



Constraints on the paleoelevation history of the Eastern Cordillera of Colombia from its palynological record

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ABSTRACT

We attempted to make an objective assessment of whether fossil pollen assemblages from the Sabana de Bogotá require surface uplift of ~2000 m since 6–3 Ma, as has been argued. We relied on recently published elevation ranges of plants for which fossil pollen has been found in sites 2000–2500 m high in the Sabana de Bogotá. The elevation ranges of fossil plants do not overlap, suggesting that those ranges may be too narrow. By weighting these elevation ranges by percentages of corresponding fossil pollen and summing them, we estimated probability density functions for past elevations. These probability distributions of past elevations overlap present-day elevations and therefore do not require surface uplift since deposition of the pollen. Fossil pollen assemblages include pollen from some plant taxa for which we do not know present-day elevation ranges, and therefore, with a more complete knowledge of elevation distributions, tighter constraints on elevations should be obtainable. The elevation of the oldest assemblage, from Tequendama, which lies at the southern edge of the Sabana de Bogotá and is thought to date from 16 to 6 Ma, is least well constrained. Although our analysis permits no change in elevation since the pollen was deposited, we consider 1000–2000 m of elevation gain since 15 Ma to be likely and consistent with an outward growth of the Eastern Cordillera.

INTRODUCTION

With many decades of study, Dutch and Colombian botanists have made the Eastern Cordillera of the Colombian Andes (Fig. 1) a test area for characterizing how tropical plants live and evolve along elevation gradients in the tropics (e.g., Hooghiemstra and Flantua, 2019). A by-product of this work has been steadily evolving images of how the Eastern Cordillera itself has risen to its present-day height in late Cenozoic time. Van der Hammen et al. (1973) suggested that the Eastern Cordillera rose to its present height largely since 3–2 Ma, and therefore since ice sheets first occupied vast areas of the Northern Hemisphere. As dating

improved, the inferred timing of surface uplift has shifted to be predominantly between 6 and 3 Ma, but still in late Cenozoic time (e.g., Hooghiemstra et al., 2006; Mora et al., 2008). If this were so, it would suggest that although the Eastern Cordillera had started to grow many tens of millions of years earlier, for some reason its surface rose abruptly since 6 Ma. Although rapid surface uplift, at nearly 1 mm/yr, does seem to have occurred in the Central Andes (e.g., Garziona et al., 2006, 2008), it is not commonly observed in the growth of most

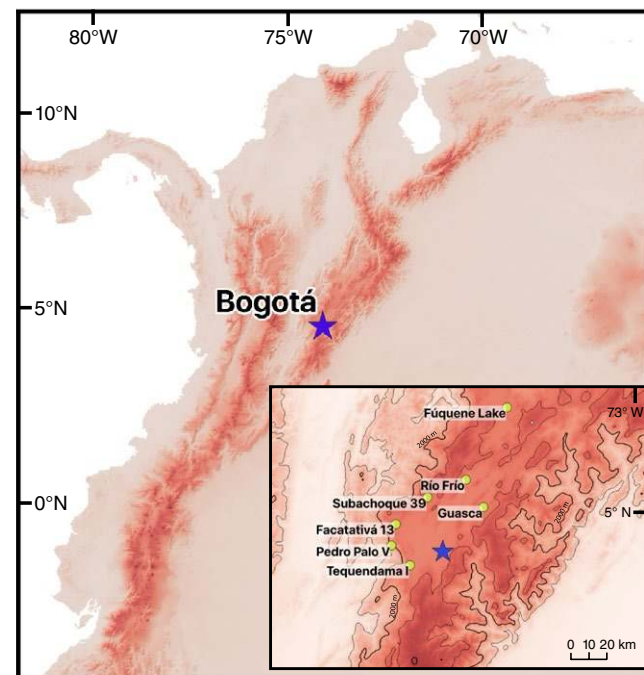


Figure 1. Map of the northwest corner of South America and the Andes. Inset: Close-up of the Sabana de Bogotá, Eastern Cordillera of Colombia, showing locations of the fossil pollen.

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mountain belts. With such considerations, we reexamined the paleobotanical evidence and arguments for a recent rise of the Eastern Cordillera.

Much evidence, consisting largely of sedimentary deposits that require nearby elevated sources of such sediment, suggests that the Eastern Cordillera began to develop as a mountain belt in Eocene or Oligocene time, if not earlier (e.g., Babault et al., 2013; Bande et al., 2012; Bayona et al., 2008, 2013; Caballero et al., 2013; Cediel et al., 2003; de la Parra et al., 2015; Gómez et al., 2003; Hoorn et al., 2010; Horton et al., 2010, 2020; Kammer et al., 2020; Martínez, 2006; Mora et al., 2010a, 2010b, 2013, 2020a, 2020b; Ochoa et al., 2012; Parra et al., 2009a, 2009b, 2012; Reyes-Harker et al., 2015; Sánchez et al., 2012; Saylor et al., 2011, 2012a, 2012b; Villamil, 1999). The building of high terrain through isostatic compensation of thickened crust obviously requires time for such crust to be shortened and thickened. Some estimates of the amount of convergence and shortening across the Eastern Cordillera range between 100 and 150 km (e.g., Bayona et al., 2008; Colletta et al., 1990; Dengo and Covey, 1993), with one as large as 170 km (Roeder and Chamberlain, 1995), but others have argued for as little as ~60–80 km (e.g., Cooper et al., 1995; Cortés et al., 2006; Kammer et al., 2020; Mora et al., 2013; Teixell et al., 2015; Tesón et al., 2013), to as little as 31.5 km (Siravo et al., 2018).

Using global positioning system (GPS) measurements, Mora-Páez et al. (2016) showed that northwest-southeast shortening across the Eastern Cordillera occurs today at only 3.7 ± 0.3 mm/yr. If constant since 6 Ma, this rate would account for only 22 km of 60–80 km or of 100–170 km of total shortening. Conversely, shortening at 3.7 ± 0.3 mm/yr since 20 or 40 Ma would be 74 ± 6 km or 148 ± 12 km, and therefore would match estimated amounts of shortening. Using receiver functions, E. Poveda et al. (2015) determined crustal thicknesses of ~60 km beneath stations in and near the Sabana de Bogotá, suggesting that Airy isostasy prevails. From traveltimes delays of *P* waves from local earthquakes, they inferred somewhat thinner crust northeast of Bogotá, but as they noted, all estimates are consistent with Airy isostatic compensation. Therefore, thickened crust accounts for the majority, if not all, of the present-day elevations (E. Poveda et al., 2015). It follows that a rapid rise of the Eastern Cordillera since only 6 Ma would require one of the following: (1) a surprisingly rapid acceleration in shortening that is not consistent with the current rate, (2) thickening of the crust not by horizontal shortening of crust, but by some other process that thickened the crust, or (3) a deeper-seated process that raised the surface without thickening the crust (e.g., Kammer et al., 2020; Siravo et al., 2019).

Consistent with doubts about a late Cenozoic acceleration of convergence and surface uplift, Anderson et al. (2015) reported temperatures inferred from branched glycerol dialkyl glycerol tetraethers (brGDGTs) in lipids from soil bacteria from three sites (Tequendama, Guasca, and Subachoque) in the Sabana de Bogotá, now ~2600 m high (Fig. 1), and these temperatures showed little change since 8–6 Ma. They inferred at most 1000 m of surface uplift since the Tequendama section was deposited, since ca. 16–6 Ma, as we discuss below.

To infer past elevations, van der Hammen, Hooghiemstra, and their colleagues relied on fossil pollen assemblages found both in outcrops and in a deep core into the Sabana de Bogotá at the southwest end of the Eastern Cordillera (Fig. 1).

Using the present-day elevation ranges of vegetation that produce the pollen found in sedimentary rock, they mapped the fossil assemblages onto modern elevations (e.g., Andriessen et al., 1993; Helmens and Van der Hammen, 1994; Hooghiemstra, 1984; Hooghiemstra and Van der Hammen, 1998; Hooghiemstra et al., 2006; Kroonenberg et al., 1990; Van der Hammen et al., 1973; Wijninga, 1996a, 1996b, 1996c, 1996d; Wijninga and Kuhry, 1990). In a brief summary of “vegetation zones,” Hooghiemstra and Ran (1994) distinguished the following zones: tropical lowland rain forest from 0 to 1000 m; a sub-Andean forest belt, or lower montane forest, from 1000 to 2300 m; an Andean forest belt, or upper montane forest, from 2300 to 3200–3500 m; subpáramo belt from 3200–3500 m to 3400–3600 m; a grass páramo belt from 3400–3600 m to 4000–4200 m; and a superpáramo belt extending from 4000 to 4200 m upward. The wide ranges of the present-day vegetation zones do not allow precise elevations to be assigned. Many tectonic interpretations of the Eastern Cordillera, however, have relied on the stated changes in elevations over the past few million years. Thus, if our paper is seen a criticism of the work by the palynologists quoted above, we hope that readers will understand that we are more critical of common, and in some cases uncritical, applications of these inferred changes in paleoelevations than of what we consider to be good work by the palynologists, despite that work possibly containing some misleading inferences of past elevations.

Recently, Groot et al. (2013) took a step beyond “vegetation zones” defined by assemblages of plants and presented elevation ranges for specific individual taxa. They stated, “Present-day altitudinal envelopes of the selected pollen taxa, often including many individual plant species, were actualized by A.M. Cleef (p. 189) based on the literature and abundant field observations...” (Groot et al., 2013, p. 189). Wijninga and Kuhry (1990, their fig. 7) had given similar, but more preliminary, summaries of present-day pollen distributions, but with some differences. We relied on the distributions of Groot et al. (2013) to assign probability density functions to elevations for various representative pollen found at different sites of different ages. Groot et al. (2013) focused on the region near the Fúquene lake (Fig. 1), which lies at an elevation of 2580 m, and as a result, they did not include elevation ranges of some taxa that currently live at low elevations. Thus, by using their data, our estimated elevation ranges are biased upward, but for sites with many lowland taxa, we added approximate elevation ranges for those taxa as well.

■ APPROACH

The differences in vegetation in different climatic settings have led to a long tradition of using paleobotanical evidence to infer past climates, and by extension past elevations. Two classes of approach have been taken.

For one, investigators assign taxonomy to a fossil plant organ, most commonly pollen, and then from similarities of environments inhabited by near living relatives of the fossil taxa, they assign a paleoclimate (e.g., Axelrod, 1957; Greenwood et al., 2003, 2005; Kershaw and Nix, 1988; Martínez et al., 2020). Approaches of this type can differ depending on whether the various

taxa are weighted in the same way or are simply used as presence versus absence data, as well as whether the absence of a taxon in a fossil assemblage, but presence in an otherwise similar modern environment, is used or ignored (e.g., Thompson et al., 2012).

