

Temperatures in tropical regions are estimated to have increased by 3° to 5°C, compared with Late Paleocene values, during the Paleocene-Eocene Thermal Maximum (PETM, 56.3 million years ago) event. We investigated the tropical forest response to this rapid warming by evaluating the palynological record of three stratigraphic sections in eastern Colombia and western Venezuela. We observed a rapid and distinct increase in plant diversity and origination rates, with a set of new taxa, mostly angiosperms, added to the existing stock of low-diversity Paleocene flora. There is no evidence for enhanced aridity in the northern Neotropics. The tropical rainforest was able to persist under elevated temperatures and high levels of atmospheric carbon dioxide, in contrast to speculations that tropical ecosystems were severely compromised by heat stress.

The Late Paleocene-Eocene Thermal Maximum [PETM, 56.3 million years ago (Ma)], lasting only ~100,000 to 200,000 years, was one of the most abrupt global warming events of the past 65 million years (1–3). The PETM is associated with a large negative carbon isotope excursion recorded in carbonate and organic materials, reflecting a massive release of ^{13}C-depleted carbon (4, 5), an ~5°C increase in mean global temperature in ~10,000 to 20,000 years (1), a rapid and transient northward migration of plants in North America (6), and a mammalian turnover in North America and Europe (7).

Efforts to understand the impact of climate change on terrestrial environments have focused on mid- to high-latitude localities, but little is known of tropical ecosystems during the PETM. Tropical temperature change is poorly constrained, but, given the magnitude of temperature change elsewhere, tropical ecosystems are thought to have suffered extensively because mean temperatures are surmised to have exceeded the ecosystems' heat tolerance (8).

For this study, three tropical terrestrial PETM sites from Colombia and Venezuela were analyzed for pollen and spore content and stable carbon isotopic composition of organic materials (Fig. 1) (9). The analysis included 317 pollen samples, 1104 morphospecies, and 37,952 individual occurrences together with 489 carbon isotopes samples, 21 plant biomarker samples, and one radiometric age (9). Localities Mar 2X (core), Riecito Mache (outcrop), and Gonzales (outcrop and well) contain sediments that accumulated in fluvial to coastal plain settings. Biostratigraphy and carbon isotope stratigraphy, using bulk $\delta^{13}C$ and plant wax *n*-alkanes, confirm the position of the PETM at the three sites (Figs. 2 and 3) (9), which is not associated with any formation boundary or major lithological or depositional environment change. The location of the

PETM is further confirmed by a U-Pb radiometric dating of a felsic volcanic tuff found within the PETM in Riecito Mache section (Fig. 3) (9).

Plant standing diversity, inferred from pollen assemblages at Mar 2X (Fig. 2D) and Riecito Mache (Fig. 3C), shows a low diversity during the Late Paleocene, followed by a significant increase during the PETM. Low-diversity Paleocene floras and an increase in Early Eocene diversity had been previously observed in tropical South America (10, 11), but the timing of the onset of the diversity changes was not resolved. Within-sample diversity in Mar 2X (9) shows a pattern similar to that for standing diversity. Paleocene samples (mean = 23.5) have fewer species than the PETM (mean = 35.9, P < 0.00449, df = 23.9), rarefied to a grain count of 150 (maintained even at a 100-grain count, Fig. 2C), whereas no significant difference is observed between the PETM and the Eocene (mean = 38.9, P < 0.33, df = 12.04). Similar diversity patterns characterize Gonzales (Fig. 3C), but within-sample diversity could not be calculated for Riecito Mache (9). The Simpson index, which measures the probability that two individuals taken at random will not belong to the same species, also reveals a similar pattern. In Mar 2X, the Simpson index is higher for the PETM (mean = 0.90) than for the Paleocene (mean = 0.76, P < 0.0008, df = 30.4), whereas the PETM and the Eocene (mean = 0.89) show no difference (P < 0.44, df = 54.8). A higher Simpson index for the PETM indicates that it has more species per sample than the Paleocene (as indicated by the higher within-sample diversity) and more evenly distributed species abundances. A similar pattern

is recorded for Gonzales, but the Simpson index is slightly higher for the Eocene. In contrast, the Simpson index of the PETM at Riecito Mache was only slightly higher than the Paleocene, but the difference is not significant (9).

