

# Permian Coal Forest offers a glimpse of late Paleozoic ecology

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Little evokes a sense of wonder about the past like moments frozen in time: the contorted bodies of Pompeii's horrified citizens fixed in their final poses, the footprints of an ancient hominin family cemented on an African savanna, the tracks of a Jurassic predator closing in on unsuspecting prey along a muddy riverbank, or tree stumps from an ancient Carboniferous rainforest buried in place by a sudden deluge (Fig. 1). These instances provide us with poignant snapshots of deep time, and just like a photograph, they also may capture some of its dynamism. In PNAS, the work by Wang et al. (1) reconstructs the vegetation of an ~300 million-year-old early Permian-aged mire that was buried and killed by a volcanic ashfall, one of a rare but increasing number of occurrences that geologists term  $T^0$  deposits (2). The study represents a high-resolution view of a Permian-aged 'Coal Forest', so-called because it accumulated atop peat (now coal), an extinct ecosystem that persisted in tropical East Asia long after its better-known Pennsylvanian-aged counterparts had all but dried up in Europe and North America (1). By using a quantitative analysis of plant fossils preserved in tuff above the coal seam, the work by Wang et al. (1) provides a 3D reconstruction of the mire vegetation before the eruption, from which patterns of heterogeneity and ecological gradients emerge. Such  $T^0$  deposits allow paleoecologists to examine the past in much the same way neoecologists appraise modern environments, and to ask questions about the conformity of observed patterns with various aspects of ecological theory.

## $T^0$ Deposits: Snapshots of Deep Time

Although plant remains are well-represented in the terrestrial fossil record, the vagaries of fossilization present numerous challenges to creating accurate depictions of ancient vegetation. An enduring and iconic image reproduced in museum dioramas the world over is of a late Paleozoic Coal Forest, with myriad bizarre plants jumbled together in a steaming tropical jungle. However, portrayals of these spectacular ecosystems are actually based on numerous lines of independent evidence, with individual plants being reconstructed from disaggregated remains at different sites before reassembly into a popular family portrait. Although im-



Fig. 1. The most classic of  $T^0$  assemblages—Fossil Grove at Victoria Park, Glasgow, Scotland, shortly after excavation in 1887. [Courtesy Culture and Sport Glasgow (Museums)].

mobile, plants shed numerous organs (leaves, seeds, and branches) during their lifetimes, and almost invariably, they are fragmented and dispersed after death. In fact, paleobotanists rarely find entire fossil plants at their original sites of growth, and they must deduce the growth habits, physiologies, and habitat preferences from remains that have suffered transport before burial. A high-fidelity record of extinct plant communities can best be achieved if they were catastrophically buried in a geological instant, with the resulting  $T^0$  deposit effectively fixing the plant relationships in time and space (3). Accordingly, plant fossil assemblages entombed in  $T^0$  deposits provide an unrivalled chance to reconstruct not only the taxonomic composition of the ancient ecosystem but also its structure, density, distribution, and synecological associations.

The vegetation described in the work by Wang et al. (1) reflects the key mechanism for the formation of  $T^0$  deposits—volcanic ash falls or surges. These events can bury landscapes in minutes to days—instantaneously from a geological perspective—and can reveal captivating ecological information. In the Czech Republic, for example, volcanic tuffs overlying Pennsylvanian-aged coal seams (4) have yielded unequivocal evidence of vines encircling

tree trunks, lianas entwined in canopy branches that fell under the weight of ash, an absence of groundcover or understory beneath trees with dense canopies, and even the impression of a spider perched on a leaf (5). Preserved articulated remains in a Pennsylvanian-aged tuff in Spain allowed reassembly of a bizarre plant that, before discovery, was almost exclusively known from spores (6). In Chemnitz, Germany, entire Early Permian forests were enclosed in volcanic ash during a violent pyroclastic surge similar to the Mount St. Helens blast (7). The superb preservation allows a glimpse into unique synecological relationships in the Permian forest, such as tree–fern trunks as nurseries for young epiphytes and lianas (8).