In the other approach, one virtually ignores taxonomy and uses only the physiognomic characteristics of different taxa (without assigning them names), including sizes and shapes of the plant organs. Most commonly, leaves are used (e.g., Spicer et al., 2009, 2011; Wolfe, 1993, 1995). Investigators first estimate the fractions (percentages) of the many characteristics in fossil assemblages, like leaves with (or without) teeth or sizes, within a given range. They then compare those fractions with corresponding fractions in modern forests growing in different climates. Virtues of this latter approach include avoiding taxonomic assignments, which can err when evolution may have altered plant organs not used in assignments of taxonomy. Moreover, for paleoaltimetry, leaf physiognomy can be used to infer moist enthalpy, and as a result, a direct inference of paleoelevations can be made without assumptions about the way in which surface temperature varied with elevation in the past (e.g., Forest et al., 1995, 1999; Spicer, 2018). In any case, applications of both methods to pollen and to leaves from the same sedimentary rock have yielded estimates of mean annual temperatures within a few degrees Celsius of one another (e.g., Fletcher et al., 2014; Greenwood et al., 2003, 2005).

We relied on a variant of the first approach—taxonomic assignments of fossil pollen and then inferences about elevations based on the assumption that their nearest living relatives provide bounds on the environments in which the fossil taxa lived.

Groot et al. (2013) reported elevation distributions that included ranges with seemingly equal likelihood and then, for most taxa, with tapered distributions at the low and high ends of elevation ranges, resulting in trapezoidal shapes if presence or absence is plotted versus elevation. Such plots resemble those in Figure 2, but for each taxon, they showed the same amplitude, whether the taxon lives in a narrow or wide elevation range. Mathematically, we can represent the probability density function (probability per unit height) of finding a particular taxon, i , at a certain elevation, z , as $P_i(z)$. It follows that

$$\int_0^H P_i(z) dz = 1.0, \tag{1}$$

where H is the maximum altitude in the region. Where Groot et al. (2013) reported a taxon to live in a narrow elevation range, the probability density (per meter of height), $P_i(z)$, would be large in that elevation range, but only over that narrow range (Fig. 2). Similarly, a taxon found at a wide range of elevations would be assigned relatively small maximum value of $P_i(z)$ in the elevation range where the taxon is present, but over that wide elevation range.

In mathematical terms, Groot et al. (2013, their fig. 3) used four elevations to describe the presence or absence of a particular taxon. For $z > z_0$ and $z > z_3$, the taxon was absent; for $z_1 < z < z_2$ the taxon was present, apparently with uniform likelihood, and for $z_0 < z < z_1$ and for $z_2 < z < z_3$, the likelihood varied linearly between z_0 and z_1 and between z_2 and z_3 . Accordingly, we assigned values to probability density functions by normalizing distributions using Equation 1, so that

$$P_i(z) = 0, z < z_0, \tag{2a}$$

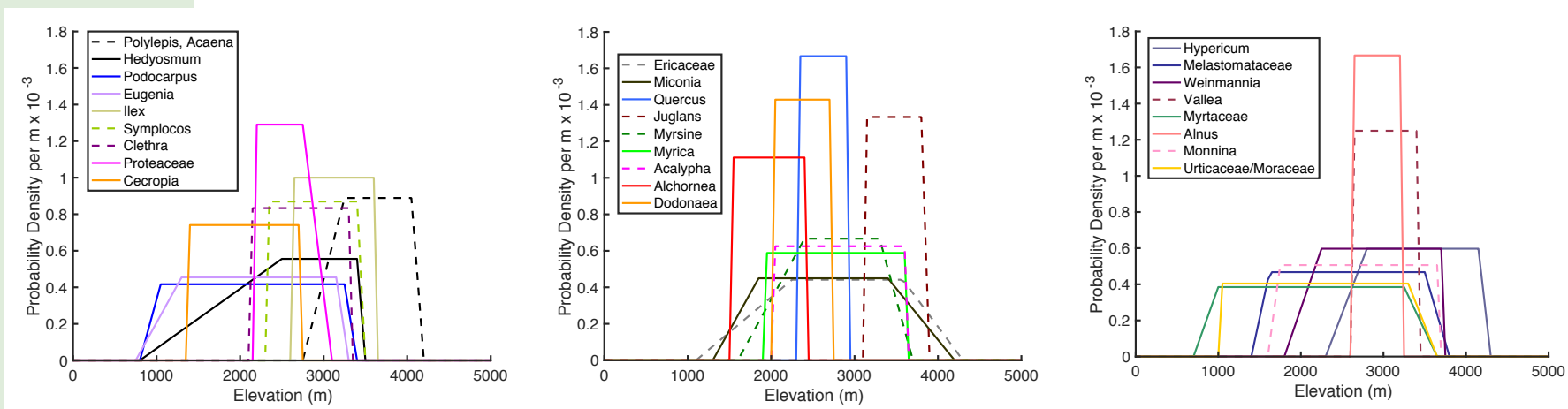


Figure 2. Probability density functions of the 26 taxa for which Groot et al. (2013) gave elevation ranges, and for which fossil pollen have been found in the sites that we considered. We use three plots so that probability density functions of individual pollen can be seen.

$$P_i(z) = P_0 \frac{z - z_0}{z_1 - z_0}, \quad z_0 < z < z_1, \quad (2b)$$

$$P_i(z) = P_0, \quad z_1 < z < z_2, \quad (2c)$$

$$P_i(z) = P_0 \frac{z_3 - z}{z_3 - z_2}, \quad z_2 < z < z_3, \quad (2d)$$

$$P_i(z) = 0, \quad z > z_3. \quad (2e)$$

It follows from Equation 1 that

$$P_0 = \frac{2}{z_3 + z_2 - z_1 - z_0}. \quad (3)$$

For fossil localities, we used published fractions of pollen over different depths in cores or sedimentary archives. Fossil pollen assemblages, or pollen spectra, are commonly scored as percent amounts of the various taxa. In all cases, percentages of pollen from each taxon varied with depth. Rather than choose percentages at some arbitrarily precise level, we took plots of pollen percentages over finite ranges of depths, and using a planimeter, we integrated those percentages to obtain average percentages that pertained to finite spans of time. The papers that we used did not present numerical data. We could not assess the age ranges that spanned the depths used to integrate percentages, but authors' discussions ignored variability and addressed similar average percentages.

We sought a probability distribution for the height, h , of a region where fossil taxa have been found. Let F_i be the fraction of a particular taxon i among N taxa found at a site. We presume that taxa with large fractions should be given the most weight. So, we assumed that each fossil taxon contributed to the probability density function of elevation by an amount $P_{h,i}(z)$, given as

$$P_{h,i}(z) = F_i P_i(z) \quad (4)$$

(where no summation convention over repeated indices is implied).

We can imagine two ways of calculating probability density functions of past elevations that take into account the different values of $P_{h,i}(z)$ for N different fossil taxa at a site.

First, we may simply sum values of $P_{h,i}(z)$:

$$P_{h,sum}(z) = \sum_{i=1}^N P_{h,i}(z). \quad (5)$$

With this approach, fossil pollen of a taxon that today grows only at low (or high) altitude would offer a finite probability that the fossil locality lay at that low (or high) altitude when the pollen was deposited. To place uncertainties on estimated elevations, we calculated cumulative probabilities, $P_{cum}(h)$:

$$P_{cum}(h) = \int_0^h P_{h,sum}(z) dz. \quad (6)$$

If we had access to elevation distributions for all fossil pollen, the value of $P_{cum}(H) = 1$. As we show below, this is not the case for any fossil pollen

assemblage. For some, however, $P_{cum}(H) > 0.9$, which implies that most of the relevant fossil pollen taxa are represented by the elevation distributions given by Groot et al. (2013). Ignoring pollen for which we do not know elevation distributions, the value of $P_{cum}(h_{mean}) = 0.5 P_{cum}(H)$ defines a mean, h_{mean} : the probability of a higher or lower elevation is 50% for each. For Gaussian statistics, values of elevations within one standard deviation, 1σ , of the mean value would occupy approximately the central two thirds of the total range of values. Although Gaussian statistics surely do not apply, we treated those heights for which the cumulative probabilities span the central 68.27% of $P_{cum}(h)$ versus h as defining 1σ bounds on the mean value, and therefore those for which $0.159 P_{cum}(H) < P_{cum}(h_{mean}) < 0.841 P_{cum}(H)$. Correspondingly, those values of $P_{cum}(h)$ for which $0.025 P_{cum}(H) < P_{cum}(h_{mean}) < 0.975 P_{cum}(H)$ define 95%, or 2σ , confidence limits.

In a second approach, we could instead calculate the product of values of $P_{h,i}(z)$:

$$P_{h,product}(z) = \prod_{i=1}^N P_{h,i}(z). \quad (7)$$

With this approach, finite probabilities, $P_{h,product}(z)$, would be restricted to elevations where all probability distributions, $P_{h,i}(z)$, are nonzero and therefore overlap. Conversely, if the present-day distributions, $P_i(z)$, of all taxa did not overlap, then $P_{h,product}(z) = 0$.

In one respect, the results were disappointing. For all but one site, the elevation ranges given by Groot et al. (2013) for at least two taxa did not overlap. So, when probability density functions are multiplied by the fraction of the corresponding taxon in the pollen spectra, $P_{h,product}(z) = 0$ in Equation 7 for all elevations. This result implies either that some of the elevation ranges given by Groot et al. (2013) are too narrow, or that some fossil pollen did not grow near the site where it was deposited. In either case, the second approach described above, using products, did not yield useful information about past elevations. Failure of this kind is not unprecedented. In a study of Eocene fossil taxa from the Copper River Formation in northeastern Nevada, Axelrod (1966) reported nearest living relatives that inhabited two widely separated elevation ranges: coast redwood forests below 150 m and fir-hemlock forests between 1400 and 2400 m in the Sierra Nevada.

In the discussion below for each region, we show three figures: (1) probability density functions (PDFs) for taxa for which Groot et al. (2013) gave elevation distributions, which show that elevation ranges do not overlap (with one exception); (2) PDFs of elevation given by Equation 5, which show the spread of permissible elevations; and (3) cumulative probabilities of elevations given by Equation 6, from which we inferred mean estimates of paleoelevations, h_{mean} and 1σ and 2σ (95%) confidence limits.

We remind readers of a limitation imposed by using the elevation distributions of Groot et al. (2013), whose focus was a pair of Holocene fossil assemblages at high elevation. Neither they nor Wijninga and Kuhry (1990) gave elevation ranges of plants today confined to low elevations. For sites that apparently were high when pollen accumulated, this has little effect, but for the oldest pollen assemblages, those of Río Frio and Tequendama, excluding plants that currently grow at low elevations, and apparently have done so for tens of millions of years (e.g., Hoorn, 1994; Ochoa et al., 2012; Salamanca

Villegas et al., 2016), biases inferences. We attempted to include, albeit crudely, elevation ranges of such taxa for these sites.

