

Floral and environmental gradients on a Late Cretaceous landscape

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Abstract. We describe an in situ fossil flora of Late Cretaceous age (~73 Ma [mega-annum or million years]) from Big Cedar Ridge in central Wyoming, USA, which we sampled using a modified line-intercept method to quantify the relative abundances of 122 taxa at 100 sites across 4 km of exposed sedimentary deposits. We also measured three physical variables at each site: paleotopographic level, grain size, and total organic content. Paleoenvironmental conditions and paleofloral composition at Big Cedar Ridge covary strongly and are highly heterogeneous on small spatial scales. The reconstructed vegetation has some similarities with extant topogenous fens, but also important differences. Non-monocot angiosperms were abundant only on wet, mineral substrates that had been disturbed shortly before preservation, consistent with the weedy life histories that are inferred for their Early Cretaceous ancestors. Many non-monocot angiosperms grew in small, dispersed populations, consistent with the hypothesis that they were biotically pollinated. Overall, non-monocot angiosperm abundance was low compared with many modern wetlands. A single species of coryphoid palm was the dominant on moist, stable, moderately organic-rich sites, a pattern seen in some subtropical to tropical wetlands in the present day. Fern thickets at Big Cedar Ridge occupied highly organic, possibly low-nutrient substrates, and were dominated by Dipteridaceae, Gleicheniaceae, Schizaeaceae, and Matoniaceae. The overall high diversity and abundance of pteridophytes is unusual in the context of modern vegetation, regardless of climate zone, and probably represents a late occurrence of pteridophyte-dominated vegetation that was common earlier in the Mesozoic. Plant distributions at Big Cedar Ridge combine aspects of pre-angiosperm and modern vegetation in a way that suggests both niche conservatism and niche evolution on geological time scales.

Key words: *angiosperms; Big Cedar Ridge, Wyoming, USA; disturbance; ferns; nutrient stress; paleoecology.*

INTRODUCTION

As phylogenetic data, techniques, and understanding have improved rapidly in recent years, it has become increasingly common to reconstruct the ecological history of groups using phylogenetic trees derived from analyses of living species (e.g., Feild et al. 2004, 2009, Davis et al. 2005, Wang et al. 2009). The basic procedure is to develop a phylogenetic tree from genetic sequence data, calibrate it to geological time using well-dated fossils of known phylogenetic position, score the terminals for an ecological trait, and then infer from parsimony or likelihood analyses the ecological preferences of dated nodes. Phylogenetic insights of this kind have led, for example, to the hypothesis that the earliest angiosperms were small woody plants of disturbed,

understorey sites in wet climates (Feild et al. 2004, 2009), to the proposition that angiosperm-dominated forests arose in the mid-Cretaceous (Davis et al. 2005, Wang et al. 2009), and to the idea that the most diverse clades of living ferns radiated in low-light environments under angiosperm canopies in the Late Cretaceous and early Cenozoic (Schneider et al. 2004, Schuettpeitz and Pryer 2009). Although the phylogenetic approach has many advantages, the ecological traits of living species exert a strong influence on conclusions about the ecology of extinct taxa. In particular, if the ecological traits or preferences of the extinct species in a group were outside the range encompassed by their living descendants, phylogenetic reconstructions will be incorrect, and this is particularly likely in lineages that are old enough to have many extinct species. Discovering if and how the past really is different from the present still requires data from the fossil record.

The purpose of this paper is to demonstrate the large amount of paleoecological information that can be

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deduced from study of an in situ fossil flora, and to give insight into landscape-scale patterns of floral distribution in the Late Cretaceous. We are particularly interested in Cretaceous vegetation because it is the geological period during which angiosperms evolved, radiated, and became common in terrestrial vegetation. The oldest widely accepted angiosperm fossils are pollen grains from the Valanginian Stage of the Early Cretaceous (140–134 Ma [Hughes 1994]). Crown group angiosperms began radiating in the Aptian (125–112 Ma [Hickey and Doyle 1977, Hochuli et al. 2006, Friis et al. 2010]), and the largest proportional increase in angiosperm diversity occurred in the Albian–Cenomanian (112–94 Ma), concurrent with origination of the major extant clades within the most diverse subgroup, the eudicots (Lidgard and Crane 1988, Lidgard and Crane 1990, Crepet et al. 2004, Friis et al. 2010).

The effect of angiosperms on Cretaceous vegetation is less well understood than the timing of their diversification. Early angiosperm fossils are rare, and assuming no overwhelming bias against their preservation, it seems unlikely they were abundant in pre-Aptian vegetation. North American Aptian palynofloras are dominated by pteridophytes and gymnosperms, with <20% of taxa and specimens attributed to angiosperms (Lupia et al. 1999). The oldest angiosperm-dominated megafossil assemblages, in the early Albian, are associated with evidence of disturbance such as fluvial channels and/or fire (Hickey and Doyle 1977). The inferred low leaf mass per area and high vein density of Albian angiosperms implies high growth rates and short leaf life spans, especially in the late Albian (Boyce et al. 2009, Brodribb and Feild 2010, Royer et al. 2010, Feild et al. 2011). Angiosperm leaves became common in many fluvial and coastal plain fossil assemblages by the Late Cretaceous, but we are not aware of studies that quantify their abundance. Proportional abundance has been measured in Late Cretaceous palynofloras, which show angiosperms increasing to an average of ~40% of grains from 100–85 million years ago, then reaching a plateau lasting until the end of the Cretaceous (Lupia et al. 1999).

Increasing proportional abundance of angiosperms appears mostly to have come at the expense of pteridophytes and possibly non-conifer gymnosperms, suggesting vegetation shifted from fern to angiosperm dominance in many settings, and that conifers were relatively unaffected (Lupia et al. 1999). This pattern could be consistent with the idea that during the Late Cretaceous angiosperm dominance continued to be highest in disturbed or open habitats that had previously been occupied mostly by ferns, as has been suggested from small angiosperm diaspore size and the rarity of large fossil angiosperm trunks (Tiffney 1984, Wing and Tiffney 1987, Wing and Boucher 1998, Eriksson 2008, Sims 2010). If many angiosperm lineages retained their ancestral ruderal life history and preference for disturbed habitats into the Late Cretaceous, it would be a

striking example of phylogenetic niche conservatism (Prinzing et al. 2001, Crisp et al. 2009) during a major evolutionary radiation.

In this paper we describe the floral and environmental gradients preserved on a Late Cretaceous (~73 Ma) landscape at Big Cedar Ridge in central Wyoming, USA. The distribution and abundance of fossil plants and their correlations with local environmental conditions yield strong inferences about their ecological preferences that are independent of both phylogenetic position and functional interpretation of morphological traits. Although vegetational patterns observed along an irregular two-dimensional transect in a single deposit, recording an instant in time, obviously cannot represent the whole globe, the patterns of plant distribution at Big Cedar Ridge do give direct evidence of the ecological roles and preferences of major plant groups on this Late Cretaceous landscape. We hope future studies will establish the generality of these patterns.

Environmental context

The Big Cedar Ridge (BCR) tuff is a bentonitic claystone bed in the middle part of the Meeteetse Formation exposed along an irregular ~4 km transect on the east side of Big Cedar Ridge, in the southeastern Bighorn Basin, Wyoming (Fig. 1). The bentonitic claystone is an altered volcanic ash erupted from the Elkhorn volcanic field in southwestern Montana, ~150 km to the northwest. Such deposits are common in the Meeteetse Formation (Hicks et al. 1995). The age of the BCR tuff is 72.7 ± 1.43 Ma, or late Campanian, which is recalculated from the published Ar/Ar age of 71.7 ± 0.7 Ma (Wing et al. 1993) using new radiometric decay constants (Min et al. 2000) and monitor mineral age (Kuiper et al. 2008). The age is also constrained by fossils (the Meeteetse Formation is here underlain by marine shale of the *Baculites grandis* Zone, (J. F. Hicks, *personal communication*) and magnetostratigraphy (just above the base of Chron 31R; W. Clyde, *personal communication*).

Leaf physiognomy (Wolfe and Upchurch 1987, Falcon-Lang 2003), wood anatomy (Falcon-Lang 2003), and climate modeling (Valdes et al. 1996) all indicate that Late Cretaceous paleoclimate in the northern Rocky Mountains was warm (mean annual temperature ~20°C) and highly equable (seasonal difference of ~4°C). Widespread coals in the Meeteetse Formation imply that precipitation was high and that any dry season was short (Lottes and Ziegler 1994), though fossil wood from slightly older rocks to the north shows intervals of narrow growth rings possibly caused by infrequent drought (Falcon-Lang 2003).

The Meeteetse Formation was deposited in delta and coastal plain settings on the western margin of the Cretaceous Interior seaway that covered large parts of central North America (Fig. 1A). Coarsening upward of the formation at BCR records the progradation of a large delta into the Cretaceous Interior Seaway. The

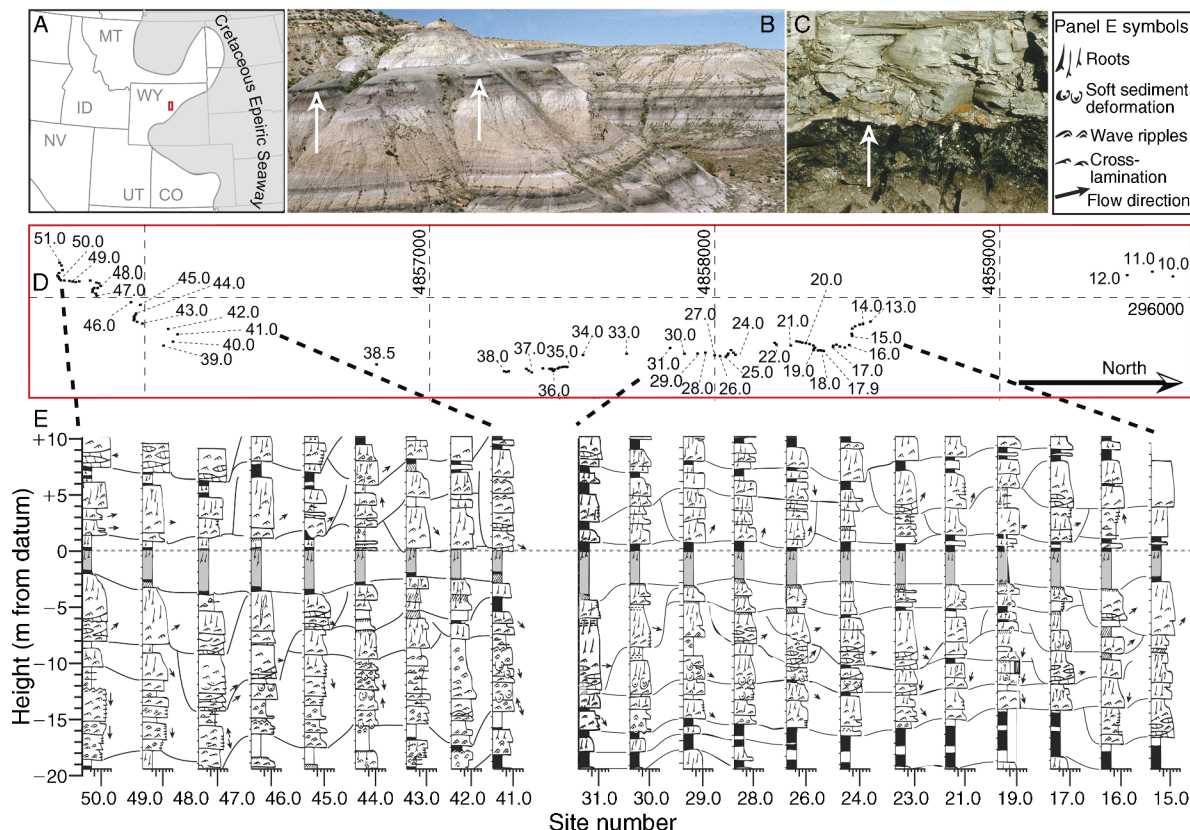


FIG. 1. The context of the Big Cedar Ridge (BCR) tuff, central Wyoming, USA. (A) Paleogeographic map showing the location of the study area near the shore of the Interior Seaway ~ 73 Ma. The paleo-coastline is from Lillegraven and Ostresh (1990). (B) Southern exposures of BCR in the vicinity of sites 43–45. White arrows point to the paleosol beneath the event bed, and bases of arrows point to delta foreset cross beds. The hill is ~ 35 m high. (C) Contact between paleosol and overlying event bed at site 22.0, indicated by white arrow; the vertical dimension of the photo is ~ 20 cm. (D) Positions of sites where the fossil flora and paleosol were sampled (UTM grid, north to right; see Supplement for site coordinates). The dashed lines show that the sections on the left are between sites 50.0 and 41.0, and the sections on the right are between sites 31.0 and 15.0. (E) Stratigraphic cross-sections through portions of the Meeteetse Formation at Big Cedar Ridge showing deltaic and fluvial deposits, coals (black units), and the position of the BCR tuff (gray-shaded unit). The symbols are in the key at the upper right of the figure. The numbers below each column indicate the closest sampling site (map view in part D). Widths of lithological columns are proportional to grain size, with coarser rock units extending farther to the right (long tick marks indicate the coarsest observed grain size, sand). Section height is in meters above and below the datum level described in *Methods*. Note variations in tuff thickness corresponding to topography on the underlying paleosol. Fluvial channels are more common to the north.

southern exposures at BCR show sandy delta foreset beds dipping up to 12° to the south or southeast, and beds in this sequence show both asymmetrical and symmetrical cross-lamination, indicating directional flow down the delta front and also reworking by waves (Fig. 1B, E). The absence of marine or trace fossils implies that this delta lobe prograded into an interdistributary bay rather than a fully marine environment. BCR exposures just 2–3 km north lack a delta foreset sequence, and the equivalent section consists of splay deposits disrupted by roots and stem casts, suggesting higher paleotopography.

