1   **Elevated CO₂, increased leaf-level productivity and water-use efficiency during the early Miocene**

3   Tammo Reichgelt[1,2], William J. D'Andrea[1], Ailín del C. Valdivia-McCarthy[1], Bethany R.S. Fox[3], Jennifer

4   M. Bannister[4], John G. Conran[5], William G. Lee[6,7], Daphne E. Lee[8]

6   [1]Lamont-Doherty Earth Observatory, Columbia University, Palisades, New York, USA.

7   [2]Department of Geosciences, University of Connecticut, Storrs, Connecticut, USA.

8   [3]Department of Biological and Geographical Sciences, University of Huddersfield, Huddersfield, UK.

9   [4]Department of Botany, University of Otago, Dunedin, New Zealand.

10   [5]ACEBB & SGC, School of Biological Sciences, The University of Adelaide, Adelaide, Australia.

11   [6]Landcare Research, Dunedin, New Zealand.

12   [7]School of Biological Sciences, University of Auckland, Auckland, New Zealand.

13   [8]Department of Geology, University of Otago, Dunedin, New Zealand.

14   Correspondence: Tammo Reichgelt (tammo.reichgelt@uconn.edu)

16   **Abstract.** Rising atmospheric CO_2 is expected to increase global temperatures, plant water-use efficiency,

17   and carbon storage in the terrestrial biosphere. A CO_2 fertilization effect on terrestrial vegetation is

18   predicted to cause global greening as the potential ecospace for forests expands. However, leaf-level

19   fertilization effects, such as increased productivity and water-use efficiency, have not been documented

20   from fossil leaves in periods of heightened atmospheric CO_2. Leaf gas-exchange rates reconstructed from

21   early Miocene fossils which grew at southern temperate and tropical latitudes, when global average

22   temperatures were 5–6°C higher than today reveal that atmospheric CO_2 was ~450–550 ppm. Early

23   Miocene CO_2 is similar to projected values for 2040AD, and consistent with Earth System Sensitivity of

24   3–7°C to a doubling of CO_2. While early Miocene leaves had photosynthetic rates similar to modern

25   plants, southern temperate leaves were more productive than modern due to a longer growing season.

26   This higher productivity was likely mirrored at northern temperate latitudes as well, where a greater

27   availability of landmass would have led to increased carbon storage in forest biomass relative to today.

28   Intrinsic water-use efficiency of both temperate and tropical forest trees was high, toward the upper limit

29   of the range for modern trees, which likely expanded the habitable range in regions that could not support

30   forests with high moisture demands under lower atmospheric CO_2. Overall, early Miocene elevated

31   atmospheric CO_2 sustained globally higher temperatures and our results reveal the first empirical

32   evidence of concomitant enhanced intrinsic water-use efficiency, indicating a forest fertilization effect.

33

34   1 Introduction

35   Terrestrial plants comprise 450 Gt of carbon, representing 80% of Earth's dry carbon (C) biomass (Bar-on

36   et al., 2018). Globally, plants draw down ~120 Gt of atmospheric C per year through photosynthesis,

37   representing the largest annual C flux on Earth (Beer et al., 2010). Total plant biomass is believed to be

38   determined in large part by atmospheric carbon dioxide concentrations (C_a), and it is predicted that future

39   increases in C_a will have a three-pronged effect on the terrestrial biosphere: 1) increased global

40   temperatures will shift the boundaries of climate zones and thereby the potential forest expanse (Rubel

41   and Kottek, 2010); 2) productivity will increase because global photosynthesis is C limited and increased

42   C_a will make more C available to the terrestrial biosphere (Zhu et al., 2016); and 3) elevated C_a will

43   increase plant water-use efficiency and reduce the threshold for physiological drought (Cernusak, 2020),

44   making more land area available for biosphere expansion (Zhou et al., 2017). Plant fossils record the

45   effect of past changes in climate, including CO_2 enrichment, and thus fossil floras provide insight into

46   changes in the carbon cycle and their effects on the terrestrial biosphere from a natural, whole-ecosystem

47   perspective.

48   The Miocene has been considered problematic for our understanding of Earth System Sensitivity

49   (ESS) to C_a, because most proxy-based C_a estimates indicate concentrations near 300 ppm (Foster et al.,

50   2017), close to pre-industrial values, yet global temperatures were 5–6 °C higher than modern (Hansen et

51   al., 2013). Enhanced radiative forcing is required to maintain such elevated early Miocene temperatures

52   (Herold et al., 2010; Hansen et al., 2013), and without elevated C_a, climate models cannot achieve such

53 high global temperatures in the Miocene (Henrot et al., 2010). The early Miocene also had an expanded

54 biosphere compared to today, including woody vegetation in locations that are currently too cold and/or

55 too dry for forests (e.g. Askin and Raine, 2000; Herold et al., 2010). A biosphere of the magnitude

56 observed in the early Miocene fossil record requires elevated temperatures and plant water-use efficiency,

57 suggesting C_a levels higher than estimated by most existing proxy reconstructions (Herold et al., 2010;

58 Henrot et al., 2010). Importantly, plant-based C_a reconstructions have challenged the consensus of low C_a

59 in the early Miocene (Kürschner and Kvaček, 2009; Reichgelt et al., 2016; Tesfamichael et al., 2017;

60 Londoño et al., 2018) and previous interpretations of alkenone-based C_a proxies are being disputed

61 (Bolton et al., 2016; Witkowski et al., 2019).

62   We applied plant gas-exchange modeling (Franks et al., 2014) to fossil leaves from the early Miocene

63 (~23 Ma) rainforest ecosystem from southern New Zealand preserved in the Foulden Maar deposit

64 (Bannister et al., 2012; Reichgelt et al., 2013; Conran et al., 2014; Lee et al., 2016) to reconstruct carbon

65 assimilation rates (A_n), intrinsic water-use efficiency (iWUE; the ratio between carbon assimilation and

66 stomatal conductance to water), and the C_a levels required to maintain these values. The same analyses

67 were performed on previously published leaf $\delta^{13}C$ and micromorphological measurements from two early

68 Miocene fossil floras from Ethiopia (Tesfamichael et al., 2017) and Panama (Londoño et al., 2018).

69 Because A_n, iWUE, and C_a are interdependent (Farquhar et al., 1980; Drake et al., 1997), we

70 reconstructed these variables in concert for each fossilized leaf recovered from these forest ecosystems.