■ HOLOCENE POLLEN DISTRIBUTIONS AS TESTS OF THE APPROACH

To test the first approach, using summed probability distributions, $P_{h,sum}(z)$, in Equation 5, and cumulative probabilities, $P_{cum}(h)$, in Equation 6, we used pollen spectra from Holocene sediment in two regions (Fig. 1): Pedro Palo and Fúquene lake (two sites). Clearly, the fossil sites are unlikely to have shifted in elevation much since Holocene time. Therefore, we might expect the comparison of modern pollen to the Holocene pollen spectra to yield the present-day elevation.

For the Laguna Pedro Palo V section zone 5, Groot et al. (2013) reported elevation ranges for 89% of the fossil pollen found by Hooghiemstra and van der Hammen (1993, their fig. 5). One taxon, *Alchornea*, dominates the pollen spectrum with 51.8% of the fossil pollen (Fig. 3A), and therefore it is no surprise that its present-day elevation distribution dominates the resulting probability distribution (Fig. 3B). The probability density function (Fig. 3B) is quite peaked, with a mean elevation of 2150 m and 1σ bounds of 1700 and 2700 m (Fig. 3C). If we treat the preponderance of *Alchornea* as a bias, and arbitrarily assign its fraction to be 10% instead of 51.8%, and therefore not much different from percentages of a couple of other taxa (Fig. 3D), the PDF becomes broader (Fig. 3E). The estimated mean elevation of 2400 m, with 1σ bounds of 1750 and 3050 m (Fig. 3F), shifts to higher elevations than when *Alchornea* dominates the spectrum. With *Alchornea* comprising 51.8% of the fossil pollen, or with 80% of *Alchornea* ignored, the 1σ bounds include the present-day elevation of 2000 m.

Hooghiemstra and van der Hammen (1993) reported two radiocarbon ages of $10,280 \pm 90$ and $10,380 \pm 90$ radiocarbon years from material within the Pedro Palo V section. When calibrated for varying production rates, these fall within ~300 yr of 12,000 cal yr B.P. (Reimer et al., 2013). Thus, the pollen was deposited during the Younger Dryas period, which began at 12,846 (± 138) cal yr B.P. (Capano et al., 2020) and ended at 11,550 ($+40/-50$) cal yr B.P. (Gulliksen et al., 1998). The Younger Dryas was a brief period of glacial conditions at high latitudes, and it is recognized as the El Abra stadial in the Colombian Andes (Kuhry et al., 1993; Schreve-Brinkman, 1978; Van der Hammen, 1974). In associating the El Abra stadial with the Younger Dryas, Van der Hammen and Hooghiemstra (1995, p. 850) stated that the “upper forest line during the El Abra stadial was ... some 600 to 800 m lower than today.” The Laguna Pedro Palo V section was taken from an elevation of ~2000 m. Correcting for this difference in climate, we might expect the pollen to suggest an elevation closer to 2600–2800 m than 2000 m. With this adjustment, the PDFs of elevations using 58% or only 10% of *Alchornea* (Figs. 3D–3F) still overlap the elevation of ~2600–2800 m adjusted for El Abra conditions.

For the Fúquene sections I (Fig. 4) and II (Fig. 5), at 2580 m, Van Geel and Van der Hammen (1973, their fig. 5) sampled two cores of Holocene sediment at opposite ends of the lake. Their differences (Figs. 4A and 5A) give an indication

of scatter in pollen spectra. The dominant taxon in both sections is Gramineae (29% and 39% of Fúquene I and II, respectively), with large amounts of “Bosque” (forest in Spanish) in each (20% and 11%, respectively). Wijninga and Kuhry (1993) assigned Gramineae to páramo environments, and Hooghiemstra and Ran (1994) gave elevations from 3400–3600 m to 4000–4200 m for the grass páramo belt. Groot et al. (2013), however, did not give elevation ranges for Gramineae. We have not been able to determine what environment is indicated by “Bosque.” Because of the major contributions of Gramineae and Bosque, we can use only 50% of the pollen from Fúquene I and only 33% from Fúquene II to estimate elevation ranges using those given by Groot et al. (2013). Both sites yielded mean elevations of 2700 m, little different from the present-day 2580 m (Figs. 4C and 5C). Moreover, 1σ bounds of 2350 and 2950 m and 2250 and 3050 m are relatively narrow.

In complicating the pollen spectra, however, two taxa dominate the population for which Groot et al. (2013) gave ranges: *Quercus* (oak) and *Alnus* (alder) (Figs. 4A and 5A). Both of these taxa immigrated from North America to the Eastern Cordillera in Pleistocene time, and hence both are absent in Pliocene and Miocene pollen assemblages (Felde et al., 2016; Hooghiemstra and Flantua, 2019; Hooghiemstra and Ran, 1994; Hooghiemstra and Van der Hammen, 2004; Hooghiemstra et al., 2006; Torres et al., 2013; Van der Hammen, 1974). Moreover, because they competed with and to some extent replaced other taxa that had thrived in the same environments for millions of years (e.g., Hooghiemstra and Van der Hammen, 2004; Torres et al., 2013), a test in which the dominant taxa are immigrants and not representative of past assemblages is less than ideal. Following Wijninga (1996b), we excluded these taxa, and analyzed the remaining ones, which comprise only 12.6% and 12.0% of the fossil pollen assemblages. For both Fúquene I and II, excluding *Quercus* and *Alnus* yields a more uniform distribution of taxa (Figs. 4D and 5D), and the resulting PDFs are less peaked (Figs. 4E and 5E) than those with *Quercus* and *Alnus* (Figs. 4B and 5B). The respective inferred mean elevations of these are 2450 m (Fig. 4F) and 2350 m (Fig. 5F), with 1σ bounds of 1750 and 3200 m and 1700 and 3100 m, which include the present-day elevation of 2580 m. If we could include Gramineae in a quantitative analysis, its inclusion might pull the inferred elevation upward. In any case, these analyses are flawed by their use of only ~12% of the fossil pollen.

The agreement between present-day elevations and those estimated for the Holocene for the three pollen spectra suggests that the approach taken here is sensible. Although the tests are imperfect because of our inability to include all fossil taxa, we proceeded to the analyses with pollen spectra of older sites.

■ FOSSIL POLLEN AND PROBABILITY DENSITY FUNCTIONS OF PAST ELEVATIONS

Pliocene Sites

We examined pollen spectra from four Pliocene sites: Guasca (ca. 3 Ma), Facatativá (3.7 ± 0.7 Ma), Subachoque (5–4 Ma), and Río Frío (5.3 ± 1.0 Ma) (e.g., Hooghiemstra et al., 2006).

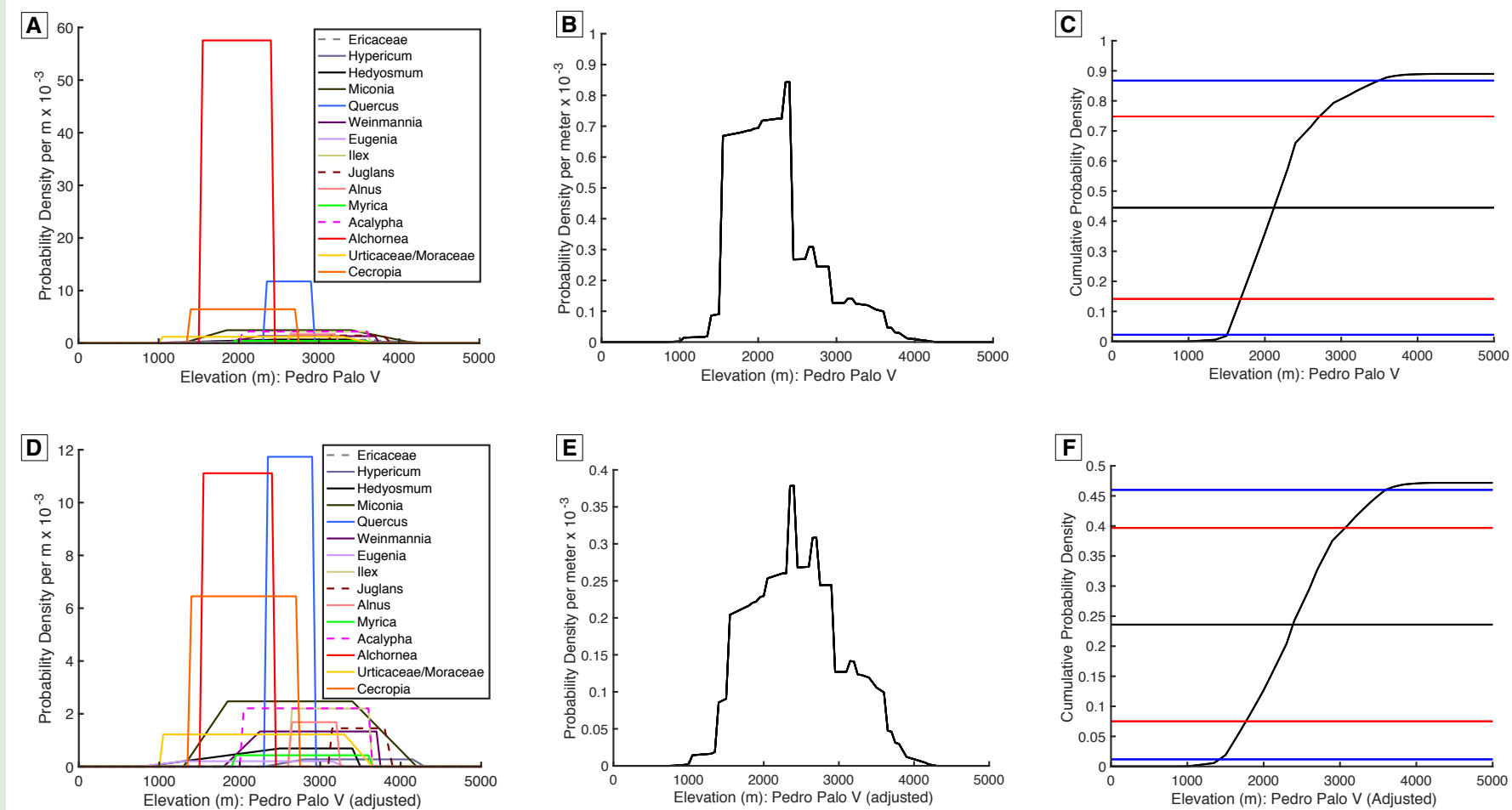


Figure 3. Probability density functions (PDFs) for pollen spectra from Pedro Palo V (Hooghiemstra and van der Hammen, 1993) presented in three ways. (A) PDFs for each taxon for which Groot et al. (2013) gave an elevation distribution. (B) PDFs of elevation given by Equation 5. (C) Cumulative probabilities of elevations given by Equation 6, where the black horizontal line defines $0.5 P_{cum}(H)$, red lines give 1σ bounds, and blue lines give 95% confidence limits. (D–F) Same as A–C, but with the fraction of *Alchornea* reduced from 51.8% to 10%.