Delta sediments at BCR are overlain by distributary channel and splay deposits alternating with paleosols. Channel bodies vary in size, with the largest being 4–8 m deep, 20–60 m wide, and having levee deposits extending hundreds of meters laterally (Fig. 1E). Paleosols

generally are low in organic matter, implying the abandoned delta lobe remained a topographic high above the swampy delta plain. The distributary channel sequence is capped by a paleosol that underlies the BCR tuff across the whole outcrop. This is the first carbon-rich paleosol above the delta deposits, though the amount of carbon varies laterally (see *Results*). Higher carbon content to the south suggests this area remained a topographic low. The lateral extent of this pre-tuff surface across the whole outcrop indicates a stable land surface formed when active deposition from the distributary channel system ceased in this area. The subsequent deposition of the BCR tuff, described in the following section, suggests that the BCR area eventually became a topographic low with respect to the surrounding landscape.

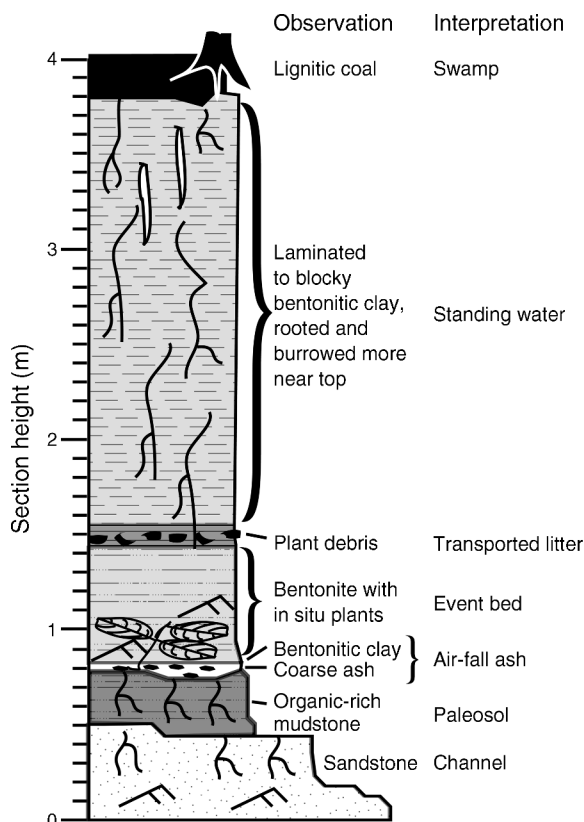


FIG. 2. Idealized stratigraphic section through the BCR tuff and associated deposits, consisting of eight units: underlying channel sand (variably present); paleosol of variable thickness and properties; thin, air-fall tuff with large biotite crystals (thickness exaggerated); thin bentonitic clay; event bed of irregularly cross-laminated tuff with abundant plant fossils, some rooted in underlying paleosol; plant debris bed consisting of horizontally laminated layers of woody, size-sorted fragments; fine blocky bentonite (altered volcanic tuff) with rare aquatic fossils; overlying lignitic coal with large wood fragments. Lithological symbols are as in Fig. 1.

Preservation of the fossil flora

The preservation of fossil plants in situ in one sedimentary unit over a distance of 4 km is unusual, but consistent with the rapid deposition of volcanic ash. The 2–5 m thick BCR tuff is underlain by the laterally extensive paleosol, and the tuff itself is composed of five depositional subunits: a thin basal volcanic ash unit, a thin clay bed, the fossil-bearing event bed, a layer of macerated plant debris, and a capping bentonitic clay deposit (Fig. 2). The BCR tuff is generally overlain by a lignitic coal.

The basal unit, only 1–3 mm thick but widespread, contains large (~1–2 mm), unworn, volcanic biotite phenocrysts and lies directly on the paleosol that formed the land surface. Similar biotite grains are also seen on the upper surfaces of some fossil leaves preserved in this unit (Fig. 3C). These crystals indicate an initial airfall of volcanic ash on the vegetation and land surface. It is

possible that some of these leaves traumatically abscised from growing plants in response to the ashfall (e.g., Burnham and Spicer 1986).

The second unit is a thin, tuffaceous clay 1–2 cm thick that is horizontally laminated with biotites and coarser tuff, which appears to have been deposited in quiet water. It may represent continued ashfall into shallow water, rather than directly onto the soil surface, implying a brief period of flooding.

The third unit, which preserves nearly all of the fossil plants, is 10–20 cm of bedded, fine-sand to silt-sized tuff that fines upward to silty clay. Asymmetrical and symmetrical small-scale cross-lamination indicates current flow and wave action. Interference bedding around some fossil plants suggests local unidirectional flow, and rolled leaves indicate an extremely turbid flow. Elsewhere laminae are predominantly horizontal, reflecting laminar flow or quiet water deposition. Fossil plants rooted in the paleosol underlying the tuff are generally bent over at the top of this unit. This bed was probably deposited as a flood of ash-laden water onto the floodplain surface from a distributary channel, though we cannot exclude the possibility of a mixture of rain and ash falling directly from the sky, then being redistributed by multidirectional, low-energy flows. Many observations show that the fossils are in situ or minimally transported: vertically compressed stems are connected to roots in the underlying paleosol (Fig. 3A, B), there is excellent preservation of thin leaves unlikely to have withstood transport, and leaves attached to axes are moderately common (Fig. 3D). Also, strong local variation in floral composition is unlikely to have been preserved in a transported assemblage (see *Results*).

The fourth unit is 1–20 cm thick, flat-laminated, and composed of ash mixed with macerated, woody plant debris resembling man-made particle board. At three sites palm stems 10–15 cm in diameter project up through units 1–3 and terminate at the top of the plant debris layer, with a few fragmentary palms leaves found at this level. The plant debris layer reflects deposition in standing water of ash mixed with abraded, size-sorted plant fragments.

The highest unit is a tuffaceous silt and clay 1–5 m thick that fines upward. It has almost no organic matter, laminations are rare, but at a few sites floating aquatic plants were found ~1 m above the pre-tuff surface. This capping clay unit represents rapid infilling with volcanic ash of a shallow lake that occupied an interdistributary depression. The low density of plant remains suggests that the lake filled in quickly, although there are branching vertical root traces in the lake-fill indicating presence of (presumably) aquatic plants.

A coal containing coniferous logs overlies the BCR tuff and signals the resumption of terrestrial deposition. Roots from this level penetrate downward through the underlying strata. The contact of the overlying lignite on lacustrine deposits provides a paleo-horizontal baseline

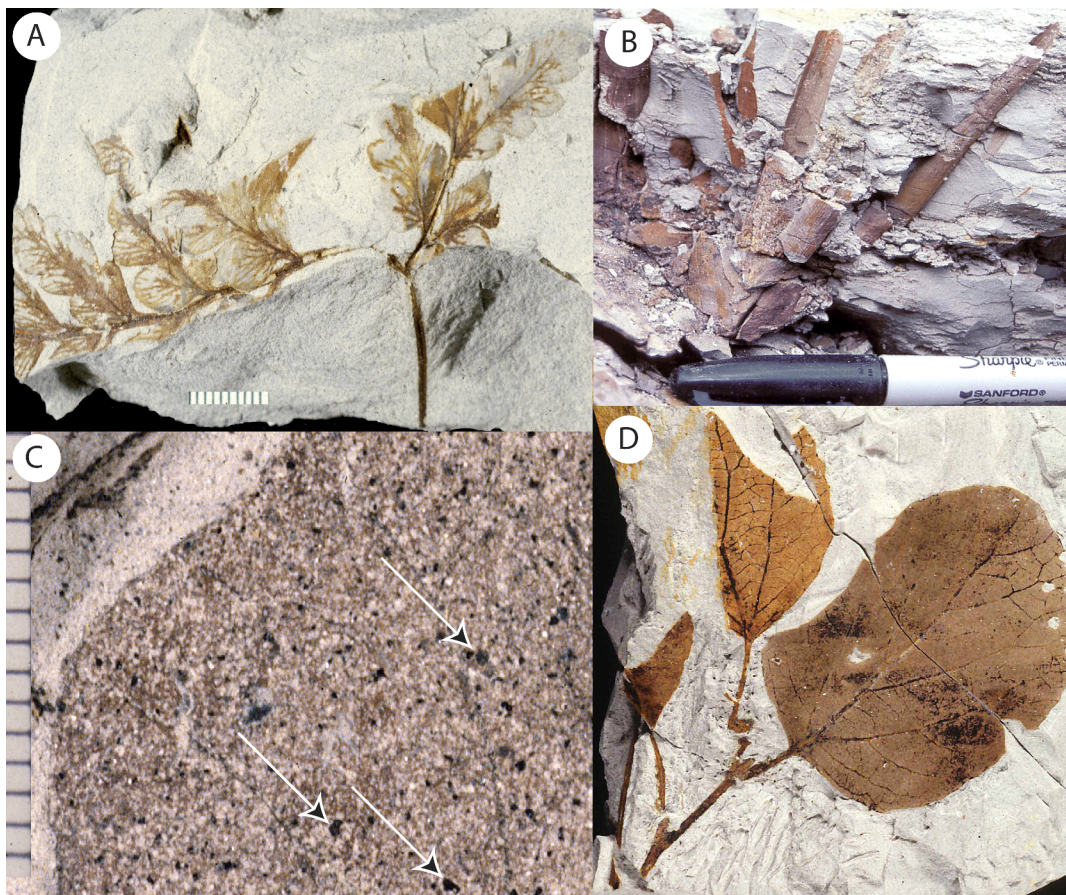


FIG. 3. Plant preservation. (A) Fern (morphotype F3) leaf with vertically oriented main stipe and horizontally oriented lamina, indicating preservation in situ in the light-gray tuff of the event bed. The scale divisions in panels (A) and (C) are millimeters. (B) Vertically oriented monocot leaves departing from one another at base of the event bed. The pen cap in panel (B) is 5 cm long. (C) Biotite phenocrysts (arrows) on surface of a dicot leaf (morphotype DN17) collected from basal, air-fall subunit. (D) Leaves of a platanaceous plant (DN5) still attached to the twig, indicating lack of transport. The largest leaf is 6 cm long.

from which the local pre-tuff topography can be reconstructed.

METHODS

Field and laboratory

The BCR flora is largely undescribed, so we segregated fossils into operational taxonomic units (henceforth “morphotypes”) for paleoecological analysis. We made large fossil collections in advance of censusing, sorted by morphotype, and then assembled a field guide containing descriptions, diagnoses, and photographs to ensure uniform identification among different census takers and over the course of the census. Based on our experience with identifying abscised leaves in extant floras (e.g., Burnham et al. 1992, Burnham 1997), our morphotypes are approximately equivalent to species.

Several new morphotypes were found during censusing. These were described and drawn in the field, then collected and preserved for photography and description. During the census, specimens with uncertain identifications were collected so their identity could be

confirmed by comparison with other material in our collections. In 2007–2008 the morphotypes were reviewed and described in more detail using the terminology of Ellis et al. (2009). This review incorporated material collected between the original 1992 census and 2007, and led to improved circumscriptions of many rare morphotypes. All uncertain identifications from the original census were checked and updated to the most recent informal taxonomy. Changes were among rare forms for which most or all census specimens had been kept, enabling us to revise the census unambiguously.

