GLOBAL BIOLOGICAL CHANGE

SPECIAL INVITED PAPER—GLOBAL BIOLOGICAL CHANGE

Plant response to a global greenhouse event 56 million years ago[1]

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- *Premise of the study:* The fossil record provides information about the long-term response of plants to CO_2-induced climate change. The Paleocene-Eocene Thermal Maximum (PETM), a 200 000-yr-long period of rapid carbon release and warming that occurred ~56 million years ago, is analogous to future anthropogenic global warming.
- *Methods:* We collected plant macrofossils in the Bighorn Basin, Wyoming, United States, from a period spanning the PETM and studied changes in floristic composition. We also compiled and summarized published records of floristic change during the PETM.
- *Key results:* There was radical floristic change in the Bighorn Basin during the PETM reflecting local or regional extirpation of mesophytic plants, notably conifers, and colonization of the area by thermophilic and dry-tolerant species, especially Fabaceae. This floristic change largely reversed itself as the PETM ended, though some immigrant species persisted and some Paleocene species never returned. Less detailed records from other parts of the world show regional variation in floristic response, but are mostly consistent with the Bighorn Basin trends.
- *Conclusions:* Despite geologically rapid extirpation, colonization, and recolonization, we detected little extinction during the PETM, suggesting the rate of climate change did not exceed the dispersal capacity of terrestrial plants. Extrapolating the response of plants from the PETM to future anthropogenic climate change likely underestimates risk because rates of climate change during the PETM may have been an order of magnitude slower than current rates of change and because the abundant, widespread species common as fossils are likely resistant to extinction.

  Key words: Paleocene-Eocene Thermal Maximum; PETM; greenhouse climate; floristic change; anthropogenic global warming

Humans have changed the composition of the atmosphere substantially over the last 150 yr, driving the concentration of CO_2 from ~280 to ~400 ppm and causing a rise in average global surface temperature of ~0.75°C. Additional increases in CO_2 to >500 ppm are likely to yield a total temperature increase of 2°–3°C in the next century (IPCC, 2007). Higher CO_2 concentrations and warmer climates will have major effects on land plants, and these are being studied at a variety of levels, from biochemical and physiological (e.g., Drake et al., 1997; Ainsworth and Long, 2005) to ecological and biogeographic (e.g., Menzel et al., 2006; Kelly and Goulden, 2008). Observations and experiments provide insight into the physiological and ecological effects of higher CO_2 and temperature over short time periods and small areas, but it is difficult to anticipate how these processes will play out over larger areas and longer periods of time (Schäfer et al., 2002; Zvereva and Kozlov, 2006; Dukes, 2007; Sitch et al., 2008), particularly the centennial to millennial time scales over which the Earth's climate and ecosystems will adjust to its changing atmosphere (Nowak et al., 2004; Archer et al., 2009; Solomon et al., 2009).

Paleontological data are essential to understanding the long-term effects of changing CO_2 and climate on plants because fossils provide the only information we have about the integrated, long-term response of ecosystems to global changes similar in magnitude to those predicted for the centuries and millennia ahead. In this paper, we describe the response of terrestrial vegetation to the largest, most rapid, and best understood global warming event known in the geological record, the Paleocene-Eocene Thermal Maximum, or PETM. In the section that follows we give a brief overview of the PETM. Following that we outline the geology and paleoenvironments of our study area in northern Wyoming, United States. We then present new data and analyses of changes in the taxonomic composition of plant macrofossil assemblages (mostly leaf fossils) during the PETM. The macrofossil data allow us to examine floristic change at a low taxonomic level compared with fossil pollen studies and with no concern that the pattern of change through time is affected by specimens that have been reworked (i.e., eroded from older sediments and redeposited during the PETM). After presenting and analyzing data from Wyoming,

we summarize floristic changes documented by fossil pollen at PETM sites in other parts of the world, discuss geographic patterns, and consider the implications of the PETM for future plant responses to anthropogenic change of the atmosphere and climate.

THE PALEOCENE-EOCENE THERMAL MAXIMUM

The PETM occurred at the beginning of the Eocene Epoch, ~56.0 million years ago (Ma) in the timescale of Gradstein et al. (2012). It lasted for ~200 thousand years (kyr) (Murphy et al., 2010) and was caused by the release of a large quantity of carbon into the atmosphere and ocean over about 10–20 kyr (Cui et al., 2011). There are three lines of evidence for this massive carbon release. First is a global decrease in the ratio of ^{13}C to ^{12}C of about 3–5‰, referred to as the negative carbon isotope excursion, or CIE (Kennett and Stott, 1991; Koch et al., 1992; McInerney and Wing, 2011). The decrease in the global ^{13}C to ^{12}C ratio shows that the carbon that was released had previously been fixed by organisms that preferred the lighter isotope, ^{12}C. Second, widespread dissolution of deep marine carbonate deposits indicates that thousands of petagrams (Pg) of carbon were dissolved in the ocean, decreasing its pH, and dissolving carbonate sediments (Zachos et al., 2005; Panchuk et al., 2008; Zeebe et al., 2009). Third, as predicted by greenhouse gas theory, the release of carbon was accompanied by a global temperature increase of 4°–8°C independently identified through a variety of geochemical analyses (Fricke et al., 1998; Sluijs et al., 2006, 2010; Zachos et al., 2006, 2007; Handley et al., 2008).

The basic outline of massive carbon release and global warming during the PETM is well established, but many important aspects of the event are unresolved. The source of the carbon is disputed, with hypothesized reservoirs including methane hydrates in the ocean floor (Dickens et al., 1995), organic-rich marine sediment heated by volcanic intrusions (Svensen et al., 2004), shallowly buried peat or coal (Kurtz et al., 2003), and permafrost (DeConto et al., 2012). Uncertainty about the source creates uncertainty about the amount of carbon released. The CIE could be explained by a relatively small release of carbon with a very negative isotopic composition, such as methane hydrates, or by a much larger release of carbon with a less-negative composition, with estimates ranging from ~1200 to ~13 000 Pg (Dickens et al., 1995; Pagani et al., 2006a; Zeebe et al., 2009; Cui et al., 2011; McInerney and Wing, 2011).

The CIE, which indicates the amount of light carbon from the release remaining in the atmosphere–ocean system, is generally recognized to have three phases: a geologically rapid "onset," a relatively long "body" or "core" of sustained negative carbon isotope composition, and a shorter "recovery" during which isotopic composition returned to normal (Bowen et al., 2006). The duration of the onset has been estimated to be 6–35 kyr (Kennett and Stott, 1991; Bowen et al., 2006; Murphy et al., 2010), with recent estimates of about 10 kyr (Cui et al., 2011). Carbon could have been released more rapidly during pulses within the onset (Bains et al., 1999; Cui et al., 2011), but the most rapid pulses consistent with surface ocean chemistry would have been one to several millennia in duration (Ridgwell and Schmidt, 2010; Robinson, 2011). Modeling of the carbon release gives peak rates of 0.3 Pg C·yr^{-1} for a methane source (less mass) to 1.7 Pg C·yr^{-1} for an organic carbon source (more mass), with atmospheric CO_2 concentration increasing from ~800 ppm prior to the PETM to either ~1500 ppm for a methane source or ~4200 ppm for an organic carbon source (Cui et al., 2011). The upper range of CO_2 increase for the PETM is more consistent with the global temperature increase of 4°–8°C (Fricke et al., 1998; Sluijs et al., 2006, 2010; Zachos et al., 2006, 2007; Handley et al., 2008).

The body of the CIE, the period of low but relatively stable carbon isotope values, is estimated to have been 80–160 kyr long, depending on the method of calibration to time and the stratigraphic section under study (Norris and Röhl, 1999; Farley and Eltgroth, 2003; Röhl et al., 2007; Aziz et al., 2008; Westerhold et al., 2009; Murphy et al., 2010). The body of the CIE may represent a quasi-stable alternate state of the global climate and carbon cycle (Bowen et al., 2006). In our study area in Wyoming, fossil soils, faunas, floras, and sediments deposited during the body of the CIE contrast strongly with those from before and after (Wing et al., 2009; Rose et al., 2012; Secord et al., 2012; Kraus et al., 2013), reinforcing the idea that the body of the CIE had a characteristic climate state in this region.

The recovery phase of the CIE is estimated to have lasted 70–80 kyr, with the bulk of the positive shift in carbon isotope composition occurring in the first ~35 kyr (Murphy et al., 2010). Sequestration of carbon from the atmosphere and ocean during the recovery is thought to be the result of both weathering and regrowth of carbon stocks in biomass, soils, and sediments (Bowen and Zachos, 2010). Rates of change during the recovery phase were probably slower than during the onset of the CIE, but it is estimated that >2000 Pg of carbon were sequestered in organic matter in the first 30–40 kyr of the recovery (Bowen and Zachos, 2010).

The PETM is broadly analogous to high-end scenarios for future anthropogenic change, although there are important differences. The magnitude of the carbon release is similar, with ~5000 Pg remaining in the fossil fuel reservoir compared to a midrange estimate of ~4500 Pg released in the PETM (Zeebe et al., 2009). Warming of 4°–8°C during the PETM overlaps at its low end with the upper range of anthropogenic warming forecast for 2100 (IPCC, 2007). The duration of the PETM, 150–200 kyr, is also consistent with model estimates for the residence time of a large anthropogenic carbon pulse in the ocean–atmosphere system (Archer et al., 2009). Climate models predict that elevated atmospheric CO_2 and attendant warming will persist for many millennia after CO_2 production ceases (Archer et al., 2009; Solomon et al., 2009). There are, however, two obvious differences between the PETM and future anthropogenic warming. The PETM began during a period that was already globally warm, with little or no polar ice and thus much less ice–albedo feedback (Winguth et al., 2010). Of great importance for biological systems is that the rates of change in atmospheric composition and climate were far slower during the PETM than they are projected to be in the future. If the earth warmed ~5°C in ~10 kyr at the onset of the PETM the average rate of temperature change was 0.05°C/century, 20–50 times slower than projected anthropogenic warming in the next century (IPCC, 2007). Even factoring in possible pulses in carbon emissions during the onset of the PETM, peak rates are estimated to have been 1.7 Pg C·yr^{-1} (Cui et al., 2011), compared with anthropogenic carbon emissions of ~9.1 Pg in 2010 (Peters et al., 2012). The slower rates of environmental change during the PETM are likely to have allowed time for plant dispersal and range change that may not be possible during the much more rapid anthropogenic change to come.

STUDY AREA AND DEPOSITIONAL ENVIRONMENTS

The Bighorn Basin in northern Wyoming is one of a series of intermontane basins that subsided as the Rocky Mountains were elevated during the Late Cretaceous and early Cenozoic (Dickinson et al., 1988). The present topographic basin is a NW-SE-oriented ovoid ~200 × 120 km, floored largely by Paleocene and Eocene rocks belonging to the Fort Union and Willwood formations. The Bighorn Mountains along the eastern and northeastern flanks of the basin were uplifted in the Late Cretaceous through the early Eocene (Hoy and Ridgway, 1997; Peyton et al., 2012). The Beartooth Range to the northwest rose during the Paleocene and early Eocene (Hickey, 1980; Decelles et al., 1991), and the Owl Creek Mountains to the south appeared at about the same time (Bown, 1980). The paleoelevation of the Rocky Mountains during the late Paleocene-early Eocene is poorly constrained, with estimates of their altitude ranging from less than 2 km to more than 4 km (McMillan et al., 2006; Fan and Dettman, 2009; Chamberlain et al., 2012). The basin floor was probably <1 km in paleoelevation (Wing and Greenwood, 1993; McMillan et al., 2006).