Taxa were divided into three groups, those for which extinction occurs in the Late Paleocene (P taxa), those whose origination occurs in the Early Eocene, including the PETM (E taxa), and those that are found in both the Paleocene and the Eocene (PE taxa). At the Mar 2X locality, standing diversity is lower for P taxa (13.6) than for E taxa (85.7; P < 0.001, df = 91.6) (Fig. 2E). Paleocene samples have a slightly higher standing diversity of PE taxa than Eocene samples (157.6 on the Paleocene side versus 135.8 on the Eocene side; P < 0.001, df = 58.542). When relative abundances are compared, the relation is similar, with P taxa less abundant in the Paleocene flora (4.6% of the assemblage) than E taxa in the Eocene flora (23.8% of the assemblage; P < 0.001, df = 107.9). The Paleocene flora at Mar 2X is composed largely of taxa that persisted into the Early Eocene, a pattern also evident in both Riecito Mache and Gonzales (Fig. 3D). Thus, our results demonstrate that the increase in tropical floral diversity during the PETM and Early Eocene resulted from the addition of a large set of new species, mostly angiosperms, to the existing, low-diversity floras that were holdovers from the Paleocene.

We assessed changes in floral composition by using a detrended correspondence analysis (DCA) and agglomerative clustering (9). The DCA shows a gradual change in flora during the PETM in the three studied sites (Figs. 2B and 3B) that is confirmed by the clustering analysis (9) (fig. S13), indicating that there was a significant change in the overall plant assemblage across the PETM. Even though we still do not know the affinities of ~85% of the flora, we were able to compare the remaining 15% (9). Diversity remained unchanged from the Paleocene into the Early Eocene for many families, including Polypodiaceae (ferns), Podocarpaceae (gymnosperms), Onagraceae, Ctenolophonaceae, Annonaceae, Moraceae, Rhizophoraceae, and Ulmaceae. However, diversity decreased in Proteaceae and increased in

Arecaceae (palms), Bombacoideae, Fabaceae, Araceae, Poaceae, and Convolvulaceae. New families also appeared (i) during the uppermost Paleocene, including Myrtaceae, Sapotaceae, and Passifloraceae; (ii) within the PETM, including Sterculioideae, Euphorbiaceae, and Pellicieraceae; and (iii) during the Early Eocene, including Olacaceae and Ericaceae. Most of these originations, such as Sapotaceae, Passifloraceae, Ericaceae, Sterculioideae, Euphorbiaceae, and Pellicieraceae, represent the oldest pollen records for each family in the neotropics (12). Relative abundances show a similar pattern (Fig. 2).

The rate of extinction increased slightly during the PETM at a rate comparable to that during intervals within the Early Eocene (Fig. 4), with the gradual extinction of a small proportion (~5%) of Paleocene flora. However, extinction does not appear different from the background extinction rates of the entire sequence (Fig. 4). In contrast, per capita rate of origination increased significantly within the PETM interval (Fig. 4). Although the rates of origination continued to be high into the Early Eocene (10), the increase in rate began within the PETM.

Overall diversity and composition analysis suggest that the onset of the PETM is concomitant with an increase in diversity produced by the addition of many taxa (with some representing new families) to the stock of preexisting Paleocene taxa. This change in diversity was permanent and not transient, as documented for temperate North America (6). Interestingly, phylogenetic molecular studies of extant ephypitic ferns (which are mostly restricted to tropical rainforest canopies) and orchids indicate a major radiation at the onset of the Eocene (13, 14).

