1 **PLANT COMMUNITY CHANGE ACROSS THE PALEOCENE-EOCENE BOUNDARY**
2 **IN THE GULF COASTAL PLAIN, CENTRAL TEXAS**

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17
18 **ABSTRACT**

19 Long-term global warming during the early Paleogene was punctuated by several short-
20 term 'hyperthermal' events, the most pronounced being the Paleocene-Eocene Thermal
21 Maximum (PETM). During this long-term warming tropical climates expanded into extra-
22 tropical areas, creating a widespread band of thermophilic flora that reached into the paratropics,
23 possibly as far north as the mid-latitude Northern Great Plains (NGP). Relatively little is known

24 about these paratropical floras, despite distribution across the Gulf Coastal Plain (GCP). We
25 assess floras from the GCP in Central Texas before and after the Paleocene Eocene Boundary
26 (PEB) to define plant ecosystem changes associated with rapid global warming in this region. At
27 the PEB these floras suggest uniform plant communities across the GCP, but with high turnover
28 rate and changes in community composition. Paleoecology and paleoclimate estimates from
29 Central Texas Paleocene and Eocene floras suggest a warm and wet environment, indicative of
30 tropical seasonal forest to tropical rainforest biomes. Fossil evidence from the GCP combined
31 with NGP data and modern tropics suggest that early Paleogene warming helped create a
32 paratropical belt that extended into mid-latitudes. Evaluating the response of fossil plant
33 communities to rapid global warming has important implications for understanding and
34 preparing for current global warming and climate change.

35

36

INTRODUCTION

37 During the early Paleogene, ~58-50 million years ago (Ma), a long-term trend of
38 increasing temperatures (e.g., Zachos et al. 2001) allowed tropical-like floras to extend outside
39 the tropics, resulting in a widespread band of thermophilic flora in sub-tropical latitudes (e.g.,
40 Harrington 2003; Wing et al. 2005; Fine and Ree 2006; Jaramillo et al. 2006; Harrington and
41 Jaramillo 2007; Jardine et al. 2012; 2018; Wing and Currano 2013; Sluijs et al. 2014). This long-
42 term trend of early Paleogene global warming culminated in the Early Eocene Climatic Optimum
43 (EECO), one of the warmest periods of the Cenozoic, from ~53-50 Ma (Zachos et al. 2001,
44 2008). Several abrupt and short-term rapid temperature increases known as ‘hyperthermal’
45 events punctuated the early Paleogene warming trend (e.g., Sluijs et al. 2006; 2009; 2014; Pagani
46 et al. 2006b; Zachos et al. 2008; 2010; McInerney and Wing 2011; Slotnick et al. 2012; Bowen

et al. 2015). These hyperthermal events were associated with numerous perturbations to climate, environment, and terrestrial and marine biota, such as pronounced negative carbon isotope excursions and increased ocean acidity (Zachos et al. 2005; 2007; Thomas 2007; Stap et al. 2009; McInerney and Wing 2011; Kraus et al. 2013; Sluijs et al. 2014; Zeebe et al. 2014; Gutjahr et al. 2017). The most pronounced of these hyperthermals is the PETM, which occurs at ~56.3 Ma and demarcates the beginning of the Eocene (e.g., Zachos et al. 2001; 2008; Westerhold et al. 2012). Warming and associated environmental changes during the PETM led to dramatic changes in biota distribution, increased evolutionary turnover rates in both marine and terrestrial environments, shifts in latitudinal range and species occurrences of marine plankton, mass extinction of benthic foraminifera, alteration in-trophic structure and taxonomic composition of terrestrial faunas, major changes in the composition of mid-latitude floral communities, and major diversification of tropical plant groups (e.g., Gingerich 2001; 2003; Wing et al. 2005; Zachos et al. 2005; Takeda and Kaiho 2007; Thomas 2007; Woodburne et al. 2009; Jaramillo et al. 2010; McInerney and Wing 2011). About two million years after the PETM the Eocene Thermal Maximum 2 (ETM2) and Hyperthermal 2 (H2) occurred in rapid succession. Both hyperthermal events were smaller in magnitude than the PETM, but caused similar biotic and geochemical changes (e.g., Lourens et al. 2005).

The early Paleogene long-term warming trend and hyperthermal events caused considerable changes in terrestrial biota, changes that are well characterized by extensively studied Bighorn Basin, Wyoming, macrofloras spanning the PETM (e.g., Wing 1998; Wing et al. 2000, 2005; McInerney and Wing 2011; Wing and Currano 2013). During the PETM, Paleocene plant taxa were almost completely replaced by new, thermophilic taxa, thought to have migrated from southern latitudes (Wing et al. 2005; McInerney and Wing 2011; Wing and Currano 2013).

70 Remarkably, during the PETM recovery phase many Paleocene taxa that had been displaced
71 returned to the Bighorn Basin and were common for the next few million years, but were then
72 displaced again by the same thermophilic taxa during the EECO (Wing et al. 2005; McInerney
73 and Wing 2011).

74 It has been suggested that immigrant plant taxa arriving in the NGP during the PETM and
75 later during the EECO came from northward dispersal of low-latitude floras in response to long-
76 term global warming (e.g., Wing et al. 2005; Harrington and Jaramillo 2007; McInerney and
77 Wing 2011; Jardine et al. 2012; Sluijs et al. 2014). However, relatively little is known about
78 early Paleogene megafloras from most of southern North America, limiting our ability to test this
79 possibility. Also coincident with early Paleogene warming was a significant rise in eustatic sea
80 level (Miller et al. 2005) dramatically changing low-lying coastal environments, such as the GCP
81 (e.g., Siesser 1984; Sluijs et al. 2014).

82 The most intensively studied floras from southern North America are from the GCP. For
83 over a century, floras have been collected and described from localities throughout the GCP
84 (e.g., Berry 1916; Crepet et al. 1975, 1980; Potter 1976; Dilcher and Manchester 1986; Taylor
85 1988; Wolf and Dilcher 2000; Harrington et al. 2003; Harrington and Jaramillo 2007; Danehy et
86 al. 2007; Jardine et al. 2012; Gardner et al. 2017; Stephenson et al. 2018). Unfortunately, age
87 control for many of these sites is poor because outcrops are relatively small and scattered,
88 making correlation difficult. Further, many early studies assumed an age for the localities based
89 on regional lithostratigraphy (Stephenson 1914; Deussen 1924; Sellards 1933), which is now
90 known to be incorrect (Weems and Edwards 2004; Yancey et al. 2010; 2012). Additionally, very
91 few studies made systematic collections or analyzed megafloreal diversity and ecology. Thus, it

92 has been difficult to assess patterns of change across the PEB in the GCP or to make
93 comparisons with early Paleogene NGP floras.

94 A few studies have reconstructed the climate and ecology of GCP floras using micro- and
95 megafloras. Wolfe and Dilcher (2000) used Climate Leaf Analysis Multivariate Program
96 (CLAMP) to estimate mean annual temperature (MAT) and mean annual precipitation (MAP)
97 for the central GCP (spanning the Wilcox Group from Texas to Arkansas) and reconstructed a
98 tropical climate for the region. Additionally, their estimates indicated an increase in MAT from
99 60 Ma (~19°C) to 56 Ma (~27°C), followed by gradual draw-down with temperatures returning
100 to 22°C at ~50 Ma, and precipitation increase from 57-56 Ma (MAP ~300 cm) (Wolfe and
101 Dilcher 2000). However, major caveats are that age control is questionable and floras sample a
102 large geographic area.