The nomenclatural status of most BCR fossils is uncertain, so in this paper we refer to morphotypes using a system of informal alphanumeric codes. Letter codes are: L = lycopsid, F = fern, CY = cycad, CO = conifer, M = monocot, DE = dicot with entire-margined leaf, and DN = dicot with nonentire leaf. (We use dicot colloquially to refer to non-monocotyledonous angiosperms because we cannot always distinguish eudicotyledons from basal angiosperms using foliar characters.) Numbers following the letter codes originally were

assigned in sequence, but because some morphotypes were lumped in the process of description, not all numbers are used in the current system. If we know the formal taxonomic name and/or higher-level affinity for a morphotype, we give this information where the morphotype is first mentioned in the text.

We censused the flora at 100 sites across the 4-km outcrop (Fig. 1D). Census sites were roughly square in plan view and 1–3 m on a side, giving a mean site area of 3–4 m². No excavation exceeded 9 m², and only four reached that size. Quarry size was limited to ensure that each site represented only a small area of the original vegetation. We estimate the 100 excavated sites had a total area of ~400 m². The first 42 sites (designated by integer numbers) spanned the entire exposed area, and were located so that the fossiliferous unit was neither deeply buried nor highly weathered. Subsequently we sampled 68 intervening sites (decimal numbers), focusing on areas with high floral variability, but with exact placement still constrained by weathering and the amount of overlying rock.

At each site we exposed the fossiliferous unit and collected it in irregular-sized blocks. Blocks were censused if they were at least 10 cm on the longest axis, and if the exposed bedding surface displayed at least one fragment identifiable to major plant group. We excluded small blocks to avoid incomplete and unidentifiable specimens; blocks lacking any identifiable fossils were ignored to save time and increase the power of the census to detect rare morphotypes.

Estimates of bedding plane cover for each taxon were made at each site using a line intercept method (Floyd and Anderson 1987, Etchberger and Krausman 1997). Excavated blocks were placed under a frame strung with 24 threads spaced at 2-cm intervals. The threads were 30 cm long and marked off in 2-cm intervals. Each block was placed in the corner of the census frame with its long axis perpendicular to the census lines, and each 2 cm increment of census line was then scored as crossing one of the recognized morphotypes, indeterminate remains assignable to one of the major plant groups, plant debris (covering an estimated 50% or 100% of the bedding surface), woody axis, charcoal, amber, or blank bedding plane. Increments crossing identifiable plant fragments were scored for that morphotype or higher taxon in preference to blank bedding plane, plant debris, wood, charcoal, or amber (i.e., identifiable remains took precedence over the other categories, and indeterminate plant remains took precedence over blank bedding plane). If an increment of census line crossed more than one identifiable fragment, the increment was scored fractionally for each morphotype. For example, if leaves of three different morphotypes were crossed by the same increment, each was scored as one-third of an increment. Every increment that crossed the census block was assigned to a category. We stopped censusing when we reached ~2000 increments or the 9-m² limit. At three sites (20.0, 30.0, and 35.0) an additional 1000 or 2000

increments were scored to test the effect of larger sample size on species diversity.

The percentage of organic carbon (% TOC) in the pre-tuff paleosol was measured at each site by low-temperature ashing (Wilde et al. 1979), and the grain-size distribution of the paleosol was measured using a Coulter counter at the Institute of Arctic and Alpine Research Sedimentology Laboratory, University of Colorado, Boulder. Color, texture, intensity of rooting (four point semiquantitative scale), and depth of rooting in the pre-tuff paleosol were observed at the 41 integer-numbered sites.

At each floral census site we measured the stratigraphic distance between the base of the ash and the bottom of the overlying coal as a means of reconstructing local topography on the pre-tuff surface. The base of the overlying coal represents the transition from subaqueous to subaerial deposition, so we assumed it was paleo-horizontal. Assuming equivalent compaction across the outcrop, the stratigraphic distance from the pre-tuff surface to the base of the coal should then be inversely related to the original elevation of the pre-tuff surface, with small distances (thinner tuff) indicating former local highs, and larger distances (thicker tuff) indicating lows in the pre-tuff surface. We transformed each stratigraphic distance by subtracting it from 5, thus making higher paleo-elevations correspond to larger values. Our measurements indicate local hummocks and depressions in the pre-tuff surface, but the slightly lower elevation of the southern outcrop compared with the north, expected from broader stratigraphic considerations, is not reflected in these measurements, probably because the regional topographic gradient was slight.

Data analyses

Floral data were arranged in a 100-site by 122-taxon matrix in which each cell contained a value representing the number of increments of a taxon at a site (Supplement). For most analyses the raw values were replaced by proportions (number of increments assigned to a given morphotype at a site divided by total number of identified increments at the site), and then transformed by taking the arcsine of the square roots of these proportions. This transformation increases the linearity of the proportions by reducing compression at the ends of the scale induced by the limiting values of 0 and 1 (Sokal and Rohlf 1995). Quantitative environmental data were arranged in a matrix of 100 sites by four variables (% TOC, % sand, silt:clay ratio, and topographic level in meters; see Supplement).

We used R version 2.7.1 for most data analyses (R Development Core Team 2007). We analyzed floral diversity at two spatial scales using the additive approach (Lande 1996), as implemented in the package stratigraph (Green 2010), which yields within- and among-sample components of species diversity. Similarity measures, resampling routines, and ordination analyses were carried out using the R packages vegan,

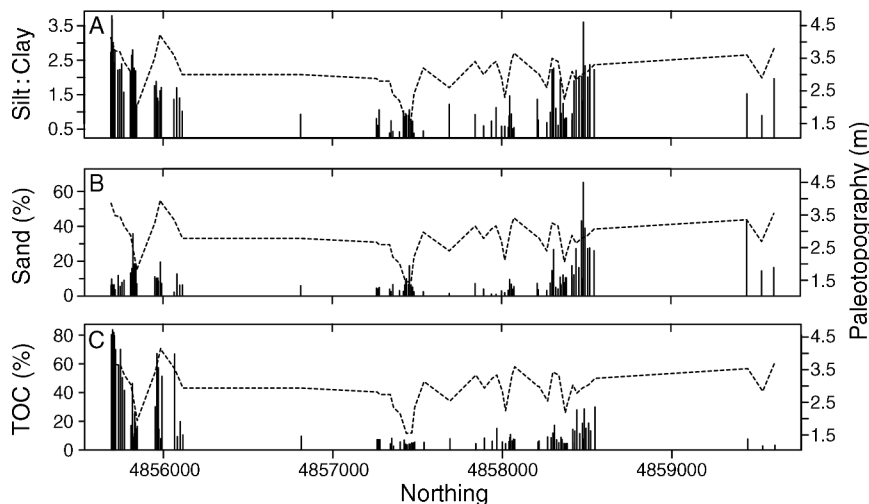


FIG. 4. Measured environmental variables at Big Cedar Ridge. Each vertical histogram line represents the value for an environmental variable at a site: (A) silt : clay ratio, (B) percentage of sand by volume, (C) percentage of total organic carbon (TOC) by mass. The dashed line represents the paleotopography of the pre-tuff paleosol surface, measured as described in *Methods* and fitted with a Lowess curve. For the 10 sites lacking one or more measurements we interpolated values using inverse distance weighting of values from the three nearest sites.

version 1.15-0 (Oksanen et al. 2008), and MASS version 7.2-42. Cluster analysis was provided by the R base package. Species accumulation curves were calculated using the software package EstimateS, version 8.2 (Colwell 2009).

RESULTS

Matrices of environmental and floral data are given in the Supplement.

Paleoenvironmental variability

There is strong variation along the outcrop in all measured environmental variables. Reconstructed topography varies from 1.2 to 4.8 m above the arbitrary horizontal baseline, TOC in the paleosol from 3% to 84%, sand from 1% to 65%, and the silt : clay ratio from 0.38 to 3.8 (Fig. 4 and Supplement).

The most conspicuous paleotopographic features are depressions in three areas: one in the northern part of the central outcrop (sites 16.4–19.3), a second in the central part of the central outcrop (sites 35.0–36.5), and a third in the southern outcrop (sites 46.0–48.0) (Fig. 4). In each of these depressions we observed fine-scale horizontal or cross-lamination in the upper 10 cm of the paleosol, indicating that bioturbation did not have time to erase primary bed-forms from sediment deposited shortly before emplacement of the BCR tuff. The low sand content in the uppermost part of the paleosol within these depressions (Fig. 4B) may indicate they were inactive channels filling with fine sediment at the time the tuff was deposited. In the largest of the channels (central outcrop sites 35.0–36.5) the flora includes several dicot morphotypes with peltate and deeply cordate leaves, as well as small, upright monocots preserved as clusters of sheathing leaves (Fig. 3B, see

Floral composition and diversity). These may have been floating and emergent aquatic forms, as would be expected in and around the margin of a small pond in an inactive channel.

Grain size of the pre-tuff surface fluctuates over small distances in association with the paleochannels, but there are larger-scale trends as well. The percentage of sand is generally highest near the north end of the central outcrop (sites 13.0–17.0) and around the channel at the south end of the outcrop (sites 47.0–48.2), although it rises to 9–18% in the channel in the middle of the central outcrop (sites 35.3, 35.6, 36.0). Across most of the central outcrop area the silt : clay ratio is <1 , whereas in the southern outcrop area it is generally >1 (Fig. 4A).

Variation in TOC is also clearly linked to position on the Big Cedar Ridge paleolandscape. Only sites in the southern outcrop (39.0–51.0) have $>40\%$ TOC in the paleosol (Fig. 4C). There is substantial heterogeneity even within the southern outcrop, where the paleosol within the paleochannel (sites 46.0–48.0) generally has lower TOC (10–30%). In the central outcrop area paleosol TOC generally is $<10\%$, but it is particularly low within the central paleochannel (sites 35.0–37.0), and then rises to 10–30% near the north end of the central outcrop. Paleosol TOC at the far northern outcrop, near sites 10.0–12.0, is $<10\%$ (Fig. 4C).

Specific types of plant debris (woody axes, fossil charcoal, amber) show little spatial pattern, but overall, plant fragments are more abundant in the southern part of the outcrop. We attribute this to the peat paleosol, some of which was probably eroded and directly redeposited in the lower part of the tuff. Wetter conditions at the southern end of the outcrop also may have favored the preservation of organic matter.

TABLE 1. Paleofloral census summary, Big Cedar Ridge (BCR) tuff, central Wyoming, USA.

Group	Cover (in cm of line intercept)			Proportion of total identified cover
	Identified to morphotype	Indeterminate but assigned to major group	Total cover	
Cryptogams	36 204	1212	37 416	0.49
Conifers	4242	64	4306	0.06
Cycads	1277	33	1310	0.02
Monocots	16 891	7261	24 152	0.31
Dicots	6549	2967	9516	0.12
All	65 162	11 537	76 699	1.00

Notes: Results are based on 423 600 cm of line intercept of fossiliferous bedding surfaces at 100 excavations spanning 4 km of outcrop (see Fig. 1 and *Methods*).

† Transect β richness calculations are according to Lande (1996), with abundance weighted as the natural log of the number of increments.

Floral composition and diversity

We scored 211 786 2-cm increments (4236 m) of line intercept in the event bed. Nearly half of the increments (48%) crossed bedding planes lacking any fossils or plant debris; 30% crossed unidentifiable plant debris. Further, 32 581 increments (15%) crossed fossils we could identify to a specific morphotype, and an additional 5769 increments (3%) crossed fossils we identified to a major plant group but could not identify to a specific morphotype because of poor preservation (Table 1). The proportion of increments per site identified to major group varies from 5% to 35%, with a weak tendency for sites at the southern, more organic, end of the outcrop to have a higher proportion of cover we could identify as belonging to one of the major groups. This probably reflects better preservation rather than greater standing biomass at the time of the ashfall, because at these sites a greater proportion of the fossils also can be assigned to a specific morphotype (i.e., details of venation are better).

Initial analyses of the Big Cedar Ridge flora (Wing et al. 1993) recognized 155 morphotypes. After revision of the original informal taxonomy, we recognize 159 vegetative and 15 reproductive morphotypes, which will be described in more detail in a later paper. The census recovered 122 of the vegetative and seven of the reproductive morphotypes (see Supplement for full data). We excluded reproductive morphotypes from our analyses so that we compare photosynthetic area of all taxa, but in any case only 19 increments (<0.05%) were assigned to reproductive structures.