71 This allows us to make inferences concerning carbon availability, productivity, and water balance in the

72 forest.

73

74 **2 Methods**

75 **2.1 Site Description**

76 Foulden Maar (Fig. 1a) is a unique *Konservat-Lagerstätte* with abundantly preserved plants and insects

77 (Kaulfuss et al., 2015; Lee et al., 2016) in southern New Zealand (45.527°S, 170.219°E). It was formed in

78 an ancient maar-diatreme lake (Fig. 1b) at the Oligocene/Miocene boundary (Fox et al., 2015; Kaulfuss,

79 2017) and consists of ~100 kyr of annually laminated diatomite (Lindqvist and Lee, 2009; Fox et al.,

80 2016). The Foulden maar-diatreme complex is part of the larger late Oligocene – late Miocene Waipiata

81 Volcanic Field that produced a variety of maar volcanoes and scoria cones (Németh and White, 2003).

82 Plant fossils used in this study were collected from a ~183 m long drill core (Fig. 1c). The Lauraceae-

83 dominated rainforest (Bannister et al., 2012) surrounding the lake grew at ~50°S (Fig. 1a). The climate

84 was marginally subtropical with a mean annual temperature of ~18°C, similar to modern day climates at

85 30°S (Reichgelt et al., 2019). The length of the growing season in this climate was ~10 months, compared

86 to 5–6 months today, as reconstructed from the surface exposure macrofossil assemblage using the

87 Climate Leaf Analysis Multivariate Program (Reichgelt et al., 2013).

88

89 **2.2 Fossil leaf anatomy and paleoecology**

90 Mummified fossil leaves were extracted from turbidite deposits that occur frequently within the Foulden

91 Maar diatomite core (Fox et al., 2015). The diatomite is loosely consolidated allowing mummified leaves

92 to be extracted using a combination of water and scalpels. After extraction, the leaves were cut into three

93 pieces: one for bulk $\delta^{13}C$ analysis, one for stomatal conductance measurements, and a third as a reference

94 specimen. Leaf $\delta^{13}C$ was measured using a Costech elemental combustion system (EA) coupled to a Delta

95 V Plus IRMS (Thermo). In order to place measured $\delta^{13}C$ on the VPDB scale, we calibrated measurements

96 using a two-point isotope calibration based on the USGS40 and USGS41 standards. Measurement

97 uncertainty was calculated by replicating ~15 samples, and applying averaged uncertainty to the

98 remaining leaves. For conductance measurements the leaves were soaked in hydrogen peroxide (H_2O_2)

99 with up to 40% dilution, with tetra-sodium pyrophosphate salt crystals ($Na_4P_2O_7 \cdot 10[H_2O]$), on a boiling

100 plate at 40–50 °C for 1–2 hours (Bannister et al., 2012). When the adaxial and abaxial cuticle layer could

101 be separated, the leaf layers were cleaned of mesophyll cell debris using small paintbrushes and both

102 layers were stained with <0.5% Crystal Violet ($C_{25}N_3H_{30}Cl$) and mounted on glass slides with glycerin

103 jelly. Conductance measurements were made on 5–8 pictures at 100× magnification using TSView

104 7.1.1.2 microscope imaging software on a Nikon Optiphot. Each picture was given bounding boxes (0.3 ×

105   0.3 mm) on which cells were counted, to calculate stomatal density, and stomatal size measurements were

106   made using ImageJ 1.48v software (Schneider et al., 2012).

107   18 distinct leaf morphotypes were identified from the Foulden Maar drill core. Descriptions and

108   justification for identification are found in the Supplementary Information. Species identifications are

109   provided, where possible, based on paleobotanical studies from the Foulden Maar surface exposures.

110   Known species recovered from the Foulden Maar drill core are *Litsea calicarioides* (Fig. S1a),

111   *Cryptocarya taieriensis* (Fig. S1b), *C. maarensis* (Fig. S1i), *Beilschmiedia otagoensis* (Fig. S2a)

112   (Lauraceae) (Bannister et al., 2012), *Laurelia otagoensis* (Fig. S2h) (Atherospermataceae) (Conran et al.,

113   2013), and *Hedycarya pluvisilva* (Fig. S2i) (Monimiaceae) (Conran et al., 2016). Otherwise, tentative

114   genus or family identifications are provided, or unspecified morphotypic qualifiers, for leaves that could

115   not be assigned a plant group. These will be henceforth be referred to as "C" (Fig. S1c), cf. Myrtaceae

116   (Fig. S1d), cf. *Ripogonum* (Fig. S1e), cf. *Myrsine* (Fig. S1f), "H" (Fig. S1g), cf.

117   Elaeocarpaceae/Cunoniaceae (Fig. S1h), cf. *Dysoxylum* (Fig. S2b), cf. *Cryptocarya* (Fig. S2c), "O" (Fig.

118   S2d), "P" (Fig. S2e), "Q" (Fig. S2f) and cf. *Endiandra* (Fig. S2g).

119   We made 375 anatomical and 80 carbon isotope measurements on 72 organically preserved fossil

120   leaves representing the 18 species collected from the Foulden Maar deposit (Fig. 1a). The affinities of

121   modern living relatives of the plant types at Foulden Maar strongly suggest that during the Miocene the

122   site was characterized by a multi-layered closed canopy rainforest ecosystem (Reichgelt et al., 2013;

123   Conran et al., 2014). In order to determine atmospheric carbon (C_a), intrinsic water-use efficiency

124   (iWUE), and carbon assimilation rates (A_n), the ecological strategies of the individual fossil species at

125   Foulden Maar need to first be established (Reichgelt and D'Andrea, 2019). Understory species rarely

126   experience light saturation and utilize respired CO_2 that has already undergone isotopic fractionation;

127   both conditions influence gas-exchange modelling results (Royer et al., 2019). Therefore, C_a