Flooding in coastal regions also has the potential to entomb extensive forested areas, with  $T^0$  deposits forming because of rapid sea-level rise or coseismic events that suddenly drop a vegetated landscape below base level. Late Quaternary drowned forests abound in tidal zones

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today (9) and may become increasingly common as global warming hastens deglaciation. In Pennsylvanian-aged strata in Alabama (10) and Illinois (11),  $T^0$  deposits formed when earthquakes rapidly dropped forested surfaces, bringing in floodwaters and sediment that entombed the drowned vegetation in growth position. Whereas many trees remain rooted in the underlying coal, the overlying mudstones contain largely complete fronds and enormous prone trees up to 33 m long. There also is good evidence for vertical tiering and even open light gaps in densely forested mires (12). Rapid sea-level rise and high sedimentation rates buried a Pennsylvanian-aged swamp in Indiana (13), preserving a standing vegetation of tall pole-like plants, an assemblage with no modern analogs. Although almost all Pennsylvanian-aged  $T^0$  deposits comprise wetland vegetation growing under humid climates, fortuitous preservation of upright conifers in coastal sabkha plains in New Mexico provided a rare glimpse of semi-arid coastal vegetation (14).

Pennsylvanian-aged strata also contain innumerable examples of in situ riparian vegetation buried in major floods. For example,  $T^0$  deposits show that several Pennsylvanian-aged plants had risen to the challenge of living in disturbance-prone wetland habitats by repeated regenerative growth after burial (15). Additionally, the upright remains of wetland forests with trees up to 6 m high are exposed at several levels along the famous Joggins Cliff, Nova Scotia (16), which was recently declared a United Nations Educational, Scientific, and Cultural Organization World Heritage Site based on its historic importance.

Although  $T^0$  deposits afford high-resolution glimpses into long extinct communities, using them to characterize an entire ecosystem would be like viewing

only a scattering of isolated frames from a motion picture. This distinction is not to denigrate these time capsules—they are one of paleobiology's greatest resources—but it is critical to keep the matter of temporal and spatial scale in mind when using them to make ecological interpretations.

#### A Matter of Scale

$T^0$  plant assemblages invite comment on matters of ancient ecosystem assembly: are there recognizable gradients, can niche partitioning be detected, etc.? Any plant (or animal) community within a given area

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will be assembled according to three basic rules (17). The first rule is a dispersal constraint: can a given organism reach the area? Together with incumbency (18), this rule alone may be sufficient to explain the composition of a community if the component species have similar habitat requirements and competitive abilities (i.e., neutral assembly) (19). However, if the species are not uniform in their physical tolerances or substitutability, environmental selection plays a fundamental role. Can the organisms live in the resource space? Thus, community composition begins to incorporate niche assembly dynamics (20), which are completed with

the final criterion, biotic interaction of a species with other site occupants. Can the organisms compete for resources in the area?

How do these matters of scale and community assembly apply to Pennsylvanian and Permian Coal Forests? In many parts of the late Paleozoic tropics, these peat-forming environments covered vast areas of coastal or alluvial plain with negligible topographic gradient. There were imperceptible changes in precipitation and microelevation, and nutrient input and disturbance levels were consistently low. Although the vegetation was clearly distributed along landscape gradients, distinct plant assemblages occurred over large areas, and ecotones were very diffuse. Plant distribution in these kinds of wetland is detectably niche-controlled at large spatial scales (11), but it seems to be highly variable and heterogeneous if only one or several disconnected relatively small areas are examined (4, 12). Thus, where dispersal limitation and a large degree of species substitutability play a role in community assembly, a small and randomly selected  $T^0$  deposit may not provide an accurate portrayal of the entire ecosystem. However, when larger scales of sampling are possible or when replicates capture identifiable environmental changes or gradients, such as those changes discussed in the work by Wang et al. (1), it becomes clear that late Paleozoic plants, unsurprisingly, record the same kinds of controls on ecological distribution that are seen in modern landscapes. They add to the growing awareness that processes such as neutral dynamics and niche segregation both operate and are strongly scale-dependent (21), as much in the past as they are today.