Dicots are by far the most diverse group overall (73 morphotypes, 60%), cryptogams are second (29 morphotypes, 24%), and the other major groups have fewer than 10 morphotypes each (Table 1, Fig. 5). Mean sample richness is 16.6 morphotypes, to which cryptogams (6.1 morphotypes) and dicots (5.8) contribute roughly equally (37% and 35%, respectively), even though on average there is less dicot cover per site. Monocots average 2.8 morphotypes per sample (17%), and on average fewer than 10% of morphotypes in a sample are conifers or cycads (Table 1). Dicots make up a much higher proportion of diversity for the whole transect than for

individual samples because of high heterogeneity among samples. Among-sample (beta) diversity is three times higher for dicots than for cryptogams, and 10–20 times higher than for the other major groups, and is also a higher proportion of total diversity for dicots than it is for other major groups (Table 1; Appendix A). Mean frequency of occurrence for morphotypes in each group is inversely related to among-sample diversity, with conifer morphotypes occurring in 31 samples on average, monocots in 23, cryptogams in 20, cycads in 11, and the average dicot morphotype occurring in only 8 samples. Clearly, conifer, monocot, and cryptogam species were on average far more ubiquitous, and the high diversity of dicots in the total flora reflects higher species density and higher turnover in species composition across the BCR landscape (Fig. 6).

Summing cover in all samples, cryptogams are 49%, monocots 31%, dicots 12%, conifers 6%, and cycads 2% (Fig. 5). The most abundant morphotype is M1, a coryphoid palm that occupies 23% of total cover and occurs at 81% of the sites (Fig. 7; Supplement). The next seven most abundant morphotypes are all ferns,

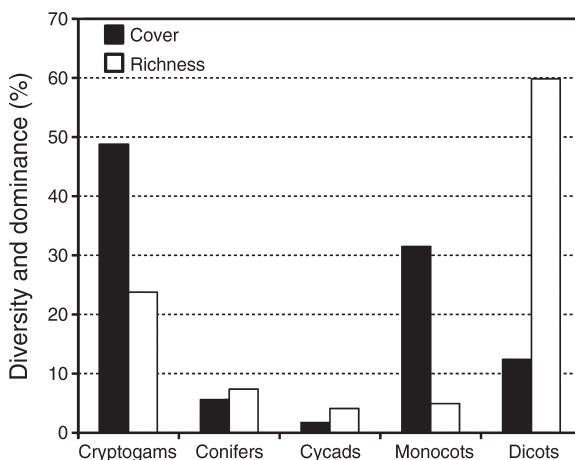


FIG. 5. Diversity (richness) and dominance (cover) of major plant groups. Note the inverse relationship between dominance and diversity.

TABLE 1. Extended.

Total richness	Mean sample richness	Standard deviation of sample richness	Transect β richness [†]	Proportion of total richness from transect β	Mean no. samples per morphotype
29	6.05	3.40	22.67	0.78	20
9	1.40	0.72	5.58	0.62	31
5	0.56	0.77	3.50	0.70	11
6	2.81	1.61	4.47	0.74	23
73	5.82	2.52	66.04	0.90	8
122	16.64	5.02	105.33	0.86	19

including species in the families Schizaeaceae (F1, *Sectilopteris psilotoides*, and F2, *Anemia fremontii*), Gleicheniaceae (F8, F9, F10), Matoniaceae (F17), and Dipteridaceae (F11). The only two conifers that account for >2% of measured cover are CO3 (probably Cupressaceae), and CO7 (*Araucarites* sp.). The most abundant cycad, CY3 (*Ctenis* sp.), accounts for 1.4% of cover. The most abundant dicot (DN14, Saxifragales?) is 2.0% of total cover, but its overall abundance is entirely the result of eight closely spaced sites in the middle outcrop (sites 35.0–36.1); it is rare everywhere else. The second most abundant dicot, DN12 (Austrobaileyales?), about 1% of total cover, also is abundant at only a few sites, most near the northern end of the outcrop.

The in situ preservation at BCR offers some clues to the stature of the plants. Only five large, vertically oriented carbonized stems were noted during excavations. Each was rooted in the underlying paleosol and ended abruptly above the top of the event bed, so we

could not assess the heights of the original plants. The largest trunks were 10–20 cm in diameter, 20–30 cm tall, and had a fibrous external morphology consistent with palms. One stem, 8 cm in diameter and ~5 cm tall, gave rise to large fern leaves belonging to morphotype F4 (Osmundaceae?). No silicified trunks were observed along the 4 km of outcrop, although silicified wood is preserved locally in the Meeteetse Formation. The rarity of large trunks suggests that trees were sparse on the BCR landscape, as does the high relative abundance of fern foliage, which would probably have been a minor component of total leaf area if the litter were derived from a forest. In addition, roughly half of the dicot leaf morphotypes are <5 cm long and have features that are common among herbs, such as being highly dissected, having deeply cordate or funnel-form bases, thin texture and poorly organized venation (Givnish 1987). Many of these leaf morphotypes are found attached to slender or fleshy-looking petioles oriented perpendicular to the

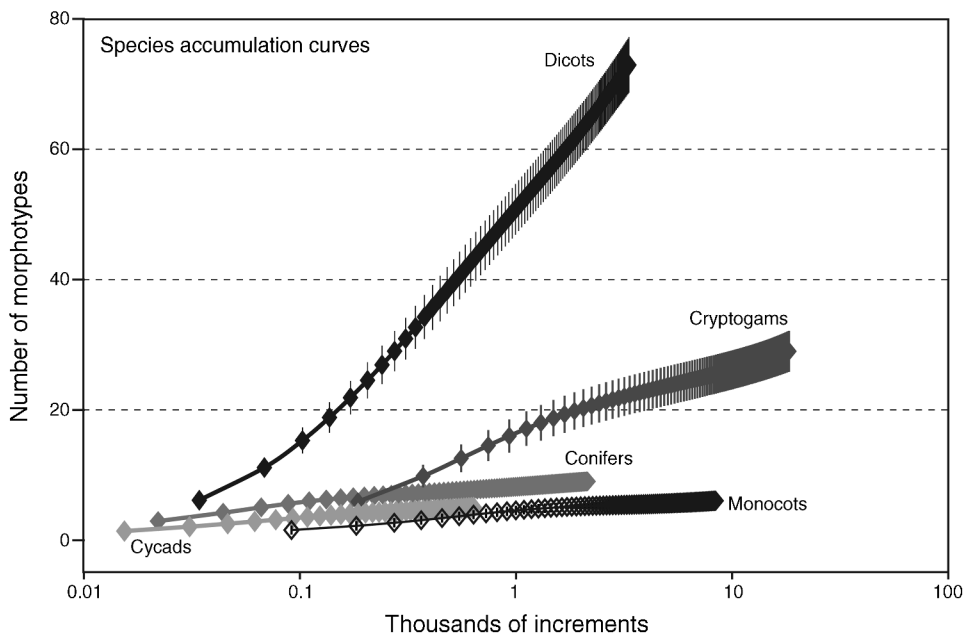


FIG. 6. Species accumulation curves for each major plant group. Estimates of richness (number of morphotypes) were made by resampling the sites by species matrix 100 times without replacement. The x-axis reflects the amount of identified cover scaled in 2-cm increments of line intercept as described in *Methods*. Gotelli and Colwell (2001) recommend scaling accumulation curves by abundance rather than by number of sites if the probability of detecting species varies by site, as is the case here. The x-axis is logarithmic to facilitate comparison of the curves. Error bars indicate \pm SD. Note the steep slope of species accumulation for dicots.

plane of the lamina, also consistent with an herbaceous, scrambling or climbing growth habit.

Floral associations

An average linkage cluster diagram constructed from quantitative Bray-Curtis dissimilarity indices grouped the sites into five major clusters with two outliers (Fig. 8, Table 2). We designate the site clusters as floral associations, each named for its dominant morphotype: F11, F1, DN14, F2, and M1. The two sites placed outside the major clusters were 14.1 and 37.1, both dominated by the gleicheniaceae fern F8 (Fig. 8). K-means clustering of the Bray-Curtis indices (Hartigan 1975, Hartigan and Wong 1979) stipulating division into five groups yielded similar results to the average linkage diagram, with only 9 of the 100 sites being assigned to different groups than in the average linkage analysis, two of those being the outliers from the average linkage tree.

Each of the five major floral associations has a moderately to strongly coherent spatial distribution (Fig. 9). All 22 sites assigned to the F11 association occur at the south end of the outcrop, but none are within the paleochannel there, which encompasses 8 of the 9 sites in the F1 association. The remaining site in the F1 association (36.5) is at the edge of the channel in the central outcrop area (Fig. 9). Eleven of the 17 sites in the DN14 association occur adjacent to one another in the middle of the paleochannel in the central outcrop area. The remaining six sites are farther north along the outcrop, of which one (19.1) is associated with a topographic low that might indicate another, smaller paleochannel. The 20 sites in the F2 association occur in the middle and northern part of the central outcrop area, with 10 of them adjacent to one another north of the deepest paleochannel, and the remaining 10 somewhat scattered. Sites in the M1 association show the widest spatial distribution, occurring all the way from the north end of the central outcrop to the paleochannel in the southern outcrop area. Within the southern paleochannel, sites belonging to the M1 association are interspersed with sites of the F1 association; along the north part of the central outcrop, sites of the M1 association are interspersed with those of the F2 association (Fig. 9).

In addition to being grouped by proximity to paleochannels, the five floral associations show differences in percent TOC and silt:clay ratio of the underlying paleosol, and in topographic level (Fig. 10; Appendix B). The mean percentage of TOC for sites in the F11 association is significantly higher than it is for all other clusters ($P \ll 0.01$; Kolmogorov-Smirnov test with Holm-Bonferroni correction for multiple tests). Mean TOC for

sites in the DN14 association is significantly lower than for all other associations ($P < 0.01$), and sites in the F1 association have significantly higher TOC than those in the F2 association ($P < 0.01$) (Fig. 10; Appendix B). Sites in the M1 association are not significantly different in percent TOC from those in the F2 or F1 associations, although the difference between M1 and F1 sites is nearly statistically significant ($P = 0.05$) with the Holm-Bonferroni correction. None of the associations have significant differences in the percentage of sand in the paleosol except for sites in the M1 association, which have more sand than the F11 sites ($P < 0.05$ with correction) (Appendix B). Differences in the topographic level and silt:clay ratio of sites belonging to different floral associations are of mixed significance, with the F11 sites being the most divergent.

The F11 association is the most distinct in terms of environmental variables (statistically distinct from the other associations in 12 of 16 Kolmogorov-Smirnov tests using the Holm-Bonferroni correction), the DN14 association sites are the next most distinct (different in 8 of 16 tests), followed by the F2 association (6 of 16 tests), and F1 and M1 associations (both distinct in only 5 of 16 tests; Appendix B). As a group, sites of the M1 association are not significantly different in any of the environmental variables from those in either the F2 association or the F1 association. The sites of the F2 and F1 associations are not statistically distinguishable except in percentage of TOC. The environmental gradients that were likely responsible for differences among floral associations are described and discussed in *Floral and environmental gradients*.