Regardless of the elevation of the surrounding mountains, the Fort Union and Willwood formations are composed mostly of sediments deposited by low-gradient streams (Neasham and Vondra, 1972; Bown and Kraus, 1981; Kraus and Aslan, 1993; Kraus, 1997; Davies-Vollum and Kraus, 2001). Coarse-grained, high-energy alluvial fan deposits exist on the northwest margin of the basin near the Beartooth Mountain front, but the rest of the early Cenozoic basin-fill is largely mudstone deposited during overbank floods, siltstone deposited by crevasse-splay channels, and fine-to-medium-grained sandstone bodies deposited by larger channel systems (Kraus, 1980, 2001; Bown and Kraus, 1981; Kraus and Aslan, 1993; Davies-Vollum and Kraus, 2001). Crevasse-splay deposits form when water in the main channel overtops the natural levee, erodes down through it, then carries coarser sediment out onto the floodplain where it is dropped. Crevasse splays are commonly channel-shaped near the breach in the levee, but become thinner and broader away from the main channel (Slingerland and Smith, 2004).

Plant macrofossils are preserved commonly in the Fort Union Formation (Fm.) (Brown, 1962; Hickey, 1980) and moderately commonly in the Willwood Fm. (Wing, 1980). Macrofossil assemblages occur in four types of fluvial subenvironments that can be recognized from sedimentary features: backswamp, alluvial ridge, channel, and ponds (Hickey, 1980; Wing et al., 1995). Tabular carbonaceous shales represent deposition in floodplain backswamps distal to the channel, areas that were flooded much of the time and had poorly aerated, wet soils (Wing, 1984a; Davies-Vollum and Kraus, 2001). In some places, floodplain backswamps graded into shallow floodplain lakes, resulting in the deposition of mudstone units with less organic matter. Macrofossils preserved in any given backswamp quarry site are derived from a very small area of the original wet floodplain vegetation, probably a fraction of a hectare (Davies-Vollum and Wing, 1998).

Fossiliferous alluvial ridge deposits are commonly ripple cross-laminated, organic silt finely interlaminated with very fine or fine sand, and occur in beds with a lensoid cross section. These beds probably represent deposition by small crevasse-splay channels on wet floodplains or distal parts of levees (Wing, 1984a; Wing et al., 1995). Sites on the alluvial ridge were elevated relative to the floodplain and, therefore, better drained and aerated than sites in the backswamp. Although deposition near the paleo-channel suggests some potential for transport of fossils before deposition, preservation of nearly complete leaves and small-scale lateral heterogeneity in floristic composition indicate that fossil assemblages in this sedimentary environment are local rather than highly transported.

Plant fossils are also preserved in fine-grained sandstone lenses, usually in mud laminae on top of decimeter to meter-scale cross-laminations (Hickey, 1980). These beds probably represent point bars or other bar forms on the floor of moderate-size fluvial channels, where plant fossils were preserved during periods of waning flow. Fossil assemblages in this sedimentary setting are generally dominated by tough leaves, wood fragments, and woody fruits and represent transported elements of channel-margin vegetation.

Pond deposits that preserve plants are fine-grained (silt or clay), horizontally laminated, preserve multiple centimeter-scale fining upward sequences, and occur in beds with lensoid cross sections that are meters to hundreds of meters across (Wing, 1984a; Wing et al., 1995). These ponds formed as the result of channel abandonment. Fossils preserved in ponds include fish and aquatic snails as well as floating and emergent aquatic plants, but they are typically dominated by tree leaves, probably derived from vegetation growing on the margin of the pond (Wing, 1984a). These assemblages also represent small areas, depending somewhat on the size of the segment of channel that was abandoned and on whether the channel was reactivated during the infill, possibly introducing some material from upstream.

In all of these fluvial subenvironments, plant fossils from any given site were likely preserved by one or a few sedimentation events that occurred in rapid succession and protected litter from degrading (Davies-Vollum and Wing, 1998; Davies-Vollum and Kraus, 2001). The short time over which fossil assemblages accumulated and the small amount of transport make each collection analogous to a "snapshot" of the original vegetation of a very small area over a short time. The snapshots are roughly similar in the amount of time and space they represent, so that differences among sites likely reflect different vegetation rather than changes in the way the vegetation was sampled by preservation. The snapshots allow us to detect rapid and short-lived events, subject to the stratigraphic density of sites and our ability to correlate them (discussed later). In addition, leaf macrofossils provide enough characters to permit recognition of species or generic-level taxa, even if higher-level affinities remain obscure. The primary limitation of our record is that it is confined to floodplain settings, providing little or no information about nondepositional areas within the basin and the surrounding mountains.

During the late Paleocene and early Eocene, the climate of the Bighorn Basin (paleolatitude ~50°N) was warm and wet compared with today, with mean annual temperatures >15°C and mean annual precipitation >100 cm (Wing and Greenwood, 1993; Fricke and Wing, 2004; Currano et al., 2008). Regional climate warmed rapidly by ~5°C at the onset of the PETM (Fricke et al., 1998; Wing et al., 2005; Secord et al., 2012), and throughout the northern Rocky Mountains, there is evidence for highly variable precipitation and stream flow and effectively drier climate (Wing et al., 2005; Kraus and Riggins, 2007; Bowen and Bowen, 2008; Foreman et al., 2012; Secord et al., 2012; Kraus et al., 2013). Soil wetness increased rapidly during the recovery phase of the CIE (Secord et al., 2012; Kraus et al., 2013), and the post-PETM temperature in the Bighorn Basin was similar to that of the late Paleocene (Wing et al., 2000).

MATERIALS AND METHODS

We collected fossil plants from 225 sites in the Fort Union and Willwood formations, distributed across a total area of ~4000 km^2 and deposited during an interval of ~7 Ma (Figs. 1, 2). All fossils are housed by the Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, which also holds detailed locality data. Ninety-six sites are Paleocene, 20 are from the PETM, and 109 are from the Eocene; 147 of the sites have an age within 1 Myr of the Paleocene-Eocene boundary (Fig. 2). We recovered a total of 314 taxa from all the sites. The number of identified specimens per site ranged from ~100 to >1000, and the volume of fossiliferous rock examined from ~0.1 m^3 to ~10 m^3. Such wide variation in sampling effort complicates interpretations of diversity, so we focused here on changes in floristic composition through time.

The age of each site was interpolated from its stratigraphic position relative to horizons of known age, assuming a uniform long-term rate of sediment accumulation between dated levels. The age model for each stratigraphic section was constructed as in previous work by Wing et al. (2000), but with new age constraints added (Secord et al., 2006; Clyde et al., 2007; Wing et al., 2009; Abels et al., 2012) and all age estimates updated to the time scale of Gradstein et al. (2012). Each site was assigned to a fluvial subenvironment using information on grain size and sedimentary features described earlier (Appendix S1; see Supplemental Data with the online version of this article).

The taxa include both formally named species and informal but unique "morphotypes." Of the 314 taxa, 90% are dispersed leaves, 8% are dispersed fruits or seeds, 1.6% are dispersed flowers, and the remaining two are an axis and a distinctive type of stipule (online Appendix S2). Thirty-two morphotaxa are thought to be represented by more than one organ, for example, leaves of the platanaceous genus *Macginitiea* and fruits called *Macginicarpa* (Manchester, 1986). Because virtually all occurrences in our data set are of dispersed organs and for the vast majority of taxa we do not know which organs go together, we treated the dispersed organs as separate taxa. Co-occurrences of dispersed organs that were once part of the same species are not likely to produce significant patterns in our data set because all but 10% of the taxa are dispersed leaves.

Leaf fossils were segregated into morphotypes and described using the terminology and procedures outlined by Ellis et al. (2009). Typical elements of the late Paleocene, PETM, and post-PETM early Eocene flora are shown in Figs. 3–5. Only 95 of the 314 morphotypes (30%) have been assigned to a family; however, we are confident that all unassigned, informal morphotypes are distinct from one another based on their unique combinations of venational and other leaf characters (Appendix S2).

For stratigraphic and multivariate analyses, we removed all sites with <5 morphotypes because they represent such a small sample of the original diversity. We then removed species that occurred at only one site. The reduced matrix has 127 species and 142 sites, including 50 Paleocene sites, 10 PETM sites, and 82 Eocene sites (Appendix S3).

All statistical analyses were performed in the program R version 2.14.2 (R Development Core Team, 2007). We recognized taxa with similar temporal ranges by plotting their occurrences with the package stratigraph (Green, 2010). Taxa that have long temporal ranges are referred to below as long-ranging taxa. To examine the similarity of sites in terms of floristic composition, we calculated Bray–Curtis distances using the presence and absence of morphotypes at sites. The Bray–Curtis distance metric was originally proposed for binomial (i.e., presence–absence) data and consistently performs well on ecological data (McCune and Grace, 2002). We then performed nonmetric multidimensional scaling (NMDS) on the Bray–Curtis distances using the metaMDS package within R. We chose NMDS for ordinations because it makes no assumptions about the distribution of species or relationships among variables (McCune and Grace, 2002). The stress of the solution decreased strongly as the number of axes increased from one to three, then became more asymptotic, so we present plots showing the first two axes of the three-axis solution.

We used analysis of similarity, or ANOSIM, to assess the statistical significance of a priori groups of sites. ANOSIM is complementary to NMDS, as both are nonparametric tests that work on ranked similarities between groups of samples (Clarke, 1993). In the first test, we used two a priori groups: PETM sites and all others. In the second test, we used three groups: Paleocene, PETM, and Eocene. In the third test, we defined six a priori groups corresponding to the five recognized depositional settings (backswamp, floodplain lake, alluvial
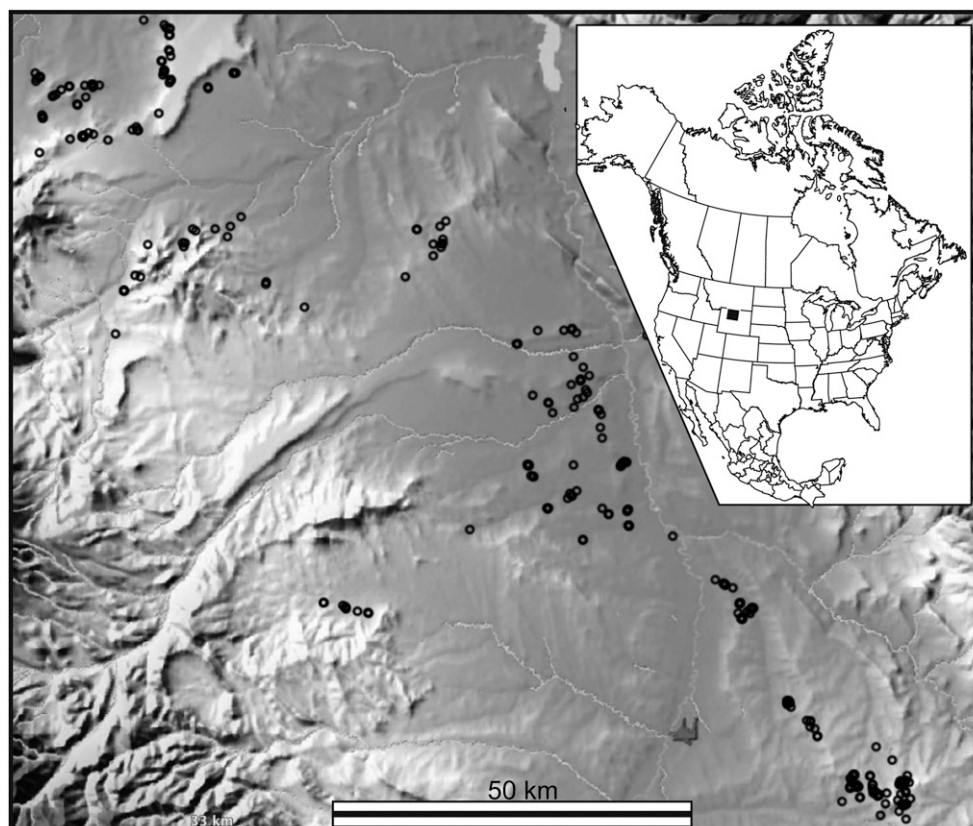

