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and M_{tr} is the primary mass in solar mass units. Inside the Hill's sphere, the motion of the satellite is controlled mainly by its primary, and perturbations from the planets can be neglected.
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52. We thank A. Morbidelli for his suggestions and constructive comments on the manuscript. We are grateful to the LISA team of the Observatoire de la Côte d'Azur (OCA), who generously provided access to their four-processor COMPAQ DEC ALPHA workstation. Simulations were also partly made on the SIVAM four-processor COMPAQ DEC ALPHA of OCA. P.M. acknowledges financial support from the Action Thématique Innovante 2001 of the French Institut National des Sciences de l'Univers. W.B. acknowledges support from the Swiss National Science Foundation. P.T. has worked on this project while staying at the OCA, thanks to the H. Poincaré fellowship 2001. This paper is dedicated to the memory of P. Farinella, who was a main contributor to past research advances on the problem of collisions between asteroids.

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Indication of Global Deforestation at the Cretaceous-Tertiary Boundary by New Zealand Fern Spike

Vivi Vajda,[1]* J. Ian Raine,[2] Christopher J. Hollis[2]

The devastating effect on terrestrial plant communities of a bolide impact at the Cretaceous-Tertiary boundary is shown in fossil pollen and spore assemblages by a diverse flora being abruptly replaced by one dominated by a few species of fern. Well documented in North America, this fern spike signals widespread deforestation due to an impact winter or massive wildfires. A Southern Hemisphere record of a fern spike, together with a large iridium anomaly, indicates that the devastation was truly global. Recovery of New Zealand plant communities followed a pattern consistent with major climatic perturbations occurring after an impact winter that was possibly preceded by global wildfires.

The abrupt replacement of a diverse plant community by one dominated by a few species of fern in numerous Cretaceous-Tertiary (K-T) boundary sites in North America (*1–5*) is compelling evidence that a giant bolide impact in the Northern Yucatan 65 million years ago (*6*) caused widespread and catastrophic disruption of terrestrial ecosystems. There has been little evidence of similar devastation in the Southern Hemisphere. Indications that the effects of the impact were less severe (*7*), however, are difficult to reconcile with knowledge that Australasian dinosaurs and marine reptiles suffered the same level of end-Cretaceous extinction as their northern cousins (*8*).

Pollen and spore assemblages from nonmarine coal and sandstone beds in the Moody Creek Mine section, West Coast, New Zealand (171°16′40″E, 42°23′18″S), let us reassess the effects of the bolide impact on terrestrial ecosystems in the Southern Hemisphere. Anomalous enrichment in iridium, chromium, cobalt, arsenic, and gold indicate that the section has an intact K-T boundary layer within a coal seam (Fig. 1). The iridium anomaly of 71 parts per billion (ppb) is the highest known from nonmarine rocks anywhere in the world [Web table 1 (*9, 10*)]. The boundary location is consistent with the last appearances of Late Cretaceous pollen species (*Tricolpites lilliei* and *Nothofagidites kaitangata*) in the underlying sample.

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Our palynological study (*11*) is based on 30 samples spanning 2.1 m (Figs. 1 and 2). In this mire setting, these assemblages are considered to be reliable representations of the pre-impact local vegetation. The Late Cretaceous assemblages are diverse, with gymnosperms dominant, ferns abundant, and angiosperms common (mean values of 57, 25, and 14%, respectively). Gymnosperms increase to ~70% in the uppermost Cretaceous at the expense of ferns and angiosperms. The K-T boundary fern spike begins with an abrupt increase in ferns to 90% of the assemblage, mainly the form genus *Laevigatosporites*, but including the only common occurrence (8%) of sphagnum moss (*Stereisporites*). Gymnosperms are greatly reduced, and angiosperms disappear completely. In searches of more than 2000 specimens per sample, no angiosperm pollen was observed over an interval of 12 cm from the base of the 40-cm-thick fern spike. The fern spike is characterized by the successive dominance of different groups, such as ground ferns (*Laevigatosporites*, *Gleichenidites*, and *Baculatisporites*) in the lower part [Web fig. 1 (*10*)] and tree ferns (*Cyathidites* and *Cibotiidites*) in the upper part. Modern relatives of these ground ferns are tolerant of open ground and acidic water-logged conditions, whereas modern tree ferns thrive in warm and humid conditions (*12*). There follows in the Moody Creek Mine succession a marked decline in ferns and a rise in gymnosperms, principally *Phyllocladidites mawsonii*. This pollen type is related to that of the extant conifer *Lagarostrobus franklinii*, which inhabits the cool-temperate rainforests of Tasmania (*13*). Angiosperms remain an insignificant component of the flora until 1.3 m above the K-T boundary. A short-lived recovery of ground ferns at the top of the fern spike may signal the first stage of regional climatic cooling, or it may be a localized phenomenon.