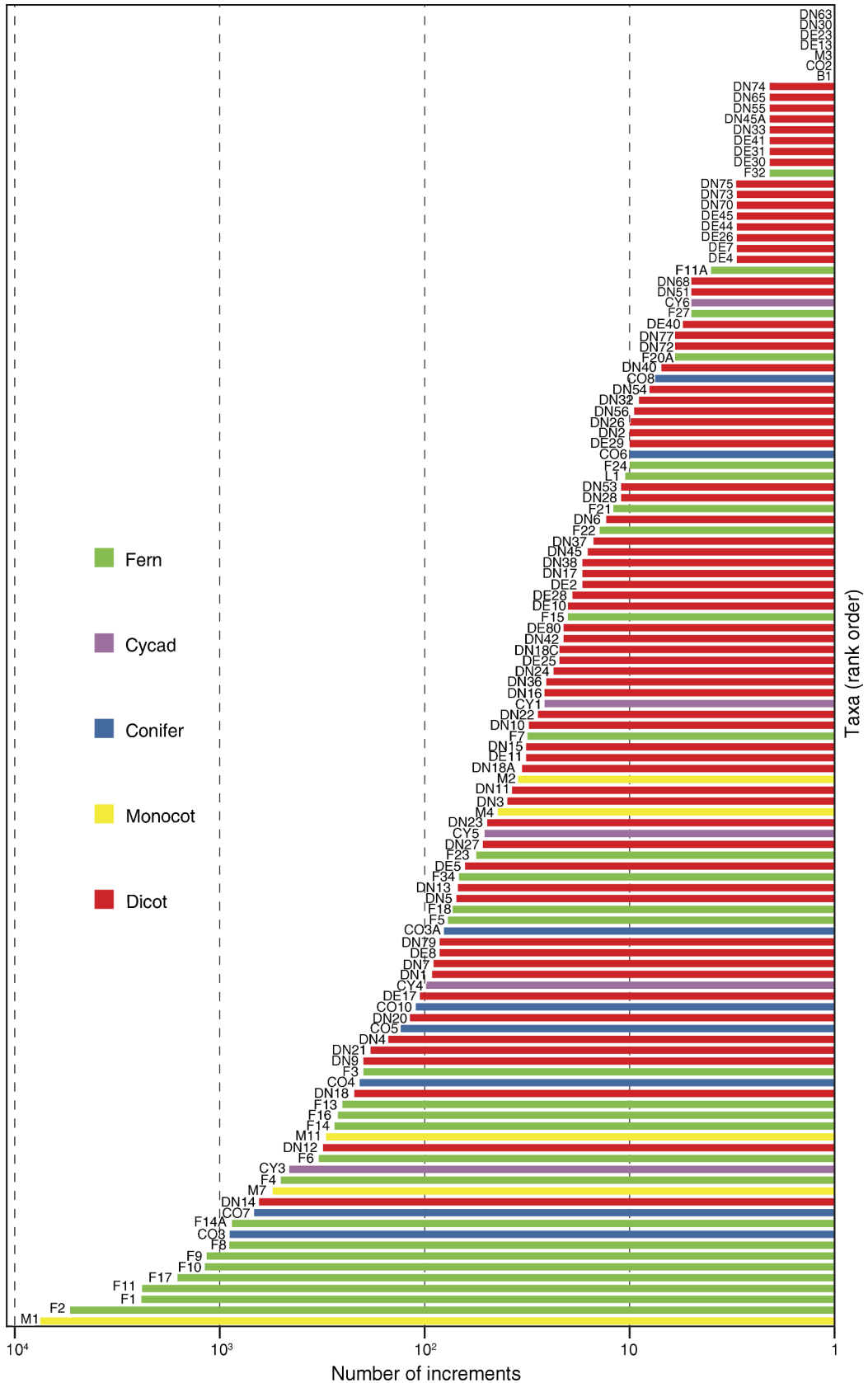
Within-site species richness is approximately equal for all five floral associations (Table 2), but sites belonging to the M1 and F2 associations have higher dominance as measured by Simpson's Index. The F11 and F1 associations have lower among-site richness than the others, and the F11 association in particular has a shallower species accumulation curve than the DN14, F2, and M1 associations because of more homogeneous floral composition among sites (Appendix C).

Floral and environmental gradients

There is very high heterogeneity in floral composition across the BCR landscape. Bray-Curtis dissimilarities (Bray and Curtis 1957, Bloom 1981, Faith et al. 1987) between pairs of sites are 0.2–1.0, with a mean of 0.75; 43% of the values are >0.8 . A Bray-Curtis index of 1.0 indicates no overlap in composition.

Mantel tests demonstrate that floral distances between pairs of sites (Jaccard's index) are highly significantly associated with inter-site distances in meters, as well as

FIG. 7. Dominance–diversity curve for summed census data. The y-axis is the number of 2-cm increments of bedding plane intercepted by each taxon (log scale). Letter-number codes denote the taxa. Colors indicate major plant groups (green, cryptogam; blue, conifer; purple, cycad; red, monocot; yellow, dicot). Note the predominance of ferns and conifers, as well as one species of palm. Full abundance data by morphotype code are given in the Supplement.



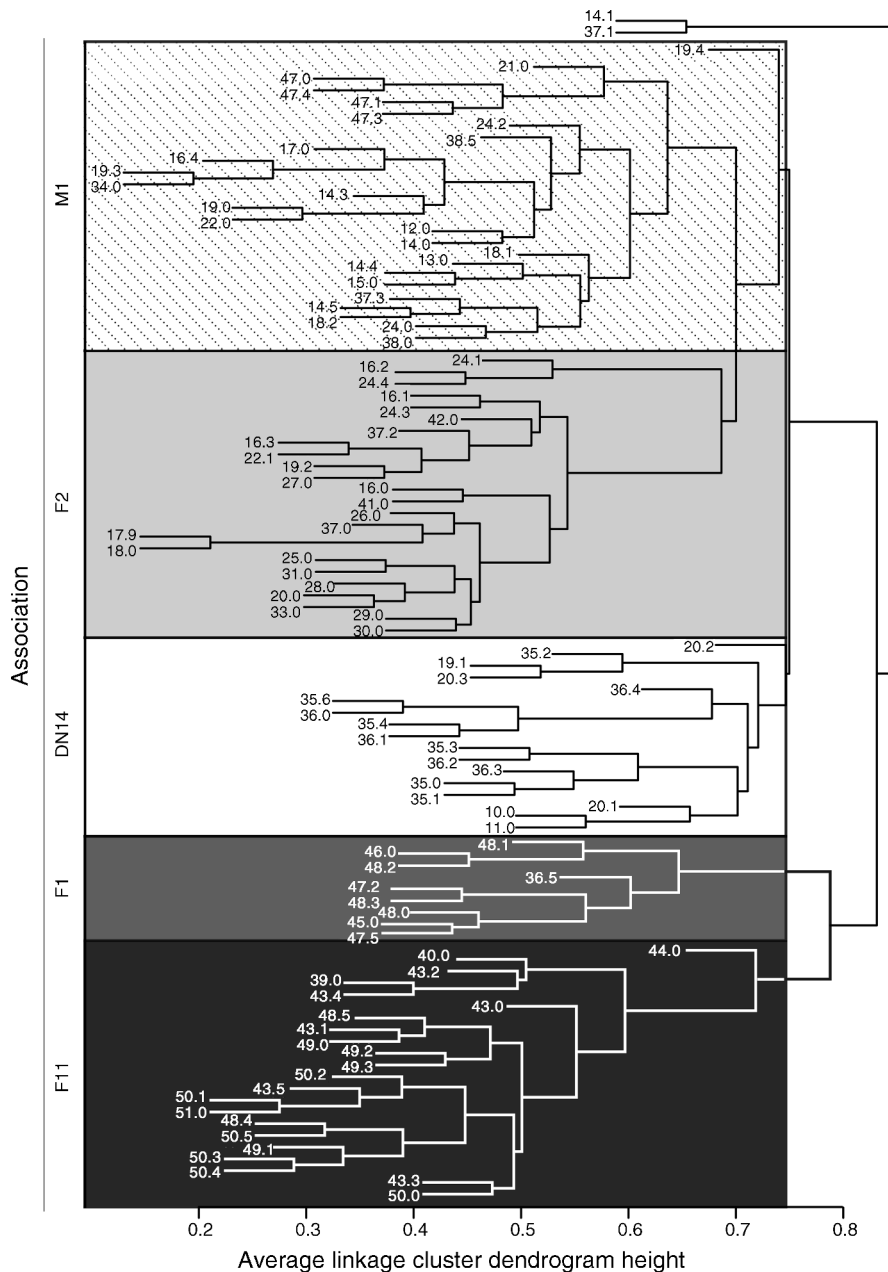


FIG. 8. Average linkage cluster diagram of BCR sites derived from Bray-Curtis dissimilarity indices. Each terminus represents a sampling site indicated by its number. Locations of selected site numbers are shown in map view in Fig. 1, and UTM coordinates are given in the Supplement. We recognize five major floral associations, referred to by their dominant taxa: F11, F1, DN14, F2, and M1.

with distances in environmental space ($P < 0.001$, Appendix D). Inter-site Jaccard's indices calculated separately for cryptogams, monocots, and dicots all show significant relationships with environmental distances. Inter-site Jaccard's indices calculated from conifer and cycad composition, however, are not significantly correlated with inter-site distances in environmental space ($P = 0.11$ and 0.828 , respectively). The most abundant conifer, CO3, is typically 1–5% of identified leaf cover, and has the lowest coefficient of

variation among sites of any morphotype at BCR. Its relative ubiquity (occurring at 93% of the sites) probably explains the absence of a correlation between Jaccard's indices calculated from conifer species abundances and the environmental distances between sites. Cycads are quite rare and undiverse (mean abundances of $<0.5\%$ except for CY3 with a mean abundance of 1.6%), making it difficult for variations in their abundances to be evaluated statistically. The absence of a significant correlation between intersite distances in meters and

TABLE 2. Abundance and diversity data for the five floral associations identified with cluster analysis (Figs. 8, 9; also see *Methods: Data analyses*).

A) Rank order values:										
Rank order	F11 association		F1 association		F2 association		M1 association		DN14 association	
	Taxa	%	Taxa	%	Taxa	%	Taxa	%	Taxa	%
1	F11	28	F1	48	F2	58	M1	68	DN14	21
2	F17	19	F9	18	M1	14	F2	7	M1	12
3	F10	11	F10	6	CO7	5	F9	3	CO3	6
4	F14A	8	M1	5	CO3	3	CO3	3	M11	6
5	CY3	4	F8	4	F8	2	CO7	2	DN12	5
6	F1	4	F14A	2	F4	2	F1	1	DN21	5
7	M7	3	F3	2	F1	2	F8	1	F16	5
8	M1	3	F13	2	DN12	1	F13	1	F4	4
9	F6	2	M7	2	DN18	1	DN4	1	CO7	3
10	CO3	2	CO3	1	CO5	1	F14	1	F13	2

B) Floral association parameters:					
Parameter	F11 association	F1 association	F2 association	M1 association	DN14 association
Total cover (cm)	17 041	7589	16 671	13 862	5466
No. sites	22	9	24	21	17
Taxa/site†	16.6	14.6	17.3	16.6	17.1
No. taxa	70	55	82	87	75
Taxa/100 cm of intercept	0.4	0.7	0.5	0.6	1.4
Taxa/site	3.2	6.1	3.4	4.1	4.4

Notes: Each floral association is named by its most abundant taxon. The most abundant 10 taxa in each association are listed in the table, with % indicating the percentage of the total identified cover in all sites assigned to that association. The lines below the 10 most abundant taxa summarize the floral data for each association.

† Mean number of taxa per site.

intersample Jaccard's indices calculated from cycad morphotype abundances probably reflects the small number of cycad morphotypes (5), their low abundances, and the small number of samples in which cycads occur ($N = 41$).

We used nonmetric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarities (Cox and Cox 2001, McCune and Grace 2002), detrended correspondence analysis (DCA) (Hill and Gauch 1980), and canonical correspondence analysis (CCA) (ter Braak 1986, 1987) to perform ordinations on the floral data. Ordination plots were visually similar regardless of method, but DCA using standard settings in the vegan package (four rescaling cycles, 26 segments, and no downweighting of rare species [Oksanen et al. 2008]) produced the strongest correlation of environmental variables with site scores.

The DCA plots show that sites belonging to four of the five floral associations occupy somewhat distinct parts of the two-dimensional ordination space (Fig. 11A). Sites assigned to the F11 association using cluster analysis plot to the right on axis 1, as do the abundant taxa at these sites: F17 (Matoniaceae), F11 (*Dipteris*, Dipteridaceae), F10 (Gleicheniaceae), and F14A (Dryopteridaceae?), along with CY3, CY4, and CY5 (Fig. 11B). Sites that preserve these morphotypes in high abundance typically rest on peat soil (Fig. 11A) and have relatively low abundances of monocots (except for M11 and M7), dicots (except for DN9, Ranunculales?), and conifers (except for CO3) (Fig. 11B; Supplement).

Sites assigned to the F1 association are adjacent to those in the F11 association in the ordination plot (these two associations link in the cluster analysis as well, seen in Fig. 9), and have axis 1 values intermediate between the F11 association sites and those belonging to the M1 and F2 associations (Fig. 11A). The F1 association separates moderately well from all other floral associations on axis three of the DCA (not shown). Floral similarities between sites in the F11 and F1 associations include moderate abundance of F10, F14A, M1, M7, and CO3 (Table 2). Sites with F1 association floras generally have intermediate levels of TOC, and many are associated with the paleochannel in the southern outcrop, but all sites with >25% sand in the substrate have low abundances of F1. Sites assigned to the M1 and F2 associations overlap broadly with one another in the lower left quadrant of the DCA, and have moderate to low amounts of TOC (Fig. 11A). They are similar in the other environmental variables as well. Cluster analysis links these associations closely (Fig. 9), but there is separation of these two associations on axis four of the DCA (not shown). They are typified by high abundances of M1, F2, CO7, CO3, and CO10, and are frequently associated with DN4 and DN18. Sites in the DN14 association form a relatively discrete cluster in the upper left quadrant of the DCA, and typically have very low TOC (Fig. 11A). These sites have high abundance of DN14 (Saxifragales?), and the emergent aquatic M11, but share moderate abundance of M1, CO3, and CO7 with sites in the M1 and F2 associations. Nearly all of

the DN14 association sites occur in paleochannels. Many of the morphotypes that plot in the upper left quadrant of the DCA are rare elsewhere on the BCR landscape.