128   reconstructed from understory species cannot be considered indicative of true global C_a. Here, we

129   determine whether a fossil leaf type was likely in the canopy or the understory, based on 1) leaf $\delta^{13}C$, 2)

130   leaf cell density, and 3) sinuosity of the epidermal cell walls. A large range of leaf $\delta^{13}C$ in a single species

131 is indicative of different levels of light saturation, which indicates that this species may preferentially

132 occur in the subcanopy or in the understory (Graham et al., 2014). Leaves in the canopy, experiencing

133 light saturation, divide epidermal cells rapidly compared to leaves in the shade, leading to high cell

134 densities and relatively high leaf mass per areas in sun-exposed leaves (Šantrůček et al., 2014). Finally, a

135 high level of anticlinal cell wall sinuosity has been interpreted as indicative of low-light conditions

136 (Kürschner, 1997; Bush et al., 2017). We consider these three lines of evidence occurring in concert as

137 indicative of a canopy or subcanopy ecological preference.

138

139 **2.3 Modelling gas-exchange**

140 Atmospheric carbon dioxide (C_a), plant photosynthesis (A_n), and intrinsic water-use efficiency (iWUE)

141 are tightly linked (Farquhar et al., 1980; Drake et al., 1997), which allows us to solve for these parameters

142 iteratively, through anatomical and carbon isotope ($\delta^{13}C$) measurements of the fossil leaves. The Franks et

143 al. (2014) gas-exchange model solves for C_a, by iteratively reconstructing A_n and leaf conductance to

144 atmospheric carbon (G_c), using a Monte Carlo approach. This means that every C_a reconstruction has an

145 associated A_n and G_c value.

146

147
$$C_a = {A_n} \Big/ {G_c \times \left(1 - \frac{C_i}{C_a}\right)} \quad (1)$$

148

149 In which C_i/C_a represents the ratio of intercellular carbon to atmospheric carbon, which can be

150 reconstructed using known leaf fractionation processes: fractionation caused by diffusion (a),

151 carboxylation (b), and fractionation caused by the preferential uptake of ^{12}C to ^{13}C in photosynthesis (Δ),

152 which is also influenced by the rate at which the leaf is photosynthesizing (Farquhar et al., 1982).

153

154
$$\frac{C_i}{C_a} = \frac{\Delta - a}{b - a} \quad (2)$$

1eof

178   G_{max} is determined using predominantly measurable anatomical features of the fossil leaf cuticle (Franks

179   and Beerling, 2009): stomatal density (SD), maximum aperture surface area (a_{max}), pore depth (p_d), and

180   the ratio of diffusivity of CO_2 in air over the molar volume of air (d/v), here taken as 0.000714 mol m^{-1} s^{-1}

181   (Marrero and Mason, 1972).

182

183
$$G_{max} = {}^{d}\!/_{v} \times SD \times \frac{a_{max}}{p_d + \frac{\pi}{2}\sqrt{a_{max}/\pi}} \quad (6)$$

184

185   In this equation, SD can be measured directly from the leaf, p_d is assumed to be the same as guard cell

186   width (gcw), and a_{max} is determined assuming a circular opening for the aperture, with the measurable

187   pore length (p_l) as the diameter (Franks et al., 2014).

188

189
$$a_{max} = \pi \times \frac{p_l}{4} \quad (7)$$

190

191   Measurements of SD, gcw and p_l used in the Franks et al. (2014) gas-exchange model are presented in

192   Table S1.

193

194   Hence, it is clear that though G_c is largely determined by measurable anatomical parameters, because A_n

195   is a component of calculating G_m, G_c is solved iteratively. However, A_n is also solved iteratively, as it is

196   dependent on C_a and the carbon saturation value (Γ), set at 40 ppm (Franks et al., 2013).

197

198
$$A_n \approx A_0 \times \frac{(C_a - \Gamma) \times (C_{a0} + 2\Gamma)}{(C_a + 2\Gamma) \times (C_{a0} - \Gamma)} \quad (8)$$

199

200   In which A_0 is the photosynthetic rate of a modern model species that can represent the fossil species'

201   photosynthetic rate, and C_{a0} is the atmospheric carbon dioxide level at which A_0 was measured. A_0 for

202   each fossil species was derived from the compilation of photosynthetic rates presented in Reichgelt and

203   D'Andrea (2019). For fossil leaves with known modern relatives, we constrained the possible A_0 range by

204   only including modern relatives within the same family or order, i.e. Lauraceae for *Litsea calicarioides*,

205   *Cryptocarya taieriensis*, *C. maarensis*, cf. *Cryptocarya*, *Beilschmiedia otagoensis* and cf. *Endiandra*,

206   Myrtaceae for cf. Myrtaceae, Liliales for cf. *Ripogonum*, Primulaceae for cf. *Myrsine*, Elaeocarpaceae and

207   Cunoniaceae for cf. Elaeocarpaceae/Cunoniaceae, Meliaceae for cf. Meliaceae, Atherospermataceae for

208   *Laurelia otagoensis,* and Laurales for *Hedycarya pluvisilva*. Then, following the method of constraining

209   A_0 of modern living relatives presented in Reichgelt and D'Andrea (2019), only A_0 values of plants with

210   similar growth forms to the fossil plants, and growing in similar light environments as Foulden Maar were

211   included. A0 and Ca0 used in the Franks et al. (2014) model, and associated ecology of fossil leaf types is

212   shown in Table S2.

213

214   The Franks et al. (2014) gas-exchange model thus iteratively solves for C_a, A_n, and G_c. However, only

215   leaves derived from canopy trees are likely to represent these values at light saturation. Moreover, plants

216   in the understory assimilate a mix of atmospheric and respired CO_2, which has therefore already

217   undergone fractionation processes, making the calculated C_i/C_a problematic. Therefore, we present the

218   results for C_a, A_n, and G_c of leaf types most likely to be derived from canopy trees separately, as they are

219   more likely to not have a systematic skew.

220   iWUE is defined as the ratio between A_n and stomatal conductance to water (Feng, 1999).