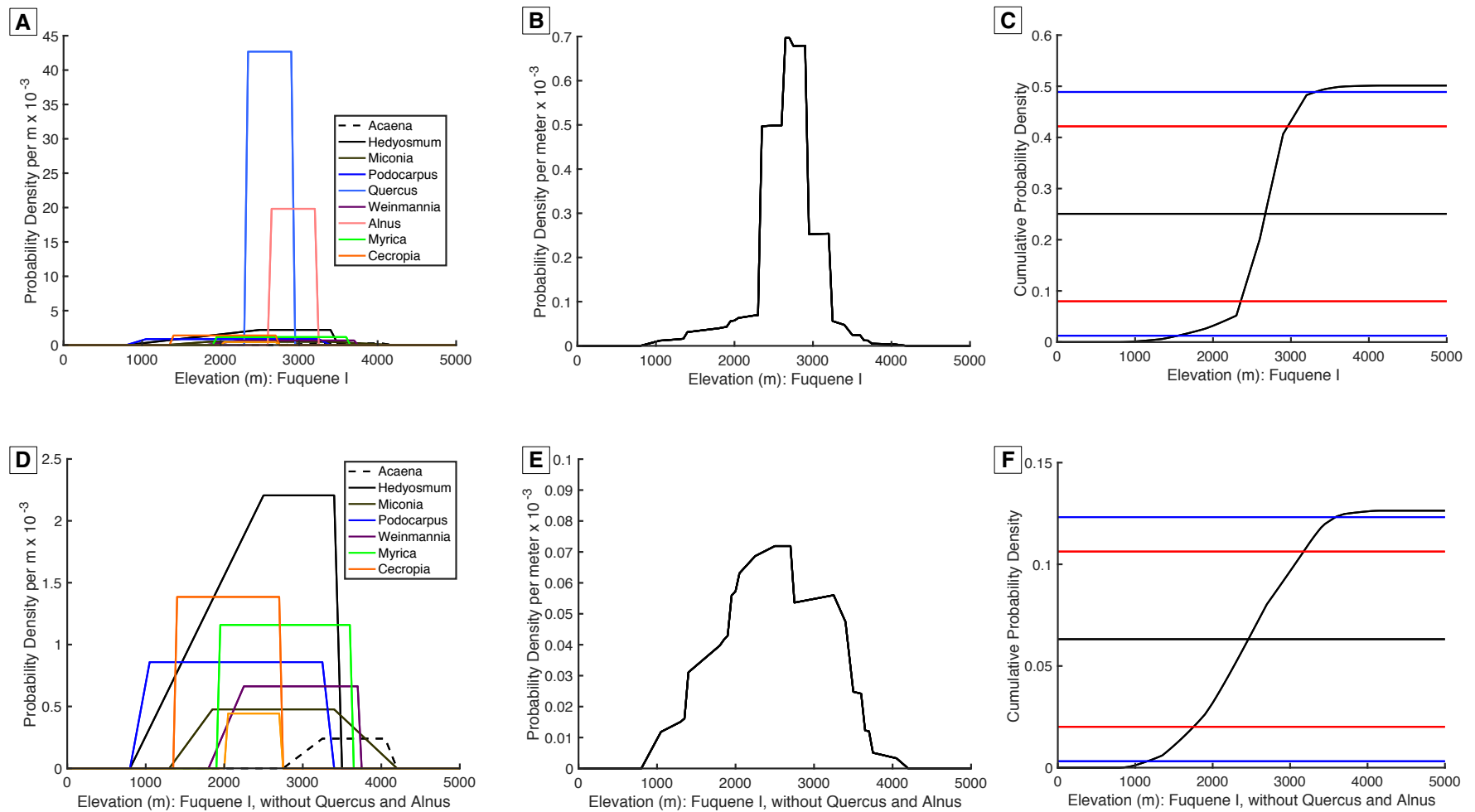


Figure 4. Probability density functions (PDFs) for pollen spectra from Fúquene I (Van Geel and Van der Hammen, 1973), as in Figure 3, presented in three ways. (A) PDFs for each taxon for which Groot et al. (2013) gave an elevation distribution. (B) PDFs of elevation given by Equation 5. (C) Cumulative probabilities of elevations given by Equation 6, where the black horizontal line defines $0.5 P_{cum}(H)$, red lines give 1σ bounds, and blue lines give 95% confidence limits. (D–F) Same as A–C but without *Quercus* (25.6%) and *Alnus* (11.9%), which dominate the pollen spectrum in A, B, and C.

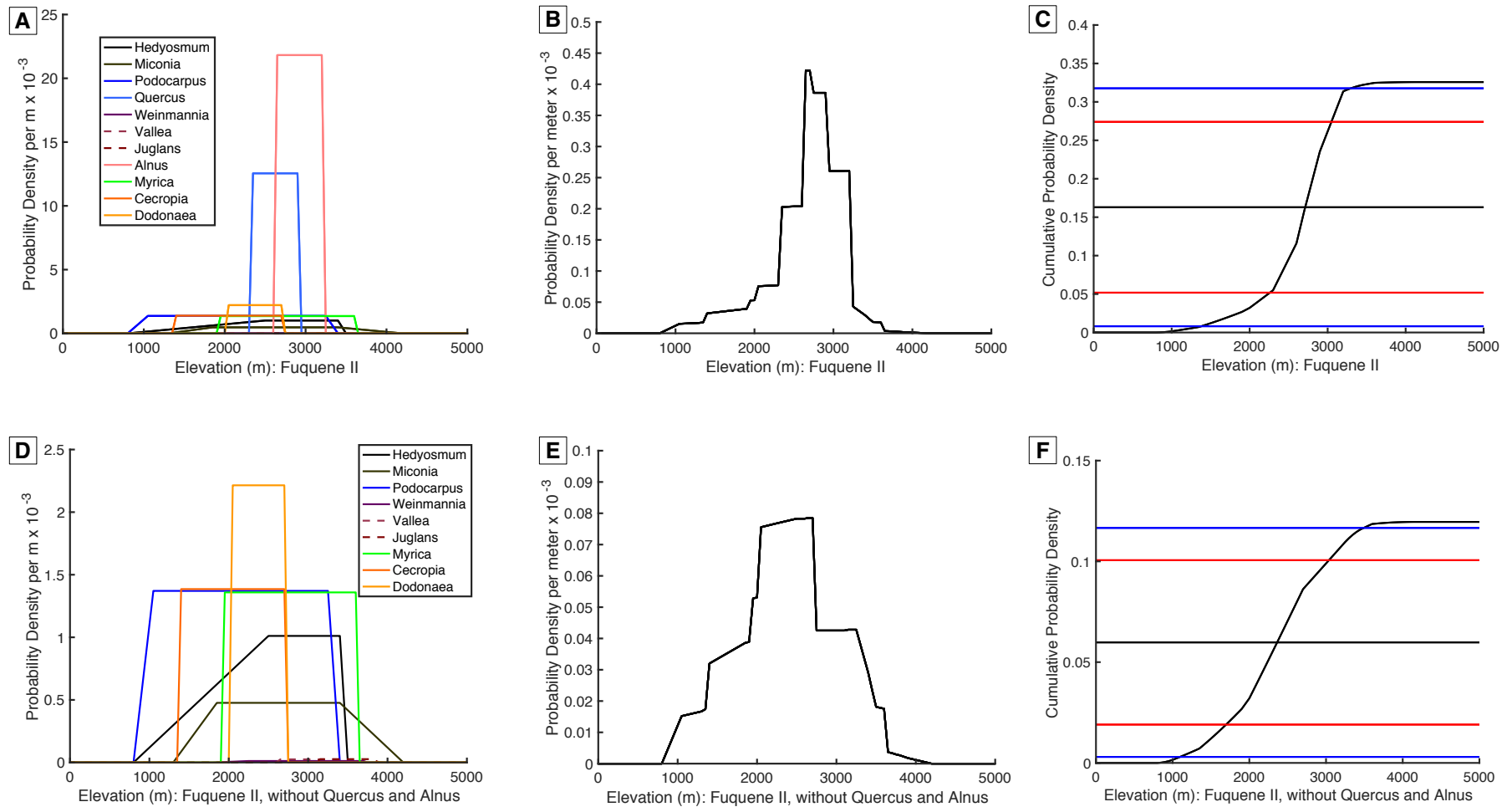


Figure 5. Probability density functions (PDFs) for pollen spectra from Fúquene II (Van Geel and Van der Hammen, 1973), as in Figure 3, presented in three ways. (A) PDFs for each taxon for which Groot et al. (2013) gave an elevation distribution. (B) PDFs of elevation given by Equation 5. (C) Cumulative probabilities of elevations given by Equation 6, where the black horizontal line defines $0.5 P_{cum}(H)$, red lines give 1σ bounds, and blue lines give 95% confidence limits. (D–F) Same as A–C but without *Quercus* (7.5%) and *Alnus* (13.1%), which dominate the pollen spectrum in A, B, and C.

Guasca Section, at 2650 m

From the mixture of pollen from plants currently living in both the subandean forest and the Andean forest, Wijninga and Kuhry (1993, fig. 5) inferred a paleoelevation of 2300 m, at the boundary between these groups. Hooghiemstra et al. (2006) suggested 2200 ± 500 m.

We examined separate intervals, B, D, and E, of a 30 m sequence of the lacustrine and fluvial sediment. Thicknesses of the intervals are ~ 1 m for B, and ~ 0.5 m for D and for E, which lie above B. Groot et al. (2013) reported elevations for $\sim 85\%$, 94% , and 98% of the pollen found by Wijninga and Kuhry (1993) in these sections. So, the approach taken here ought not be strongly biased by the absence of pollen from key taxa.

The probability density functions all show broad maxima between 1500 and 3400 m (Fig. 6). The cumulative probability distributions indicate the following mean elevations and 1σ ranges: for interval B, 2500 m with 1σ bounds of 1850 and 3250 m (Fig. 6C); for interval D, 2200 m with 1σ bounds of 1550 and 3000 m (Fig. 6F); and for interval E, 2400 m with 1σ bounds of 1800 and 3150 m (Fig. 6I), compared with Wijninga and Kuhry's (1993) inferred elevation of ~ 2300 m or 2200 ± 500 m of Hooghiemstra et al. (2006). These paleoelevation ranges also agree with the present-day 2650 m and therefore offer little support for a change in elevation since the pollen was deposited.

Facativá 13 Section, at 2750 m (Wijninga, 1996b, their fig. 6, part B)

We used pollen spectra between depths of 100 and 280 cm. Wijninga (1996b, p. 157) wrote: "Modern analogs of these Pliocene vegetations do not exist, because of immigration of plant taxa and evolution of ecosystems; cautious use of the modern vegetation zonation as a reference allows inference of the altitude of sediment deposition." Groot et al. (2013) presented elevation ranges for 87% of the taxa that Wijninga (1996b) found. Among those missing from the study by Groot et al. (2013) are small fractions of lowland taxa from the palm family: *Palmae psilate* (2.3%), other *Palmae* (1.7%), and *Iriartea* (1.1%).