Temperature and precipitation are important factors affecting plant communities. Estimates of PETM mean annual temperature (MAT) from tropical latitudes are scarce. By using both published literature and TEX_{86} values from a nearby marine core [P2 core (Fig. 1 and fig. S14) (9)], we estimate that tropical temperatures during the PETM increased by ~3°C in the northern Neotropics and that mean temperatures were between 31° and 34°C (±2°C) during the peak of global

[1]Smithsonian Tropical Research Institute, Box 0843-03092, Balboa, Ancon Republic of Panama. [2]Department of Biological Sciences, East Tennessee State University, Johnson City, TN 37614–14850, USA. [3]Colombian Petroleum Institute, Km 7 Via Piedecuesta, Bucaramanga, Colombia. [4]Institute of Geosciences, Goethe University Frankfurt, Altenhöferallee 1, D-60438 Frankfurt am Main, Germany. [5]Department of Geology and Geophysics, Yale University, New Haven, CT 06520, USA. [6]Department of Geological Sciences, Indiana University, Bloomington, IN 47405, USA. [7]Department of Geology, University of Saskatchewan, 114 Science Place, Saskatoon SK, Canada. [8]Department of Geological Sciences and Engineering, Missouri University of Science and Technology, Rolla, MO 65409–0140, USA. [9]Paleoflora Limitada, Calle 9 No. 9-09, Zapatoca, Colombia. [10]Department of Geology, University of Minnesota, Minneapolis, MN 55455–0231, USA. [11]Corporación Geológica Ares, Calle 57 N.24-11 ofic. 202, Bogotá, Colombia. [12]Petróleos de Venezuela S.A. (PDVSA) Exploración, Nucleoteca La Concepción, Maracaibo, Venezuela. [13]PDVSA Exploración, Edificio Guaraguao Puerto de la Cruz, Venezuela. [14]Goucher College, 1021 Dulaney Valley Road, Baltimore, MD 21204, USA. [15]Royal Netherlands Institute for Sea Research (NIOZ), Department of Marine Organic Biogeochemistry, Post Office Box 59, 1790 AB, Den Burg, Texel, Netherlands. [16]Department of Geological Sciences, University of Caldas, Manizales, Colombia. [17]Paleosedes, Tv 27 No. 57-49 Bogota, Colombia. [18]Université Paul Sabatier, CU Ponsan Bellevue, Rue Maurice Becanne, 31078 Tolulouse CX 04, France. [19]Agencia Nacional de Hidrocarburos, Bogotá, Colombia. [20]Department of Geosciences, Boise State University, Boise, ID 83725–1535, USA. [21]Valencia Geoservices, Tucson, AZ 85712, USA. [22]School of Earth and Environmental Sciences, Washington State University, Pullman, WA 99164–2812, USA.

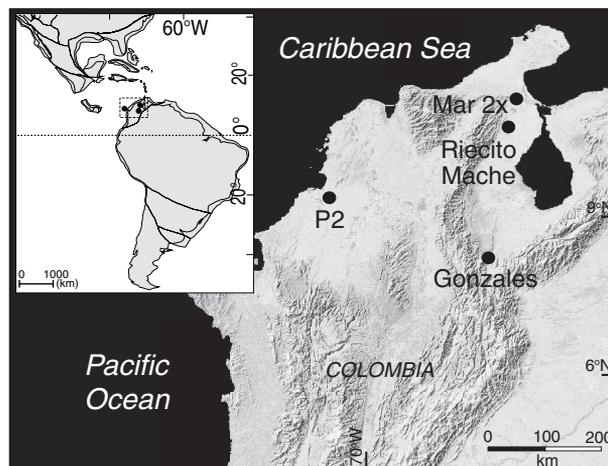*To whom correspondence should be addressed. E-mail: jaramilloc@si.edu

Fig. 1. Geographical location of the studied sections. Inset shows the Late Paleocene paleogeographic location of the studied sections [paleogeographic map after (27)]. Note that the northern Andes had not been uplifted yet, and most of Central America was still underwater.