221

222    $$iWUE = \frac{A_n}{G_w} \quad (9)$$

223

224   Due to the different rates at which carbon dioxide and water vapor diffuse in air, a transformation of G_c is

225   required to calculate G_w.

226

227 $$G_w = 1.6 \times G_c \ (10)$$

228

229 Finally, cumulative annual carbon uptake through photosynthesis (A_{tot}) can be calculated in gC m^{-2} yr^{-1},

230 by transferring from moles to grams, including a measure for the relative time the leaf is assimilating

231 carbon (ζ), and a measure for the absolute amount of time that the leaf was assimilating carbon.

232

233 $$A_{tot} = (2.6 \times \zeta \times A_n \times GS) \times 12 \ (11)$$

234

235 In which GS is the length of the growing season, which we can derive from the fossil plant assemblage

236 (Reichgelt et al., 2019), using the method of Spicer et al. (2009). G_w, A_{tot}, and iWUE values for *Litsea*

237 *calicarioides*, *Cryptocarya taieriensis*, *C. maarensis*, cf. Elaeocarpaceae/Cunoniaceae, and cf. Myrtaceae

238 are presented in Table S3. The modern reference A_n and G_w data is derived from Maire et al. (2015),

239 which included coordinates, habit, A_n and G_w data, from which we could then calculate iWUE and A_{tot}.

240

241 **2.4 Comparison to Earth System Sensitivity**

242 Earth System Sensitivity to C_a (ESS) is the amount of temperature increase expected under a doubling of

243 atmospheric CO_2. This sensitivity is likely not static in Earth's history and is dependent on, among other

244 aspects, continental configuration and ocean circulation patterns (Royer, 2016). ESS is likely to have been

245 between 3–7°C for the Neogene (Hansen et al., 2013; Royer, 2016), meaning that a doubling of C_a

246 compared to pre-industrial levels would have led to an increase of global average surface temperatures

247 (T_s) of 3–7°C compared to modern. Using this expected ESS, we calculated the expected C_a using the

248 methodology of Hansen et al. (2013).

249   Compiled deep-sea benthic foraminifera $\delta^{18}O$ data of the last 30 million years (Zachos et al., 2001)

250 were averaged into 20 kyr time bins. Deep-sea temperatures (T_d) were then calculated using the linear

251 transfer functions of Hansen et al. (2013), which depend on the presence of sea-ice.

252

253
$$T_d = 5 - 8 \times \frac{\delta^{18}O - 1.75}{3} \; IF \; (\delta^{18}O < 3.25) (12)$$

254
$$T_d = 1 - 4.4 \times \frac{\delta^{18}O - 3.25}{3} \; IF \; (\delta^{18}O > 3.25) (13)$$

255

256   T_s was then calculated for post-Pliocene using:

257

258
$$T_s = 2 \times T_d + 12.25 \; (14)$$

259   For the Pliocene:

260
$$T_s = 2.5 \times T_d + 12.15 \; (15)$$

261

262   And for pre-Pliocene we assumed that T_s changed linearly with T_d, by a factor of 1.5.

263

264
$$\Delta T_s = 1.5 \times \Delta T_d \; (16)$$

265

266   C_a based on an ESS range of 3–7°C was then calculated using the resulting T_s.

267

268
$$C_a = 310 \times \frac{T_{s[x]} - T_{s[0]}}{2 \times ESS} + 310 \; (17)$$

269

270   In which $T_{s[x]}$ is the calculated average global surface temperature at time x, and $T_{s[0]}$ is the modern day

271   average global surface temperature.

272

273   **3 Results and Discussion**

274   **3.1 Southern Temperate Rainforest Paleoecology**

275   Modern day Lauraceae rainforests in New Zealand have a single dominant canopy tree, *Beilschmiedia*

276   *tawa*, and their farthest southern extent is ~42°S (Leathwick, 2001), the farthest southern occurrence of

277   any arborescent Lauraceae species in the world. Rainforests at higher latitudes in New Zealand are

278   usually dominated by Nothofagaceae or Podocarpaceae, and the only modern-day forests at ~50°S are the

279   Magellanic Subpolar Forests in southern South America. Low-growing Podocarpaceae/Nothofagaceae

280   forests, similar to modern forests in southern New Zealand and southern South America, dominated

281   Antarctic vegetation during the early Miocene (Askin and Raine, 2000) and the Foulden Maar rainforest

282   included at least ten Lauraceae species (Bannister et al., 2012), emphasizing the expanded biosphere

283   potential in the early Miocene compared to today (Herold et al., 2010).

284   We identify *L. calicarioides*, *C. maarensis*, *C. taieriensis*, cf. Elaeocarpaceae/Cunoniaceae, and cf.

285   Myrtaceae as the most probable canopy components because they lack 1) the large range of leaf $\delta^{13}C$

286   values, relatively low overall leaf $\delta^{13}C$ values (Graham et al., 2014), 2) low cell densities typical of

287   understory components (Kürschner, 1997; Bush et al., 2017) (Fig. 2 a,b), and 3) the undulating or sinuous

288   cell walls typical of understory components (Kürschner, 1997; Bush et al., 2017). The most likely

289   subcanopy or understory taxa were cf. *Ripogonum*, cf. *Myrsine*, "O", and cf. *Dysoxylum*, because leaf

290   fossils of these types have both low leaf $\delta^{13}C$ and sinuous or undulating cells (Fig. S1e,f, S2b,d). *H.*

291   *pluvisilva*, *L. otagoensis*, cf. *Cryptocarya*, cf. *Endiandra*, *B. otagoensis*, "C", "H", "P", and "Q", all

292   displayed some variation in these features and occurred in relative low abundance, and are therefore

293   considered of uncertain ecological affinity.