The strong correlation of DCA axis 1 with soil TOC is evident from the shading of points in Fig. 11A. The bivariate correlation of axis 1 scores of sites with their percentage of TOC is high ($r^2 = 0.65$, $P < 0.001$), suggesting that TOC, or a factor correlated with it, exerted a strong influence on plant distributions. This is also evident in the CCA ordination, where %TOC has the highest loading of any variable we measured (Fig. 12).

Examining the abundances of individual morphotypes against %TOC in the paleosol shows that many of those that are abundant at sites with TOC >50% are also common at a few sites with TOC <40%. In contrast, morphotypes that are abundant at some sites with low TOC are never abundant at sites with TOC >40%. The correlation between high TOC and plant species abundances is thus asymmetrical.

In the present day, preservation of high levels of organic matter in soils formed under warm climates requires long periods of flooding, low pH, or both (Gore 1983). Since decay rates are likely to have been similar in the Cretaceous, and BCR existed in a subtropical climate, high TOC probably indicates one or both of these factors were involved. Floral gradients correlated with TOC may reflect the inability of some species to live on substrates that were permanently wet or acidic.

Although there are no gradients in site richness expressed in the ordination, on average samples in the lower left quadrant (M1 and F2 associations) have lower evenness than the rest (mean Simpson's index for lower left quadrant samples is 0.56, for all other samples, 0.73; Kolmogorov-Smirnoff test $D = 0.404$, $P = 0.0004$) reflecting the high dominance of M1 and F2 at these sites.

DISCUSSION

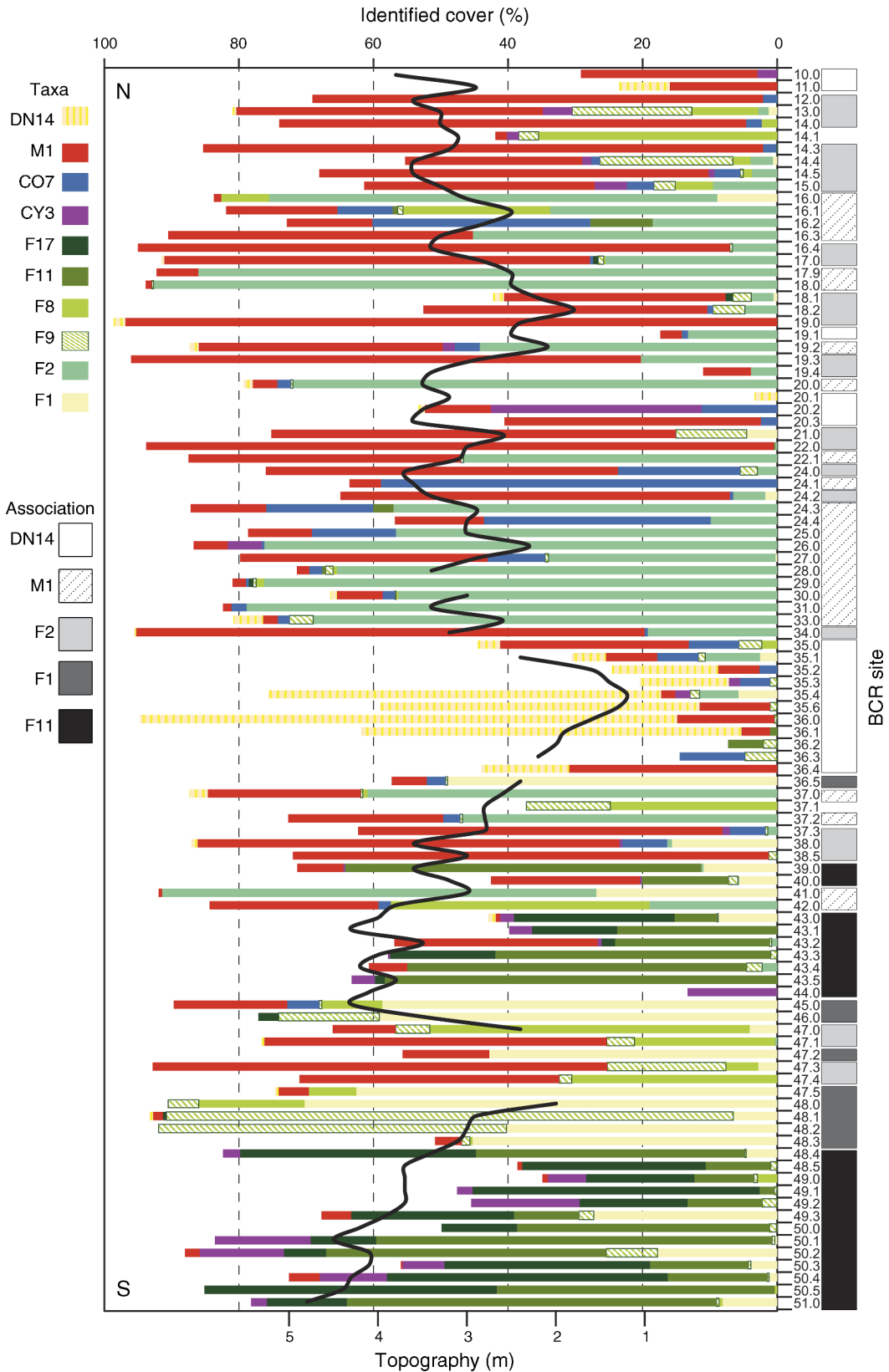
All of the sedimentological and depositional data, as well as the abundant preservation of plant fossils and organic carbon, indicate that the Big Cedar Ridge tuff preserved a wetland ecosystem. Within this setting the preservation of in situ plant fossils and the soil they grew on allows us to directly assess spatial variation in floral composition and its correlation with soil characteristics. Our results show that (1) soils and floral composition varied markedly and in a correlated way across the BCR landscape, (2) the strongest predictor of floral composition is the amount of organic matter in the soil, (3) the vegetation was dominated by ferns (especially on peaty

soils) and palms (on organic-rich mud), and (4) dicots were highly diverse because of their heterogeneity among sites but dominant only at a few sites with mineral substrate and associated evidence for recent disturbance. Here we compare the inferred vegetation types of the BCR landscape with similar modern environments, and the inferred growth habits and strategies of some BCR plants with those of their probable living relatives. We ask if extant relatives of BCR fossils still form similar vegetational associations and live in similar environments.

Diversity.—The BCR flora is among the richest local compression fossil assemblages of any time or place, with a total of 122 morphotypes from the ~400 m² of excavated area. This is more species than were found at two sites famous for their diversity: the early Paleocene Castle Rock “rain forest” in Colorado (~104 leaf taxa [Johnson and Ellis 2002, Ellis et al. 2003]), and the subtropical early Eocene site at Laguna del Hunco, Argentina (102 leaf taxa [Wilf et al. 2003]). We are not able to correct for differences in sampling effort because the other sites were censused by leaf count rather than line intercept, but all three floras have been intensively sampled by paleobotanical standards, meaning many person-weeks of collecting. There are differences in depositional setting among the three floras, with Castle Rock being a nearly in situ fluvial wetland something like BCR, though forested, and Laguna del Hunco being a crater lake into which plant remains were probably transported from surrounding terrain.

The mean richness of BCR collecting sites (16.6 morphotypes in ~3–4 m²) is also high compared with many fossil compression assemblages representing warm, wet vegetation (e.g., Wing and DiMichele 1995, Wilf et al. 2003, Wing et al. 2009). Richness at BCR is not particularly high, however, compared with modern herbaceous wetland vegetation. Fens in Iowa average 12 species per 0.25-m² quadrat, and 80 species per fen (Nekola 2004). Midwestern U.S. fens as small as 80 ha can have >500 species (Amon et al. 2002). Freshwater coastal marshes in Louisiana average 8–12 species per m² (Mancera et al. 2005), and transects of temperate to subtropical North American wetland vegetation that are hundreds to thousands of meters long commonly record 50–200 species (e.g., Laliberte et al. 2007, Flinn et al. 2008, Peirson and Evans 2008, Carr et al. 2009). The high diversity of BCR relative to other fossil assemblages probably reflects unusual preservation of herbaceous as well as the few woody plants, rather than high diversity of the original flora compared with extant floras in similar habitats.

FIG. 9. Proportional abundance of the 10 most common morphotypes by site. The black curve indicates the reconstructed topography. Sites are arranged ordinally with north to the right, but distances are not proportional. Site designations across the bottom are color coded according to membership in the five floral associations derived from the cluster analysis. See *Results: Floral composition and diversity*.



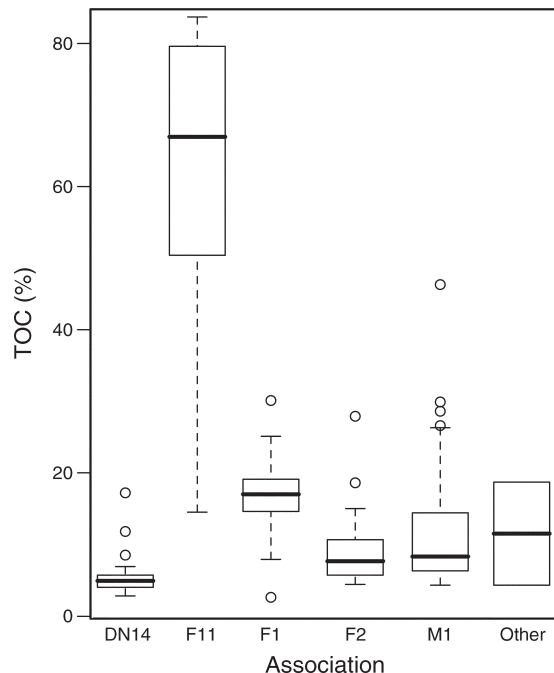


FIG. 10. Boxplot showing differences in percentage TOC among sites belonging to the different floral associations defined by cluster analysis. Thick horizontal lines are mean values, rectangles indicate \pm SD, "whiskers" are \pm 2SD, and circles are outlier points.

Although total floral diversity at BCR is not particularly high compared with modern wetland vegetation, the number and proportion of pteridophyte species is high, with 29 morphotypes (24% of total plant diversity) in the flora as a whole, and >6 species of pteridophytes per $\sim 3\text{--}4\text{ m}^2$ site. Fern diversity of 20 species/ha is considered high in temperate eastern North America (Karst et al. 2005), and much larger areas (>1000 ha) support similar numbers of species (Greer et al. 1997). Quadrats of 16 m^2 in Quebec include 0–6 species, and 50-m^2 plots include no more than 7 species (Karst et al. 2005). Even in the tropics small areas do not necessarily support many more species of pteridophytes than are found at BCR. Lwanga et al. (1998) found 0–15 species of ferns in a large number of 2×100 m transects at 12 study forests in Uganda. With 33–50 such transects per forest, a much larger sampling area than at BCR, they recovered 29.5 species on average. Kessler (2001) used plots of 400 m^2 to assess pteridophyte diversity at 65 mid-elevation forested sites in tropical Bolivia, a region of globally high pteridophyte diversity (Kreft et al. 2010). Mean pteridophyte richness per plot ranged from 0 to 47.9 species, and the mean number of terrestrial pteridophytes per plot ranged from 0 to 20.9 species (Kessler 2001). Working at four widely separated sites in terra firma forest of lowland Amazonia, Tuomisto and Poulsen (2000) found 24–32 species of terrestrial pteridophytes per $0.65\text{--}1.0$ ha plot. Subplots of 100 m^2 include 1–18 species, with the mean

number of species per subplot varying from 5 to 10 species depending on the site.

The proportion of species at BCR that are pteridophytes is also high relative to modern floras. A global survey shows that pteridophytes on average account for 8% of species in montane biomes, 6.8% in moist broad-leaved forest biomes, and 3.6% in all continental biomes (Kreft et al. 2010), compared with 24% of species at BCR, which was neither montane nor fully tropical.