103 Danehy et al. (2007) described the Red Hot Truck Stop (RHTS) macroflora in western
104 Mississippi, one of the few megafloras in the GCP to be confidently dated as very early Eocene
105 (~1.6 million years post-PETM). Their results indicated tropical and subtropical climates during
106 the early Eocene based on occurrences of monocotyledonous angiosperms (monocots) and taxa
107 from the families Lauraceae, Myrtaceae, Fabaceae, and Juglandaceae. Analyses of GCP
108 palynofloras from eastern Mississippi, western Alabama and Georgia, including from the RHTS,
109 indicated increased taxonomic richness during the late Paleocene along with rapid turnover,
110 decreased diversity, and late Paleocene to early Eocene extinctions (Harrington and Jaramillo,
111 2007). The palynoflora comprises plant families associated with temperate and tropical affinities
112 (Harrington and Jaramillo 2007), similar to the RHTS megaflora (Danehey et al. 2007). These
113 dramatic changes in floral composition and diversity spanning the PEB across the GCP suggest

114 that early Paleogene environmental changes influenced tropical ecosystems and that early
115 Paleogene dispersal of plant taxa across North America likely tracks climate change (Di).

116 Another area where megafloras and microfloras are common, and relatively well
117 constrained in age, is in the upper Wilcox and lower Claiborne in Central Texas (Berry 1916;
118 Yancey et al. 2010; Dickey and Yancey 2010; Gardner et al. 2017; Stephenson et al. 2018).
119 Extensive new collections of macrofloras from well-documented deposits in Bastrop County,
120 Texas (Denison et al. 2017; Demchuk et al. 2019) present an excellent opportunity to examine a
121 PEB floral record from southern North America in the context of both sedimentological setting
122 and changing climate. We use fossil leaves from Central Texas to describe and assess the floral
123 composition and paleoecology of GCP floras across the PEB. These trends and characteristics
124 are then compared to other GCP floras, and to Big Basin NGP floras, to determine if paratropical
125 forest communities migrated north from the GCP during early Paleogene hyperthermal events
126 and warming, then contracted back to the GCP during cool periods.

127

128 Geologic Framework

129 This study is focused on uppermost Wilcox and lowermost Claiborne deposits in Bastrop
130 County. These two groups are present across the entire GCP (Fig. 1A; Baker 1995; Weems and
131 Edwards 2004), although pronounced lateral facies changes result in different formations being
132 defined in different regions. Conversely, some units that include quite different lithologies
133 laterally, such as the Sabinetown, bear the same name. In Texas calcareous microfossils are rare
134 in the onshore Wilcox, which severely limits high-resolution surface and subsurface correlations
135 at local and regional scales.

Wilcox outcrops in Texas have a long history of interpretation as fluvio-deltaic deposits (e.g., Plummer 1933, Harris, 1962; Fisher and McGowen 1967; Baker 1995). However, they include extensive tidal to nearshore marine deposits, based on tidal sedimentary structures and marine trace fossils that indicate deposition in an overall mesotidal coastal setting (Breyer and McCabe 1986; O’Keefe et al. 2005; Denison et al. 2017; Demchuk et al. 2019; Ambrose et al. 2020). Thus, all floras in this study would have been strongly influenced by and adapted to coastal environments. In modern environments, a variety of micro-habitats develop along coastal areas in response to tidal influences and salinity gradients (e.g., Sternberg et al. 1991). Plant community composition can respond to changes in salinity as sea level varies, a pattern observed in lower, middle, and upper marsh habitats due to varying salinity gradients (e.g., Gough and Grace 1998).

Pollen and spores indicate that PEB low-lying Central Texas GCP landscape was populated with abundant palms and moderately diverse dicotyledonous angiosperms (e.g., O’Keefe et al., 2005; Denison et al., 2017; Stephenson et al., 2018). This landscape with lagoons and marshes was dissected by tidal channels and transitioned offshore to a tidally-dominated shallow-shelf. Sea level rise during the PETM, driven by heat-induced expanding ocean volumes (Denison 2021), caused landward translation of deposition across the GCP (Sluijs et al. 2014). In Central Texas, this translation can be seen as progradational parasequences of the Sabinetown give way to the shallow marine transgression represented by the ‘Dark Band.’ A hiatus of unknown, but likely long-term duration, separates Wilcox sediments from the Carrizo (lowermost Claiborne). The boundary is demarcated by a *Glossifungites* ichnofacies with burrows into the subjacent ‘Dark Band’. In the intervening c. 4 Ma missing at this boundary, possibly representing all or most upper Wilcox time, sediment translated across an exposed

159 coastal plain into shelf edge deltas and deepwater turbidites. In Central Texas the Carrizo has
160 tidal sedimentary structures and robust *Ophiomorpha*, possibly prograding tidal delta deposits on
161 a shallow shelf (see discussion below; Yancey et al. 2010; 2012; Sluijs et al. 2014; Denison et al.
162 2017).

163 Microfossil studies show that seasonal euxinic photic zone conditions developed along
164 the GCP at the PEB leading to shelf eutrophication, facilitating carbon burial along continental
165 margins, ultimately acting as negative feedbacks to carbon input and global warming (Sluijs et
166 al. 2014). Coastal habitats, which are submerged or partially submerged, often reduce turbulent
167 flow and dampen wave energy while plant roots trap sediment and prevent resuspension of
168 sediment (Duarte et al. 2013). As a result, these coastal regions act as large carbon sinks,
169 influence basin accommodation space, regulate nutrient fluxes, and provide a form of climatic
170 regulation (Duarte et al. 2013). In this scenario, coastal plant communities within the GCP,
171 specifically those with tidal marsh, mangrove, and hardwood hammock characteristics, may have
172 played an essential role in sediment accumulation across the PEB.

173

174 *Paleogene Gulf Coastal Plain deposits in Central Texas.*— There are several locations in the
175 Bastrop area where uppermost Wilcox and lowermost Claiborne are exposed (Fig. 1). In Central
176 Texas the pertinent stratigraphic succession is, in ascending order, Calvert Bluff and Sabinetown
177 of the upper Wilcox, a ‘Dark Band’ unit, and the Carrizo of the lowermost Claiborne (Fig. 2;
178 Denison et al. 2017; Demchuk et al. 2019).

179 The uppermost Calvert Bluff is late Paleocene in age. At Pancake Rocks in Tahitian
180 Village it consists of sand-dominated tidal flats with small, depauperate trace fossils that are

181 dissected by sand-filled tidal channels with robust *Ophiomorpha* (Denison et al. 2017; Ambrose
182 et al. 2020).

183 Above a basal transgressive lag, the Sabinetown in the Bastrop area is a series of
184 progradational parasequences that become progressively thicker up-section (Denison et al. 2017).
185 Each parasequence consists of marine siltstones that become more heterolithic upwards and
186 transition into muddy tidal heterolithics capped by sand-dominated tidal heterolithics, locally
187 with extensive bioturbation. The uppermost parasequence has planar cross bedding, wavy and
188 flaser bedding in the upper part. In contrast, at its type locality the Sabinetown was described as
189 mainly glauconitic sand in the lower part (30 feet), overlain by brown clay (40 feet), sand (25
190 feet) and lignitic clay (15 feet) (Plummer 1933). The Sabinetown is latest Paleocene in age
191 (Denison et al. 2017). Scattered fossil leaves are common in the Sabinetown but never in high
192 abundance.

193 Between the uppermost Sabinetown and the base of the Carrizo is the ‘Dark Band’ (Fig.
194 1B, 1C, 2; Denison et al. 2017). The ‘Dark Band’ has not been formally defined nor assigned to a
195 formation or group. It is presently interpreted as the uppermost Wilcox unit, deposited during the
196 PETM, making it earliest Eocene in age (e.g., Denison et al. 2017; Gardner et al. 2017;
197 Stephenson et al. 2018; Demchuk et al. 2018, 2019). It has an erosive base, making it
198 disconformable with the underlying Sabinetown (Denison et al. 2017; Demchuk et al. 2019).