294

295   **3.2 Earliest Miocene CO₂**

296   Gas-exchange modeling (Franks et al., 2014) of canopy leaves throughout the Foulden Maar core

297   indicates that C_a was 445 +618 / -100 ppm, whereas understory elements experienced a higher C_a of 622

298   +3017 / -161 ppm (Fig. 2c), consistent with understory plants assimilating respired CO_2 that has

299   undergone prior fractionation processes, as well as experiencing elevated levels of C_a under the canopy

300   (Graham et al., 2014; Royer et al., 2017). Prior work on the Foulden Maar core established three different

301   phases based on bulk organic $\delta^{13}C$ (Fig. 1c), fatty acid $\delta^{13}C$, and fatty acid δD: Phase I (80–105 m depth)

302   with high $\delta^{13}C$ and low δD, Phase II (55–65 m depth) with low $\delta^{13}C$ and high δD, and Phase III (0–45 m

303   depth) with high $\delta^{13}C$ and low δD (Reichgelt et al., 2016). Phase III can be further subdivided into Phase

304   IIIa (30–45 m depth) and IIIb (0–20 m depth), as Phase IIIa exhibits a period of low fatty acid $\delta^{13}C$ and

305   high δD, which is not expressed in bulk organic $\delta^{13}C$ (Reichgelt et al., 2016). Gas-exchange modelling on

306   leaves from these phases (Fig. 1c) suggest that during Phase II and IIIa C_a may have been elevated (C_a =

307   529 +1159 / -125 and C_a = 538 +769 / -181 ppm, respectively) compared to Phase I and Phase IIIb (C_a =

308   444 +572 / -95 and 442 +1219 / -110 ppm, respectively) (Fig. 3).

309   The advantage of using gas-exchange modeling to reconstruct C_a from multiple species is that the

310   uncertainty is quantified and constrained, greatly reducing the potential for systematic error in the final

311   estimate (Reichgelt and D'Andrea, 2019; Royer et al., 2019). Along with the enhanced accuracy comes a

312   more comprehensive appraisal of uncertainty than is achieved using other proxy approaches (Fig. 4).

313   Proxy error propagation is based on mechanistic variability, grounded in known physical and

314   physiological limits of plant gas-exchange that are understood to be universal (Franks et al., 2014). This

315   differs from empirical proxies, whose uncertainty representation is based on calibration error of modern-

316   day observations without mechanistic constraints. Our canopy C_a estimate (445 +618 / -100 ppm, Fig. 2c)

317   is independent of calibration error, based on universal gas-exchange mechanisms, and represents plant

318   vegetative organs of multiple plant species that directly interacted with the available pool of atmospheric

319   carbon dioxide. Previous C_a estimates from the Oligocene/Miocene boundary based on boron isotopes

320   and paleosol carbonates are generally lower than our estimates (Ji et al., 2018; Greenop et al., 2019) (Fig.

321   4b), whereas C_a estimates based on stomatal index and recent alkenone-based C_a estimates are more

322   similar to our results (Kürschner et al., 2008; Super et al., 2018).

323   Reconstructions of globally elevated temperatures of 5–6 °C in the early Miocene (Hansen et al.,

324   2013) with a C_a of ~300 ppm (Ji et al., 2018; Greenop et al., 2019) upsets the expected ESS to C_a during

325   this period (Henrot et al., 2010). Geochemical C_a proxy estimates consistently produce C_a estimates that

326   are too low to satisfy ESS to C_a prior to the Pliocene (Royer, 2016) (Fig. 4a,b). Estimates from the fossil

327   leaf-based stomatal index proxy for C_a (Kürschner et al., 2008) on the other hand do indicate a positive

328   correlation between temperature and C_a in the Neogene (Fig. 4a). At present, there are too few studies that

329   reconstruct C_a using gas-exchange modeling to allow for a full comparison to other C_a proxies; however,

330   our C_a estimates of ~450–550 ppm are in line with the ESS to C_a in the early Miocene (Fig. 4a,b), based

331   on modelling experiments (Herold et al., 2010; Henrot et al., 2010). Moreover, thus far, Neogene C_a

332   estimates reconstructed using gas-exchange methods (Reichgelt et al., 2016; Tesfamichael et al., 2017;

333   Londoño et al., 2018; Moraweck et al., 2019) appear to agree with the suggested ESS to C_a (Fig. 4a,b).

334   Bulk organic and leaf wax $\delta^{13}C$ values reveal a ~4‰ decrease at Foulden Maar over a 10-meter

335   interval at the beginning of Phase II (55–65 m depth), likely representing a time period of <10 kyr (Fox et

336   al., 2016). This shift in isotopic composition suggests a substantial change in the global carbon cycle

337   (Reichgelt et al., 2016). Results presented here show a ~100 ppm C_a increase (from ~450 to 550) from

338   Phase I to Phase II (Fig. 3). The C_a values stay near 550 ppm throughout Phase II and Phase IIIa,

339   representing a 20–40 kyr time period (Fig. 3). Absolute dating of Foulden Maar based on paleomagnetic

340   reversals in the core, annual lamination of lake sediments, and basalt-derived Ar/Ar dates indicates that

341   the deposition of the Foulden Maar sediment coincided with the termination of the earliest Miocene (Mi-

342   1) glaciation of Antarctica (Fox et al., 2015). An increase in C_a from ~450 to ~550 ppm at the termination

343   of Mi-1 is consistent with modeling studies indicating that $C_a > 500$ ppm is necessary to terminate a large-

344   scale Antarctic glaciation (DeConto et al., 2008).

345

346   **3.3 Elevated CO₂ and the early Miocene biosphere**

347   The Foulden Maar Miocene rainforest was primarily evergreen (Lee et al., 2016). The main Miocene

348   canopy trees at Foulden Maar, *Litsea calicarioides*, *Cryptocarya taieriensis*, *C. maarensis*, cf.

349   Elaeocarpaceae/Cunoniaceae and cf. Myrtaceae, had relatively high iWUE (Miocene iWUE first quartile

350   [Q_1] – third quartile [Q_3] = 70–101) compared to modern evergreen trees (evergreen iWUE Q_1–Q_3 = 31–

351   73) (Fig. 5a). Reconstructed iWUE from tropical early Miocene plants (Tesfamichael et al., 2017;

352   Londoño et al., 2018) is slightly higher (Q_1–Q_3 = 80–125) (Fig. 5a). The difference between reconstructed

353   Miocene iWUE and that of modern deciduous trees is greater still (deciduous iWUE Q_1–Q_3 = 27–52),

354   consistent with the expectation that increased C_a favors evergreen trees (Niinemets et al., 2011; Soh et al.,

355   2019). In contrast to iWUE, reconstructed conductance to water (G_w) for Miocene trees is similar to the

356   modern-day range at the same latitude (Fig. 5b), a somewhat surprising result because G_w is expected to

357   be reduced in high C_a climates (Franks and Beerling, 2009). Increased atmospheric evaporative demand

358   in combination with a longer growing season in a warmer climate would facilitate a relatively high

359   hydraulic flux to the atmosphere, despite higher iWUE and similar G_w (Frank et al., 2015). Furthermore, a

360   longer growing season also results in increased total annual carbon flux (A_{tot}) to the biosphere (Fig. 5c).