- Wang J, Pfefferkorn HW, Zhang Y, Feng Z (2012) Permian vegetational Pompeii from Inner Mongolia and its implications for landscape paleoecology and paleobiogeography of Cathaysia. *Proc Natl Acad Sci USA* 109:4927–4932.
- Johnson KR (2007) Palaeobotany: Forests frozen in time. *Nature* 447:786–787.
- DiMichele WA, Falcon-Lang HJ (2011) Pennsylvanian 'fossil forests' in growth position ( $T^0$  assemblages): Origin, taphonomic bias and palaeoecological insights. *J Geol Soc London* 168:585–605.
- Opluštil S, et al. (2009) A Middle Pennsylvanian (Bolsonian) peat-forming forest preserved *in situ* in volcanic ash of the Whetstone Horizon in the Radnice Basin, Czech Republic. *Rev Palaeobot Palynol* 155:234–274.
- Selden PA, Penney D (2010) Fossil spiders. *Biol Rev Camb Philos Soc* 85:171–206.
- Wagner RH (1989) A late Stephanian forest swamp with *Sporangioctrobus* fossilized by volcanic ash fall in the Puertollano Basin, central Spain. *Int J Coal Geol* 12:523–552.
- Rößler R (2006) Two remarkable Permian petrified forests: Correlation, comparison and significance. *Geol Soc Spec Publication* 265:39–63.
- Rößler R (2000) The late Palaeozoic tree fern *Psaronius*—an ecosystem unto itself. *Rev Palaeobot Palynol* 108:55–74.
- Fedje DW, Josenhans H (2000) Drowned forests and archaeology on the continental shelf of British Columbia, Canada. *Geology* 28:99–102.
- Gastaldo RA, Stevanovic-Walls I, Ware WN (2004) Erect forests are evidence for coseismic base-level changes in Pennsylvanian cyclothems of the Black Warrior Basin, USA. *AAPG Studies in Geology* 51:219–238.
- DiMichele WA, Falcon-Lang HJ, Nelson WJ, Elrick SD, Ames PR (2007) Ecological gradients within a Pennsylvanian mire forest. *Geology* 35:415–418.
- Gastaldo RA, Stevanovic-Walls IM, Ware WN, Greb SF (2004) Community heterogeneity of Early Pennsylvanian peat mires. *Geology* 32:693–696.
- DiMichele WA, Nelson WJ, Elrick S, Ames PR (2009) Catastrophically buried Middle Pennsylvanian *Sigillaria* and calamitean sphenopsids from Indiana, USA: What kind of vegetation was this? *Palaio* 24:159–166.
- Falcon-Lang HJ, et al. (2011) Pennsylvanian coniferopsid forests in sabkha facies reveal the nature of seasonal tropical biome. *Geology* 39:371–374.
- Gastaldo RA (1992) Regenerative growth in fossil horsetails following burial by alluvium. *Hist Biol* 6:203–220.
- Calder JH, Gibling MR, Scott AC, Davies SJ, Hebert BL (2006) A fossil lycopsid forest succession in the classic Joggins section of Nova Scotia: Paleoecology of a disturbance-prone Pennsylvanian wetland. *Spec Pap Geol Soc Am* 299:169–195.
- Belyea LR, Lancaster J (1999) Assembly rules within a contingent ecology. *Oikos* 86:402–416.
- Massot M, Clobert J, Lecomte J, Barbault R (1994) Incumbent advantage in common lizards and their colonizing ability. *J Anim Ecol* 63:431–440.
- Hubbell SP (2001) The Unified Neutral Theory of Biodiversity and Biogeography. *Monogr Pop Biol* 32:1–448.
- Silvertown J (2004) Plant coexistence and the niche. *Trends Ecol Evol* 19:605–611.
- Weiher E, et al. (2011) Advances, challenges and a developing synthesis of ecological community assembly theory. *Philos Trans R Soc Lond B Biol Sci* 366:2403–2413.