199 The ‘Dark Band’ has been eroded in all three locations by channels (Fig. 1C), and
200 elsewhere in the region by the Carrizo and/or Pleistocene deposits (Harris 1962). Tidal channel-
201 fill deposits consist of sand and mud and commonly end with a subbituminous coal of varying
202 thicknesses. Channel deposits contain abundant fossil leaves.

203 Palynological analyses of the ‘Dark Band’ show a spike in *Cicatricosisporites* sp. fern
204 spores, the last occurrence of *Spinaepollis* sp. angiosperm pollen, an acme of the dinocyst
205 *Apectodinium homomorphum*, a worldwide indicator for the PETM (Denison, 2021), and a lack
206 of Paleocene-restricted pollen taxa (Denison et al. 2017; Gardner et al. 2017; Stephenson et al.
207 2018; Demchuk et al. 2018, 2019). Additionally, preliminary results of compound-specific
208 isotope analyses of samples from the ‘Dark Band’ show a weak negative excursion in $\delta^{13}\text{C}$
209 (Demchuk et al. 2018). Based on the carbon isotope excursion, pollen biostratigraphy, and *A.*
210 *homomorphum* acme, the ‘Dark Band’ has been interpreted to represent the PETM (Demchuk et
211 al. 2018), albeit attenuated due to the up-dip location and bounding hiatuses. Channel deposits
212 that erode into the ‘Dark Band’ may be younger than the ‘Dark Band’; however, due to the way
213 that the channels migrate within the ‘Dark Band’ and the fact that both the channels and the
214 ‘Dark Band’ are capped by an erosive unconformity, the age relationships of the channels and
215 the ‘Dark Band’ are difficult to determine. Importantly, fossil leaves are abundant within the
216 ‘Dark Band’ and the channel-fills that erode it (Fig. 2), making it possible to assess the GCP
217 megafloral record across the PEB.

218 Above the ‘Dark Band’, and the channel deposits that erode into it, the Carrizo is
219 interpreted as early Eocene in age (Fig. 1B, 1C, 2). It unconformably overlies the ‘Dark Band’,
220 and *Thalassinoides* from a *Glossifungites* surface extend down into the ‘Dark Band’ (Denison et
221 al. 2017). It consists of fine-grained cross-bedded sands that contain abundant robust
222 *Ophiomorpha*, indicating deposition on an open marine shelf. Up-section, silt laminae become
223 increasingly abundant indicating a small-scale regression, then decrease and the sands become
224 better sorted, indicating renewed transgression and a return to open shelf conditions. Within

225 these sand deposits, usually in the mud layers, are pieces of woody debris and occasional well-
226 preserved fossil leaves (Yancey et al. 2010).

227 Gardner et al. (2017) and Stephenson et al. (2018) used fungi and other non-pollen
228 palynomorphs to assess the palynoecology of the upper Sabinetown–lower Carrizo strata
229 exposed near Bastrop in a series of vertical transects from Red Bluff, Golf Course, and
230 Manawianui sites (Fig. 1C). This work suggests that upper Sabinetown deposition took place on
231 a shallow shelf offshore from a tidal marsh bordered by an onshore hardwood wetland and fern
232 savanna. The ‘Dark Band’ was deposited in a tidal lagoon or shallow shelf offshore from a fire-
233 prone fern-dominated savannah (Stephenson et al. 2018). Channel-fill at the Golf Course is
234 derived from hardwood hammocks, mangroves, and sawgrass marshes (Stephenson et al. 2018).
235 Carrizo palynofloral assemblages indicate an abrupt change in depositional environment to a
236 shallow marine shelf offshore from a brackish tidal marsh, bordered by a palm savannah
237 (Stephenson et al. 2018), consistent with the sedimentological evidence.

238

239 METHODS

240 Fossil Collection and Description

241 Fossil leaves were collected from uppermost Wilcox and lowermost Claiborne outcrops
242 along the Colorado River, near Bastrop (Fig. 1B, 1C). Locality JW1802, from the uppermost
243 Sabinetown at an outcrop on Copperas Creek, a small tributary of the Colorado River (Fig 1B,
244 1C). Locality JW1801, a channel-fill exposed at the Pine Forest Golf Club course along the
245 Colorado River in Tahitian Village, TX (Fig. 1B, 1C). Locality JW1803, an outcrop of Carrizo at
246 the southern end of Manawianui Drive in Tahitian Village, TX (Fig. 1B, 1C). These three

247 locations will be referred to as ‘Copperas Creek’ (JW1802), ‘Golf Course’ (JW1801), and
248 ‘Manawianui’ (JW1803) respectively.

249 Voucher collections, in which the best-preserved specimens and specimens of any
250 unknown morphotypes were collected, were made at all sites. Census collections of fossil leaves,
251 in which at least 300 specimens were examined, identified, and tallied, were made from Golf
252 Course and Manawianui. Poor preservation and sparse fossils at Copperas Creek precluded a
253 census collection. Specimens identified and tallied during these collection activities comprise the
254 ‘field census’ (Supplementary Material, Tables 1, 2). Representative samples of each
255 morphotype, all unknown specimens, and well-preserved specimens that document morphotype
256 variability were collected during the census collections. All collected specimens were given
257 laboratory identification numbers and are housed at Baylor University, comprising the ‘lab
258 census’ (Supplementary Material, Tables 1, 2, 3). Field census data were used for diversity
259 analysis, while lab census material was used for estimating paleoecology and paleoclimate
260 values.

261 Fossil non-monocotyledonous angiosperm leaves (referred to herein as dicots) were
262 described using the ‘Manual of Leaf Architecture’ (Ellis et al. 2009). Monocotyledonous
263 angiosperms (monocots) and ferns were described primarily using venation characteristics.
264 Based on the features observed when making these descriptions, the fossils from each locality
265 were divided into morphotypes (e.g., Ellis et al. 2009; Peppe et al. 2008) (Supplementary
266 Material, Table 4).

267 In addition, fossil leaves of late Paleocene and early Eocene age from GCP localities in
268 northeastern Texas, Tennessee, Arkansas, and Kentucky (Fig. 1A) that are housed at the Florida

269 Museum of Natural History, were assessed and photographed for comparison with Bastrop
270 morphotypes (Supplementary Material, Table 5).

271

272 Diversity Analyses

273 Floral diversity based entirely on our quantitative collections (field census) was evaluated
274 using PAST (Hammer et al. 2001). Abundance counts of Golf Course and Manawianui material
275 were used to determine diversity (Shannon, Simpson, and Equitability Indices), dominance
276 (Berger-Parker Dominance), and evenness (Shannon Index divided by the natural log of species
277 richness; Harper 1999; Morris et al. 2014) of the flora. Bray Curtis Dissimilarity (Legendre and
278 Legendre 1998) and Jaccard's Index of Similarity (Real and Vargas 1996) were used to compare
279 community compositions.