Identification of a similar succession of spore and pollen assemblages in a nearby marine K-T boundary section at mid-Waipara River, Canterbury (172°34′56″E, 43°3′44″S), indicates that the fern-to-gymnosperm succession reflects New Zealand–wide changes in vegetation through the K-T transition (Fig. 2). Further, although the spore and pollen records have been blurred by transport and mixing of terrestrial debris in this shallow marine setting, the well-defined boundary (*14*) and biostratigraphic control (*15, 16*) help constrain the duration of the Paleocene floral succession. General trends at mid-Waipara are similar to those reported from a marine section in Hokkaido, Japan (*17*), where the fern spike also separates mixed forest Cretaceous assemblages from gymnosperm-dominated Paleocene assemblages. The floral succession at Moody Creek Mine is similar to that in nonmarine K-T sections in North America, where the fern spike is made up of groups such as *Laevigatosporites* and *Cyathidiites* (*1, 3–5*). The North America fern spike also marks significant floral turnover from angiosperm-rich Cretaceous floras to gymnosperm-dominated ones (*2, 18, 19*).

Our results indicate that the devastation of forests after the K-T boundary impact was a global phenomenon. Even the geographically isolated vegetation of New Zealand, far from the impact site, was severely affected. We recognize five phases in the floral succession: (i) abrupt extinction or local disappearance of terrestrial vegetation due to prolonged darkness, freezing ground temperatures, possibly extensive wildfires, and acid rain (*20*); (ii) colonization of a waterlogged, acidic, cool landscape by a succession of moss and ground ferns; (iii) expansion of tree ferns in the upper part of the fern spike at both Moody Creek Mine and mid-Waipara (Fig. 2), indicating that a regional change to warm humid conditions followed earliest Paleocene cooling; (iv) decline in tree ferns before a long-term rise in cool-temperate gymnosperms, consistent with evidence in the marine record for climatic cooling in the early Paleocene (*16, 21*); and (v) recovery of angiosperms to near Cretaceous levels, possibly related to a warming climate in the late early Paleocene.

The relative importance of the impact winter versus extensive wildfires in causing devastation of terrestrial plant communities is the subject of current debate (*22, 23*). A prolonged impact winter is thought to have resulted from the impact's generation of a global dust cloud that cut off sunlight for a period ranging from several months to years (*24*). Freezing ground temperatures and light levels too low for photosynthesis for one or more growing seasons would have caused the extinction of many terrestrial plants. Continued cool and low-light conditions for several years would have stifled the germination of seeds and recovery of the warm-climate vegetation of the Cretaceous.

I has also been argued, based on the abundance of sootlike carbon and other inferred combustion products (*25–27*), that the bolide impact ignited extensive forest fires. It was initially suggested (*25*) that the fires would have been mainly restricted to North America, but subsequent models have indicated that thermal radiation generated by the ballistic reentry of ejecta may have led to spontaneous outbreaks of wildfires worldwide (*28*). The presence of fullerenes in New Zealand K-T boundary clays (*27*) supports the theory of the occurrence of local wildfires. However, although wildfires may explain the widespread devastation of forests, they do not explain the succession observed in the New Zealand palynological record or the prolonged delay in recovery of Cretaceous-type floras.

The fern spike (of both ground and tree ferns) extends into the upper part of the earliest Paleocene *Guembelitria cretacea* foraminiferal zone (P0) in the mid-Waipara and Hokkaido marine sections (*15, 17*), implying a duration of ~30,000 years. Radiolarian biostratigraphy (*16*) indicates that the interval of gymnosperm dominance may have lasted for 1 million years. These time frames are far greater than the predicted duration of months to hundreds of years for climatic changes directly associated with an impact event, such as impact winter and greenhouse warming (*20, 24*). The New Zealand vegetation record supports evidence from the local marine record (*16, 21*) and South Atlantic deep sea cores (*29*) that the K-T boundary impact, through mass extinction of oceanic plankton and mass injection of CO_2 into the atmosphere, caused major disruption of the carbon cycle, which resulted in pronounced climatic oscillations for at least 1 million years of the early Cenozoic.