Fig. 1.   Map of the Bighorn Basin, Wyoming, showing positions of the sites from which macrofloras were collected for this study.
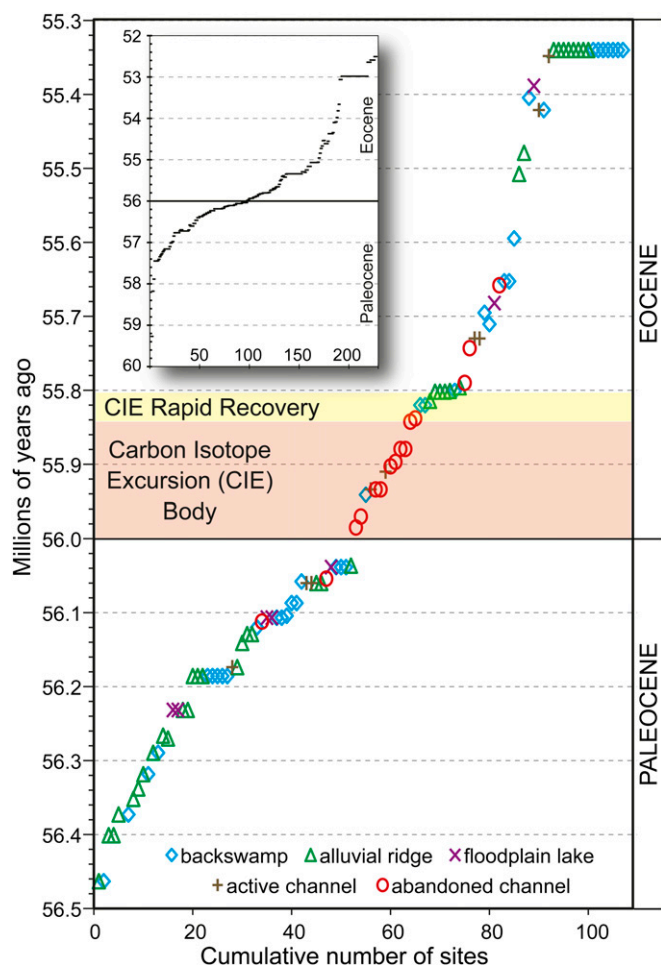
Fig. 2. Distribution of Bighorn Basin plant macrofossil sites in time. Inset figure shows the interval from 60 to 52 million years ago (Ma); the main figure shows the interval around the Paleocene-Eocene Thermal Maximum. The Carbon Isotope Excursion (CIE) is the global, negative shift in the carbon isotope composition of the atmosphere, ocean, and biosphere that indicates the release of thousands of petagrams of organic carbon. The body of the CIE was a period of sustained negative carbon isotope composition that corresponds to the warmest climate. See section on the Paleocene-Eocene Thermal Maximum for more detail on the CIE. Site symbols in the main figure vary by depositional environment (see key).

ridge, active channel, and abandoned channel) and two sites that were not characterized. Finally, to test whether changes in floristic composition across the study interval result from changes in the frequency of different depositional environments, we restricted our analysis to only sites representing the abandoned channel environment and used the a priori groups of the Paleocene, PETM, and Eocene. Abandoned channels are the only depositional environment with more than one site in each interval (4 Paleocene, 8 PETM, and 10 Eocene). For all tests, we set ANOSIM to perform 999 iterations of a procedure in which sites were randomly assigned to groups, then Bray–Curtis distances within and between groups were compared between the randomly constituted and a priori groups.

Last, we examined floristic turnover across the PETM at the taxonomic level of plant families. The abundance and diversity of angiosperm families varies strongly with climate (Punyasena, 2008; Punyasena et al., 2008), so we expected climatic shifts during the Paleocene–Eocene transition to have changed floristic composition at the family as well as at the species level. We calculated ubiquity for each family during the Paleocene, PETM, and post-PETM periods as the sum of the number of occurrences of all morphotypes assigned to the family in the time interval divided by the total number of possible occurrences for the family (i.e., the number of occurrences if every morphotype belonging

to the family in the whole data set occurred at every site in the time interval). The ubiquity scores vary from 0 (no occurrences of the family in the time interval) to 1 (every morphotype assigned to the family occurs at every site in the time interval). Although only 30% of morphotypes have been assigned to families, we do not think the probability of placing a morphotype in a family varies systematically through our record, and thus the ubiquity of families should reflect real floristic change.

RESULTS

The most striking pattern in our data is the distinctiveness of floras from the PETM, which results both from species that occur only at PETM sites and others that never occur during the PETM but are common before and after (Fig. 6). We recognize five groups of taxa that have different temporal distributions relative to the PETM. Group I taxa occur only in the Paleocene, last occurring in the final 200 kyr of the epoch prior to the PETM. Group II taxa occur only or mostly during the PETM. Group III taxa occur throughout the late Paleocene, PETM, and early Eocene. Group IV plants first appear in the 500 kyr following the PETM. Group V species occur throughout the late Paleocene-early Eocene except during the body of the CIE, which marks the period of highest temperatures and greatest water stress (Secord et al., 2012; Kraus et al., 2013).

The NMDS analysis (Fig. 7) demonstrates the distinctiveness of floral samples from the body of the CIE in the multidimensional space defined by species occurrences. Paleocene and post-PETM Eocene sites overlap broadly in composition, because of the large number of taxa that occur both before and after the PETM (group V). Cupressaceous conifers such as *Metasequoia occidentalis* (Newberry) Chaney (Fig. 3A) and *Glyptostrobus europaeus* (Brongniart) Heer typically dominate backswamp fossil assemblages both during the late Paleocene and in the early Eocene following the body of the CIE, along with eudicots such as *Corylites* Gardner (Fig. 3C), *Averrhoites affinis* (Newberry) Hickey (Fig. 5E), cf. *Phoebe* Nees, and the fern *Allantoidiopsis erosa* (Lesquereux) Knowlton & Maxon. Alluvial ridge sites in both epochs commonly contain fossils of *Ginkgo adiantoides* Heer (3F), the eudicots "*Ficus*" *planicostata* Lesquereux (Fig. 3B), *Cercidiphyllum genetrix* (Newberry) Hickey (Fig. 3J), *Zizyphoides flabella* (Newberry) Crane, Manchester & Dilcher (Fig. 3G), *Macginitiea gracilis* (Lesquereux) Wolfe & Wehr (Fig. 3E), *Fagopsiphyllum groenlandicum* (Heer) Manchester (Fig. 3I), and *Platanus raynoldsii*, and the monocot *Zingiberopsis isonervosa* Hickey. Sites from the recovery phase of the CIE tend to be dominated by long-ranging taxa (group V) and characteristic Eocene forms (group IV), and are not very different in composition from latest Paleocene and early Eocene sites (Fig. 7). A few typical PETM taxa, for example "*Artocarpus*" *lessigiana* (Lesquereux) Knowlton, do occur at one or two sites in the recovery interval. (We use generic names in quotes to indicate that the binomial is valid but probably incorrectly assigned to genus.)

The different average composition of Paleocene and post-PETM sites reflects both regional extinction (group I) and immigration (group IV). Paleocene backswamps commonly have *Browniea serrata* (Newberry) Manchester & Hickey (Fig. 3D), *Davidia antiqua* (Newberry) Manchester (Fig. 3H), and *Beringiophyllum cupanioides* (Newberry) Manchester, Crane & Golovneva, but these are absent (*Browniea*, *Davidia*) or extremely uncommon (*Beringiophyllum*) following the PETM. Eocene backswamps commonly have abundant leaves of *Alnus* Miller (Fig. 5G), which does not occur as a macrofossil in the