280

281 Vein Density Scaled Leaf Area Determination

282 Much of the collected material was fragmentary, making it difficult to reconstruct leaf
283 area. In cases where the leaf was not complete enough to estimate leaf area, we used the vein
284 density method (Sack et al. 2015; Merkhofer et al. 2015) to estimate leaf area. We then used the
285 vein density estimated leaf area to calculate leaf mass per area and leaf area in paleoclimate
286 reconstructions. Photographs of all specimens were taken using a high-resolution camera (Nikon
287 D330, DX-VR, 18-55 mm). All photographs included a scale bar, locality, and specimen ID. Vein
288 density was measured on all specimens with well-preserved secondary veins. Secondary (2°)
289 veins were identified using the definition of Ellis et al. (2009) and included all regular, inter-,
290 interior, and minor secondaries. Four or more rectangular boxes were placed on the photographs
291 of preserved leaf fragments using Adobe Photoshop CC 2019. These boxes were located on the

basal, middle (2), and apical thirds of the leaf following the protocols of Sack et al. (2012) and Merkhofer et al. (2015). If those locations were not available, the boxes were fit on the available preserved area. Vein density is defined as total vein length divided by the rectangle area (Sack et al. 2012). The area of each rectangle was sized to include at least two 2° veins. After measuring and recording the area of each box, lengths of all secondary veins were measured and recorded. All measurements were made in ImageJ (Schneider et al. 2012). After calculating the average vein length density (mm/mm²) for all specimens, the estimated area of each leaf was scaled using the regression method of Sack et. al (2012):

$$\log_{10}(\text{leaf area cm}^2) = 1.96 - 2.04 \times \log_{10}(\text{subsampled } 2^\circ \text{ vein density cm/cm}^2) \quad (\text{Eq.1})$$

The natural log of the estimated leaf area (recorded in mm²) was used to categorize each leaf into the following leaf size classes: leptophyll, nanophyll, microphyll, notophyll, mesophyll, and megaphyll; which are defined as greater than 2.12 mm², 4.32 mm², 6.51 mm², 8.01 mm², 9.11 mm², and 11.42 mm², respectively (Webb 1959).

Leaf Mass per Area

To calculate leaf mass per area (M_a, g/m²) the vein-scaled areas were used in combination with petiole widths using the woody dicot regression from Royer et al. (2007):

$$\log[M_a] = 0.3820 \times \log[PW^2/A] + 3.070 \quad (\text{Eq.2})$$

When possible, leaf area was determined from direct measurement of leaf area in ImageJ.

However, as most of the fossils are leaf fragments, most leaf areas were estimated from vein

density, and ~96% of estimated M_a used vein-scaled areas. All leaves measured were non-sessile

315 with observable petioles. If the entire petiole was not present, the width of the exposed primary
316 vein merging with the uppermost section of the petiole was measured following the protocol of
317 Royer et al. (2007; 2012). The leaf mass per area was then compared to modern sites (Peppe et
318 al. 2018; Royer et al. 2012) to assess ecological habitat.

319

320

Paleoclimate

321

Univariate and multivariate methods were used to estimate MAT and MAP for Golf
322 Course. Leaf margin analysis (LMA), a univariate climate model, which uses the presence and
323 absence of teeth in woody dicot angiosperm leaves, was used to estimate MAT (Miller et al.
324 2006; Peppe et al. 2011). Leaf area analysis (LAA), a univariate climate model, which uses the
325 average leaf size of an entire flora, was used to estimate MAP (Wilf et al. 1998; Peppe et al.
326 2011). Digital leaf physiognomy (DiLP) was used to estimate mean MAT and MAP (Peppe et
327 al., 2011). DiLP is a multivariate climate model that utilizes multiple size and shape
328 characteristics of fossil leaves to estimate MAT and MAP. All fossil woody dicot leaves with
329 $\geq 25\%$ preservation were measured using the protocols described in Royer et al. (2005) and
330 Peppe et al. (2011). For specimens that were at least 25% complete, but where leaf area could not
331 be digitally measured, the vein-scaled leaf area was used in both LAA and DiLP.

332

333

RESULTS

334

Floral Composition and Characteristics

335

Copperas Creek megaflora fossils (JW1802), of latest Paleocene age, are relatively
336 poorly preserved and commonly occur in mats between siltstone laminae. A total of 11
337 morphotypes, consisting of 91% dicots and 9% monocots, were identified and described (Table

1, Fig. 3A). Of the 10 dicots, 63% have toothed margins. Golf Course megaflora fossils, of early Eocene age, are better preserved and have a total of 26 morphotypes. The Golf Course flora is comprised of 84% dicots, 8% monocots, and 8% ferns (Table 1, Fig. 3A), with 32% of the dicots having toothed margins. Manawianui megaflora fossils (JW1803), also early Eocene in age, consist of 13 morphotypes with preservation similar to Golf Course. Manawianui flora is comprised of 77% dicots, 15% monocots, and 8% ferns (Table 1, Fig. 3A), with 60% of dicots having a toothed margin.

Copperas Creek lab collection consists of 54 specimens composed of 12 morphotypes. Dicots BT-02 and BT-15 were the two most abundant morphotypes (Supplementary Material Table 3). Golf Course field census collection yielded 310 specimens composed of 10 morphotypes. Morphotypes BT-01 and BT-02 made up >50% of the collection (Supplementary Material Table 1). Golf Course lab collection, a combination of specimens collected during census collection and a voucher collection from multiple channel fills, consists of 200 specimens composed of 23 morphotypes (Supplementary Material Table 1). BT-01 and BT-02 were also the most abundant morphotypes in the lab collection (~40% of the collection). Manawianui field census collection yielded 344 specimens composed of 13 morphotypes. BT-30, a monocot, made up >40% of the collection (Supplementary Material Table 2). Manawianui lab collection had 108 specimens composed of 13 morphotypes, with BT-23 (palm) and BT-34 (dicot/laurel) the most abundant morphotypes (Supplementary Material Table 2).

Several morphotypes were shared among the localities. Two morphotypes, BT-02 and BT-28, were present in all three localities (Supplementary Material Table 4). BT-01 and BT-29 were present at Golf Course and Manawianui, BT-21 was present at Copperas Creek and Golf Course, and BT-34 was present at Copperas Creek and Manawianui (Supplementary Material

361 Table 4). Fossil leaves observed from other localities within the GCP (Fig. 1A) share
362 morphotypes in common with those found in Central Texas (this study), including BT-02, BT-
363 05, BT-06, BT-09, BT-12, BT-14, BT-20, BT-23, BT-30, BT-34, BT-35 and BT-37
364 (Supplementary Material Table 5).

365

366 Species Richness and Diversity

367 Rarefaction curves for Golf Course and Manawianui display similar species richness (10
368 and 13 morphotypes, respectively) and plateau, indicating the sites have been well sampled (Fig.
369 3B). Floras also have very similar levels of diversity and dominance (Table 2). However, despite
370 these similarities, they have markedly different compositions, demonstrated by a Bray Curtis
371 Dissimilarity value of 0.966 and Jaccard's Index of Similarity of 0.095 (Table 3).

372

373 Paleoecology

374 All floras have similar site mean and median M_a and are comprised primarily of taxa
375 reconstructed to be deciduous, though there is a small component of evergreen taxa in each flora.
376 For Copperas Creek mean M_a is 93 g/m² (maximum 213 g/m² and minimum 41 g/m²;
377 Supplementary Material Fig. 1), and 2 of the 6 morphotypes (BT-36, BT-37) are likely
378 evergreen. Mean M_a for Golf Course is 93 g/m² (maximum upper 177 g/m² and minimum 51
379 g/m² (Supplementary Material Fig. 1), and four morphotypes (BT-04, BT-05, BT-06, and BT-12)
380 are likely evergreen. Manawianui has one morphotype (BT-35) that is likely evergreen, with
381 mean M_a of 84 g/m² (maximum 134 g/m² and minimum 53 g/m²; Supplementary Material Fig.
382 1).

Although mean M_a is similar between sites, distribution at each locality is considerably different (Fig. 4). In particular, Golf Course has a much wider distribution of M_a than Copperas Creek and Manawianui (Fig. 4), suggesting taphonomic differences between sites or that the Golf Course represents a different ecosystem from the other two sites.