Wijninga's (1996b) pollen spectra and the elevation ranges of Groot et al. (2013) show a broad peak in the probability density function centered near 2500 m, between 1500 and 3500 m (Fig. 7). Wijninga (1996b) inferred a paleoelevation of 2000–2500 m. The cumulative probability distribution defines a mean elevation of 2500 m, with 1σ bounds of 1700 and 3200 (Fig. 7C), which surround the present-day elevation of 2750 m.

Subachoque 39 Section, at 2820 m (Wijninga and Kuhry, 1990, fig. 4)

We used pollen spectra averaged over a 40-cm-thick layer. Groot et al. (2013) gave elevation ranges for much of the fossil pollen (69%). Wijninga and Kuhry (1990, p. 263), however, noted that some tens of percent of the fossil pollen could not be identified: "The high percentage of unidentifiable pollen

(Fig. 4, right) is explained by the number of taxonomically unrecognized and badly corroded or folded pollen grains recorded in the pollen analysis." They also noted (p. 265): "As can be observed in the general diagram (Fig. 4, left), taxa from the Andean-subandean forest belt predominate (average, 64%). The next largest group is that of the subandean lower tropical elements (average, 29%). The lower tropical forest elements are significantly represented (average, 4%). Both the high Andean vegetation elements (average, 1%) and the paramo elements (average, 2%) are poorly represented. As a preliminary conclusion, this section would probably represent a subandean forest, because the majority of the taxa belong to the Andean-subandean group and the subandean-lower tropical group." The present-day elevation range of subandean forests is 1000–2300 m (Hooghiemstra and Ran, 1994).

The probability density function shows a broad maximum near 2500 m (Fig. 8), not far from the present-day elevation of 2820 m. The cumulative probability distribution defines a mean elevation of 2450 m and 1σ bounds 1700 and 3100 m. Although the mean inferred paleoelevation is ~ 370 m below the present-day elevation of 2820 m, the 1σ bounds include that value.

Wijninga and Kuhry (1990, p. 268) inferred that the Subachoque site rose ~ 1000 m since it was deposited, and they based that inference in part on fossil fruits of plants that currently live at low elevations. They also allowed for a change in the elevation distribution of plants: "The altitudinal distribution and the floristic composition of the zonal vegetation types at that time may have been different from the present-day situation." Obviously, if this were so, the approach that we take here, of using the present-day altitude ranges of modern plants to infer past elevations, would be flawed. In any case, although we cannot rule out a 1000 m rise since the Subachoque 39 section was deposited, our analysis does not require a change in elevation since deposition at 5–4 Ma.

Río Frío 17 Section, at 3165 m (Wijninga, 1996c, fig. 5)

We used pollen spectra from a 5-cm-thick layer. Wijninga (1996c) gave an age of 5.3 ± 1.0 Ma, based on fission tracks; from the pollen and macrofossils, he inferred that the past elevation was no higher than 1500 m. Hooghiemstra et al. (2006) suggested a paleoelevation between 500 and 1500 m. The probability density function based on only 29% of the fossil pollen (Fig. 9), however, shows a broad maximum between 1500 and 3500 m. The cumulative probability distribution (Fig. 9C) shows a mean of 2500 m, with 1σ bounds of 1650 and 3150 m. These bounds do not quite include the present-day elevation of 3165 m. The 15 m difference, however, is negligible compared to subsequent sea-level drop of many tens of meters (e.g., Miller et al., 2005).

For this site, many taxa with abundant fossil pollen were not included by Groot et al. (2013), including three from the palm family: *Palmae psilate* (27.6%), *Palmae reticulate* (19.6%), and *Iriartea* (13.8%). Consequently, the estimate of past elevations using Equation 5 will be biased toward higher values than seem likely. Also, important, however, is Gramineae (16.1%), which commonly is associated with high elevations. Finally, the dominant taxon among

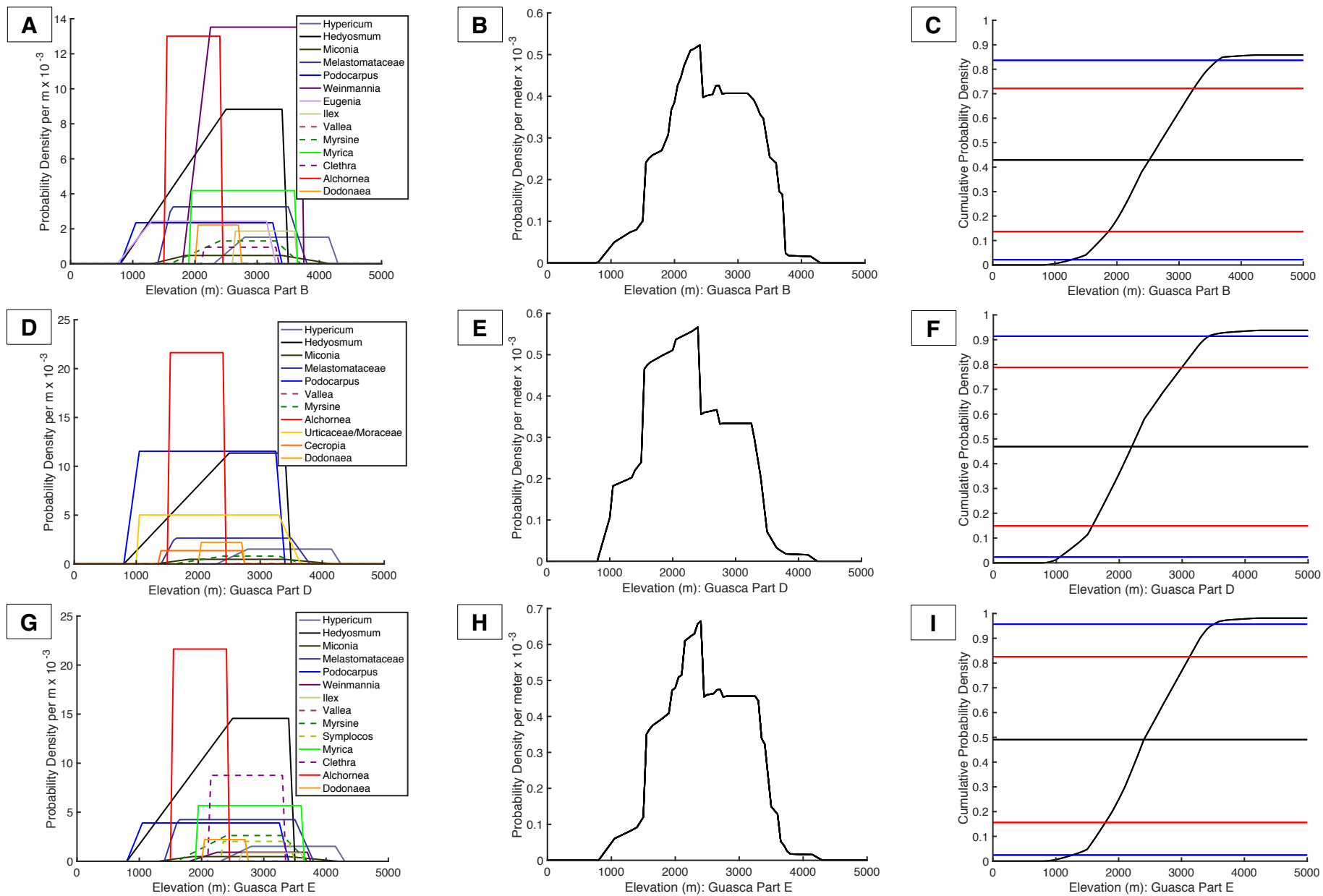


Figure 6. Probability density functions (PDFs) for pollen spectra from Guasca (Wijninga and Kuhry, 1993) presented in three ways, where (A–C) correspond to section B, (D–G) correspond to section D, and (G–I) correspond to section E. (A, D, and G) PDFs for each taxon for which Groot et al. (2013) gave an elevation distribution. (B, E, and H) PDFs of elevation given by Equation 5. (C, F, and I) Cumulative probabilities of elevations given by Equation 6, where the black horizontal line defines $0.5 P_{cum}(H)$, red lines give 1σ bounds, and blue lines give 95% confidence limits.

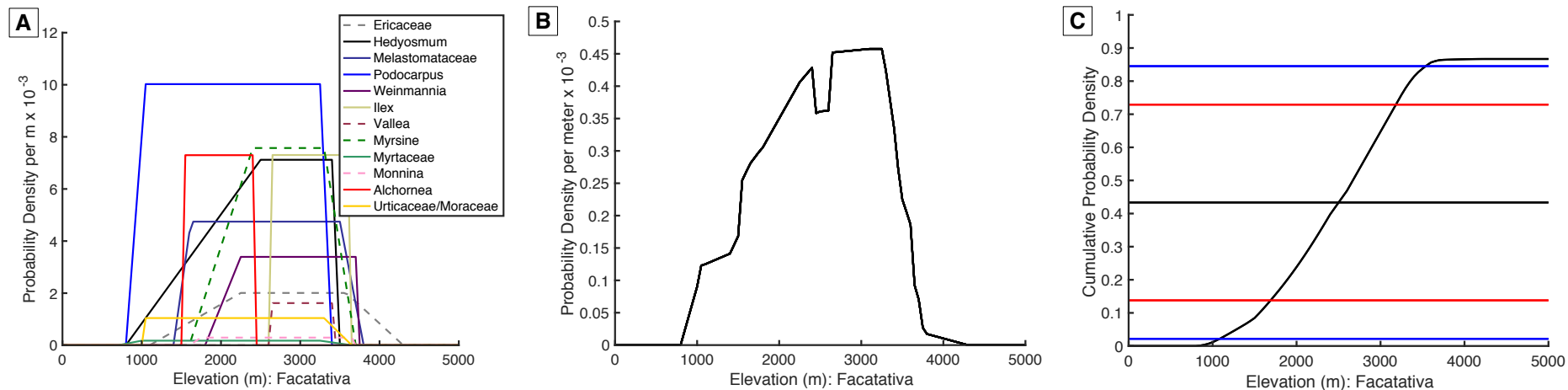


Figure 7. Probability density functions (PDFs) for pollen spectra from Facatativa 13 section (Wijninga, 1996b) presented in three ways. (A) PDFs for each taxon for which Groot et al. (2013) gave an elevation distribution. (B) PDFs of elevation given by Equation 5. (C) Cumulative probabilities of elevations given by Equation 6, where the black horizontal line defines $0.5 P_{cum}(H)$, red lines give 1σ bounds, and blue lines give 95% confidence limits.