Fig. 3.   Typical plant fossils of the late Paleocene in the Bighorn Basin, Wyoming. (A) *Metasequoia occidentalis* (Cupressaceae, USNM 558831); (B) "*Ficus*" *planicostata* (Lauraceae?, USNM 558832); (C) *Corylites* sp. (associated with inflorescences of *Cranea wyomingensis* Manchester; Betulaceae, USNM 558833); (D) *Browniea serrata* (Cornales, USNM 539835); (E) *Macginitiea gracilis* (Platanaceae, USNM 558834); (F) *Ginkgo adiantoides* (Ginkgoaceae, USNM 558835); (G) *Zizyphoides flabella* (Newberry) Crane, Manchester & Dilcher (Trochodendraceae, USNM 558836); (H) *Davidia antiqua* (Cornaceae, USNM 539838); (I) *Fagopsiphyllum groenlandicum* (Fagaceae, USNM 558837); (J) *Cercidiphyllum genetrix* (Newberrry) Hickey (Cercidiphyllaceae, USNM 539837). Scale bar markings are in millimeters.
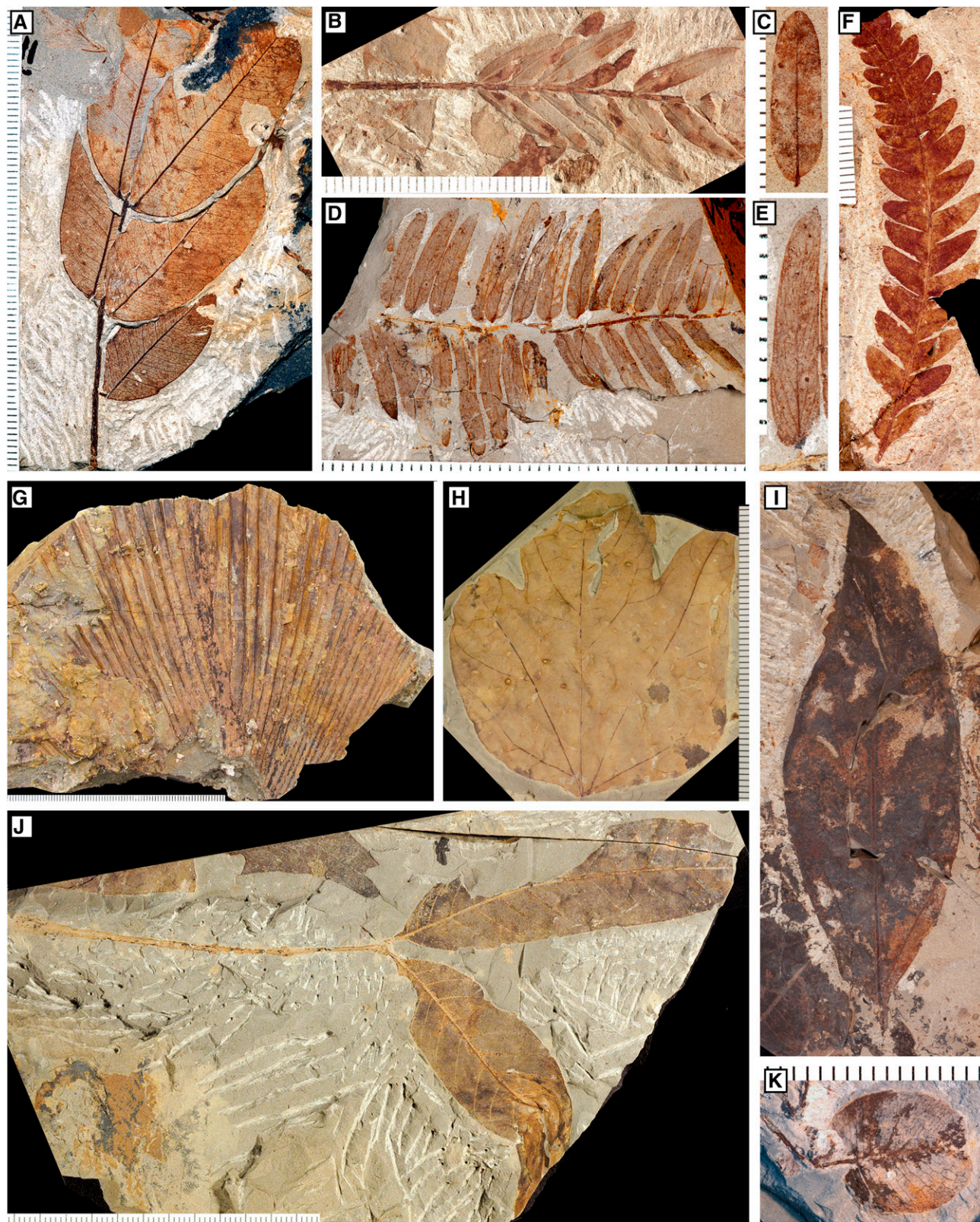
Fig. 4.   Typical plant fossils of the Paleocene-Eocene Thermal Maximum in the Bighorn Basin, Wyoming. (A) cf. *Copaifera* (Fabaceae, USNM 558838); (B) *Parvileguminophyllum coloradensis* (Fabaceae, USNM 558839); (C) closeup of (B); (D) leaf type WW020 (Fabaceae, USNM 558840); (E) closeup of (D); (F) cf. "*Rhus*" *nigricans* (Sapindaceae?, USNM 558841); (G) *Sabalites* sp. (Arecaceae, USNM 558842); (H) cf. *Gyrocarpus* (Hernandiaceae, USNM 558843); (I) cf. *Phoebe* (Lauraceae, USNM 558844); (J) leaf type WW004 (family unknown, USNM 558845); (K) *Salvinia preauriculata* (Salviniaceae, USNM 558846). Scale bar markings are in millimeters.
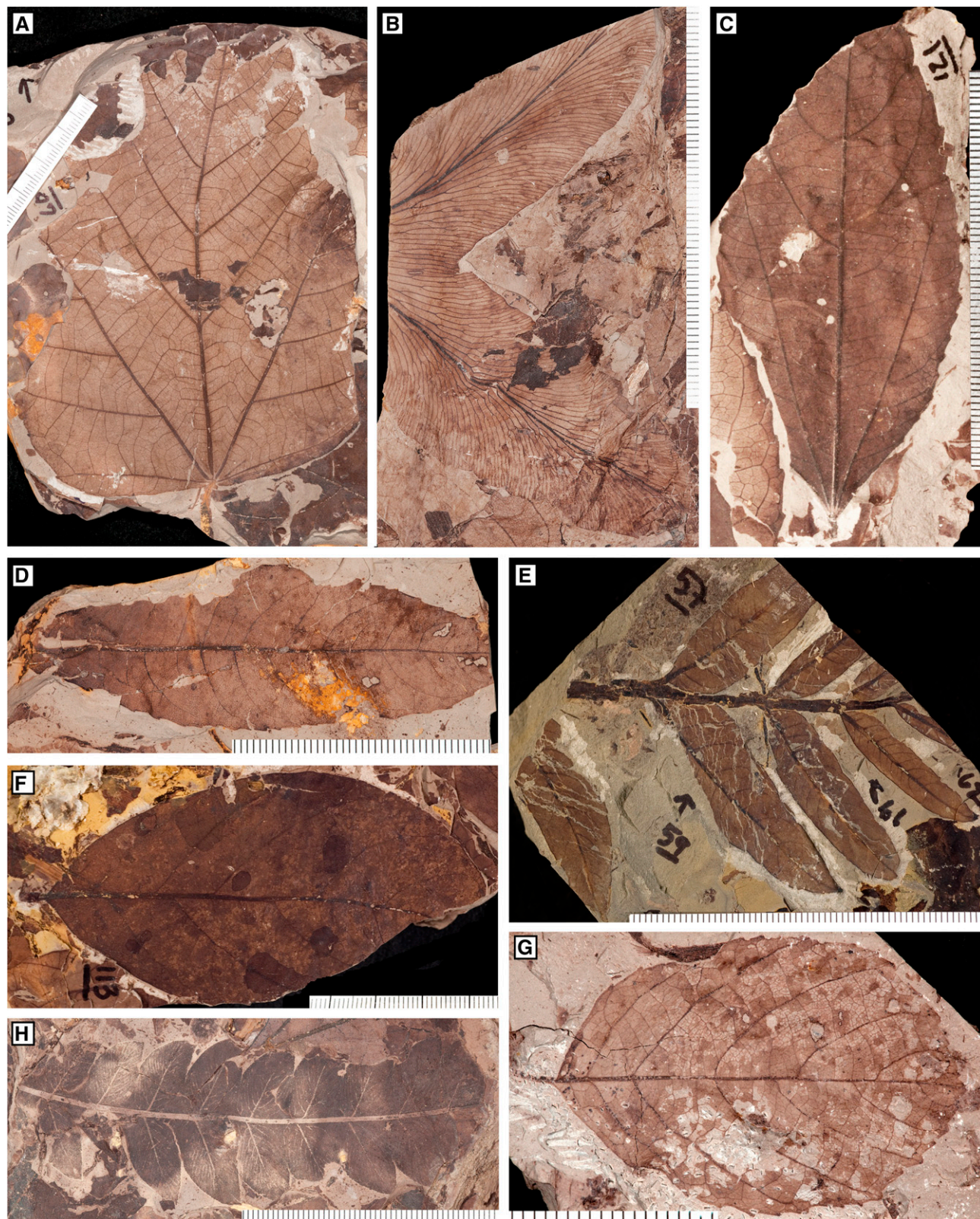
Fig. 5. Typical plant fossils of the early Eocene in the Bighorn Basin, Wyoming. (A) *"Dombeya" novi-mundi* Hickey (Malvaceae, USNM 539885); (B) *Lygodium kaulfussi* (Schizaeaceae, USNM 558847); (C) *Populus cinnamomoides* (Salicaceae, USNM 558848); (D) *Platycarya casta-neopsis* (Lesquereux) Wing and Hickey (Juglandaceae, USNM 558849); (E) *Averrhoites affinis* (family unknown, USNM 539858); (F) leaf type WW061 (Lauraceae?, USNM 539920); (G) *Alnus* sp. (Betulaceae, USNM 539817); (H) *Cnemidaria magna* (Cyatheaceae, USNM 558850). Scale bar markings are in millimeters.

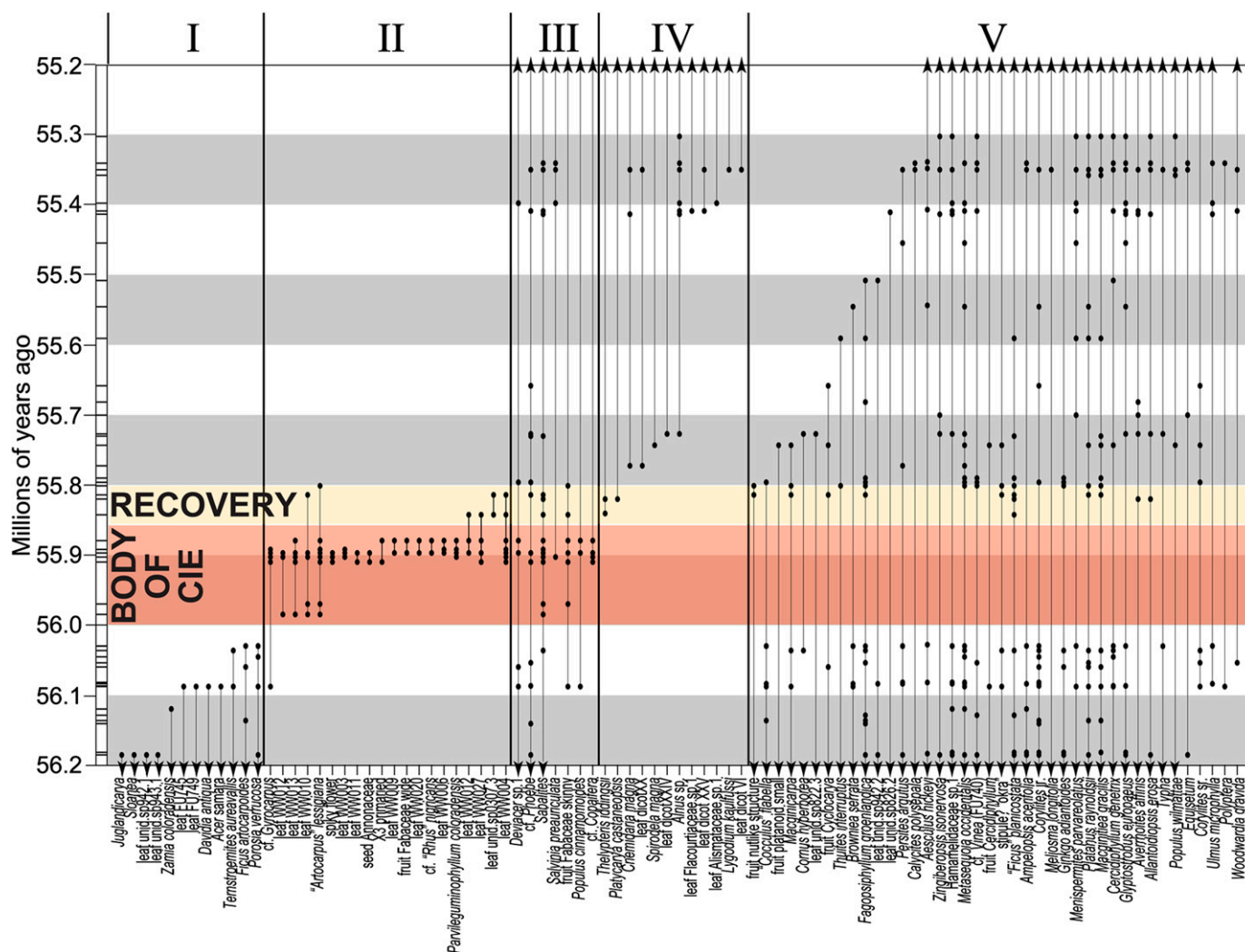Fig. 6. Temporal distributions of 91 common plant fossil taxa in the Bighorn Basin during the Paleocene-Eocene transition. Five types of temporal range are: (I) Paleocene only; (II) wholly or mostly confined to the PETM; (III) long-ranging but also occurring in the PETM; (IV) first appearing in the immediate post-PETM interval; and (V) long-ranging but not present in the PETM.

Paleocene of the Bighorn Basin in spite of alder-like pollen being common in the pollen and spore assemblages, or palynoflora (Harrington, 2001). "*Dombeya*" *novi-mundi* Hickey (Fig. 5A), and *Platycarya castaneopsis* (Lesquereux) Wing & Hickey (Fig. 5D) are also common in post-PETM backswamp assemblages, particularly in the later early Eocene. *Populus cinnamomoides* (Lesquereux) MacGinitie (Fig. 5C) is found in both PETM and later early Eocene assemblages and may have one latest Paleocene occurrence. Backswamp and alluvial ridge sites in the post-PETM Eocene commonly have the ferns *Lygodium kaulfussi* Heer (Fig. 5B) and *Cnemidaria* (*Hemitelia*) *magna* (Knowlton) Hickey (Fig. 5H), which are not known from the Paleocene (Wing, 1998). Some backswamp sites in the early Eocene, and many abandoned channels from the body of the CIE and after, preserved the floating aquatic fern *Salvinia preauriculata* Berry (Fig. 4K), which is not known from the Paleocene. In sum, although several plants species do not cross from the Paleocene to the Eocene (group I) and several other species first appear in the Eocene (group IV), there is strong continuity from the late Paleocene into the post-PETM early Eocene (groups III and V).