Paleoclimate

MAT and MAP were reconstructed for Golf Course. Climate was not reconstructed for the other two sites because they had too few morphotypes to produce reliable climate estimates. MAT estimates using LMA were $21.2 (\pm 3.4)$ and $18.6 ^\circ\text{C} (\pm 4.8 ^\circ\text{C})$ using the Miller et al. (2006) and Peppe et al. (2011) models, respectively (Table 4). MAP estimates using the Wilf (1998) and Peppe et al. (2011) LAA regressions were $197.5 (+85.3, - 59.6)$ and $191.7 (+161.1, - 87.6)$, respectively (Table 4). DiLP MAT and MAP estimates were $22.4 ^\circ\text{C} (\pm 4.0^\circ\text{C})$ and $250.1 \text{ cm/yr} (+205.6/-112.8)$ (Table 4). These climate reconstructions indicate warm and wet adapted flora, similar to a modern sub-tropical to tropical seasonal forest biome (Fig. 5A).

DISCUSSION

Composition and Diversity of Central Texas Gulf Coastal Plain Floras

We observed a considerable Paleocene to Eocene change in floral composition in Central Texas GCP floras. The late Paleocene Copperas Creek flora was dominated by dicots. Monocots were present but were much less abundant in both the number of morphotypes and collected specimens when compared to the younger localities (Table 1). Further, unlike Golf Course and Manawianui, ferns and gymnosperms were not present at Copperas Creek. Additionally, two dicots dominated the assemblage and legume-like fruits were relatively common. Given the

406 floral composition and dominance of a few taxa in the total assemblage, we suggest that the flora
407 was probably low in species richness and diversity. However, this could not be assessed further
408 because the flora was not amenable to systematic collecting. Despite the lack of systematic
409 collections, the flora was sufficiently well preserved to compare the taxonomic composition of
410 the flora with the other two sites.

411 The Golf Course flora, comprising 26 morphotypes, contains nearly twice as many
412 morphotypes as Copperas Creek and Manawianui (11 and 13 morphotypes, respectively, Table
413 1). Four taxa (3 dicots, 1 palm) dominate the flora, with other morphotypes being relatively rare.
414 Despite relatively high morphotype richness in the voucher collection, the census collection
415 yielded only 10 morphotypes, indicating that our extensive voucher sampling yielded rare
416 morphotypes not represented in the census collection. Differences in species richness between
417 sites could be due to differences in floras or in taphonomy. Golf Course voucher and census
418 collections were made from different locations along a lateral transect: differences in species
419 richness between voucher and census collections could reflect a heterogeneous landscape. In this
420 scenario, the voucher collection, from several different channel cut-and-fill bodies, could have
421 sampled a broader diversity of taxa on the landscape. Alternatively, Golf Course material was
422 collected from a fluvially-dominated channel distinctly different from marine-deposits at
423 Copperas Creek and Manawianui. These dramatic differences in depositional environments
424 imply that taphonomic processes leading to preservation of the three floras were very different.
425 Much higher species richness at Golf Course-is likely due to taphonomic processes rather than
426 real differences in species richness on the landscape.

427 Floral composition at Copperas Creek and Golf Course is markedly different. Only two
428 morphotypes persisted from Copperas Creek to Golf Course (BT-02 and BT-01), both of which

429 are more abundant in the Golf Course assemblage. Relative to Copperas Creek there is a nearly
430 complete turnover in dicot morphotype composition, the appearance of ferns, and an overall
431 increase in abundance of palms and ferns at Golf Course. This suggests a major change in floral
432 composition from Copperas Creek to Golf Course (Supplementary Material Table 4). However,
433 the appearance of turnover could be due to the taphonomic controls or the local absence of a
434 particular taxa.

435 Manawianui was dominated by palms and a laurel-like morphotype (BT-34)
436 (Supplementary Material Table 2, Appendix Fig. 30). Voucher and census collections yielded 13
437 distinct morphotypes and rarefaction indicates that the collection was well-sampled (Fig. 3B). Of
438 the 11 latest Paleocene Copperas Creek morphotypes that may have been extirpated or were
439 locally absent prior to deposition of Golf Course (Supplementary Material Table 4), two are
440 found to occur again in the early Eocene Manawianui flora (BT-28 and BT-34). Morphotype BT-
441 02, which is high in abundance at Golf Course, decreased in abundance at Manawianui, returning
442 to an abundance similar to Copperas Creek. Much like between Copperas Creek and Golf
443 Course, there is a near complete turnover in taxonomic composition between Golf Course and
444 Manawianui.

445 Despite this turnover in taxonomic composition, species richness of census collections
446 and overall floral diversity were similar (Table 2), though the Berger-Parker Dominance value
447 was greater at Manawianui (Table 2), indicating the site was dominated by fewer taxa. Similarity
448 indices based on census collections (Bray Curtis Dissimilarity and Jaccard's Index of Similarity)
449 indicate that floral composition is significantly different (Table 3). These diversity and similarity
450 indices suggest that although there was significant floral turnover between Golf Course and
451 Manawianui, it had little effect on overall floral diversity. Sample sizes of Golf Course and

452 Manawianui collections were similar and rarefaction curves indicate that floras were well
453 sampled (Fig. 3; Supplementary Tables 1, 2, and 3), suggesting that differences in species
454 richness, diversity, and composition reflect real differences. However, given dramatic differences
455 in depositional environments between the sites, it is likely that some differences are related to
456 taphonomic processes. At this stage it is difficult to determine if the change through time is a
457 result of taphonomic differences due to different depositional settings, and additional collections
458 are needed to resolve this question. Regardless, the proportion of monocot, dicot, gymnosperm,
459 and fern taxa in GCP floras changed through time (Fig 3A), with an overall increase in palm and
460 fern abundance (Fig 3A). For comparison, the proportion of monocots, dicots, gymnosperms,
461 and ferns were estimated for Bighorn Basin late Paleocene, PETM, and early Eocene floras
462 (Wing and Currano 2013). Similar to the Bastrop flora, in Bighorn Basin there was an overall
463 increase in palm abundance and decrease in dicot abundance post-PETM. This supports the
464 hypothesis of a latitudinally widespread thermophilic flora with similar composition from the
465 GCP into the NGP, at least as far north as Bighorn Basin.

466

467 Gulf Coastal Plain Early Paleogene Floras

468 We compared our Bastrop collections to historical Wilcox and Claiborne collections from
469 Central Texas, Tennessee, and southwestern Kentucky, housed at the University of Florida
470 Natural History Museum (Fig. 1A). Unfortunately, due to issues with stratigraphic nomenclature
471 and imprecise dating at most historical GCP collecting locations, it was not possible to determine
472 if collections were Paleocene or Eocene. Nonetheless, historical floras are a good reflection of
473 early Paleogene GCP floras and thus provide a useful comparison to our Central Texas floras.
474 Floras we examined from across the GCP and southeastern United States share at least 15

475 morphotypes with our Bastrop floras (Supplementary Material Table 5). The most common
476 morphotypes to appear in other GCP localities were BT-02, BT-20, BT-23, and BT-34, which we
477 tentatively assign to the Juglandaceae, Arecaceae, and Lauraceae families, respectively.

478 BT-02, the lanceolate, usually entire, Juglandaceous-type leaf, was the most common
479 morphotype that we found to co-occur in Bastrop sites and other GCP floras we assessed
480 (Supplementary Material Fig. 1A, 4B, 8B). Berry (1916) described several fossil leaf
481 morphotypes similar to BT-02, suggesting it commonly occurred across the GCP. Dilcher and
482 Manchester (1986) created a new genus, *Oreoroa*, for a middle Eocene-age (Claiborne
483 equivalent) fossil leaf with characteristics very similar to BT-02 to accommodate leaves similar
484 to the extant genera *Oreomunnea* and *Alfaroa*. We suggest that BT-02, and all comparable
485 morphotypes from historical GCP floras, are probably affiliated with *Oreoroa*, but additional
486 study is needed for confirmation. In particular, BT-02 is closely similar to *O. claibornensis*,
487 described by Manchester and Dilcher (1986), from Claiborne localities in Mississippi,
488 Tennessee, and Kentucky, suggesting it might be the same species or a closely related one.
489 Extant *Oreomunnea* and *Alfaroa* are evergreen tree genera that grow in montane/sub-montane
490 tropical rain forests in Central America, which is ecologically similar to our reconstructions for
491 the Bastrop Paleogene floras.