warmth [see (9) for a detailed explanation]. To reconstruct regional hydrology, we classified plant families according to the rainfall preferences using Gentry's neotropical plant data set (15) into dry- versus wet-preferred habitats (9) (table S9). Both Paleocene and Eocene are dominated by families indicating wet habitats, with no significant difference across the Paleocene-Eocene (Paleocene = 64%, Eocene = 61%, P < 0.49, df = 32.5), and low abundance of dry elements (e.g., Poaceae) that represents <2% of the assemblage (Paleocene = 0.7%, Eocene = 2%), all suggesting that no increase in aridity occurred across the PETM. This conclusion is further supported by stable carbon and hydrogen isotope (D/H) compositions of higher-plant–derived n-alkanes at site Mar 2X. A negative carbon isotope excursion (CIE) is evident in all n-alkanes measured and ranges between 2 and 3 per mil (‰), roughly matching bulk organic $^{13}C/^{12}C$ (δ^{13}C) trends (Fig. 1 and fig S11) (9). At the onset of the PETM, n-alkane D/H compositions become more D-depleted (~35‰) and do not return to pre-PETM values within the measured

section (9) (fig. S12). Changes in the D/H composition of plant lipids are related to changes in biosynthetic fractionation (related to a plant's specific water-use efficiency), meteoric water D/H composition, amount of precipitation, and moisture recycling in forest ecosystems. Given the setting of these sites and the observed increase in tropical rainforest diversity, the negative shift in the hydrogen isotope value (δD) of n-alkanes likely reflects the predominance of D-depleted precipitation related to increased precipitation during rainout events (e.g., amount effects).

If we assume that our compound-specific δ^{13}C record captures the maximum extent of the CIE within the body of the PETM, a much smaller CIE is observed at Mar 2X relative to the ~4.6‰ excursion recorded globally (16). In addition to the atmospheric carbon isotopic composition, environmental parameters in tropical rainforests that influence n-alkane δ^{13}C values include water stress (17), ecosystem changes (related to changes in net isotope fractionation) (16), and canopy effects (18). It is possible that the smaller CIE recorded