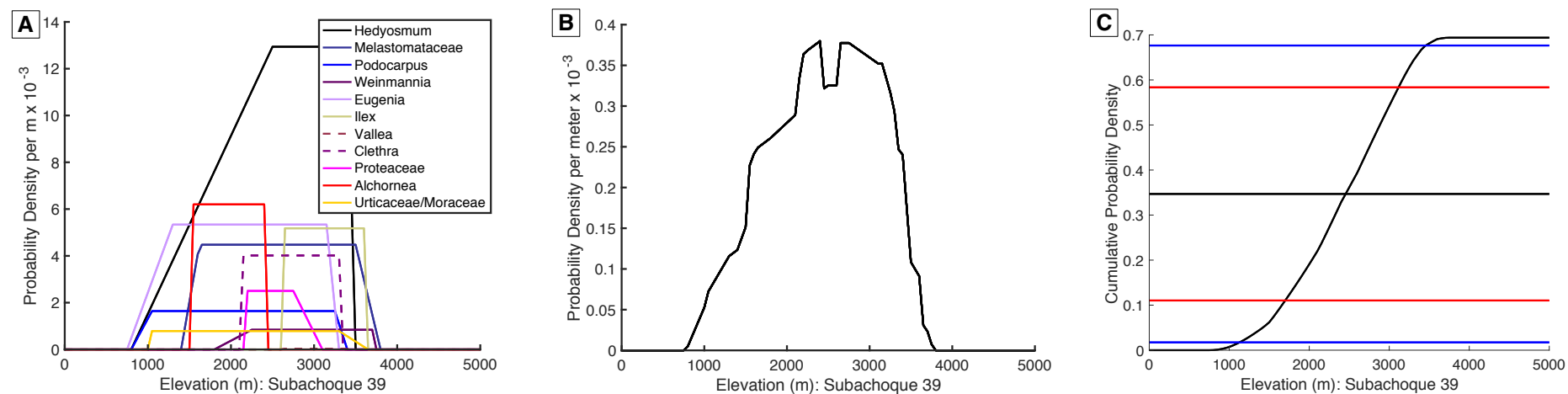


Figure 8. Probability density functions (PDFs) for pollen spectra from Subachoque 39 section (Wijninga, 1996b) presented in three ways. (A) PDFs for each taxon for which Groot et al. (2013) gave an elevation distribution. (B) PDFs of elevation given by Equation 5. (C) Cumulative probabilities of elevations given by Equation 6, where the black horizontal line defines $0.5 P_{cum}(H)$, red lines give 1σ bounds, and blue lines give 95% confidence limits.

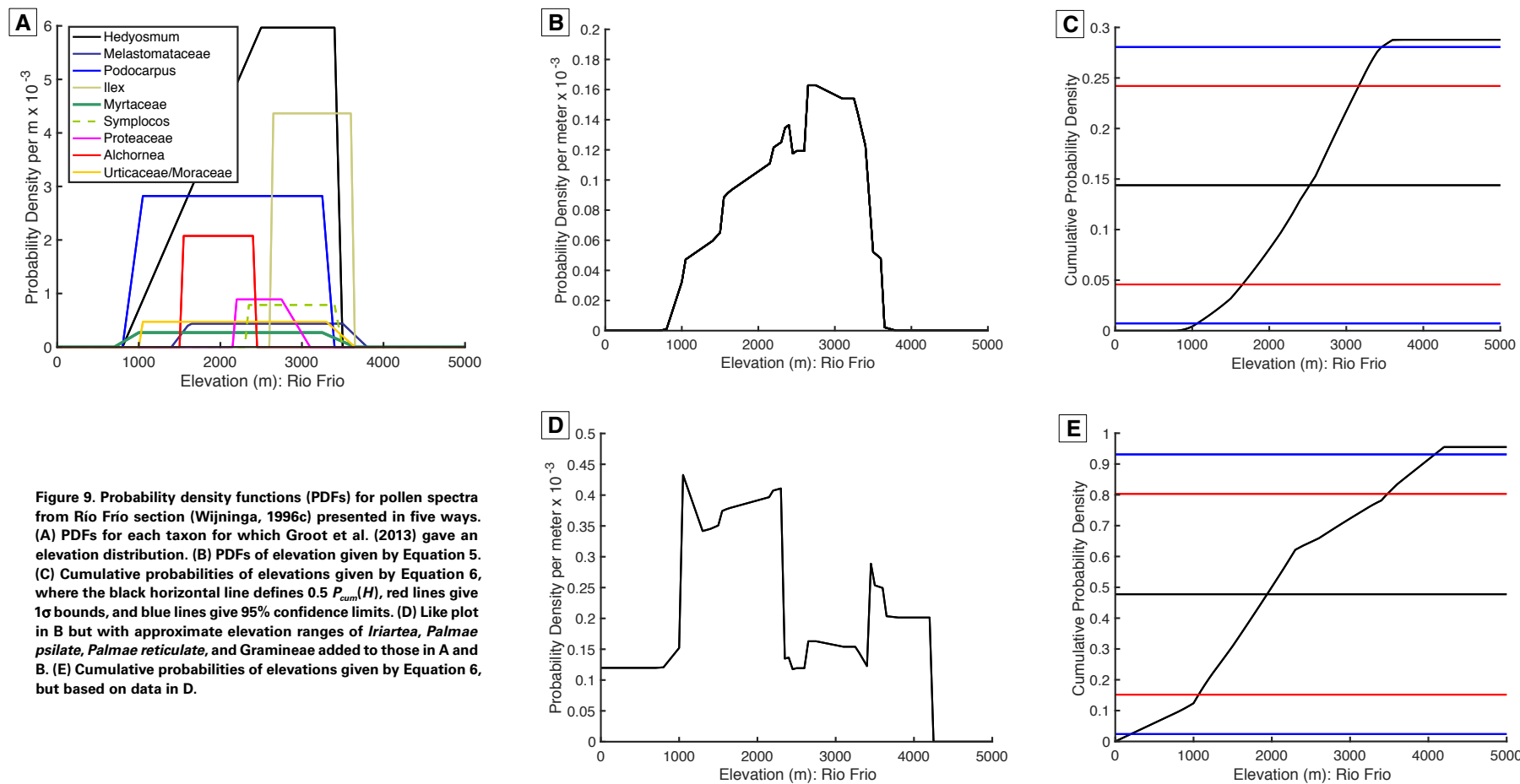


Figure 9. Probability density functions (PDFs) for pollen spectra from Rio Frio section (Wijninga, 1996c) presented in five ways. (A) PDFs for each taxon for which Groot et al. (2013) gave an elevation distribution. (B) PDFs of elevation given by Equation 5. (C) Cumulative probabilities of elevations given by Equation 6, where the black horizontal line defines $0.5 P_{cum}(H)$, red lines give 1σ bounds, and blue lines give 95% confidence limits. (D) Like plot in B but with approximate elevation ranges of *Iriartea*, *Palmae psilate*, *Palmae reticulata*, and Gramineae added to those in A and B. (E) Cumulative probabilities of elevations given by Equation 6, but based on data in D.

the 29% of the assemblage that we used is *Hedyosmum*, which is found at a wide range of elevations (Fig. 2) and cannot place a tight constraint on past altitudes (Martínez et al., 2013).

It is possible to place crude constraints on elevation ranges of *Palmae psilate*, *Palmae reticulate*, *Iriartea*, and Gramineae. Bacon et al. (2018) stated that the palm *Iriartea deltoidea* is confined to elevations below 1000–1300 m. Other palms grow higher; the palm *Wettinia lanata* grows in a narrow range of between 2100 and 2600 m in the Eastern Cordillera (Bacon et al., 2016). Wijninga (1996a, 1996c) included *Palmae* in the subandean-lower tropical forest belt between 1000 and 2300 m. If we assume that *Palmae psilate* and *Palmae reticulate* lived within that elevation range, and that Gramineae grows in the grass-páramo belt between 3400 and 4200 m (Hooghiemstra and Ran, 1994), then inclusion of these four taxa with these ranges raises the probability density function at low elevations (Fig. 9D) and lowers the estimated elevation range to a mean of 1950 m but with wide 1σ bounds of 1050 and 3450 m (Fig. 9E). A mean elevation of 1950 m points toward an elevation lower than that today, as Wijninga (1996c) and Hooghiemstra et al. (2006) had inferred, but the revised 1σ bounds include the present-day elevation of 3165 m.

Miocene Site

Tequendama Sections, at 2475 m

We examined pollen spectra from Wijninga (1996a), and specifically those from his figures 8 and 12. The age of this material has not been constrained well. Wijninga (1996a) inferred a middle Miocene age, but allowed for a Pliocene age; Hooghiemstra et al. (2006) suggested 17–11 Ma; from magnetostratigraphy, but without an absolute age to tie the sequence, Anderson et al. (2015) suggested ages between 7.6 and 6.1 Ma. We allow for an age between ca. 16 and 6 Ma.

We used Wijninga's (1996a) three divisions from his Tequendama I section (shown in his fig. 8): layers A, B, and C, with thicknesses of ~250 mm, 550 mm, and 1.2 m. Groot et al. (2013) reported elevations for only 29%, 29%, and 46% of the taxa from those layers. The greater fraction for section C is due in large part to the large percentage of *Podocarpus*: 28% in section C, but only 8% in section A and 8.5% in section B. We also examined layers B and C, with thicknesses of ~3 m and ~1.5 m, respectively, from the Tequendama II section (also shown in his fig. 12). Because Groot et al. (2013) reported elevation distributions for only a few percent of the fossil pollen, however, we present no quantitative analysis.

Among the numerous fossil pollen not represented in the compilation of modern data with elevations (Fig. 2), *Iriartea* is the dominant taxon in all of Tequendama IA, IB, and IC layers. In Tequendama IIB and IIC, *Mauritia* is dominant, with >60% of the pollen. Wijninga (1996a, p. 118) associated both *Iriartea* and *Mauritia* with lowland environments. One species of the former, *Iriartea deltoidea*, reaches no higher than 1300 m (Bacon et al., 2018). Wijninga (1996a) reported that *Mauritia*, which today is common to the Amazon Basin, does not grow higher than 700 m. Wijninga (1996a, p. 125) suggested that

the “co-occurrence of montane and lowland pollen taxa... is in general due to streams draining montane areas.”

From the fossil pollen and some macrofossils, Wijninga (1996a) inferred a paleoelevation no higher than 700 m. He also allowed for warmer climate, by 3 °C, which would allow a higher Miocene elevation, by ~500 m, but still ~1150 m lower than that today. The probability density functions for elevations of Tequendama IA, IB, and IC show broad maxima between ~2000 and 3300 m, and centered at 2150–2300 m (Fig. 10), which are little different from the present elevation of 2475 m. The 1σ bounds of 1550–2950 m, 1550–2950 m, and 1450–2950 m include the present elevation (Figs. 10C, 10F, and 10I). These results offer no support for significant uplift of the site relative to sea level, but with the omission of large numbers of taxa that current live at low elevations, a low elevation makes for a sensible inference.