361   Early Miocene trees at 50°S likely assimilated A_{tot} Q_1–Q_3 = 265–696 gC m^{-2} yr^{-1}, in comparison to A_{tot}

362   Q_1–Q_3 = 108–182 gC m^{-2} yr^{-1} in modern evergreen forests, and A_{tot} Q_1–Q_3 = 249–410 gC m^{-2} yr^{-1} in

363   modern deciduous forests at the same latitude (Fig. 5c). Tropical trees appear to have slightly higher total

364   annual carbon flux (A_{tot} Q_1–Q_3 = 596–1220 gC m^{-2} yr^{-1}) than today (A_{tot} Q_1–Q_3 = 329–721 gC m^{-2} yr^{-1}).

365   Although this estimate cannot take the number of leaves per unit area into account, the results provide

366   strong evidence for enhanced productivity in "greener" worlds.

367

368   **4 Conclusions**

369   Leaf-level gas-exchange derived C_a estimates suggest that early Miocene atmospheric CO_2 was higher

370   than pre-industrial levels at 450–550 ppm, further solidifying the growing consensus of relatively high

371   early Miocene global temperatures maintained by high atmospheric CO_2 (Kürschner et al., 2009;

372   Tesfamichael et al., 2017; Super et al., 2018; Londoño et al., 2018; Moraweck et al., 2019). A relatively

373   high C_a in the early Miocene also satisfies an Earth System Sensitivity of 3–7°C (Hansen et al., 2013;

374   Royer, 2016). A potential shift in atmospheric CO_2 from 450 to 550, and back to 450, is recorded in the

375   100 kyr of sedimentation and leaf deposition at Foulden Maar. A disruption of the regional carbon and

376   hydrological cycle was also recorded in leaf-wax $\delta^{13}C$ and δD (Reichgelt et al., 2016), and may be linked

377   to the Antarctic deglaciation at the termination of the Mi-1 (DeConto et al., 2008; Fox et al., 2015;

378   Liebrand et al., 2017).

379   The first record is provided of increased Miocene leaf-level intrinsic water-use efficiency in both

380   temperate New Zealand and the tropics, and we provide evidence for increased leaf-level productivity in

381   temperate New Zealand. Enhanced productivity and water-use efficiency on other landmasses in

382   temperate latitudes during the early Miocene, such as North America, Australia, and Asia, would have

383   had a major impact on the global carbon and water cycles. Our gas-exchange results from New Zealand,

384   supplemented with results from Ethiopia (Tesfamichael et al., 2017) and Panama (Londoño et al., 2018)

385   provide empirical evidence for high water-use efficiency in the globally warmer world of the early

386   Miocene, associated with elevated C_a. Tropical trees with high water-use efficiency compared to modern,

387   would have likely facilitated forest survival in climates where currently tropical savannas and grasslands

388   exist. An overall higher water-use efficiency in the early Miocene tropics is corroborated by the spread of

389   C_4 grasslands in the late Miocene, when reduced CO_2 levels started favoring the more efficient C_4

390   photosynthetic pathway (Strömberg, 2011; Polissar et al., 2016).

391   Emission scenarios suggest that atmospheric CO_2 will reach our reconstructed early Miocene values of

392   450 ppm by 2030–2040 CE. While the global temperature response may lag the C_a increase, and forest

393   habitat expansion is hampered by the slow dispersal and growth rate of climax forest trees and

394   anthropogenic influence (e.g., forest fragmentation and fire), early Miocene water-use efficiency and

395   productivity estimates provide insight into the near future-biosphere potential, as well as into selective

396   pressures that influence the types of plants that may proliferate under future elevated C_a.

397

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403

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407 contributed to the final manuscript.

408

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410

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621   S., Peñuelas, J., Poulter, B., Pugh, T. A. M., Stocker, B. D., Viovy, N., Wang, X., Wang, Y., Xiao, Z.,
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626   Figure and Figure legends

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628
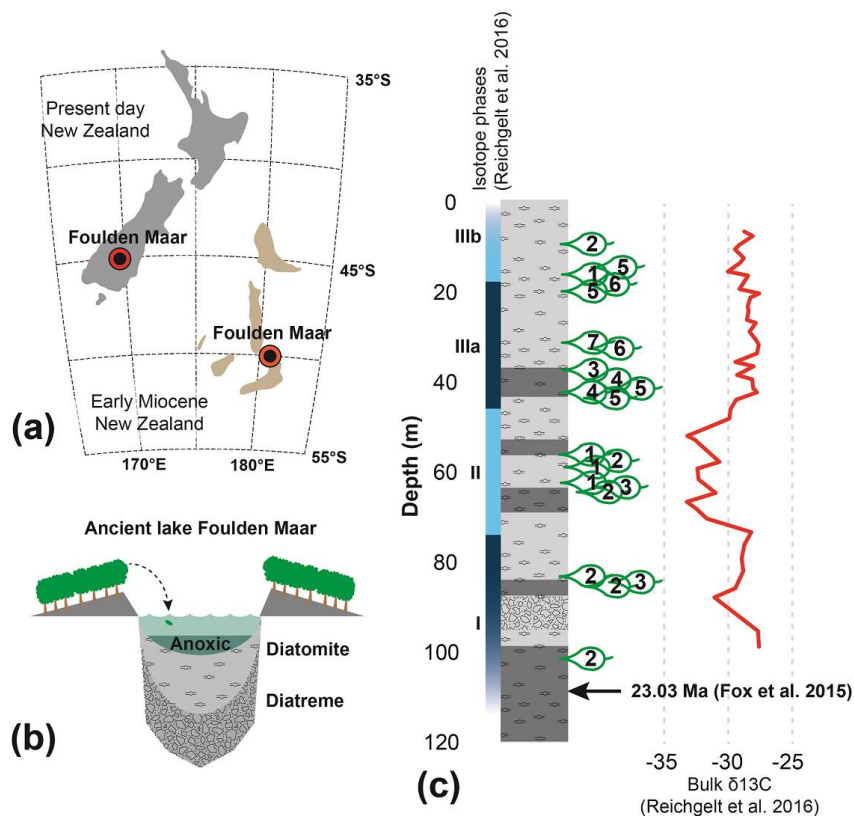
Figure 1. Foulden Maar site information. (a) Location of the Foulden Maar deposit and paleogeographic