492 In addition to fossil leaves of *Oreoroa* (BT-02), abundant *Momipites*-type pollen,
493 morphotypes interpreted to have an affinity to Juglandaceae, have been described from the
494 Bastrop localities (Stephenson et al. 2018), and other locations across the GCP (Elsik and
495 Crabaugh 2001; Dickey and Yancey 2010). It is likely that *Oreoroa* sp. produced *Momipites*
496 pollen, supporting our tentative affiliation between BT-02 and *Oreoroa*. Further, it demonstrates
497 that *Oreoroa* was an important early Paleogene taxon across the GCP.

498 BT-34 is a species within the Lauraceae family that is present in Texas and Tennessee
499 Claiborne localities. It was likely an evergreen tree or shrub, possibly in the genus *Cinnamomum*.
500 This morphotype is absent from Golf Course, but is present at Copperas Creek and Manawianui
501 (Supplementary Material Table 5, Fig. 3A, 9D), suggesting that while it may have been
502 extirpated from Central Texas during or near the PEB, it was an important and persistent early
503 Paleogene taxon across the GCP. In addition, a member of the Lauraceae family, though
504 morphologically distinct from BT-34, was described at a Mississippi early Eocene locality
505 (Danehy et al. 2007), suggesting the family was present across the entire GCP during the early
506 Paleogene.

507 BT-20 and BT-23, fan palms from the Arecaceae family, possibly in the subfamily
508 Coryphoideae (Gomez-Navarro et al. 2009), appear throughout the GCP in the Wilcox and
509 Claiborne in Tennessee and Texas (Supplementary Material Table 5, Fig. 6E, 8D) indicating they
510 were important parts of the early Paleogene flora. Macrofossil palms appear to be very similar in
511 morphology between GCP sites, but more analysis is needed to determine if they are the same
512 species. Multiple palm pollen types have also been identified at Bastrop, including *Arecipites*-,
513 *Pandanus*-, and *Butia*-types (Stephenson et al. 2018).

514 We document a dramatic increase in palm abundance from Golf Course to Manawianui.
515 This same pattern was also noted in palm pollen abundance during the PETM from nearshore
516 marine deposits in Mississippi (Sluijs et al. 2014), suggesting that the increase in palms in the
517 GCP is related to environmental perturbations at the PEB. Further, one of the taxa that appears in
518 the body of the negative CIE in the Bighorn Basin was a palm (Wing et al. 2005), which supports
519 this supposition. More comparative work is needed, but it is plausible that the Bighorn Basin
520 palm was sourced from the GCP.

During the Paleocene and Eocene, palms experienced a significant radiation event (Gomez-Navarro et al. 2009), which coincides with the early Paleogene long-term global warming(e.g., Zachos et al. 2007). The trend observed in Central Texas early Paleogene floras (this study, Stephenson et al., 2018) and GCP palynofloras (Sluijs et al. 2014) is an increased palm abundance from the late Paleocene into the early/mid Eocene, which coincides with this radiation event (Harley 2006; Dranfield et al. 2005). Hyperthermal events may have acted as catalysts, providing opportunities for palm species to increase in abundance and diversity in subtropical areas (e.g. the GCP), as well as higher latitudes, such as the Bighorn Basin.

The GCP would have been a dynamic mosaic of coastal and offshore environments during the early Paleogene, generated by repeated transgressions and regressions. Warm early Paleogene climates created a sub-tropical/tropical coastal environment across the GCP. Our Bastrop material and comparisons to other GCP floras reveals a large proportion of shared morphotypes during the early Paleogene across the GCP, supporting the concept of a widespread band of thermophilic flora expanding into subtropical latitudes, composed of similar taxa across the region (e.g., Harrington, 2003; Fine and Ree 2006; Jaramillo et al. 2006; Harrington and Jaramillo 2007; Jardine et al. 2012; 2018). Further, it is plausible that during hyperthermal events the band of thermophilic flora would have expanded northward in response to a decreased latitudinal temperature gradient. GCP taxa, and particularly those that were widespread and not only restricted to coastal areas (i.e. morphotypes present further inland in places like Tennessee, Arkansas, and Kentucky), are plausible sources for PETM floras found in the NGP (e.g., Wing et al. 2005; Currano and Wing 2013; McInerny and Wing 2011). However, more detailed floral descriptions and accurate dating of floras from across the GCP are necessary to test this.

We were only able to reconstruct paleoclimate for Golf Course because the other two localities did not have enough taxa for reliable reconstructions (e.g., Burnham et al. 1992). MAT and MAP estimates for Golf Course indicate a tropical seasonal forest to a tropical rainforest biome (Fig. 5A). The Bastrop DiLP estimated MAT, 22.4°C (+/- 4°C), overlaps within uncertainty with Wolfe and Dilcher (2000) central GCP CLAMP estimates for 58-57 Ma and 56-55 Ma, 23-24°C and 27°C (+/- 1.8°C), respectively. DiLP MAP estimates for Golf Course suggest a wet environment (Fig.5a), similar to the CLAMP mean growing season precipitation estimate of >400 cm (Wolfe and Dilcher 2000). Our paleoclimate estimates also support previous data suggesting a warm and wet environment in the GCP during the early Paleogene (Wolfe and Dilcher 2000; Harrington et al. 2004; Danehy et al. 2007).

Of note, our MAT estimates from Bastrop are somewhat cooler than sea surface temperature (SST) and mean annual air temperature (MAAT) for the PETM from other regions in the GCP (e.g., Sluijs et al. 2014), but overlap within the range of uncertainty of SST and MAAT estimates for the late Paleocene (Sluijs et al. 2014) and early Eocene (Keating-Bitoni et al. 2011; Sessa et al. 2012). This offset in temperatures between our Golf Course floral estimates and SST and MAAT estimates based on TEX₈₆ and MBT-CBT paleothermometers may be due to methodological differences between the proxies. Alternatively, they could reflect real differences in temperature, suggesting that coastal terrestrial environments were slightly cooler than nearshore marine environments during deposition of Golf Course sediments.

Fossil assemblage paleoecology can be assessed using methods from Royer et al. (2007), summarized and applied in Peppe et al. (2018). Values less than ~87 g/m² can be broadly categorized as deciduous, greater than ~129 g/m² are broadly categorized as evergreen, and ~111

567 g/m^2 is considered to be intermediate between the two. Paleoecological reconstructions of the
568 three floras using M_a reveal noticeable changes through time, which likely reflect markedly
569 different ecosystems and sedimentary environments at the time of deposition, and potentially
570 changes in paleoclimate between floras. Copperas Creek floral distribution is most similar to
571 distributions seen in modern swamp/riparian tropical seasonal forests, but the proportion of
572 morphotypes is different (Fig. 4), possibly due to marine influence on floras. Wilcox and
573 Claiborne outcrops near Bastrop have recently been interpreted as coastal marine and paralic
574 deposits, with an environment of deposition within and offshore from a tide-dominated deltaic
575 system, including tidal lagoons, tidal channels and bars, tidal marshes, and peat-producing
576 topogenous mires (Denison et al. 2017; O’Keefe et al. 2017; Stephenson et al. 2018). Plant
577 communities in these types of environments are often low in diversity due to such harsh,
578 changing environments (Mitsch and Gosselink 2015), and need to be tolerant of salt spray, tidal
579 changes, brackish water, and possibly winds. Marine influence likely would have affected leaf
580 mass per area distribution at Copperas Creek, which potentially explains the higher proportion of
581 taxa with a very low M_a as compared to modern floras (Fig. 4).