in this study resulted from ecosystem turnover and the prevalence of flora with higher water-use efficiencies. Alternatively, temporal changes in the carbon isotopic composition could be attributable to changes in mean annual precipitation (MAP), given that relations between total carbon isotope fractionation during carbon fixation and MAP have been observed today (16). A smaller CIE could imply that MAP decreased in the tropics, an interpretation unsupported by floral assemblages or by the δD record, which displays a negative shift (~–35‰) during the onset of the PETM. However, we cannot exclude the possibility that changes in moisture recycling also influenced the D/H record. Indeed, it is difficult to explain the totality of the carbon isotope record in light of our understanding of the PETM elsewhere. For example, carbon isotope compositions return to pre-event values by the end of the PETM, albeit slightly more negative as observed globally. However, the recovery phase at our localities is not accompanied by changes in vegetation, inconsistent with our assumption that ecosystem
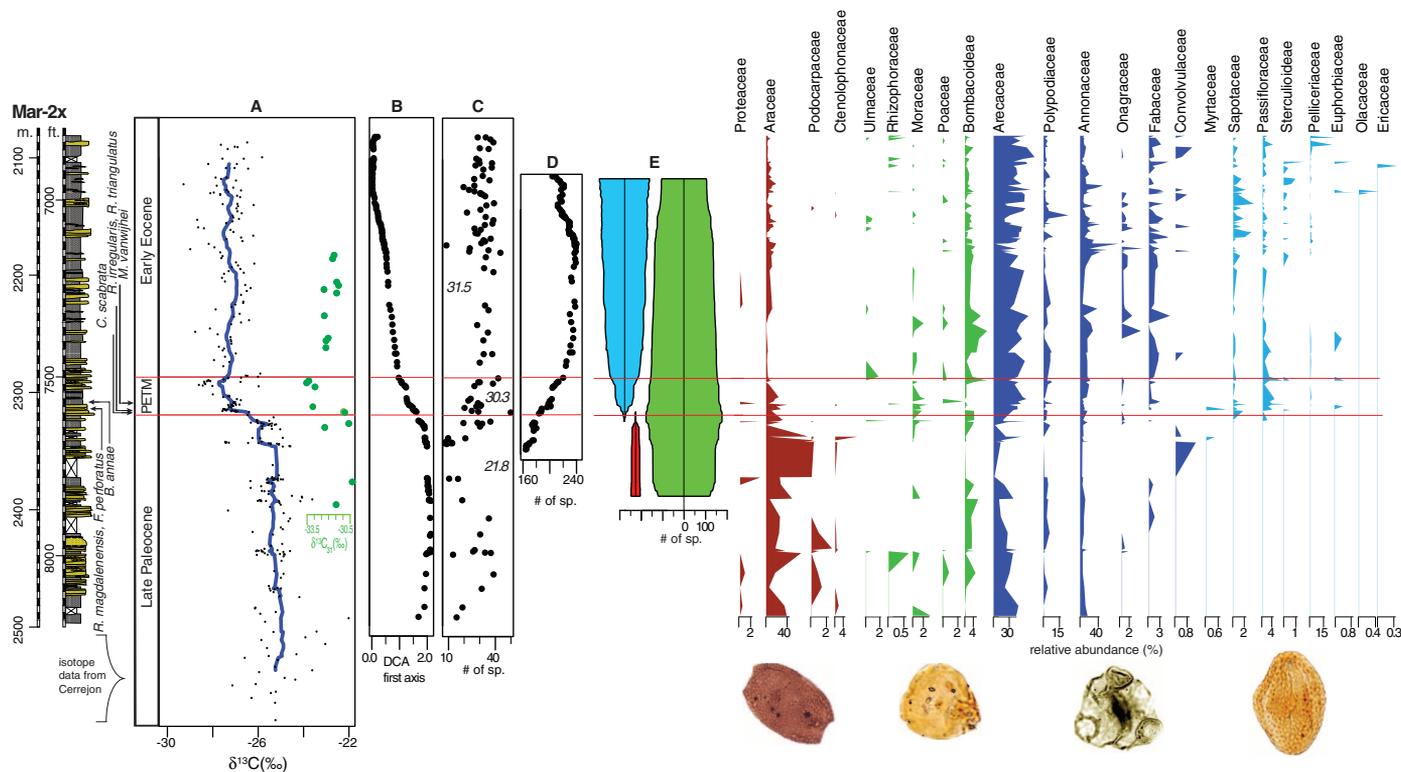
Fig. 2. Changes in palynofloral diversity and composition across the PETM in the Mar 2X core. The lithological description of the core and key biostratigraphic events are shown to the left. (**A**) δ^{13}C values of bulk organic matter across the PETM. Isotope data from the lowest part of the section was previously published (28). Blue line corresponds to a 20-point running mean of bulk data. (Inset) δ^{13}C values of the C$_{31}$ n-alkanes (n-C$_{31}$) showing a pattern similar to those of n-C$_{25}$, n-C$_{27}$, and n-C$_{29}$ (fig. S11). (**B**) First axis of a DCA, which explains 34.9% of the total variance in species composition along the stratigraphic profile. Paleocene palynofloras are distinct from Eocene palynofloras, with a gradual transition during the PETM. (**C**) Within-sample (rarefied) diversity at a count of 100 grains. The Paleocene (mean = 21.8) is less diverse than the PETM (30.3), and the PETM and Eocene (31.5) are very similar. (**D**) Pollen and spore standing diversity using the range-through method and eliminating edge effect and