Perhaps ironically, Tequendama IC is the one pollen assemblage that overlaps with present-day elevations that we can use (for 46% of the fossil pollen; Fig. 10G). They overlap in the narrow range of 2300 m to 2450 m, which virtually includes the present-day elevation.

As with the Río Frío 17 section, we may add lowland taxa for which Groot et al. (2013) did not report elevation ranges. Following Wijninga (1996c), we assume that the palm *Mauritia* is confined to elevations below 700 m. Its dominance, 66%, of the pollen from the Tequendama IIB and IIC sections virtually guarantees deposition at low elevations. For the Tequendama IA, IB, and IC sections, however, *Mauritia* contributes no more than ~4% of the pollen. The abundance of *Iriartea*, as for Río Frío, also calls for lower-elevation ranges than when that taxon is omitted. With the inclusion of *Mauritia* and *Iriartea*, plus small amounts (<1%–2%) of *Palmae psilate*, *Palmae reticulate*, and Gramineae, the probability density functions show maxima at low elevations and decrease with elevation (Figs. 11A–11C). Calculated mean elevations are accordingly low: 1550 m for Tequendama IA, 950 m for IB, and 1700 m for IC, but 1σ bounds are: between 400 and 2800 m for Tequendama IA, between 300 and 2500 m for IB, and between 600 and 2800 m for IC, all of which include the present-day elevation of 2475 m for these sites (Figs. 11D–11F).

Although the 1σ bounds on past elevations include the present-day elevation of 2475 m, and therefore do not require any elevation gain of the Tequendama region, we consider Wijninga (1996a) and Hooghiemstra et al. (2006) to have been justified in drawing such an inference. First, the preponderance of *Mauritia* in the Tequendama II section makes high elevations for it seem unlikely. Second, for the Tequendama I section, the probabilities that layers Tequendama IA, IB, and IC lay below the present-day elevation are 77%, 84%, and 76%, but, therefore, only 23%, 16%, and 24% that they lay above the present-day elevation. Finally, geologic evidence supports an increase in elevation since mid-Miocene time.

In the present day, GPS sites southwest of the Sabana de Bogotá move toward the Sabana at ~1 mm/yr (Mora-Páez et al., 2016, 2020). If steady for 15 m.y., ~15 km of convergence would have occurred. Such shortening across a region 60 km wide implies an average strain of 0.25. If such strain were negligible in the low area southwest of the Sabana de Bogotá, and a maximum at its southern edge, where the Tequendama section lies (Fig. 1), then crust there would have shortened and

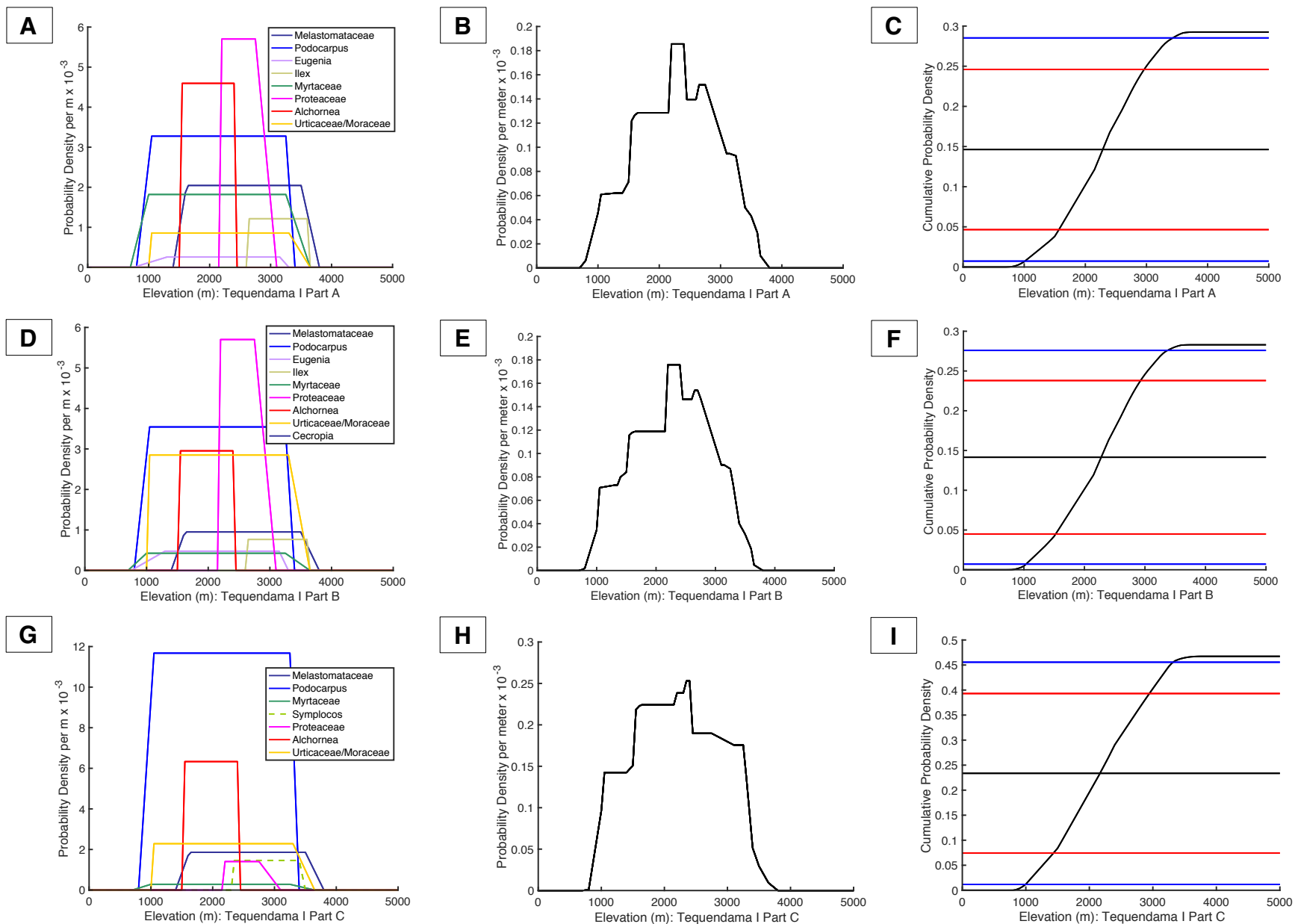


Figure 10. Probability density functions (PDFs) for pollen spectra from Tequendama I part A (A–C), part B (D–F), and part C (G–I) (Wijninga, 1996c) presented in three ways. (A, D, and G) PDFs for each taxon for which Groot et al. (2013) gave an elevation distribution. (B, E, and H) PDFs of elevation given by Equation 5. (C, F, and I) Cumulative probabilities of elevations given by Equation 6, where the black horizontal line defines 0.5 $P_{cum}(H)$, red lines give 1σ bounds, and blue lines give 95% confidence limits.

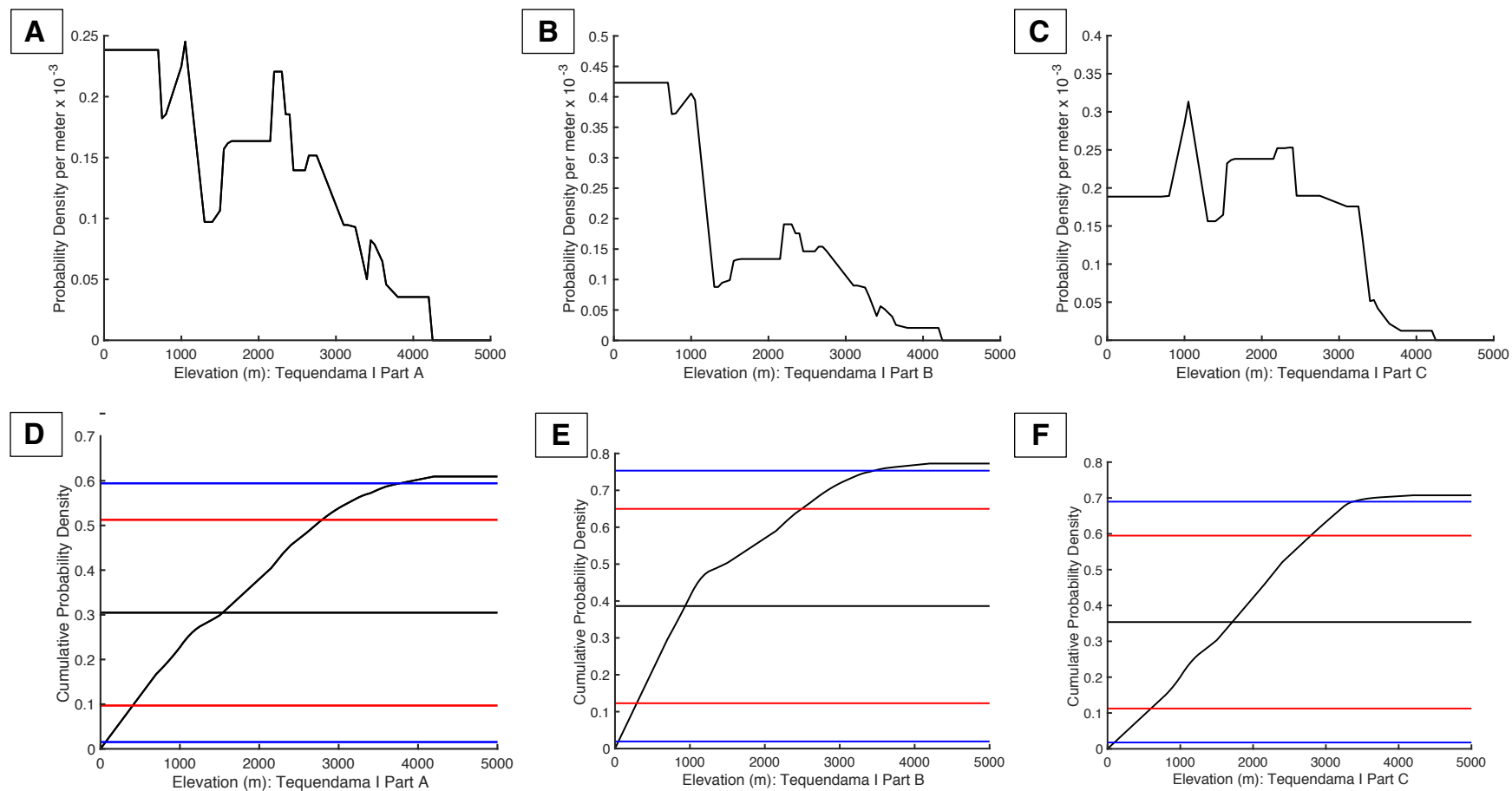


Figure 11. Probability density functions (PDFs) for pollen spectra from Tequendama I part A (A and D), part B (B and E), and part C (D and F), like those in Figure 10, but with approximate elevation ranges of *Mauritia*, *Iriartea*, *Palmae psilate*, *Palmae reticulata*, and Gramineae included. (A–C) PDFs of elevation given by Equation 5. (D–F) Cumulative probabilities of elevations given by Equation 6, where the black horizontal line defines $0.5 P_{cum}(H)$, red lines give 1σ bounds, and blue lines give 95% confidence limits.

thickened by 50%. If initially 40 km thick, like that in surrounding lowlands, that crust would have thickened by 20 km to its current value beneath the Sabana de Bogotá (E. Poveda et al., 2015). Thus, whereas a 2000 m increase in elevation since 6–5 Ma seems fast, such an increase on the edge of an already high Sabana de Bogotá since 16 Ma seems reasonable. This does not require that the entire Eastern Cordillera rose en masse since 16–6 Ma, or that the rate of surface uplift accelerated during the past few million years (e.g., Mora et al., 2008, 2013).