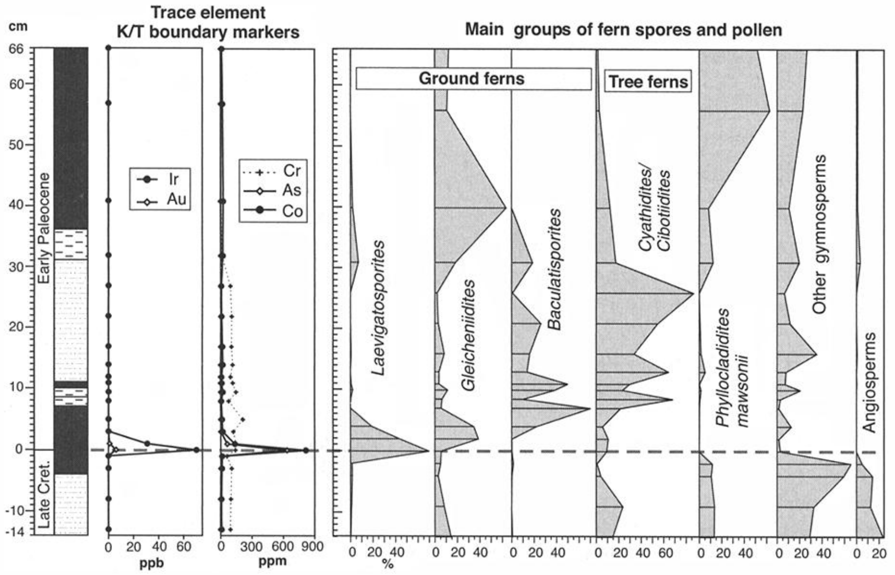

Fig. 1. Geochemical signature and abundance of main spore and pollen groups through the K-T boundary interval at Moody Creek Mine. The fact that only two samples at the K-T boundary yielded Ir values above the detection limit is consistent with very low values of Au, As, and Co outside the boundary zone (*9, 10*).

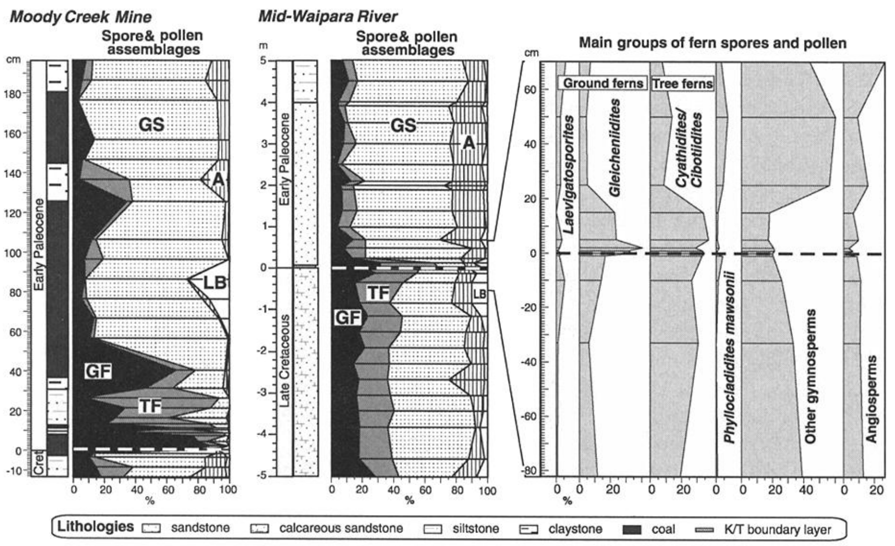

Fig. 2. Comparison of pollen and spore records from Moody Creek Mine and mid-Waipara River K-T boundary sections. GF, ground ferns; TF, tree ferns; GS, gymnosperms; A, angiosperms; LB, lycopods and bryophytes (including *Sphagnum*).

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9. Milled whole rock samples were analyzed by neutron activation analysis with detection limits for iridium of 1 ppb in coals and 3 ppb in siliclastics (Becquerel Laboratories, New South Wales, Australia). [Web table 1 (*10*)].
10. Supplementary Web material is available on *Science* Online at www.sciencemag.org/cgi/content/full/294/5547/1700/DC1.
11. Standard palynological processing methods included treatment by hydrochloric acid, hydrofluoric acid, and Schulze reagent and sieving at 6 μm. Residues were mounted on slides in glycerine jelly and sealed for examination under transmitted light. Relative abundance is based on counts of >300 whole specimens (pollen + spores). Slides, residues, and bulk material are deposited in the Paleontology Collection, Institute of Geological and Nuclear Sciences, New Zealand.
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Tree Diversity in Tropical Rain Forests: A Validation of the Intermediate Disturbance Hypothesis

Jean-François Molino* and Daniel Sabatier

The "intermediate disturbance hypothesis," which postulates maximum diversity at intermediate regimes of disturbance, has never been clearly proved to apply to species-rich tropical forest tree communities and to local-scale canopy disturbances that modify light environments. This hypothesis was tested on a sample of 17,000 trees in a Guianan forest, 10 years after a silvicultural experiment that added to natural treefall gaps a wide range of disturbance intensities. Species richness, standardized to eliminate density effects, peaked at intermediate disturbance levels, particularly when disturbance intensity was estimated through the percentage of stems of strongly light-dependent species.