single-occurrence species. Note increase in diversity at the onset of the PETM. (**E**) Eocene-restricted taxa (blue) are more diverse than Paleocene-restricted taxa (red), whereas diversity of taxa that cross the Paleocene into the Eocene (green) does not change. Increase in diversity at the onset of the PETM is due to a large addition of taxa to the preexisting Paleocene flora. Family relative abundances are shown to the right of the figure. Families that are more abundant in the Paleocene are shown in purple; families that do not change in abundance across the Paleocene/Eocene transition, green; families that are more abundant in the Eocene, dark blue; and families that originate at the latest Paleocene, PETM, or Early Eocene, light blue. Images in the lower left correspond to distinct taxa of the sequence: *Retidiporites magdalenensis* (Proteaceae), *Momipites africanus* (Moraceae), *Corsinipollenites undulatus* (Onagraceae), and *Rhoipites guianensis* (Sterculioideae).
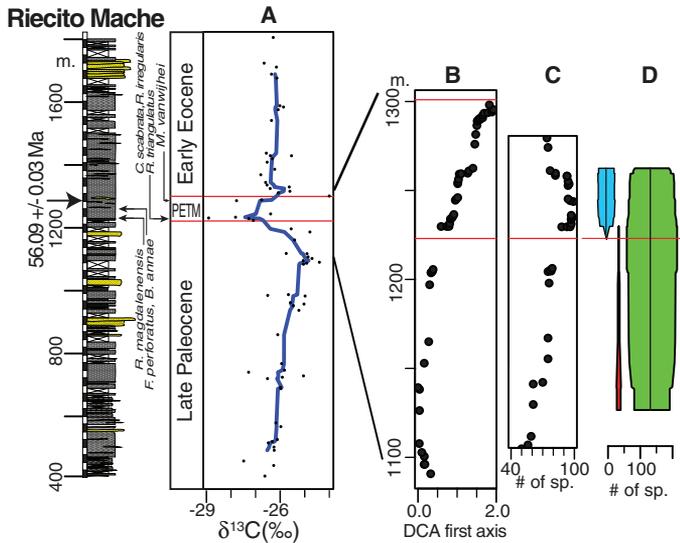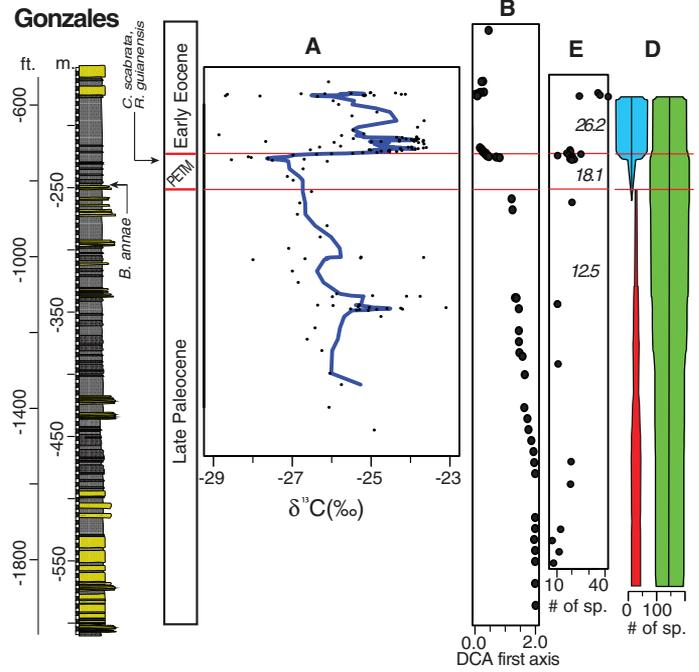
Fig. 3. Changes in palynofloral diversity and composition across the PETM at Riecito Mache and Gonzales. Lithological description of the section, key biostratigraphic events, and a radiometric age of a volcanic tuff dated by the U-Pb zircon radiometric method are shown to the left. (**A**) $\delta^{13}C$ values of bulk organic matter across the PETM. Blue line corresponds to a 7-point running mean of bulk data. (**B**) First axis of a DCA, which explains 22.2% (Riecito Mache) and 34.6% (Gonzales) of the total variance in species composition along the stratigraphic profile. (**C**) Pollen and spore standing diversity using the range-through method and eliminating edge effect and single-occurrence species. Note the increase in diversity at the onset of the PETM. (**D**) PETM-restricted taxa (blue) are more diverse than Paleocene-