In contrast to the strong similarity between late Paleocene floras and those that postdate the body of the CIE, fossil assemblages from within the body of the CIE are almost entirely different from those that precede or follow them. All fossil assemblages from the body of the CIE have this distinctive composition. This is reflected in Fig. 7, where PETM sites occupy a completely different part of the multivariate space than Paleocene and later Eocene floras. The distinctiveness of the PETM floras is the result both of the absence of long-ranging taxa such as those mentioned above (group V), and the presence of many species that are largely confined to the body of the CIE (group II). Among the most common of the PETM plants are three members of Fabaceae: cf. *Copaifera* L. (Fig. 4A), *Parvileguminophyllum coloradensis* (Knowlton) Call & Dilcher (Fig. 4B, C), and an undescribed species with tiny leaflets we informally designate WW020 (Fig. 4D, E). Other common PETM plant species include *Populus cinnamomoides* (Berry) MacGinitie (Fig. 5C), an undescribed pinnately compound leaf we informally designate WW004 (Fig. 4J), cf. *Gyrocarpus* Jacquin (Fig. 4H), "*Artocarpus*" *lessigiana*, and cf. *Rhus nigricans* (Lesquereux)
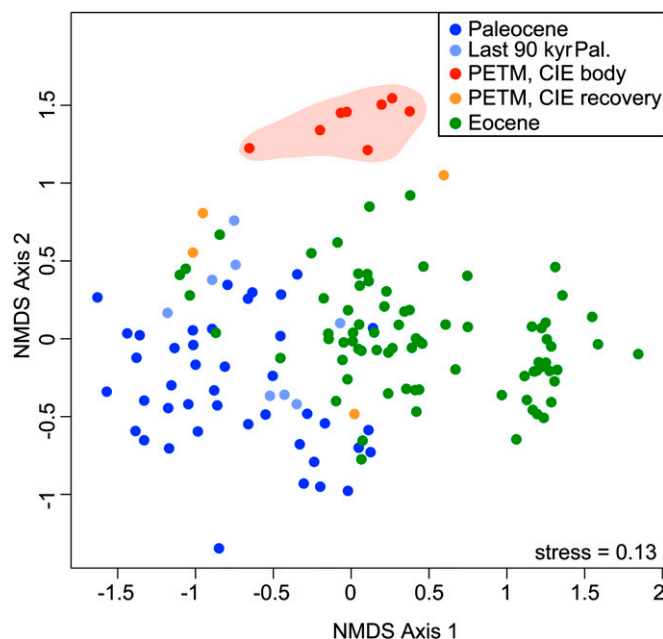
Fig. 7.   Nonmetric multidimensional scaling analysis of the sites by species presence–absence matrix (see online Appendix S3). Sites are coded by age as indicated in the key. Sites from the body of the Carbon Isotope Excursion (CIE) occupy a distinct region of the plot, showing they are compositionally distinct from Paleocene and Eocene sites, which overlap in composition. The two Paleocene sites most similar in composition to the PETM sites are from the last 90 kyr prior to the onset of the CIE.

Knowlton (Fig. 4F). Palm leaf fragments (Fig. 4G; *Sabalites* Saporta sp.) are also ubiquitous in PETM assemblages but less common before and after.
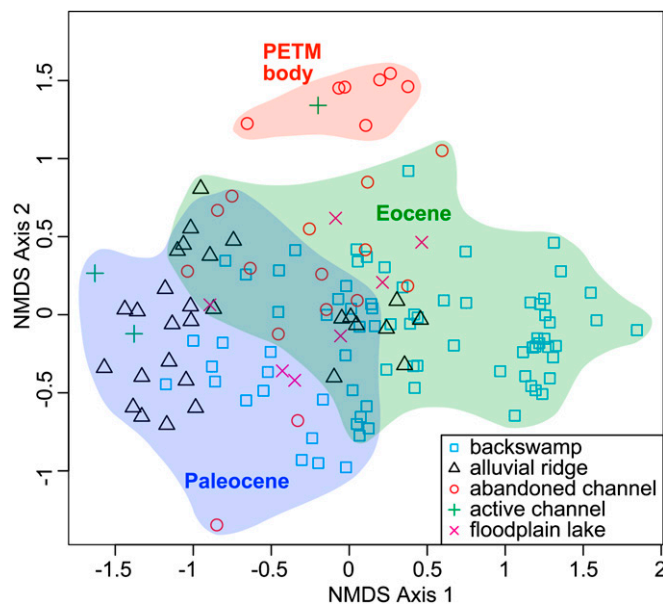

Fig. 8.   Nonmetric multidimensional scaling analysis of the sites by species presence–absence matrix. Sites are coded by depositional environment as indicated in the key. Overlay shapes indicate time-period groupings as in Fig. 7. Environment of deposition influenced floristic composition, but does not overwhelm the pattern of temporal change. See text for additional discussion.
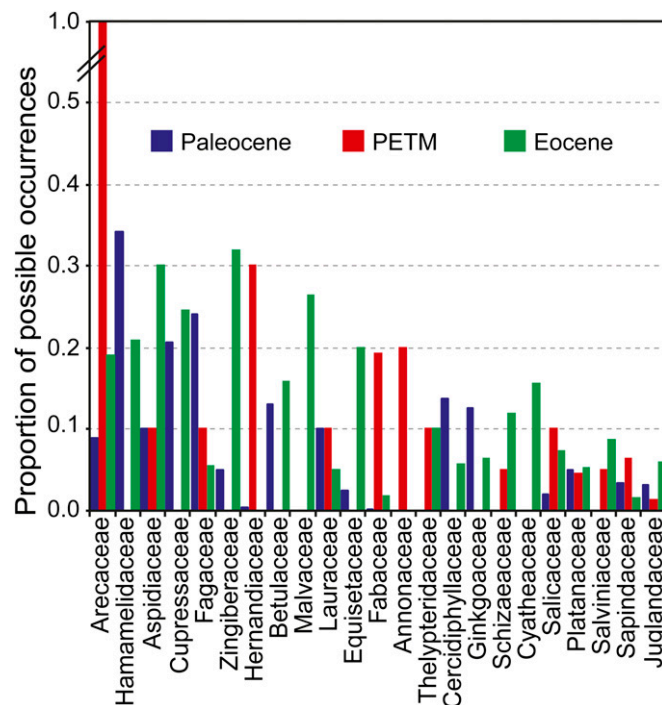

Fig. 9.   Family-level comparison of Paleocene, PETM, and Eocene macrofloras from the Bighorn Basin. The proportion for each family in a time period is calculated as its possible number of occurrences (i.e., the number of occurrences if every morphotype in the family occurred at every site in the time interval) divided by the actual number of occurrences of all morphotypes in the family. See Results section for additional description.

The Paleocene sites with the greatest similarity to those from the body of the CIE are from the last ~90 kyr prior to the PETM (Fig. 7). This similarity results from the first appearances of cf. *Gyrocarpus*, and probably *Populus cinnamomoides* and "*Artocarpus*" *lessigiana* (one specimen each). Interestingly, the Eocene floras with the greatest similarity to those of the PETM do not come from the time immediately following the PETM, but rather from a later, prolonged period of warm climate at about 53 Ma, sometimes called the Early Eocene Climatic Optimum (EECO). The similarity between the PETM and EECO sites reflects shared taxa such as *Populus cinnamomoides* and cf. *Copaifera*, although there are many species present during the EECO that were not present during the PETM, and vice versa.

The ANOSIM analysis demonstrates that the differences in floristic composition described above are greater than would be expected if fossils from each time period were a random sample of a homogeneous flora. Using three a priori groups (Paleocene, PETM and post-PETM Eocene), $R = 0.49$ and $P < 0.001$. Using two a priori groups (PETM and non-PETM) produces a similar result, with $R = 0.47$ and $P < 0.001$.

As mentioned, floras of the same age vary somewhat in composition according to depositional environment, reflecting original heterogeneity of floodplain subenvironments and vegetation. The commonness of the different subenvironments varied through time, for example, backswamps were abundant in the late Paleocene and post-PETM Eocene but are totally absent from the PETM, whereas abandoned channels are more common during the PETM than before or after. If different subenvironments

preserve different types of plants, then changing abundance of subenvironments through time could cause change in floristic composition.

To examine this possibility, we show the same NMDS analysis as in Fig. 7, but with the sites coded by depositional environment rather than by time period (Fig. 8). Although sites from different depositional environments overlap in the two-dimensional NMDS plot, there are different centroids for sites from backswamp, alluvial ridge, and abandoned channel environments. ANOSIM confirms there are significant differences in floristic composition among depositional environments ($R = 0.33$, $P < 0.001$), raising the possibility that the large floristic change we see during the body of the CIE is partly driven by differences in local environments (which could itself be driven by larger climate change). However, when we consider only sites from the abandoned channel environment, we still find a significant difference between Paleocene, PETM and Eocene sites. This ANOSIM yields a higher R (0.73) and equal significance ($P < 0.001$) to the ANOSIM using all sites. Floristic differences among the time periods cannot be explained by changes in depositional environment alone.

To illustrate changes in floristic composition at a higher taxonomic level, we have plotted the proportion of occurrences assigned to each family in the Paleocene, PETM and post-PETM Eocene (Fig. 9). The PETM stands out from the surrounding time intervals in family composition just as it does in species composition. Arecaceae occur at every PETM site, compared with less than 20% of Paleocene and other Eocene sites. Other families that are more ubiquitous during the PETM are Fabaceae, Annonaceae, and Hernandiaceae. Conversely, many families rarely occur in the PETM compared with the Paleocene and post-PETM Eocene. Hamamelidaceae, Cupressaceae, Betulaceae, Cercidiphyllaceae, and Ginkgoaceae are most striking in this regard because they are moderately ubiquitous before and after the PETM, but completely absent during the event.

INTERPRETATION OF PETM FLORISTIC CHANGE IN THE BIGHORN BASIN

The plant macrofossil record from the Bighorn Basin clearly demonstrates that increased atmospheric CO_2, ~5°C of warming, and seasonal or perennial decrease in water availability during the PETM were associated with a major change in the composition of floodplain vegetation. The change in floristic composition during the PETM was evident from the first sites collected (Wing et al., 2005), but the additional sites and taxa reported here confirm the unusual floristic composition of the PETM and demonstrate for the first time that long-ranging taxa reappeared during the recovery phase of the CIE. The additional sites, and persistent distinctiveness of the PETM flora when only abandoned channel assemblages are considered, give us confidence that the floristic changes during the PETM represent real changes in the original floodplain vegetation rather than local changes in the production, transport, preservation, or sampling of plant fossils.

The absence of nearly all common Paleocene species during the PETM (group V taxa in Fig. 6) indicates that they were extirpated or became extremely rare in our study area. Although local extirpation reached very high levels, the reappearance of most Paleocene taxa during the recovery phase of the CIE or in the early post-PETM period indicates that actual extinction rates were low (only group 1 taxa of Fig. 6 are possible extinctions). Because of the strong warming and drying that took place with the onset of the PETM, we infer that the species missing from the PETM were those that preferred cooler and/or more mesic conditions. This is consistent with their family-level affinities in Betulaceae, Juglandaceae, Cupressaceae, and other clades that have many extant species in warm-temperate, mesic climates. Although most mesic species were locally or regionally extirpated during the PETM, other populations of the same species must have survived at higher elevations or farther north and recolonized the floodplains of the Bighorn Basin as climate became cooler and wetter again during the recovery phase of the CIE. Current evidence helps little to distinguish high-elevation from high-latitude refugia for these group V species. Some lineages (e.g., Juglandaceae, Betulaceae, and Cupressaceae) are present in PETM palynofloras (Wing et al., 2005). These pollen grains might have been eroded from underlying Paleocene sediments and redeposited during the PETM, or alternately, they might have been produced by populations of mesic species that survived the PETM in montane refugia surrounding the Bighorn Basin.