In the context of present-day vegetation, the pteridophyte diversity recovered from BCR (presumed to represent terrestrial pteridophytes because of the absence of evidence for a canopy), is high for a small area of warm, coastal wetland at mid-latitude. The high species density and high proportional diversity of pteridophytes at BCR is consistent with the idea that ferns were a larger proportion of herbaceous plant diversity in the Late Cretaceous than they are today, and were replaced by monocotyledonous angiosperms in many wetland habitats. Compilations of Cretaceous pollen and macrofossil records show that the relative diversity of pteridophytes declined through much of the Late Cretaceous, but that they typically composed 20–40% of species in local floras, even to the end of the period (Lidgard and Crane 1988, Crane and Lidgard 1989, Lidgard and Crane 1990, Lupia et al. 1999, Nagalingum et al. 2002), making the high pteridophyte diversity at BCR typical of its time.

Fossil fern thickets.—The rarity of fossil trunks and the high abundance of foliage of Schizaeaceae (F1, F2, F5), Dipteridaceae (F11), Gleicheniaceae (F8, F9, F10), Matoniaceae (F17), and Dryopteridaceae (F14A) implies that much of the BCR landscape was occupied by low-statured vegetation dominated by ferns, a "fern thicket." Fern thickets are today minor landscape elements in both temperate and tropical settings. Temperate fern thickets (e.g., *Matteuccia struthiopteris* [Flinn et al. 2008]) form underneath forests dominated by either angiosperms or conifers, and ferns have been shown to inhibit successful establishment of temperate deciduous forest trees, probably by light competition in the seedling phase (George and Bazzaz 1999). One temperate fern, *Pteridium aquilinum*, even dominates extensive patches of open country, probably because of the deep shade cast by its frond mats, the thick accumulation of litter beneath its canopy, and the toxic compounds in its leaves that slow their decomposition and deter herbivory (Marrs et al. 2000, Griffiths and Filan 2007). *Pteridium* does not do well in saturated soils, however (McGlone et al. 2005, Marrs and Watt 2006).

Fern thickets also occur in the subtropics. *Lygodium microphyllum* (Schizaeaceae) has become an invasive weed in subtropical Florida, dominant in large gaps created by tree falls and other disturbances, and favoring disturbed sites with wet soils (Pemberton and Ferriter 1998, Lynch et al. 2009). A species of *Lygodium* (morphotype F5) occurs at BCR, and though it is not

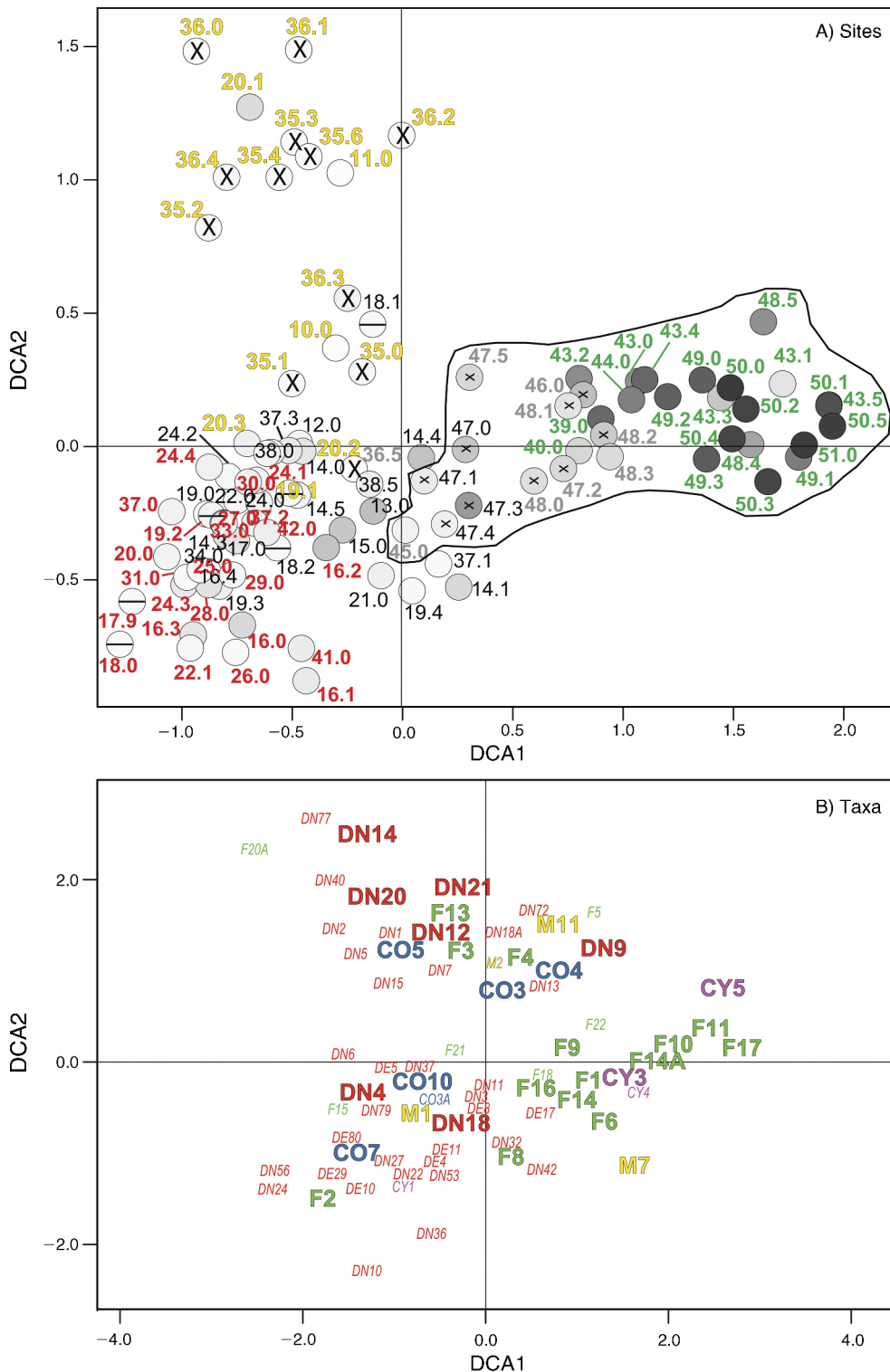


FIG. 11. Detrended correspondence analysis (DCA) of (A) BCR samples and (B) morphotypes. Shading of site symbols varies directly and continuously with the total organic carbon (TOC) of the sub-tuff paleosol (0% TOC, white; 100% TOC, black). The colors of the numbers indicate which cluster each site belongs to (green, F11 association; gray, F1 association; black, F2 association; red, M1 association; yellow, DN14 association). Site symbols with a large X are within the large paleochannel in the central outcrop, sites with a small x are within the paleochannel in the southern outcrop, and sites with a horizontal line are in a small paleochannel near the north end of the main outcrop. Sites from the southern outcrop are enclosed by a black line. Morphotype designations are color coded by major plant group (green, cryptogams; magenta, cycads; blue, conifers; yellow, monocots; red, non-monocot angiosperms). The 30 most abundant morphotypes are indicated by larger font sizes.

abundant, Schizaeaceae is the most abundant fern family at BCR because F1 and F2 are both widespread and common.

Fern thickets dominated by Gleicheniaceae are common in wet, particularly upland, tropical regions, where species of *Gleichenia*, *Dicranopteris*, *Sticherus* and other genera can sometimes make up 75% of cover over areas of >1 ha (Walker 1994, Cohen et al. 1995, Walker and Boneta 1995, Russell and Vitousek 1997, Russell et al. 1998, Ohi and Bussmann 2004, Amatangelo and Vitousek 2009). Typically, these gleicheniaceo fern thickets occur on highly leached, nutrient-poor soils, or are associated with recent (and often frequent) disturbance. Some fern thickets grow following anthropogenic disturbance, and/or are formed by introduced species that may not be limited by specialized parasites and predators, but others form following massive natural disturbance events (Spicer et al. 1985). Once established, gleicheniaceo ferns generate thick accumulations of organic matter on and above the soil surface through slow decay of their marcescent leaf tissues (Russell and Vitousek 1997, Amatangelo and Vitousek 2009). The layers of living fronds (>1 m deep), dead fronds/stipes (~1 m deep) and a root mat (~35 cm deep) create dense shade, and release few nutrients via decay, preventing woody plants from colonizing and allowing the ferns to maintain dominance for decades (Slocum et al. 2006).

Did the fern thickets at BCR grow in areas strongly affected by disturbance and/or nutrient limitation? The answer varies by the type of fern thicket. Sites dominated by F2 are not associated with channels or other indicators of disturbance, they have moderate soil organic content, and they are spatially interspersed with sites dominated by palms. Thus we have no evidence that dominance by F2 was correlated with high levels of disturbance or nutrient stress. In contrast, sites dominated by F1 have moderately high organic levels and evidence of channeling, and sites dominated by F11 have very high levels of organic matter. The high soil organic matter at F11-association sites could indicate some degree of nutrient stress, with N and/or P limitation being common on peat substrates in wetlands today (Stanek et al. 1977, Verhoeven 1986, Vitt and Chee 1990, Bridgman and Richardson 1993, Bedford et al. 1999, Lahteenoja et al. 2009). Nevertheless, even the most organic-rich soils at BCR have at least 15% silt and clay, and the upper delta plain depositional setting we infer would have been subject to intermittent flooding from nearby channels, which would likely have supplied nutrients dissolved during weathering of volcanic areas to the west. In light of these observations, it is unlikely that any part of the BCR landscape had the very low nutrient levels commonly found, for example, in ombrogenous bogs (Verhoeven 1986, Pastor et al. 2002).

The role of disturbance in generating the fern thickets at BCR is hard to evaluate. Highly organic soils, seen particularly under the F11 association, must have required some years or decades to accumulate, making

it unlikely that disturbance would have come in the form of erosion or major depositional events that would have left clastic deposits. Other sources of disturbance, such as fires and grazing by large herbivores, might have left less sedimentary evidence. Fossil charcoal is common in most rocks of the Meeteetse Formation, but we did not observe unusually high concentrations of it in the fern-dominated areas of BCR. We searched for, but did not find, trackways indicating the passage of large animals. The best we can say is that we found no evidence for frequent or recent disturbance of the fern thickets at BCR.

If the fern thickets at BCR were neither strongly nutrient limited nor early successional, then the dominance of ferns over much of this subtropical, coastal landscape is quite unusual in the context of modern vegetation, in which monocotyledonous angiosperms (typically grasses or sedges) dominate warm-climate wetlands (e.g., Loveless 1959, Gore 1983, Clarkson et al. 2004). Fern-dominated fossil floras, on the other hand, have been widely reported from Cretaceous rocks (Rushforth 1971, Harris 1981, Crabtree 1988, Skog and Dilcher 1994, Cantrill 1996, Van Konijnenburg-Van Cittert 2002, Nagalingum and Cantrill 2006, Deng et al. 2008). Many of these are in situ or minimally transported assemblages, for which the relative abundance of fern foliage can be taken as a rough indication of their relative abundance in the original vegetation. Fossil floras dominated by ferns are less common in the Late Cretaceous than in the Early Cretaceous, but the evidence from BCR suggests that as late as the latest Campanian, schizaeaceous, dipteridaceous, gleicheniaceo, and matoniaceous ferns were still able to dominate the vegetation of a habitat they no longer command today: warm coastal wetlands without strong nutrient limitation or frequent disturbance.