582 In contrast to Copperas Creek, Golf Course M_a distribution was most similar to a modern
583 non-riparian tropical seasonal forest (Fig. 4). This is very similar to biome reconstructions based
584 on our paleoclimate estimates, which also suggest a tropical seasonal forest or tropical rainforest
585 biome (Fig. 5A). Non-riparian floral characteristics in fluvial-channel cut-and-fill Golf Course
586 deposits shows that material sourced from the neighboring floral community, which included
587 deciduous and evergreen morphotypes, was transported into fluvial channels. As most leaves are
588 well preserved, with at least 50% of the leaf being present, transport was relatively limited,
589 suggesting a parautochthonous flora that reflects relatively nearby vegetation.

590 Notably, Golf Course floral composition and M_a distribution is significantly different
591 from younger and older floras. Thus, we suggest that the wide distribution in M_a may result from
592 new taxa establishing territory in the GCP while previous taxa were extirpated. Morphotypes
593 unique to Golf Course may represent species filling new niches created during early Eocene
594 rapid warming events, as a result of climate change and extirpation of Paleocene floras.

595 Alternatively, this difference could be due to the depositional environment, as Golf Course
596 samples come from a different depositional environment than Copperas Creek or Manawianui.

597 M_a distribution of the-Golf Course megaf flora suggests a mixture of evergreen, semi-
598 evergreen, and deciduous taxa, similar to paleoecological reconstruction interpretations based on
599 palynofloras. Taxonomic composition and palynofloral distribution-from the ‘Dark Band’ has
600 been interpreted to represent transport from a range of peat-producing environments, from
601 hardwood hammock to sawgrass marshes (Stephenson et al. 2018). Hardwood hammocks
602 typically comprise a mixture of diverse evergreen and semi-deciduous tree and shrub species,
603 often with a closed canopy (Mitsch and Gosselink 2015), similar to the Golf Course
604 reconstructed distribution of leaf mass per area.

605 Manawianui M_a distribution is very different from Copperas Creek and Golf Course
606 distributions, and also does not resemble any modern-day tropical rainforest or tropical seasonal
607 forest distributions (Fig. 4). Distribution of the Manawianui flora is primarily deciduous with
608 ~30% of the flora being between 100-120 g/m², suggesting these floras may have been semi-
609 evergreen. Notably, a palm (BT-23) was the dominant morphotype here. Palms are not
610 represented in the M_a distribution because vein density and M_a protocols are not applicable to
611 monocotyledonous taxa without discrete petioles (Royer et al. 2007; 2012). Inclined heterolithics
612 and an increase in palm abundance suggest a tidal-channel meander, possibly surrounding a tidal

613 marsh, rich in palms, deciduous to semi-evergreen shrubs, and scattered ferns. Shannon and
614 Simpson (1-D) Index values for Manawianui indicate low diversity with moderately high
615 evenness. Salt marshes are typically low in diversity with a variety of plant compositions
616 depending on salinity gradient (Mitsch and Gosselink 2015), a potential analog for Manawianui.

617

618 Early Paleogene Plant Communities

619 Plant community change at Bastrop can be related to early Paleogene patterns of floral
620 response in other regions. In higher latitudes (Arctic, 70-80°N), the PETM flora is characterized
621 by a decrease in conifer abundance and an increase in angiosperm abundance (Sluijs et al. 2006),
622 associated with high water availability and runoff. In the tropics, there was a significant late
623 Paleocene to Eocene diversity increase, suggesting that high temperatures and change in
624 precipitation during the PETM did not exceed the tolerance of tropical vegetation, and instead
625 may have promoted diversification (Jaramillo et al. 2010).

626 At RHTS Harrington (2003) interpreted Wasatchian palynoflora containing the PEB as
627 warm-adapted vegetation with a diversity that remained unchanged across the PEB, similar to
628 our observations in Bastrop. However, Harrington and Jaramillo (2007) recorded pollen data
629 from the GCP in eastern Mississippi, western Alabama and Georgia showing increased
630 taxonomic richness during the late Paleocene, followed by rapid turnover, decreased diversity,
631 and extinction from the late Paleocene into the early Eocene, suggesting that environmental
632 changes during these rapid warming events influenced tropical ecosystems. Pollen and spores
633 from the eastern GCP showed continued low diversity until the EECO (Frederiksen 1980, 1988).
634 The Bastrop flora exhibits a similar trend in diversity increase from Golf Course to Manawianui,
635 but an increase in palm abundance, supporting the hypothesis of palm radiation during the early

636 Paleogene (Harley 2006; Dranfield et al. 2008; Gomez-Navarro et al. 2009; Sluijs et al. 2014;
637 Stephenson et al. 2018). Collectively, early Paleogene fossil evidence throughout the GCP
638 demonstrates floral change across the PEB, possibly in several phases.

639 When comparing species richness of GCP Bastrop and Bighorn Basin early Paleogene
640 floras (Fig. 3B), the Bastrop flora has a higher species richness (Fig. 3B). This higher richness
641 could be attributed to the latitudinal diversity gradient, especially since the Bastrop GCP MAT
642 and MAP suggest a warm and wet environment. Since GCP taxa would have already been
643 adapted to a warmer climate than Bighorn Basin flora, it may have allowed for higher rates of
644 migration in the GCP due to the local taxa already being thermophilic. Despite differences in
645 species richness, paleoecological reconstructions for Central Texas and Bighorn Basin floras are
646 similar. MAT and MAP ranges of Golf Course and Hubble Bubble localities (Fig. 5A) suggest
647 some shared range of MAT and MAP (Fig. 5A, Table 4), with Golf Course estimated to be
648 wetter and warmer. Remarkably, LMA distribution of Central Texas latest Paleocene and PETM
649 floras and Bighorn Basin PETM floras (Currano et al. 2008) are very similar (Fig. 5B). This
650 evidence that Central Texas PEB and Bighorn Basin PETM-floras had a similar ecology supports
651 the hypothesis of early Paleogene expansion of thermophilic taxa into paratropical latitudes from
652 the GCP into the NGP.

653 In summary, fossil evidence from the GCP combined with data from the NGP and the
654 tropics suggests that climate warming associated with the PETM helped create a widespread
655 band of thermophilic taxa that extended into the mid-latitudes. This northward floral expansion
656 may have pushed taxa into environments where they were influenced by heat and moisture
657 tolerance thresholds, increasing rates of floral turnover (Jaramillo et al. 2010; McInerney and
658 Wing 2011; Wing and Currano 2013). Understanding the variation and dynamics of floral and

659 faunal response to rapid global warming will be essential for responses to current and future
660 climate change, as farmlands and food production are likely to be affected.

661

662 CONCLUSIONS AND FUTURE WORK

663 Paleocene-Eocene macrofossil floras of the Central Texas GCP suggest a high turnover
664 rate and change in plant community composition at the Paleocene-Eocene boundary in response
665 to rapid global warming. High floral turnover in Central Texas suggests continuous response to a
666 changing environment. Lack of change in diversity suggests plant communities were not limited
667 by heat tolerance thresholds, but instead were influenced by changes within the environment
668 such as salinity, sea level, and the introduction of new thermophilic taxa. Similar morphotypes
669 throughout the Wilcox and Claiborne of the southeastern GCP support the hypothesis of a
670 widespread band composed of thermophilic taxa that expanded into the mid-latitudes during the
671 early Paleogene. Several morphotypes in the Central Texas GCP late Paleocene flora may also
672 be present in the Bighorn Basin PETM flora, although more descriptions and comparisons are
673 necessary to confirm this. Similarities in M_a distributions of Central Texas GCP PEB and NGP
674 PETM floras suggests an environment comparable to that of Copperas Creek and Golf Course,
675 supporting the hypothesis of early Paleogene expansion of paratropical environments into
676 northern latitudes. Additional datasets of GCP floras and refined age constraints are necessary to
677 further evaluate the composition and transition of flora at the PEB across the southeastern USA
678 and relationships between GCP and NGP floras.