reconstruction of early Miocene New Zealand (Boyden et al., 2011; Lee et al., 2014). (b) Schematic

reconstruction of the Foulden Maar depositional environment. (c) Stratigraphic column of the Foulden

Maar core (Fox et al., 2015), with sample locations and bulk organic $\delta^{13}C$ (Reichgelt et al., 2016).

633

634   Fig. 2

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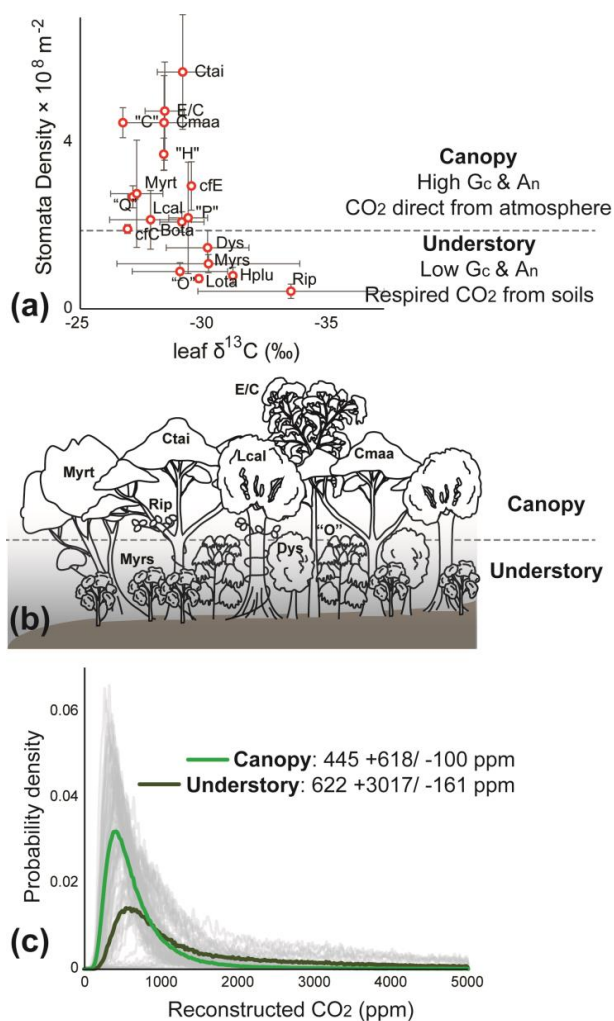
Figure 2. Foulden Maar paleoecology and atmospheric CO₂ reconstructions. (a) δ^{13}C values and

stomatal density from the fossil leaves of Foulden Maar provide constraints to distinguish canopy leaf

types from understory, because understory leaves tend to have a high range of δ^{13}C and low cell density

(Graham et al., 2014; Bush et al., 2017). **(b)** Paleoecological reconstruction of the dense rainforest at

Foulden Maar with a canopy comprising *Litsea calicarioides* (Lcal), *Cryptocarya taieriensis* (Ctai), *C.*

maarensis (Cmaa), cf. Elaeocarpaceae/Cunoniaceae (E/C), and cf. Myrtaceae (Myrt), and an understory

comprising cf. *Myrsine* (Myrs), cf. *Ripogonum* (Rip), cf. *Dysoxylum* (Dys), and leaf type "O". *Hedycarya*

643   *pluvisilva* (Hplu), *Laurelia otagoensis* (Lota), *Beilschmiedia otagoensis* (Bota), cf. *Cryptocarya* (cfC), cf.

644   *Endiandra* (cfE), and leaf types "C", "H", "P", and "Q" could not be ecologically placed with certainty.

645   **(c)** Probability density distributions of C_a reconstructions from canopy (thick light green line) and

646   understory components (thick dark green line) using a gas-exchange model (Franks et al., 2014). Grey

647   curves represent 1000 Monte Carlo reconstructions on a single fossil leaf.

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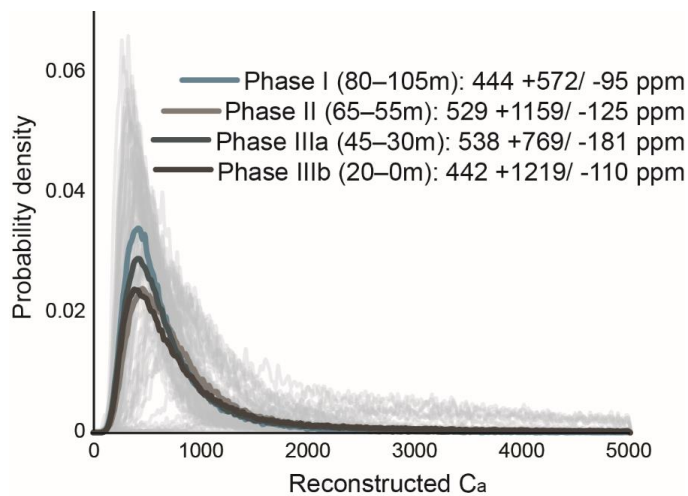
649

650   **Figure 3.** Probability density distributions of Ca reconstructions using a gas-exchange model (Franks et

651   al., 2014), divided by bulk carbon isotope phases (Fig. 1c).