Plants that are for the most part temporally restricted to the PETM (group II taxa in Fig. 6) presumably extended their ranges northward onto Bighorn Basin floodplains as CO_2 increased and climate warmed and became drier near the onset of the CIE. These northward range extensions are difficult to document because macrofossil assemblages from the latest Paleocene of the southern United States and Mexico are not well known or dated. The distinctive pinnately lobed leaf type "*Artocarpus*" *lessigiana* is, however, widely distributed in Late Cretaceous and Paleocene rocks of the southern Rocky Mountains and Gulf Coastal Plain (Berry, 1916; Knowlton, 1930; Ellis et al., 2003). It is also present at most PETM sites in the Bighorn Basin, but absent from the Paleocene with the possible exception of one specimen from the youngest pre-PETM sample. The geographic and temporal distribution of "*Artocarpus*" *lessigiana* is consistent with a northward range extension of many hundreds of kilometers at, or shortly before, the onset of the PETM, but it is difficult to constrain the rate of range change.

The climatic preferences of close living relatives of PETM plants might aid interpretation of climatic changes. We only know the affinities of three taxa below the level of family, of which two have extant relatives living in dry tropical forest. Fossils here referred to as cf. *Copaifera* probably belong to the genus *Copaifera*, which is widely distributed from southern Mexico and the Caribbean to Paraguay and includes four species in Africa (Renner, 2004). Many living *Copaifera* species inhabit seasonally dry tropical climates, and though some tolerate seasonally wet soils, are less likely to grow in permanently waterlogged soils (Oliveira-Filhoa and Ratter, 1995; Teixeira et al., 2008). PETM fossil leaves and fruits with strong resemblance to the pantropical genus *Gyrocarpus* (Hernandiaceae) are currently under study (Manchester and Wing, 2012). Living species of *Gyrocarpus* commonly occur in tropical climates with a strong dry season (Michalak et al., 2010). *Populus cinnamomoides* is less obviously tied to dry tropical climate, with many extant, recently diverged species in the genus having north temperate distributions (Levsen et al., 2012). *Populus cinnamomoides*, though, is an early diverging lineage in a clade that is largely tropical (Manchester et al., 2006).

Many taxa common in the PETM of the Bighorn Basin, including the three just mentioned, are very similar or identical to taxa described from late early Eocene deposits in the Green River Fm. of southern Wyoming, Colorado, and Utah. (Bighorn Basin leaves called cf. *Copaifera* are nearly identical to *Swartzia wardelli* MacGinitie, cf. *Gyrocarpus* is probably equivalent to *Lindera varifolia* MacGinitie (Manchester and Wing, 2012), cf. "*Rhus*" *nigricans* is similar to "*Rhus*" *nigricans*, and *Parvileguminophyllum coloradensis* and *Populus cinnamomoides* are probably present in both formations.) The Green River Fm. is a dominantly lacustrine unit, but both evaporitic deposits and paleobotanical evidence indicate the climate was warm and at least seasonally dry (Macginitie, 1969; Smoot, 1983; Wilf, 2000). Regardless of systematic affinities, the size and shape features of PETM leaves in the Bighorn Basin are most similar to those seen in living dry tropical forests (Peppe et al., 2011). The stratigraphic distributions of many PETM species are also consistent with a preference for warm, seasonally dry climate because they are absent from the Bighorn Basin during the cooler, wetter periods of the early Eocene and reappear during the globally warm phase near the end of the early Eocene (EECO of Zachos et al., 2001).

In sum, there is considerable evidence that the species that appeared in the Bighorn Basin during the PETM preferred seasonally dry tropical climates, that they arrived in the area as close to the onset of the event as can be expected given the constraints of sampling, and that their local populations in the Bighorn Basin were extirpated as temperature declined and soils became wetter during the recovery phase of the CIE. Like most of the Paleocene species that were locally extirpated at the onset of the CIE, then returned to the Bighorn Basin afterward, most of the thermophilic species of the PETM did not go extinct when climate cooled after the PETM. Rather, they persisted elsewhere during the cooler part of the early Eocene (Wing et al., 2000), then returned to the Bighorn Basin several million years later during the EECO.

Two taxa with first appearances in the recovery phase of the CIE deserve special mention. The juglandaceous genus *Platycarya* Siebold & Zuccarini (Fig. 5D) has long been associated with the base of the Eocene in North America (Frederiksen, 1979; Wing, 1984b), but our more detailed record now shows that the first appearance of the genus (both pollen and leaf fossils) was during the recovery phase of the CIE, 150–200 kyr after the beginning of the Eocene (Wing et al., 2003, 2005). Pollen similar to *Tilia* L. [referred to *Intratriporopollenites instructus* (Potonié) Thomson and Pflug] also has a first appearance in Wyoming during the recovery phase of the CIE (Harrington, 2001; Wing et al., 2003). Both *Platycarya* and *I. instructus* are known from the Paleocene of western Europe (Harrington, 2003), so although their intercontinental range expansion across Arctic land bridges may have taken place during the PETM, their spread to the midlatitudes in the Rocky Mountains was delayed until the waning phase of the hyperthermal. Northern Wyoming may have been too hot and/or dry for these plants during the body of the CIE.

A narrow focus on the onset of the CIE may overestimate the concentration of climatic and biotic change occurring at that time. Secord et al. (2010) presented carbon and oxygen isotopic data from mammalian teeth and soil nodules that suggest warming of as much as 5°C in the Bighorn Basin during the 10–50 kyr prior to the onset of the CIE. Changes in fossil soil horizons in the uppermost 10–15 m of Paleocene rocks in the southeastern

Bighorn Basin also give evidence for drying and warming in the tens of millennia prior to the onset of the CIE (Wing et al., 2009; Kraus et al., 2013). Shallow shelf marine sediments in New Jersey also indicate substantial warming in the oceans during the last millennia before the CIE (Sluijs et al., 2007). Some of the plant extirpation and colonization events that appear to take place at the onset of the CIE in the Bighorn Basin might be spread over the last 30 kyr of the Paleocene; we lack fossil sites from this period that could detect floristic change during the pre-PETM warming. Even with current sampling, the single occurrences of cf. *Gyrocarpus* and *Populus cinnamomoides* approximately 100 kyr before the onset of the CIE suggest that floral changes seen strongly at the onset of the event were already beginning.

So far we have discussed floristic change in the context of climatic change during the PETM, but the large (70–400%) increase in atmospheric concentration of CO_2 that caused the climate change (Zeebe et al., 2009; Cui et al., 2011) could also have had direct effects on terrestrial vegetation. Direct results of higher CO_2 expected and/or observed in living plants include higher growth rates (Körner et al., 2005; McMahon et al., 2010), increased water-use efficiency (Lockwood, 1999; Schäfer et al., 2002; Körner, 2003), higher thermal tolerance (Wang et al., 2012), and higher N demand (Nowak et al., 2004; Hoosbeek et al., 2011). Increases in plant productivity and water-use efficiency caused by higher CO_2 concentrations may also increase soil moisture and carbon storage (Heath et al., 2005; Hoosbeek et al., 2011), though the relationships are complex (Schäfer et al., 2002).

Several changes in plants, soils, and sediments during the PETM in the Bighorn Basin and other parts of the Rocky Mountains speak to expectations from the physiological models and experiments mentioned. The great increase in the ubiquity (and abundance) of Fabaceae during the body of the PETM is consistent with the prediction and observation that plants with N-fixing symbionts are more successful under higher CO_2 concentration because they are less limited by soil nitrogen (Nowak et al., 2004).

Changes in PETM sediments and fossil soils have been interpreted as the result of highly intermittent stream flow and less stable floodplains (Foreman et al., 2012; Kraus et al., 2013). Flashy stream discharge could result from less rapid soil water uptake by plants whose stomata have closed in response to higher CO_2, an effect that has been invoked to explain similar sedimentological changes at the Triassic-Jurassic boundary (Steinthorsdottir et al., 2012). Although legume dominance and flashy stream discharge are expected effects of higher CO_2 concentration, they could also be explained solely by more seasonal precipitation and water stress during the PETM.

Some studies of extant systems show higher atmospheric CO_2 concentration can increase plant productivity and soil moisture, resulting in more soil organic matter (Heath et al., 2005; Hoosbeek et al., 2011). The evidence from fossil soils during the PETM is not consistent with this prediction; instead PETM soils suggest greater fluctuation in water tables and overall drier soils containing less organic matter (Kraus and Riggins, 2007; Adams et al., 2011; Kraus et al., 2013). The decrease in soil organic matter during the PETM may reflect drier soils, but also summer temperatures as high as 35°–40°C (Snell et al., 2013), and accelerated soil respiration during the PETM and the immediately preceding part of the Paleocene (Secord et al., 2010).

Evidence for direct effects of increased CO_2 concentration on plants, soils, and terrestrial ecosystems during the PETM is equivocal. Increases in abundance, diversity, and ubiquity

of Fabaceae, as well as increases in herbivore feeding rate (Currano et al., 2008), are consistent with higher CO_2 levels but also with climate change. Decreases in organic carbon and other soil features are not consistent with higher NPP and wetter soils caused by higher CO_2, but increases in temperature and seasonality of precipitation might have overwhelmed the direct effects of CO_2.

FLORISTIC CHANGE DURING THE PETM IN OTHER REGIONS

The Bighorn Basin is the only area with a stratigraphically dense record of plant macrofossils through the late Paleocene and early Eocene that is also firmly correlated to the CIE. Having a record from only one region, though, severely limits understanding of a global event like the PETM. Climate change at the PETM,

particularly precipitation, varied with latitude and proximity to coastlines (Winguth et al., 2010; Huber and Caballero, 2011). Therefore we summarize here floristic changes in other parts of the world (Table 1; Fig. 10). These sites vary in terms of the confidence with which they can be correlated to the PETM, but most have evidence of the CIE, and all have been correlated to the Paleocene-Eocene boundary interval through regional or global biostratigraphy.