restricted taxa (red), whereas diversity of taxa that cross from the Paleocene into the PETM (green) does not change. Increase in diversity at the onset of the PETM is due to a large addition of taxa to the preexisting Paleocene flora. (**E**) Within-sample (rarefied) diversity at a count of 100 grains. The PETM (mean = 18.1) is more diverse than the Paleocene (12.5) and less diverse than the Eocene (26.2).
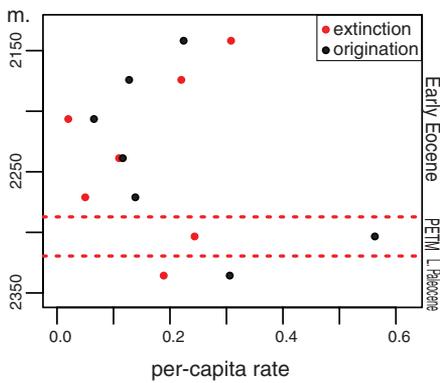

Fig. 4. Per capita rates of origination and extinction per 200,000 years (the time span of the PETM) in Mar 2X. The per capita extinction rate (red) shows a slight increase in extinction during the PETM that is comparable to other intervals in the Eocene. The per capita origination rate (black) shows a spike in origination during the PETM.

turnover was the cause for the relatively ^{13}C-enriched CIE. More likely, a smaller CIE from this study could simply be the result of incomplete recovery of the PETM maxima.

Today, most tropical rainforests are found at MAT below 27.5°C. Many have argued that tropical communities live near their climatic optimum (*19*) and that higher temperatures could be deleterious to the health of tropical ecosystems (*8, 19–23*). Indeed, tropical warming during the PETM is surmised to have produced intolerable

conditions for tropical ecosystems (*8, 21*), although 31° to 34°C is still within the maximum tolerance of leaf temperature of some tropical plants (*24*). We recognize that further studies toward the center of the South American continent need to be performed in order to understand the effects of warming in more continental tropical settings. However, at our sites in northern South America, tropical forests were maintained during the warmth of the PETM (~31° to 34°C). Greenhouse experiments have shown that high levels of CO_2 together with high levels of soil moisture improve the performance of plants under high temperatures (*25*), and it is possible that higher Paleogene CO_2 levels (*26*) contributed to their success. Higher precipitation amounts could have been as important as high CO_2. Precipitation reconstruction from a nearby Late Paleocene site, Cerrejon, indicate high precipitation regimes: about 3.2 m of rain per year (*11*). Our data, including a –35% shift in leaf-wax δD values, no increase in plant abundance of dry indicators (e.g., Poaceae), absence of a large plant extinction, high plant diversity, and high abundance of families typical of wet tropical rainforests (such as Annonaceae, Passifloraceae, Sapotaceae, Araceae, and Arecaceae), suggest that precipitation in the northern Neotropics during the PETM was either similar to Paleocene levels (3.2 m/year) or higher. Indeed, it is possible that rainforest families in general, which have been present in the Neotropics since the Paleocene (*11*), have the genetic variability to cope with high temperatures, CO_2, and rainfall (*25*).

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Conditional Cooperation and Costly Monitoring Explain Success in Forest Commons Management

Devesh Rustagi,[1]* Stefanie Engel,[1] Michael Kosfeld[2]*

Recent evidence suggests that prosocial behaviors like conditional cooperation and costly norm enforcement can stabilize large-scale cooperation for commons management. However, field evidence on the extent to which variation in these behaviors among actual commons users accounts for natural commons outcomes is altogether missing. Here, we combine experimental measures of conditional cooperation and survey measures on costly monitoring among 49 forest user groups in Ethiopia with measures of natural forest commons outcomes to show that (i) groups vary in conditional cooperator share, (ii) groups with larger conditional cooperator share are more successful in forest commons management, and (iii) costly monitoring is a key instrument with which conditional cooperators enforce cooperation. Our findings are consistent with models of gene-culture coevolution on human cooperation and provide external validity to laboratory experiments on social dilemmas.