652

653   Fig. 4

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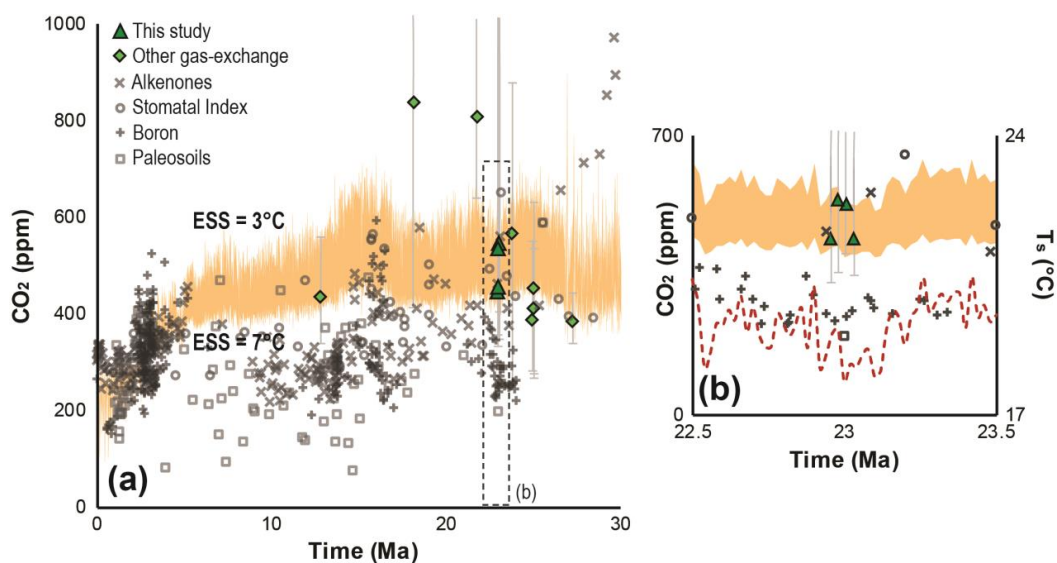
Figure 4. Neogene Earth System Sensitivity (ESS) and C_a reconstructions. Calculated C_a levels for an

ESS range of 3–7 °C (orange shaded area) for the last 30 Ma **(a)**, and for the interval between 22.5–23.5

Ma **(b)**, the red dashed line in **(b)** indicates the global average surface temperature (T_s) in the earliest

Miocene (Hansen et al., 2013). The ESS envelope was determined using deep-sea $\delta^{18}O$ of benthic

foraminifera (Zachos et al., 2001) and the transform function approach from Hansen et al. (2013)

(Supplementary Information). Proxy-based Neogene C_a reconstructions are derived from a previously

published compilation (Foster et al., 2017) and are supplemented with more recently published data (Ji

et al., 2019; Londoño et al., 2018; Super et al., 2018; Greenop et al., 2019; Moraweck et al., 2019,

Steinthorsdottir et al., 2019). Error bars on gas-exchange based proxy estimates represent ±1σ.

664

665   Fig. 5

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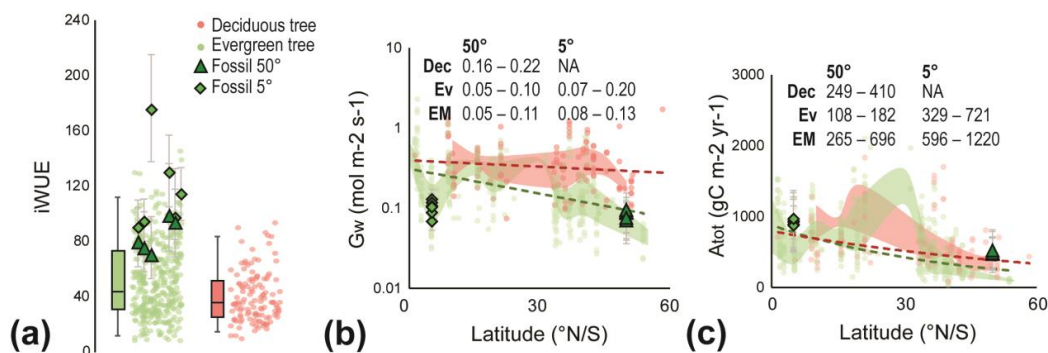
Figure 5. Early Miocene leaf-level physiological parameters of canopy trees. (a) Intrinsic water-use

efficiency (iWUE) of evergreen (green circles) and deciduous trees (red circles) based on modern leaf-

level measurements (Maire et al., 2015), and fossil reconstructions (green triangles and diamonds). Error

bars on fossil-derived data indicate $\pm 1\sigma$, box-and-whisker plots indicate median, first and third quartile

(Q1 and Q3), and 95% confidence interval of modern leaves of canopy trees. Individual datapoints are

randomized on the x-axis for a clearer depiction of the distribution. **(b)** Conductance to water (G_w) from

modern evergreen (Ev) and deciduous (Dec) trees (Maire et al., 2015) and fossils (EM) from different

latitudes. The shaded red and green areas indicate the Q1–Q3 range of modern evergreen and deciduous

trees, respectively, and the dashed lines indicate the overall linear trend with latitude. Text in panel is the

Q1–Q3 range for each group, grouped in 5° latitude bins. **(c)** Total annual carbon flux per unit leaf area

(A_{tot}) from modern evergreen (Ev) and deciduous (Dec) trees (Maire et al., 2015) and fossils (EM) from

different latitudes. The shaded red and green areas indicate the Q1–Q3 range of modern evergreen and

deciduous trees, respectively, and the dashed lines indicate the overall exponential trend with latitude.

Text in panel is the Q1–Q3 range for each group, grouped in 5° latitude bins.

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Data availability. All raw measurement data on fossil leaves generated for this paper is available in the

online supplementary information. Raw measurements on fossil leaves from Ethiopia (Tesfamichael et

al., 2017) and Panama (Londoño et al., 2018), $\delta^{18}O$ measurements (Zachos et al., 2001), and iWUE, G_w

685   and A_n measurements on modern plants (Maire et al., 2015) are available through the cited original

686   works.

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