Southwest Pacific—The region with the greatest density of plant sites spanning the PETM is New Zealand. During the PETM, New Zealand was at high middle southern latitudes (50–55° S) and was a low-lying, isolated land mass. The southwest Pacific had exceptionally warm surface water for its latitude, even given the overall low latitudinal temperature gradients of the Paleogene greenhouse world (Hollis et al., 2009). High

TABLE 1.   Summary of site information and patterns of floristic change at PETM sites.

| Map no.	Nation/Ocean	Site	Latitude	Longitude	Paleoenvironment	Fossil type	PETM change
1	Arctic	Lomonosov Ridge, IODP 302, Hole 4A	88	136	Open marine	Palynoflora, biomarkers	Conifer decrease, thermophilic angiosperm increase
2	Spitsbergen	Nordenskiøldfjellet	78	15	Marine	Palynoflora	Conifer decrease
3	North Sea	Core 22/10a-4	58	2	Deep marine, restricted basin	Palynoflora	Conifer decrease, thermophilic angiosperm increase
4	Belgium	Hoegaarden	51	5	Paludal, coastal plain	Wood	No data on change, dominated by Cupressaceae during PETM
4	Belgium	Kallo Borehole	51	4	Lagoonal/shallow marine	Palynoflora	Minor change, abundant reworked pollen
5	England	Cobham lignite	51	0	Paludal, coastal plain	Palynoflora, charcoal mesofossils	Minor change, abundant Cupressaceae, decrease in fire frequency
6	Austria	St. Pankraz	48	13	Open marine	Palynoflora	Minor change, abundant reworked pollen
7	US	Farmers Butte, ND	47	−102	Floodplain	Palynoflora	Minor change, appearance of European immigrants
8	US	Chalk Butte, WY	44	−106	Floodplain	Leaves, palynoflora	Minor change, European immigrants in CIE recovery
9	US	Bighorn Basin, WY multiple sections	44	−108	Floodplain	Leaves, palynoflora	Major extirpation of temperate plants, immigration of dry tropical forms
10	Spain	Ermua section	43	2	Open marine	Palynoflora	Conifer decrease, thermophilic angiosperm increase
11	USA	Oak Grove Core, VA	38	−77	Shallow marine-shelf	Palynoflora	Minor change, European immigrants in recovery phase
12	USA	Harrell core, MS	32	−89	Near shore shallow marine	Palynoflora	35% extinction?
13	Colombia-Venezuela	multiple cores	8	−72	Coastal plain-prodelta	Palynoflora	Diversity increase within tropical lineages
14	Tanzania	Tanzania Drilling Project Site 14	−9	40	Open marine, outer shelf-upper slope	Palynoflora, biomarkers	Minor change, evidence of longer dry periods
15	New Zealand	Tawanui	−40	176	Open marine, upper slope	Palynoflora	Minor change, abundant reworked pollen
15	New Zealand	Tui-1	−40	173	Near shore marine	Palynoflora	Thermophilic angiosperm increase
15	New Zealand	Kumara	−43	171	Paludal, coastal plain	Palynoflora	Conifer decrease, thermophilic angiosperm increase
15	New Zealand	Kakahu	−45	170	Paludal, coastal plain	Palynoflora, leaves, cuticle, charcoal mesofossils	Conifer decrease, thermophilic angiosperm increase
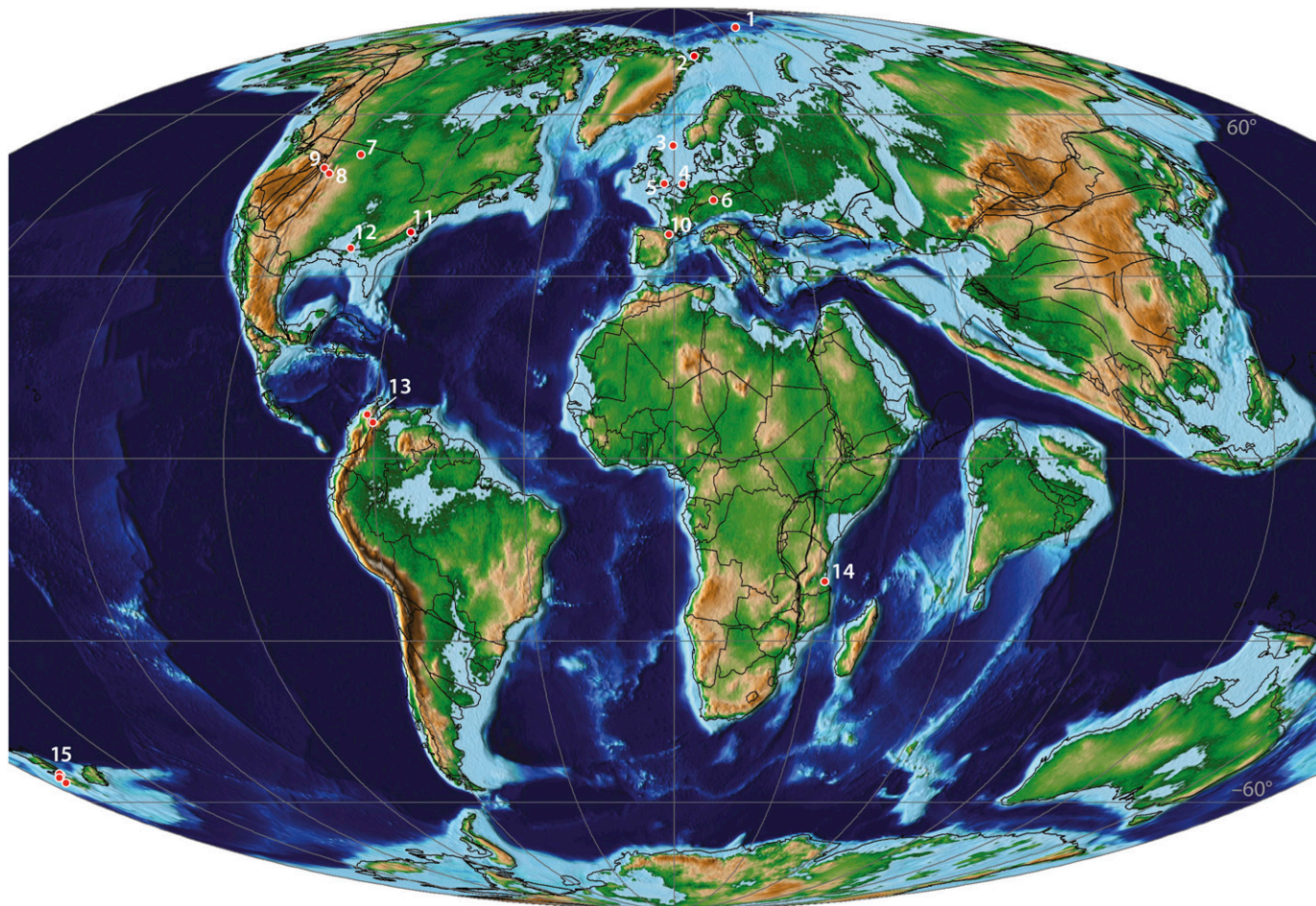
Fig. 10.   Global paleogeographic reconstruction for 56 Ma showing positions of sites in Table 1 and mentioned in text. Paleogeographic positions from C. Scotese, PALEOMAP project.

southern latitudes are thought to have experienced even hotter, wetter climate during the PETM than before or after (Robert and Kennett, 1994; Crouch, et al., 2003; Crouch and Brinkhuis, 2005).

Palynofloras from the Kumara-2 core on the western side of the South Island record moderate change in floristic composition across the PETM. Changes at the onset of the CIE include the first occurrences of the tropical mangrove palm *Nypa* Steck., and *Cupaneidites* Cookson & Pike, a thermophilic eudicot probably belonging to Sapindaceae, along with an increase in the abundance of other probable warm-climate eudicots in the families Malvaceae and Myrtaceae (Crouch et al., 2009; Handley et al., 2011). Also at the onset of the PETM there was a decline in the abundance of probable temperate elements such as podocarpaceous conifers and Proteaceae (Crouch et al., 2009; Handley et al., 2011). Conifer abundance increased upward into the latter part of the PETM, and overall the palynoflora returns to a composition similar to that seen in the late Paleocene, though with thermophilic pollen types being less abundant (Handley et al., 2011). The higher abundance of oleananes, a biomarker for angiosperms, near the base of the PETM is consistent with the pollen flora (Handley et al., 2011.

The Tawanui outcrop near the south end of the North Island preserves terrestrial pollen and spores in a deep marine environment not far from the paleoshoreline, but all terrestrial

fossils underwent considerable transport prior to preservation (Crouch and Visscher, 2003). In general, the proportion of terrestrial pollen and spores increased during the PETM, which is taken as an indication of higher runoff. Crouch and Visscher (2003) considered the pollen and spores to represent four types of vegetation: conifer-dominated rainforest with abundant podocarps, lowland rainforest with Casuarinaceae, heathlands dominated by ferns, and *Nypa*-dominated mangrove forest. During the PETM, there were relatively minor changes in the proportions of species or vegetation types to one another.

Dispersed cuticle, leaf fossils, and pollen and spores from the coal-bearing Kakahu region on the east side of the South Island are also thought to record changes across the PETM, though the correlation to the Paleocene-Eocene boundary is by pollen/ spore biostratigraphy and a carbon isotope record is lacking (Pole, 2010). Pollen indicate a shift from conifer- to angiosperm-dominated vegetation with abundant grains linked to Casuarinaceae (Pole, 2010). Fossil charcoal is also exceptionally abundant in the sediments thought to be deposited during the PETM, raising the possibility that intervals of wet climate, during which thick coal seams formed, alternated with periods dry enough for wildfire (Pole, 2010).

Two factors suggest that New Zealand might have been buffered from climatic and floristic changes during the PETM. The isolation

of New Zealand from other land masses (Crouch and Visscher, 2003) would have made dispersal to the island difficult, limiting the number of immigrant taxa. Furthermore, changes in temperature and precipitation might have been subdued compared with many other parts of the earth because of maritime buffering of temperature change and the short distances that water vapor would have to travel from sea-surface to land. Subdued floristic change during the PETM is to be expected in such a protected environment.

Low latitudes—The low-latitude record of floristic change across the PETM is restricted to three areas: subtropical East Africa, tropical South America, and subtropical North America.

Cores of nearshore marine sequences from Tanzania preserve palynofloras and plant biomarkers from the Paleocene-Eocene boundary at ~18°S (Handley et al., 2012). There are no obvious changes in palynofloral composition across the PETM, but there are major fluctuations in the chain length of higher plant epicuticular waxes (*n*-alkanes) that may signal shifts in the composition of the vegetation or in climate (Handley et al., 2012). An increase in the deuterium to hydrogen ratio of *n*-alkanes has been interpreted as reflecting greater evapotranspiration and plant water-use efficiency, and other lines of evidence suggest episodic heavy rainfall and higher rates of erosion (O'Halloran et al., 2010; Handley et al., 2012).

Palynofloras from paleotropical Colombia and Venezuela provide our only record of tropical rainforest during the PETM (Jaramillo et al., 2010). Broad-scale studies have demonstrated that floristic diversity increased strongly from the Paleocene to the Eocene in northern South America, with the new forms arising within existing tropical lineages (Jaramillo, 2002; Jaramillo et al., 2006). Higher resolution studies show that the rate of diversity increase inflects upward at the time of the PETM, indicating that global warming did not exceed the heat tolerance of these plants living near the equator (Jaramillo et al., 2010). Carbon isotope data are, however, consistent with higher water stress on tropical plants during the PETM. The negative CIE measured in leaf waxes from this area is small (2–3‰) compared with the approximately −5‰ CIE measured in leaf waxes from other regions (McInerney and Wing, 2011). The small CIE could reflect increased closure of stomata during the PETM to conserve water, which would have slowed diffusion of atmospheric CO_2 into leaves, decreasing their discrimination against ^{13}C, thereby partially offsetting the decrease in the carbon isotopic composition of the atmosphere (Jaramillo et al., 2010).

Studies of pollen from marginal marine deposits in the Gulf Coastal Plain of the United States (about 35°N paleolatitude) initially suggested a 35% decrease in plant diversity across the PETM (Harrington and Jaramillo, 2007). The decrease in diversity was attributed to extinction of plants that were unable to survive the higher temperatures of the PETM and the inability of plants adapted to hot climates to disperse to the southern shores of North America from across the Tethys Seaway (Harrington and Jaramillo, 2007). More recent work may indicate a minor hiatus in deposition during part of the PETM in this area (van Roij, 2009) and raises the possibility that the diversity decline occurred in post-PETM time, which would coincide with a cooling, rather than warming, climate phase (Wing et al., 2000).