Maintaining large-scale cooperation for the provision of public goods and the management of common property is fraught with the infamous cooperation dilemma in which free riders enjoy group benefits without bearing the cost of their provision. The conventional analysis, based on the assumption of self-regarding individuals, predicts zero cooperation under these conditions (*1, 2*). Yet extensive field evidence underlines that many groups are able to manage their commons, albeit with varying degrees of success (*3, 4*). This marked deviation from the conventional hypothesis as well as the variation in management success necessitates a coherent theory of human collective behavior that explains well the observed variation in cooperation outcomes. In addition to structural factors like resource characteristics, group size, and socioeconomic heterogeneity (*3–5*), recent findings suggest that social behaviors, such as the norm of conditional cooperation (individual cooperation being conditional on the cooperation of others) together with the costly enforcement of this norm, may play an important role in stabilizing large-scale cooperation (*6–8*).

Much of the evidence for conditional cooperation comes from behavioral laboratory experiments with student participants showing that individuals display a considerable heterogeneity in their behavioral disposition to cooperate. Although a large proportion of participants reveal conditionally cooperative behavior, a nontrivial share meets the conventional assumption by behaving as free riders (*9–14*). Because conditional cooperators do not cooperate if many group members ride for free, the composition of a group becomes decisive for the prospects of maintaining cooperation. Whereas voluntary cooperation may be achieved in groups with larger share of conditional cooperators (*15, 16*), in heterogeneous groups costly norm enforcement is needed to attain cooperation (*6, 17–21*). Evidence shows that many individuals, in particular those with a high propensity to cooperate, are willing to enforce cooperation even at a personal cost (*17, 22–26*) and that this has a positive effect on group members' contribution (*17, 19, 27, 28*).

The large body of evidence for conditional cooperation and costly norm enforcement is compelling. However, unless the relations between these behaviors and the way they affect outcomes of commons management are investigated in a concrete field setting, where one can account for context-specific information regarding relevant structural factors, their ultimate impact for commons management is hard to evaluate (*29–31*). Although previous studies have conducted be-havioral experiments with diverse populations including commons users (*26, 32–36*) and have tentatively documented the importance of local enforcement in the field (*21, 37*), reliable evidence on the extent to which variation in conditional cooperation and costly norm enforcement among commons users affects natural commons outcomes is altogether missing.

We combined data on natural outcomes of commons management with experimental measures of conditional cooperation among 679 individuals from 49 commons user groups to investigate whether groups with larger share of conditional cooperators achieve better outcomes (*38*). We also measured costly enforcement through survey data on monitoring, an important input for the detection and punishment of free riding in our context, to analyze the extent to which monitoring plays a role in sustaining commons outcomes by conditional cooperators. In doing so, we aimed to underline the conditions under which local enforcement of commons management is predicted to work.

Our research strategy was to carry out these investigations in a field setting where individuals in a group face a natural commons dilemma and use costly enforcement mechanisms to overcome this dilemma and where there exists a reliable measure of cooperation outcomes in commons management. We conducted our study in the context of a major forest commons management program launched to save local forests and livelihoods in the Bale region of Ethiopia. Under the program, groups of the Bale Oromo people were given secure tenure rights to use and manage their forests as common property resources (*39*). In return, these groups are required to maintain their forest cover, for which they are allowed to implement local rules regarding forest use, for instance, the amount of fuelwood a member is allowed to harvest for self-consumption and sale. While managing their forest as a common property, group members confront cooperation dilemmas, because each member is better off when every member in the group cooperates by adhering to internal rules; however, violating the rules leads to higher payoffs, for instance, from the sale of extra fuelwood, implying that individual members might have little incentive to cooperate. To overcome this first-order dilemma, members have the option to engage in costly monitoring, which involves conducting patrols through the forest. Such patrols not only deter

[1]Institute for Environmental Decisions, Eidgenössische Technische Hochschule (ETH) Zurich, Universitätsstrasse 22, CH-8092 Zurich, Switzerland. [2]Faculty of Economics and Business Administration, Johann Wolfgang Goethe University Frankfurt, Grüneburgplatz 1, D-60323 Frankfurt am Main, Germany.

*To whom correspondence should be addressed. E-mail: devesh.rustagi@env.ethz.ch (D.R.); kosfeld@econ.uni-frankfurt.de (M.K.)