The proposition that "the highest diversity is maintained at intermediate scales of disturbance" (*1*), known as the "intermediate disturbance hypothesis," remains largely untested for the highly diverse rain forest tree communities, and for the most prevalent patch-size disturbances (*2*) in such communities, canopy light gaps (*3*). This model is particularly difficult to study in this case because (i) trees are long-lived, thus, data sets large enough to cover temporal and spatial variations of tree species richness and their relationships with disturbances are very few (*4–6*), and (ii) the mechanisms through which light gaps influence tree regeneration are still not fully elucidated (*3*). Until now, most studies have focused on the pioneer guild and early gap phases, and on the pioneer/nonpioneer and gap/nongap contrasts, because both conceptual objects are rather easily circumscribed in the field: shade-intolerant pioneer species germinate exclusively in open places, and newly opened gaps can be delimited through canopy height measurement (*7*). These approaches have demonstrated the existence of interspecific differences in light requirements among tropical forest trees, but have given little evidence of gap partitioning by pioneers (*3*), thus failing to convince all ecologists that the intermediate disturbance hypothesis could explain the maintenance of high tree species diversity in tropical rain forests.

In a study of the variation in species richness of tree saplings during early gap-phase regeneration in a 50-ha plot at Barro Colorado Island (BCI), Panama, Hubbell *et al.* concluded that this hypothesis should be rejected in favor of another model, the recruitment limitation hypothesis (*8*). According to this hypothesis, the effects of dispersal- and recruitment-limitation on tree species diversity outweigh those of disturbance. Although the opening of gaps in mature forest does enlarge the choice of available niches, these would not necessarily be filled by the most adapted species, but rather by those whose propagules are abundant enough at the right place and the right time. The observed increase in species richness with gap size is thus attributed by the authors only to a steep increase in stem density (*8*).

We tested the intermediate disturbance hypothesis at Paracou, French Guiana [Supplemental fig. 1 (*9*)] (*10, 11*). We selected ten 20 m by 250 m transects, three in untouched control areas and the remainder in seven 9-ha plots commercially logged in 1986–88 (*12*), associated or not with selective felling of noncommercial trees for fuel and with thinning by poison-girdling (Fig. 1) (*10, 11*). Through 1995 (transects in control areas) and 1996–97 (other transects), we censused all trees with a dbh (diameter at breast height, or trunk diameter at 1.3 m) ≥2 cm in our 5-ha study area. All were tagged, mapped, measured, and identified to species (*13*) (>17,000 stems belonging to 546 species). From former independent studies, we distinguished two nested groups of species: a set of 97 heliophilic (sun-loving) species, including 61 pioneer, strictly gap-dependent species [Supplemental table 2 (*9*)].

After excluding swampy and seasonally flooded areas (8.8% of total area), we partitioned our transects in 20 m by 20 m *terra firme* quadrats. In each quadrat, we estimated the light-gap disturbance level through lost basal area (LBA) of removed, killed, naturally fallen, or dead trees of dbh ≥10 cm from 1987 to 1994, in the 40 m by 40 m area in which it was centered. Hereafter, we refer to the cumulated LBA over this 8-year period for each quadrat as its LBA. Of these 99 quadrats, 32 had been crossed by skid trails where logging operations, apart from the opening of canopy light gaps, resulted in increased disturbances of understory and soil. Because such disturbances are not taken into account in LBA as defined above, trail quadrats were excluded from analyses involving this disturbance indicator. LBA varied from 0 to 24.6 m^2/ha (1.94 to 27.2 m^2/ha for trail quadrats).

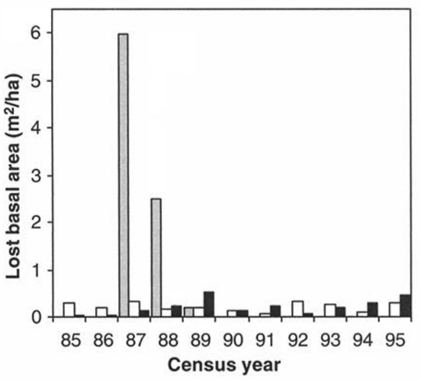

Fig. 1. Annual distribution of disturbances, estimated using LBA, in the seven treated transects (3.5 ha) at Paracou between 1985 and 1995. Gray, artificial disturbances; white, natural treefalls; black, standing dead trees. Years are those of censuses: artificial deaths in 1986 were recorded in 1987. Many trees poisoned in 1988 actually died in 1989.

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