The response of tropical lowland vegetation to the PETM is of particular interest because of the high average temperatures in the tropics (Winguth et al., 2010; Huber and Caballero, 2011). Huber (2008) suggested that initial PETM warming

exceeded the physiological tolerances of tropical plants, resulting in a die-off of terrestrial vegetation, which in turn contributed more carbon to the ocean and atmosphere upon decay. Although all known low-latitude paleobotanical records for the PETM are coastal and thus would have had more equable climates than continental interiors, there is no evidence for major extinction or dieback of tropical plants during the PETM.

Europe and the North Sea—A number of middle latitude sites in western Europe preserve records of floristic change during the PETM. Schmitz and colleagues (Schmitz et al., 2001; Schmitz and Pujalte, 2003) recovered terrestrial palynomorphs from deep marine deposits near Ermua in the Tremp Basin of northern Spain (~37°N paleolatitude). The samples are depauperate, probably because of the marine environment, but still give some insight into vegetational change during the PETM. The most common pollen type in the late Paleocene just below the PETM is that of Cupressaceae, *Taxodiaceapollenites hiatus* (Potonié) Kremp. Angiosperm palynomorphs are markedly more diverse within the PETM than below or above it, and nine of the species in the PETM are found only at that time. The most abundant sporomorphs within the PETM are ferns, although angiosperms are also common (Schmitz et al., 2001; Schmitz and Pujalte, 2003). Sedimentological data and fossil pollen/spores from multiple stratigraphic sections across the Tremp Basin suggest that late Paleocene coastal swamps dominated by cupressaceous conifers gave way to angiosperm–fern vegetation growing in a climate with extreme variation in water availability during the PETM (Schmitz et al., 2001; Schmitz and Pujalte, 2003, 2007).

The St. Pankraz outcrop in the Austrian Alps preserves deep marine sediments deposited near the north shore of Tethys at the time of the PETM (Hofmann et al., 2011). As in many marine depositional settings, reworked Cretaceous and Paleocene pollen and spores are common along with those thought to be derived from plants living during the PETM (Hofmann et al., 2011). Only two samples in this stratigraphic section are from within the PETM, but they document the first occurrences of three Eocene pollen types. Cupressaceous pollen is rare in the PETM samples, and overall the palynoflora is consistent with a warm, humid but not tropical climate (Hofmann et al., 2011).

During the late Paleocene-early Eocene, northern Europe from Germany to England was a low-lying coastal plain supporting paludal, lagoonal, and shallow marine environments, and small fluctuations in sea level alternately inundated or exposed vast areas (Collinson et al., 2003; Fairon-Demaret et al., 2003; Steurbaut et al., 2003). Freshwater swamps around the fringes of the marine environment were generally dominated by cupressaceous conifers, probably related to *Glyptostrobus* (Fairon-Demaret et al., 2003). The Kallo borehole in Belgium produced a succession of palynofloras from the late Paleocene, PETM, and early Eocene (Steurbaut et al., 2003). Throughout the core, reworked pollen and spores are common, and small fluctuations in sea level on the shallow shelf generated large variations in the relative proportion of marine and terrestrial palynoflora (Steurbaut et al., 2003). Overall the terrestrial flora is composed of Cupressaceae, Juglandaceae, Myricaceae, Tiliaceae, and palms—a typical mix for the subtropical greenhouse vegetation of northern Europe at this time. There are no major changes in the composition of terrestrial vegetation associated with the PETM (Steurbaut et al., 2003).

The Cobham Lignite of southeastern England represents highly organic deposition in a coastal swamp near the time of

the Paleocene-Eocene boundary (Collinson et al., 2003, 2009). Carbon isotope measurements through the 2-m-thick lignite are thought to indicate that the onset of the CIE occurred during its deposition, and biostratigraphic correlation confirms that the lignite formed at about the time of the PETM. Pollen and spores from the Cobham Lignite reveal few last appearances of common taxa at the PETM onset and only minor shifts in relative abundances (Collinson et al., 2009). The floristic composition of PETM samples can be statistically distinguished from late Paleocene samples, but this is thought mostly to reflect a decrease in fire frequency and an increase in the wetness of the substrate, including an increase in the abundance of cupressaceous conifers (Collinson et al., 2009), which contrasts with the decrease in conifer abundance seen in many PETM sections.

Core 22/10a-4 from the North Sea, north of Britain, preserves the PETM in organic-rich marine sediments that were deposited in a restricted marine environment surrounded by Scandinavia, Britain, and Greenland during rifting of this part of the North Atlantic (Kender et al., 2012). The late Paleocene is dominated by pollen of cupressaceous and pinaceous conifers, but their abundance drops sharply just before the onset of the CIE, and the proportion of alder (*Alnipollenites* Potonié) pollen rises, along with ferns and fungal spores (Kender et al., 2012). Alder pollen declines later in the PETM and hickory-type pollen (*Caryapollenites* G. V. Raatz ex R. Potonié), and moss spores become abundant. The decrease in cupressaceous pollen near the onset of the PETM was attributed to changes in coastal plain area, changes in temperature and precipitation regime, or both (Kender et al., 2012).

Most European stratigraphic sections that preserve the PETM were deposited in marine environments where palynofloral composition is strongly influenced by distance to shoreline, dispersability of pollen, and differential preservation of various pollen types. Most contain substantial amounts of reworked material, which may well smooth out short-lived changes in terrestrial flora associated with the PETM. The records from Cobham and the North Sea appear to have the least reworked material, but they record essentially opposite floristic changes (increase vs. decrease in cupressaceous conifers, respectively), leaving it difficult to generalize about northern European vegetational change during the PETM.

The Arctic—Two cores of marine sediments have yielded terrestrial palynomorphs from the PETM in the Arctic, one from central Spitsbergen at ~70°N paleolatitude (Harding et al., 2011) and the other from the Lomonosov Ridge of the central Arctic Ocean at ~80°N paleolatitude (Sluijs et al., 2006, 2008; Schouten et al., 2007). The Spitsbergen palynoflora has only rare angiosperm pollen, but there is an abundance peak of the fern spore *Cicatricosisporites* Potonié & Gelletich near the base of the PETM, ~5 kyr following the onset, which could be consistent with increasing wetness (Harding et al., 2011).

Palynofloras from Lomonosov Ridge generally have abundant conifer pollen during the late Paleocene, but dominance shifts to angiosperms during the PETM (Sluijs et al., 2006), a pattern somewhat at odds with that in biomarkers, which suggest decreases in both gymnosperm and angiosperm abundance during the CIE (Schouten et al., 2007). The isotopic composition of angiosperm- and gymnosperm-specific biomarkers suggests that water-use efficiency of angiosperms decreased during the PETM, while that of conifers remained unchanged (Schouten et al., 2007). In contrast to evidence of dryness and fluctuating discharge at midlatitudes, high latitudes appear to have been wetter as well as warmer during the PETM, and continental runoff was high (Pagani et al., 2006b; Sluijs et al., 2006; Cui et al., 2011; Dypvik et al., 2011; Harding et al., 2011; Kender et al., 2012).

DISCUSSION AND CONCLUSIONS

Several key conclusions emerge from synthesizing the results of our detailed study of floristic change through the PETM in the Bighorn Basin with other results from around the globe. First, there is no evidence for dramatically increased rates of extinction among terrestrial plants at the time of the PETM in any region or local stratigraphic section. This is not a trivial result, because some groups of organisms, notably benthic foraminifera, did experience extinction rates of 35–50% during the PETM (Thomas, 2007).

Second, in the Bighorn Basin, rates of local extirpation were exceptionally high. Eighty-eight percent (46 of 52) of plant taxa present in the last 100 kyr of the Paleocene are not recorded in the PETM, and four of those that are present in the PETM are known only from the recovery phase of the CIE, as CO_2 concentration was declining and climate became cooler and wetter again. Local extirpation is not seen in other PETM floral records. These extirpations might be hard to detect in palynofloras, which have lower taxonomic resolution and are more subject to reworking and thus smearing of temporal patterns, but it is also possible that the vegetation of continental interiors was more affected than that of the coastal regions from which the pollen records come.

Third, the Bighorn Basin record shows very high levels of range extension, with only 23% (6 of 26) of plants in the PETM having earlier occurrences in the region. A few of these range extensions were clearly intercontinental, with the lineages present in Europe prior to their occurrences in North America. As with the extirpations, range extensions are not prominent in the pollen and spore data from elsewhere in the world, but a combination of lower taxonomic and temporal resolution could be disguising the pattern. Some tropical range extensions are seen even on the isolated landmass of New Zealand.

Fourth, the botanical affinities and foliar physiognomy of the winners and losers during the PETM in the Bighorn Basin suggest higher temperature and increased water stress in midlatitude continental interiors during the PETM, as do geological lines of evidence. This contrasts with high latitudes, where water availability and runoff appears to have been higher during the PETM. Evidence from the tropics is equivocal.

Fifth, most records of floristic change show that conifers decreased in abundance near the onset of the PETM wherever they had formerly been abundant; this includes decreases in Podocarpaceae in New Zealand and declines in Cupressaceae in the middle to high latitudes of the northern hemisphere in regions that remained wet (the Arctic and North Sea) as well as those that became drier (Wyoming, Spain). The simultaneous decline in abundance of different lineages of conifers in different regions with different precipitation regimes raises the possibility that higher temperatures were an underlying cause. There is little evidence from studies of extant conifers that they would be competitively disadvantaged by higher CO_2 (Hyvönen et al., 2007). Possibly conifers were less able than angiosperms to increase growth rates under higher temperatures and higher rates of evapotranspiration (Lusk et al., 2003; de Boer et al., 2012).

The value of the fossil record of the PETM is that it provides data on the integrated long-term response of real, fully complex ecosystems to a major increase in CO_2 and temperature. The results of the PETM "experiment" indicate that at rates of environmental forcing that are probably 1/10th to 1/20th those predicted for the near future, the dominant mode by which plants responded was through range change. Low levels of plant extinction during the PETM imply that plant populations were able to disperse to refugia and persist there for >100 kyr. The vast difference in rate between the PETM and future climate change complicates our efforts to use the past as a way of understanding the future; nevertheless, the PETM example shows that large, slow (by anthropogenic standards) changes in climate did not cause high levels of extinction among the abundant and widespread species of plants that make up the fossil record.

Projections of the effects of anthropogenic global warming on terrestrial plants are controversial, but some models anticipate high levels of extinction (15–30%) during the decades and centuries ahead under climate scenarios that anticipate far less warming than occurred during the PETM (Thomas et al., 2004). At first blush, one might think that the high extinction rates anticipated for the future reflect much faster climate change, but this cannot be the reason because such models assume infinite dispersal capacity even in scenarios that produce substantial extinction. Extinction is predicted because the climatic envelopes of many species are not projected to exist anywhere in the future.

How can this apparent contradiction between modeling and the fossil record be resolved? Montane regions surrounding the Bighorn Basin might have provided nearby refugia for cool-adapted plants, reducing extinction rates, but such altitudinal refugia cannot explain the low extinction rates seen in all other PETM records. Alternately, the low extinction observed at the PETM in the Bighorn Basin, as well as in other regions, might be misleadingly low because the rare species with small ranges that are most vulnerable to climatically driven extinction are also very unlikely to be sampled. It might also be that extinction rates for extant plants are overpredicted by methods that assume the current climate region occupied by a species is a full expression of its climatic tolerances. If current distributions reflect competition, disturbance, and history as well as climatic limitation, many species may survive better under climate change than would be predicted by models that assume a strict climate envelope derived from the current distribution.

We cannot yet resolve the apparent contradiction between models and the fossil record, but it is worth a much greater effort to improve the record of plant response to past global climate change and to improve our ability to compare models and data. Data about the past are hard to get and hard to interpret, but data about the future are impossible to get without waiting an unacceptably long time.

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