■ CAVEATS

The approach that we have taken contains many assumptions that can be challenged.

We used present-day elevation ranges of plants given by Groot et al. (2013), but plants surely do not sense elevation. They respond more to temperature and to moisture as manifested not just as mean annual amounts, but also as seasonal variations (e.g., Spicer, 2018). Moreover, differing amounts of soil moisture will affect evapotranspiration and resulting surface energy fluxes from soil to air. Except for the late Quaternary Pedro Palo V section, we have ignored differences between present-day and past climates. Such differences tend to be greater at high than low latitudes, and therefore even if the mean temperature of Earth at 15–3 Ma was, for example, 3 °C warmer than today, that greater warmth seems likely to have been smaller, and perhaps negligible in the Eastern Cordillera. Before 4–3 Ma, however, the eastern tropical Pacific Ocean was warmer than today by ~4 °C, as it is during major El Niño events (e.g., Dekens et al., 2007; Lawrence et al., 2006; Ravelo et al., 2006; Wara et al., 2005; Wycech et al., 2020). Assuming that modern El Niño teleconnections apply to past climates, the Sabana de Bogotá before 4–3 Ma would have been warmer by ~2 °C than today (Pérez-Angel and Molnar, 2017). In addition, during El Niño, the Sabana de Bogotá not only receives less rain than normal, but dry periods are longer, and soil moisture is reduced (e.g., G. Poveda and Mesa, 1997; G. Poveda et al., 2001, 2011). Spicer (2018) pointed out that surface temperatures as a function of elevation in dry and wet environments can differ. Thus, before 4–3 Ma, when the Eastern Cordillera may have been drier, surface temperatures might not have followed the present-day trend of 6 °C/km of elevation (e.g., Pérez-Angel et al., 2020), and elevation ranges of present-day vegetation might have differed from those today. Nevertheless, ignoring likely climatic differences between Miocene–Pliocene and present-day climates in the Eastern Cordillera is not likely to have introduced an error of more than 500 m in estimated elevation ranges. Moreover, if we have erred in this way, because of the warm dry past climate, we would have underestimated past elevations perhaps by 300–500 m.

When using fossil plant organs to make taxonomic assignments, pollen is not the best choice. First, winds can carry pollen both upslope and downslope, as can insects, birds, and other animals, and rivers can transport it downslope. Moreover, different plants disperse their pollen different distances, though Kuentz et al. (2007) found only short-distance insect-transported pollen in the Peruvian Andes between 2000 and 4500 m. Second, rarely can pollen be used to infer

species, only genus (e.g., Cain, 1940; Mander and Punyasena, 2014; Meyer, 2007); flowers, for example, are much more diagnostic than pollen (e.g., Spicer, 2018). The diversity of habitats of species of the same genus can be large; for example, those of the *Quercus* genus (oaks) live in both moist temperate environments and arid warm ones, as well as the “upper montane forest” zone of the Eastern Cordillera (e.g., Hooghiemstra and Ran, 1994). In their study of the past elevations of a part of the Peruvian Andes, Martínez et al. (2020) not only exploited, but relied on other plant organs like leaves and wood to draw inferences about paleoelevations that are somewhat more precise than those that we present.

The approach taken here also assumes negligible evolution. From an examination of modern plants in different biomes, Crisp et al. (2009, p. 754) showed that “closely related species were more ecologically similar than would be expected by chance.” Thus, taxa thriving in a given environment seem to evolve together within the changing environment. Different parts of plants, however, evolve in response to different environmental changes. Pollen consists of small hard grains that might not be sensitive to local environments and to changes in them, while other plant organs, like seeds and flowers, might evolve to adapt to new environments. Meyer (2007, p. 156) pointed out that “morphological characters, particularly those with a reproductive function such as pollen and seeds or fruits, may have evolved differently than the more climate-sensitive physiological tolerances of a taxon through time.” Because modern plants may have evolved and adapted to environments that differ from those of the plants that produced the fossil pollen (e.g., Spicer, 2018), assigning a paleoenvironment on the basis of fossil pollen that resembles pollen produced by a modern plant carries an attendant risk. Although applications to early Cenozoic fossil pollen assemblages have yielded results similar to those obtained from other approaches (e.g., Fletcher et al., 2014, Greenwood et al., 2003, 2005), younger assemblages seem more likely to yield reliable results than older ones (e.g., Meyer, 2007).

■ DISCUSSION, IN LIEU OF CONCLUSIONS

Despite these caveats, one might draw a spectrum of diverse, even mutually exclusive, inferences from the analysis that we present.

First, modern distributions of vegetation may be either too poorly known or unreliable for some other reason to be used to infer past elevations. Because the elevation ranges of living taxa associated with fossil pollen taxa do not overlap, the second approach described above and represented mathematically by Equation 7 cannot be applied. The lack of overlap in elevation ranges of that modern vegetation implies some error in what we have done.

Second, ignoring this failing and applying the other approach of summing probability distributions, represented mathematically by Equations 5 and 6, leads to the conclusion that the Pliocene fossil pollen assemblages require no resolvable difference between present-day and likely past elevations, and therefore no change in elevation at these sites since ca. 5 Ma.

This conclusion seems robust for some sites, and specifically those for which Groot et al. (2013) reported modern elevations for >80% of the fossil

pollen, the Guasca sections B, D, and E and Facatativá 13. The paleoaltitudes that we infer differ little from those inferred by the palynologists who analyzed the fossil pollen: for Guasca, 1σ bounds of 1850 and 3250 m, 1550 and 3000 m, and 1800 and 3150 m versus 2300 m (Wijninga and Kuhry, 1993) or 2200 ± 500 m (Hooghiemstra et al., 2006); and for Facatativá 13, 1σ bounds of 1700 and 3200 m versus paleoaltitudes of 2000–2500 m (Wijninga, 1996b) or 2000 ± 500 m (Hooghiemstra et al., 2006). If we differ in interpretation from Hooghiemstra et al. (2006), Wijninga (1996b), or Wijninga and Kuhry (1993), it would be because we see no evidence of elevation change since deposits accumulated at these sites at ca. 3 Ma (Guasca) and 3.7 ± 0.7 Ma (Facatativá), whereas they inferred changes of $\sim 500 \pm 500$ m.

For elevations of older Pliocene fossil assemblages, Subachoque 39 (5–4 Ma and at 2820 m today) and Río Frío 17 (5.3 ± 1.0 Ma and at 3165 m today), Groot et al. (2013) reported modern elevations for nearly 69% and only 29% of the fossil pollen, respectively. Our analysis differs more with published results for these sites than for younger assemblages.

For Subachoque 39, Wijninga and Kuhry (1990) inferred 1000 m of surface uplift, though with fossil fruits playing a role in their inference, and Hooghiemstra et al. (2006) reported a paleoelevation of 1000 ± 500 m, which implies 1800 ± 500 m of surface uplift. Our mean elevation of 2450 m and 1σ bounds 1700 and 3100 m, however, differ little from the present-day 2820 m, and we consider negligible change in elevation to be a justifiable conclusion.

For Río Frío, using fossil taxa with modern elevation distributions given by Groot et al. (2013), we obtained a mean elevation of 2450 m, with 1σ bounds of 1650 and 3150 m, which nearly includes the present-day elevation, and would include the present-day elevation if we included corrections for past temperatures and sea level. Because the compilation of Groot et al. (2013) does not include many taxa current living at low elevations, we included approximate elevation ranges for them and then recalculated probability density functions of elevations (Figs. 9D and 9E). The recalculated mean of 1950 m is below that based solely on the elevation ranges of Groot et al. (2013), but the 1σ bounds of 1050 and 3450 m span the present-day elevation. Although we are less confident in asserting no elevation change since the pollen was deposited than for the younger sites, we cannot reject the hypothesis that there has been no change in the elevation of the Río Frío 17 site.

Finally, for Tequendama, a Miocene assemblage, but one that otherwise has not been precisely dated, our inferred paleoelevations do not require a change in elevation since the material was deposited, but our inability to assign modern elevations to many fossil taxa, particularly those that live at low elevations today, makes such a deduction risky as best. As for Río Frío, we added to the elevation distributions of Groot et al. (2013) using crude estimates for other taxa, most of which today live at low elevation, and we recalculated the PDFs of elevations for three layers in the Tequendama I section. Although the 1σ bounds on elevation encompass present-day elevations, estimated means are lower than the present-day elevation of 2475 m, and lower elevations seem likely. Mountain belts commonly grow outward, once they have reached limiting elevations, but not upward (e.g., the Tibetan Plateau is the

pressure gauge of Asia; Molnar and Tapponnier, 1978). As the Tequendama site lies on the southwestern edge of the Sabana de Bogotá, and therefore of the Eastern Cordillera, an elevation gain of 1000–2000 m there since ca. 15 Ma seems geologically plausible, if not likely.

We could turn the question posed here around and ask: If the paleoelevation ranges that we infer are valid, then how do we account for the abundances of pollen assemblages that include many genera like *Palmae*, *Iriartea*, and *Mauritia* that today are confined to low elevations? As Wijninga and Kuhry (1990) pointed out, present-day altitude distributions might not be representative of those in early Pliocene or Miocene time. More precisely, perhaps ancestors of these taxa lived at higher elevations than their living descendants do today. As an example, Bacon et al. (2016) showed that *Iriarteae* and *Wettinia*, which are in subfamilies of palms, share common ancestors before they diverged in early Cenozoic time, but some species of *Wettinia* today live as high as 2600 m, and more than one species lives above 2000 m (Restrepo Correa et al., 2016). Among the caveats discussed above, evolution might make the approach that we have taken inappropriate (e.g., Meyer, 2007; Spicer, 2018).

Although the analysis that we present here does not allow firm conclusions to be drawn, it offers no support for a late Cenozoic, since ca. 5 Ma, acceleration in the growth of the Eastern Cordillera.

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