679 Floral and faunal responses during the rapid and long-term warming events of the early
680 Paleogene are important as proxies for possible biota responses to current and future global
681 warming. Coastal plant compositions and distributions will likely depend on sediment

682 accumulation, keeping pace with rising sea levels (Watson and Burne 2009), heat tolerance
683 thresholds (Wing and Currano 2013), and immigration of new or invasive species (Dukes and
684 Mooney 1999). Marshes, swamps, and coastal lagoons are not only important ecological habitats,
685 but also act as carbon sinks. As global temperatures continue to rise at an alarming rate,
686 important ecological habitats are increasingly threatened due to adaptation and evolution limiting
687 the response rate of these habitats. Ongoing destruction of coastal environments (salt marshes,
688 tidal lagoons, hardwood hammocks, mangrove forests) has been well documented (Watson and
689 Byrne 2009) because of the recognized ecological and biogeochemical importance of such
690 habitats. Current global warming is occurring at a faster rate than what has been calculated at the
691 PEB. As these habitats play an important role in carbon sequestration and are already being
692 destroyed due to anthropogenic effects (Watson and Byrne 2009), they may not be able to keep
693 up with the pace of current climate change and essential carbon sinks could be lost.

694

695 ACKNOWLEDGEMENTS

696 JDW acknowledges Baylor University Department of Geosciences, Baylor University
697 Graduate School, the Paleontological Society, and the Dallas Paleontological Society for
698 financial support. Aly Baumgartner, Brittany Davis, Kathy Denison, Andrew Flynn, Danielle
699 Gygi, Joe Milligan, and Anna Peppe assisted in the field and lab. Steve Manchester facilitated
700 and assisted with JDW's visit to the Florida Museum of Natural History. We thank two
701 anonymous reviewers for comments that considerably improved this paper.

702

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- 1058 FIG. 1 — **A)** Location of collection sites within the Gulf Coastal Plain, specifically the Wilcox-
1059 Carrizo location in Texas. Bastrop, TX and Austin, TX are represented by the black star and red
1060 dot respectively. **B)** Geological map with collection sites. Each census location is indicated

within the red box (modified from Denison et al., 2017, with permission). C) Fence diagram of stratigraphy relationships in Tahitian Village, TX (edited from Denison et al., 2017, with permission). Approximate locations of three fossil leaf sites, JW1802, JW1801, JW1803 are indicated by circles 1, 2, and 3 respectively.

FIG. 2 — Stratigraphic relationships of sampled localities: not to scale (edited from Demchuk et al., 2019, with permission). Leaves indicate fossil leaf presence and relative abundance in each locality. Pollen data from Denison et al. (2017).

FIG. 3— A) Early Paleogene plant composition of Bighorn Basin, WY and Bastrop, TX (% monocot, dicot, gymnosperm, and fern). Bighorn Basin late Paleocene, PETM, and early Eocene compositions are averages of taxa presence/absence data from Wing and Currano (2013), Appendix S3. ‘Late Paleocene’ is an average from sites SLW9436, SLW8212, SLW8213, SLW945, SLW867, SLW868, SLW931, SLW9421, SLW9136, SLW9150, SLW9154, SLW947. ‘PETM’ is an average of sites Jons.Site.SLW, HubbleBubble, Deep.Sand.SLW, Steep.Face.SLW, SLW0606, Caterpillar.invasion, First.PETM.SLW. Early Eocene is an average from sites SLW8830.WCS, SLW9141.WCS, SLW9142.WCS, BR1.5, SLW845.SLW87, SLW8412.RR2., SLW9143.same_, SLW9144.same_, SLW9145.same_. B) Rarefaction curves for Bastrop, TX and Bighorn Basin, WY are grey and black, respectively. Rarefaction curve labels: i. Manwianui, ii. Golf Course, iii. HubbleBubble (PETM), iv. Tiffanian5 (late Paleocene), v. Clarkforkian 3 (latest Paleocene), vi. Wasatchian 2 (early Eocene).

FIG. 4 — Distribution of LMA values for Copperas Creek, Golf Course, and Manawianui. Black bars in each column that represent modern day tropical LMA distributions from Peppe et al. (2011) have been overlain with Central Texas LMA distributions. Copperas Creek distribution is most similar to modern swamp/riparian tropical seasonal forest, Golf Course is most similar to non-riparian tropical seasonal forest, and Manawianui distribution is an overall poor fit for modern-day tropical forest LMA distributions.

FIG. 5 —A) Biome perimeter based on estimated MAP and MAT. Blue and orange shaded boxes represent standard error of average estimated MAT and MAP for Central Texas ‘PETM’ and Bighorn Basin PETM floras respectively. MAT and MAP were estimated via DiLP (Whittaker-1975; Peppe et al. 2011). B) Estimated LMA distributions of fossil flora from Bighorn Basin, WY, and GCP, Central Texas. The Royer et al. (2007) method was used to estimate all LMA values. Bighorn Basin data are from Currano et al. (2008) supplemental data. Latest Paleocene: USNM 416413, ‘Clarkforkian 3’ (55.9 Ma); PETM: USNM 42384

TABLE 1 —Central Texas Paleocene-Eocene boundary fossil flora characteristics. Tabulation of number of morphotypes, composition, and margin characteristics of PEB flora from the GCP of Central Texas.

TABLE 2 —Diversity values for Golf Course and Manawianui flora from Bastrop, Texas. Floral diversity was assessed using PAST (Hammer et al. 2001) from quantitative (census) collections.

TABLE 3 — Diversity comparisons of the Golf Course and Manawianui census collections. See methods for equations.

1107 TABLE 4 — Paleoclimate estimates using univariate and multivariate methods. Table includes
1108 average leaf mass per area, number of species processed, Leaf Margin Analysis MAT estimate,
1109 Leaf-area analysis MAP estimate, and DiLP MAT/MAP estimates. Bighorn Basin data for the
1110 PETM Hubble Bubble locality sourced from Peppe et al. 2011.

1111

1112

A

B

Table 1

Locality	# morphotypes	% dicot	% monocot	% fern	Margin (% Toothed)
Manawianui	13	77	15	8	60
Golf Course	26	84	8	8	39
Copperas Creek	11	91	9	0	63

Table 2

Locality	Shannon Index	Simpson Index (1-D)	Equitability (Evenness)	Berger-Parker Dominance
Manawianui	1.913	0.776	0.746	0.416
Golf Course	1.764	0.781	0.766	0.339

Table 3

Communities	Bray Curtis Dissimilarity	Jaccard's Index of Similarity
Golf Course vs Manawianui	0.966	0.095

Table 4

PETM Locality	Average leaf mass per area (g/m ²)	r of woody dicotyledonous angiosperm species
ghorn Basin (Hubble Bubb	89	29
CP central Texas (JW180	93	26

woody dicotyledonous angiosperm specie	DiLP MAT estimate	Leaf Margin analysis MAT estimate	Regional DiLP MAT estimate	DiLP MAP estimate
	(°C)	(°C)	(°C)	
16	20.3	17.9	20.2	147 (+121, -66)
20	18.6	20.3	22.4	250.1 (+205.6, -112.8)

Leaf-area analysis MAP
estimate

146 (+120, -66)

131.6 (+101.5, -57.3)

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Supplemental Material

[Palaaios_SupMat_2022_reducedfile 2.pdf](#)