Dicot paleoecology.—Dicot dominance at BCR is restricted to sites near the major channels that have mineral soil. The inferred habitat is therefore one with high water availability, high nutrient levels, and high light levels resulting from the recent disturbance associated with channel erosion. Although a few of the dicots may have been floating or emergent aquatics (inferred from their peltate leaves) these were rare, and we infer from the depositional setting that the common dicot morphotypes were early-successional herbs and woody plants. This inference is supported by the morphology of dicot leaves, which often are small in size, cordate or dissected, and have slender petioles positioned at an angle to the lamina, as is typical of many herbs and vines. As in the Early Cretaceous (Hickey and Doyle 1977), dicots were not a major contributor to vegetation in what were probably the more stable, competitive, and resource-limited parts of the BCR landscape (Wing and Boucher 1998). The high abundance of dicots in the most disturbed habitats at BCR is consistent with hypotheses that rapid growth in rich habitats was an important aspect of flowering plant

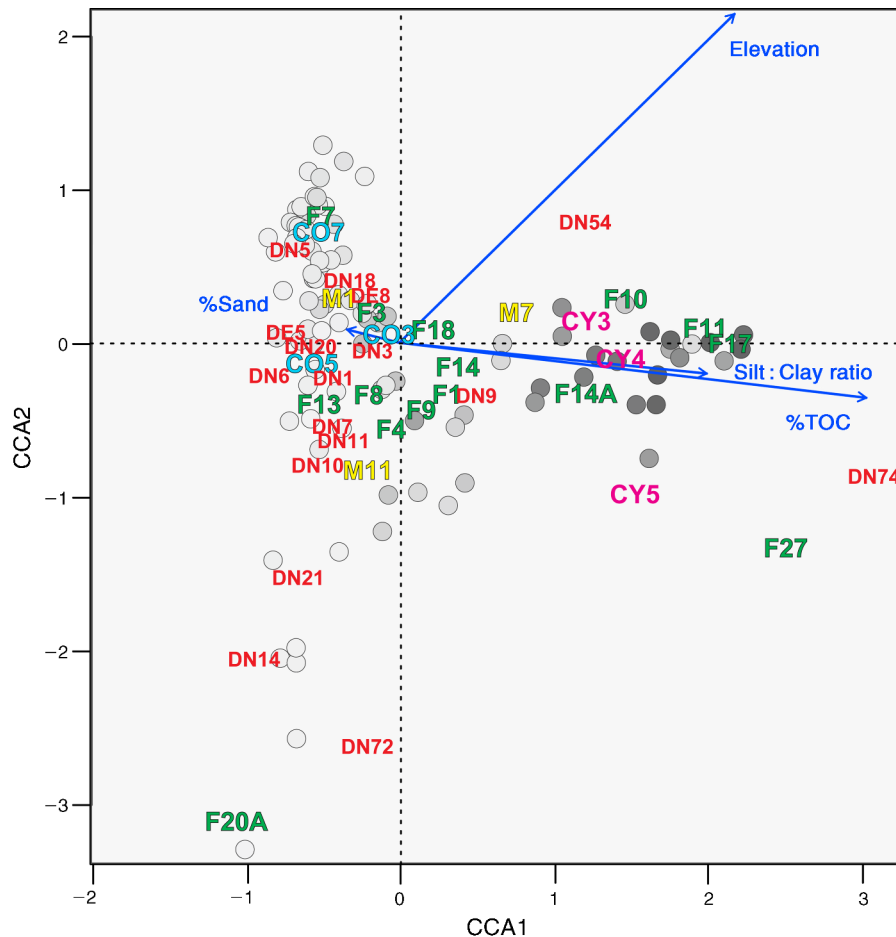


FIG. 12. Canonical correspondence analysis showing the relationship between site positions based on floral composition and four measured environmental variables: percentage total organic carbon (TOC), topographic level (elevation), percentage sand, and silt:clay ratio. Site symbols are shaded and morphotype designations are colored as in Fig. 11.

success in the Cretaceous (Hickey and Doyle 1977, Bond 1989, Wing and Boucher 1998, Philippe et al. 2008, Berendse and Scheffer 2009, Boyce et al. 2009, Bond and Scott 2010, Brodribb and Feild 2010, Royer et al. 2010).

Dicots are rare, yet have high beta diversity across all BCR habitats, except the area with the strongest evidence for disturbance, thus indicating that dicot populations were small and dispersed at the local scale except in disturbed areas. It has been argued that reproductive success in patchy populations is facilitated by biotic pollination (e.g., Regal 1982 and references therein), although more recent reviews show little difference in pollen limitation of reproductive success between biotically and abiotically pollinated species (Knight et al. 2005). Nevertheless, pollen transport has been shown to limit reproductive success in some abiotically pollinated plants living in fragmented habitats (Friedman and Barrett 2009). The rarity and dispersed occurrence of dicots at BCR is consistent with biotic pollination among these Late Cretaceous angiosperms (Wing et al. 1993), and furthermore, there is

direct evidence for entomophily in the morphology of many Late Cretaceous angiosperm flowers (Crepet 1984, Friis et al. 2006) and pollen types (Hu et al. 2008).

Some authors have portrayed angiosperm success in the Cretaceous as primarily the result of the capacity for rapid growth (e.g., Midgley and Bond 1991, Taylor and Hickey 1996, Boyce et al. 2009, Brodribb and Feild 2010, Royer et al. 2010), whereas others have favored the importance of insect pollination that permitted spatially dispersed populations to persist (e.g., Regal 1977, Crepet 1984). At BCR we find evidence for both attributes: dicot abundance centered in the most nutrient-rich and disturbed part of the landscape, where high growth rates would have been most advantageous, and a scattering of rare individuals across the landscape that is consistent with dispersed populations connected by insect pollination. If the distribution pattern of dicots at BCR is typical of Late Cretaceous landscapes, this suggests that both rapid growth rate and biotic pollination were important to the success of the group. Although we do not yet know the phylogenetic position

of most BCR dicots we are confident that many belong to eudicot lineages, suggesting that rapid growth and biotic pollination were part of the ecological strategy of derived angiosperm lineages in the Late Cretaceous.

Palm paleoecology.—As the single most abundant species at BCR, the coryphoid palm M1 was recovered from all habitat types, although it is most dominant on sites with moderate levels of organic matter and no evidence for recent disturbance. High abundance in what we infer to be stable, nutrient-rich habitats leads us to hypothesize that M1 was a competitive dominant among BCR plants. Work in the modern Neotropics documents palms as dominant in many poorly drained or flooded habitats (Tomlinson 1979, Svenning 2001). In tropical wetland vegetation a single species of palm may make up 60–70% of the understory plant cover, and their high abundance limits establishment of seedlings and saplings of other species through shading, thus influencing tree composition (Svenning 2001). Palms of low stature (e.g., *Sabal* and *Serenoa*) are also abundant to dominant in coastal lowlands of the southeastern United States, where a combination of tolerance to stress and disturbance (slow growth rates, long leaf life spans, tolerance of low nutrient soils, and fire resistance) allows them to persist in high abundance (e.g., Abrahamson 2007). These palmetto thickets of southeastern North America, where combined nutrient stress and regular fire favor palm cover, provide an alternate modern analog for palm-dominated vegetation at BCR, but we find no fossil evidence for either low nutrient levels or regular fires, at least relative to the rest of the BCR landscape. Dominance of part of a landscape by palms has been observed in at least one other Late Cretaceous flora (from Europe), where, as at BCR, palms have highest abundance in fine-grained wetland deposits and dicots are more abundant in coarser channel-margin sediments (Herman and Kvaček 2007).

Gradients on the BCR landscape.—In living wetland vegetation, even small changes in topography often have a strong effect on floral composition (e.g., Carr et al. 2009). The strong influence of topography on species composition reflects multiple edaphic characteristics that vary with site elevation: flood frequency, fire frequency, and a host of chemical attributes of soil including pH, oxygen, and nutrient availability (e.g., Schalles and Shure 1989, Svenning 2001, De Steven and Toner 2004, Bowles et al. 2005, Dick and Gilliam 2007, Laliberte et al. 2007).

Given the strong relationship between topography and floral composition on extant landscapes, it is surprising that at BCR the topographic variable has a relatively weak (though highly significant) correlation with floral composition. This may reflect the difficulty of accurately measuring paleotopography on the ancient landscape. The lower, wetter conditions at the south end of the BCR outcrop suggested by our stratigraphic and sedimentological data (see *Development of the BCR landscape*) may have been associated with lower topography, but a very low gradient would have been impossible to measure.

Therefore, topography might have covaried more strongly with floral composition (and other environmental variables) than our results indicate.

Although we cannot directly measure the environmental gradients at BCR, we infer from the geological context and soil data that the landscape was perennially moist to wet, and that the environmental gradients most important for floral composition were probably disturbance (in the form of channel erosion/deposition), and nutrient availability (negatively associated with soil organic matter). Although much of variation in floral composition is correlated with soil/environment variables, the Mantel tests show that floral composition varies even more strongly with simple distance than with environmental proxies. This suggests that variation in the composition of vegetation was also caused by patchiness in colonization and growth, and/or by environmental variables we are currently unable to measure. This is particularly evident in the alternation of F2- and M1-dominated localities at small spatial scales in the absence of any clear pattern of variation in the substrate. The insignificant differences in substrate characteristics between sites of the M1 and F2 associations, and their interspersed spatial arrangement, suggests that the difference in floral composition reflects either an unobserved environmental variable (such as light), or the unpredictable occupation of space by individual palms, which might dominate the sites in which they occur simply because they are large plants compared with the ferns.

Evolution of ecological strategies.—Although the BCR fossil plant assemblage is unusually well preserved, it is far from unique, and therefore the kind of information we present here can be (and has been) obtained for fossil assemblages of many ages (DiMichele and Gastaldo 2009). Fossil floras that preserve information about vegetational and habitat heterogeneity on a scale of meters to hundreds of meters are known from every interval of geological time since the advent of vascular land plants (e.g., Devonian [Andrews et al. 1977]; Carboniferous [Wnuk and Pfefferkorn 1987, DiMichele and Nelson 1989, Gastaldo et al. 2004, DiMichele et al. 2009, Oplustil et al. 2009]; Permian [Pfefferkorn and Jun 2007]; Triassic [Cúneo et al. 2003, Artabe et al. 2007]; Jurassic [Spicer and Hill 1979]; Cretaceous [Cantrill 1996]; and Cenozoic [Gemmill and Johnson 1997, Davies-Vollum and Wing 1998, Williams et al. 2003, 2009]). The fossil record clearly documents changes in ecological strategies and preferences of organisms through time. There is considerable work involved in making the “snapshot reconstruction” of a single place and time, of course, but in aggregate many such snapshots yield a moving picture of the evolution of ecological strategies and preferences within lineages over geological time. Such data can be used to test hypotheses developed from phylogenetic inferences or observations of ecological processes in the present, potentially establishing the strength of phylogenetic inferences

about the evolution of ecological traits, and the generality of ecological trends and patterns observed among the 1% of species that happen to be alive today.

CONCLUSIONS

1) The Big Cedar Ridge tuff preserves in situ or minimally transported plant fossils that record the species composition and relative abundances of plants in an ~74 million-year-old wetland growing on a subtropical delta plain.

2) Floral composition and paleosol features measured at 100 sites spaced along a 4-km transect indicate strong gradients in environmental conditions and floral composition. We recognized five floral associations: two types of fern thickets dominated by pteridophytes that occurred on the most organic-rich substrates; a third type of fern thicket occurring on moderately organic soil; palm-dominated vegetation in the same environment; and dicot-dominated vegetation associated with mineral soils in abandoned channel scours.

3) The distributions of species and paleosol characteristics suggest that nutrient stress and disturbance were the major factors controlling floral composition, with ferns in the families Gleicheniaceae, Dipteridaceae, and Matoniaceae dominant at the most stressed sites, dicots dominant only at the most disturbed sites, and palms mixed with some conifers and schizaeaceous ferns most abundant at sites that were neither highly stressed nor highly disturbed. The environmental gradients we infer for the BCR landscape are among the important factors determining floral composition in many present-day wetland environments.

4) The overall high dominance and diversity of ferns at BCR is not seen in similar climates or habitats today, and would be unusual in any modern environment. Fern-dominated fossil assemblages such as BCR are moderately common in the Cretaceous, indicating that pteridophytes have lost ground (literally) with respect to other plant groups, mostly angiosperms, since the Campanian Age.

5) The overall rarity and high beta diversity of dicots at BCR is consistent with the hypothesis that many Late Cretaceous angiosperms were insect pollinated and occurred in spatially dispersed populations. The high abundance of dicots in the most disturbed habitats is consistent with hypotheses that rapid growth and short generation times were important aspects of flowering plant success in the Cretaceous.

6) In general, fossil floras preserved in situ provide a remarkable opportunity to reconstruct the relationships between extinct plants and their growth environments, and to gain insight into the way earlier members of extant lineages lived and interacted with the physical environment and one another. The distribution of fossil plants on ancient landscapes can be a source of ideas about how plant ecological strategies have evolved through geological time, and of data for testing paleoecological hypotheses derived from studying phy-

logenetically “basal” extant species or from studying the functional morphology of fossils. Ongoing studies of similar deposits in other places will establish if the patterns described here were geographically widespread. We hope that this study provides an example of how much ecological information can be preserved in the spatial distribution of fossil plants, and its value in developing and testing paleoecological hypotheses.

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SUPPLEMENTAL MATERIAL

Appendix A

Additive diversity analyses of BCR census data (*Ecological Archives* M082-001-A1).

Appendix B

Significance tests of environmental differences between floral associations data (*Ecological Archives* M082-001-A2).

Appendix C

Species accumulation curves for floral associations recognized from cluster analysis data (*Ecological Archives* M082-001-A3).

Appendix D

A table of Mantel tests showing statistical significance of the association between floral distance, spatial distance, and environmental distance data (*Ecological Archives* M082-001-A4).

Supplement

Floral morphotype abundances and environmental data for each site at Big Cedar Ridge (*Ecological Archives* M082-001-S1).