Title: Arabica-like flavour in a heat tolerant wild coffee species

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Abstract

There are numerous factors to consider when developing climate resilient coffee crops, including the ability to tolerate altered climatic conditions, meet agronomic and value chain criteria, and satisfy consumer preferences for flavour (aroma and taste). We evaluated the sensory characteristics and key environmental requirements for the enigmatic narrow-leaved coffee (*Coffea stenophylla*), a wild species from Upper West Africa[1]. We confirm historical reports of a superior flavour[1-3], and uniquely and remarkably, reveal a sensory profile analogous to high quality Arabica coffee. We demonstrate that this species grows and crops under the same range of key climatic conditions as (sensorially inferior) robusta and Liberica coffee[4-9], and has a mean annual temperature 6.2–6.8ºC higher than Arabica coffee, even under equivalent rainfall conditions. This species substantially broadens the climate envelope

for high quality coffee, and could provide an important resource for the development of climate resilient coffee crop plants.

Main

Coffee is a ubiquitous beverage that drives a multibillion dollar global coffee industry[10], supports the economy of several tropical countries, and provides livelihoods for more than 100 million coffee farmers[11]. Despite its global success, the coffee supply chain is beset with challenges, including cyclic price volatility, extreme weather events, increases in the prevalence and severity of pests and diseases, and even modern-day slavery. In addition to these constraints and issues, and compounding them, are the negative influences of accelerated climate change[12]. Successful coffee farming occurs within a relatively narrow climatic envelope and is susceptible to weather perturbations throughout its growth and life cycle, rendering it sensitive to climate change. Future-proofing the supply chain under climate change is seen as a major objective for the coffee sector, but so far there has been limited progress. There are three main resiliency pathways for coffee: (1) the relocation of coffee farming to areas with suitable climates, especially to higher elevations; (2) adapting coffee farming practices (e.g. the use of irrigation, shade or improved shade, cover mulching, etc.); and (3) the development of either adapted coffee crops cultivars (via plant breeding) or the use of new coffee crop species. Relocation of coffee farming to higher elevations offers considerable long-term potential for high elevation coffee producing countries, such as Ethiopia, but there are disadvantages, including competing land use and loss of livelihoods for lower elevation farming communities[4]. Irrigation is effective against low rainfall, and other farm adaptation interventions may offer some potential; both imply additional costs. Progress on breeding climate resilient coffee crop plants is at an early stage, with attention focused on the two main coffee crop species, Arabica (*Coffea arabica*)[13] and robusta (*C. canephora*)[14].

In 2019/20 Arabica contributed c. 56% of global production, robusta 43%, and Liberica coffee (*C. liberica*) less than 1%[10]. Within the context of long-term climate change, it has been argued that Arabica alone does not have the potential to attain the level of climate resiliency required for adaptation[15] under existing climate change projections[12]. Arabica is a cool-tropical plant, originating from the highlands (1,000–2,200 m) of Ethiopia and South Sudan[16]; in the wild and in cultivation is has an optimum mean (annual) temperature range of 18–22ºC[5,6]. For Arabica, there appears to be no evidence of climate partitioning, or useful (physical or physiological) climate resilience attributes, over its indigenous range or in cultivation[5,7,17]. Robusta coffee is a predominately low elevation species (50–1,500 m), occurring naturally across much of wet-tropical Africa[18], and is adapted to higher mean temperatures of 24–26ºC[8] or perhaps even higher to 30ºC[9]. It is also resistant to the prevalent strains of coffee leaf rust (*Hemileia vastatrix* Berk. & Broome), a serious constraint for Arabica farming in Central and South America. For these reasons, robusta is often mooted as the replacement species for Arabica under a scenario of increasing temperatures and declining and increasingly erratic rainfall. However, robusta may require as much or more rainfall (soil moisture) as Arabica, relative to other climate variables (e.g. air temperatures), and could be more temperature sensitive than previously supposed (≤16.2–24.1ºC under a revised estimate of optimal range[9]). There is a well-defined price difference between the two species, with Arabica achieving higher prices[10] due to its superior taste. Robusta and Liberica are excluded from the higher value specialty coffee sector, which is currently the sole preserve of Arabica. *Coffea eugenioides,* a very minor crop species, has an excellent flavour and has started to gain attention as a niche-market, high-end coffee, but its seeds (coffee beans) are small (less than half the size of Arabica seeds) and yields are low[19].

Amongst the other 120 coffee species[15] there are numerous species able to grow in warmer and drier environments relative to Arabica, robusta and Liberica, and some markedly so[18]. So far, however, none of these species have demonstrated the required flavour and agronomic attributes for wide-scale commercial success.

In this respect, *C. stenophylla* (hereafter given as stenophylla), a species endemic to Guinea, Sierra Leone, and Ivory Coast (Fig. 1), is of considerable interest[1]. Several historical references (1834–1929) indicate that this species has an excellent taste[1], as good as 'best Mocha'[2] , and possibly superior to all other coffees , including Arabica[3]. However, given their age and context, these claims have been heavily caveated[1], and sensory praise for this species has not been universal[20]. In its native habitat, stenophylla is a species of low elevation (c. 400 m), hot-tropical environments. It is also reported to be drought tolerant and have partial resistance to coffee leaf rust, as reviewed by Davis et al.[1]. The seeds of stenophylla are about the same size or slightly smaller than Arabica.

There has been no published sensory information for stenophylla since the 1920s, probably due to its scarcity in cultivation and rarity in the wild: it has not been in general cultivation since the 1920s[1], and is threatened with extinction in the wild[15]. Poor yield has been given as the main reason stenophylla failed to become established as a major global coffee crop species[21], although competition from robusta coffee, whose early progress towards becoming a global commodity coincides with the decline of stenophylla farming, is likely to be a major contributing factor[15]. Based on the number of flowers/fruits per node and shoot, stenophylla yields are likely to be less than Arabica and robusta, although commercially viable yields are evident[1,20].

Following the rediscovery of wild populations of stenophylla in Sierra Leone in 2019[1], in May 2020 we obtained a sample of wild-collected stenophylla coffee beans (seeds) from Sierra Leone. A second sample was obtained in October 2020, via the *Coffea* Biological

Resources Center (BRC *Coffea*) on Reunion Island (originally collected from the forests of eastern Ivory Coast). These samples and other accessions were evaluated by five professional, independent sensory panels, using two protocols (see Methods and Supplementary Information), in mid to late 2020 and early 2021.

In a sensory evaluation employing the CIRAD protocol (four panels and 15 judges) a high overall quality score was awarded for stenophylla. Two Arabica samples, one of high quality (from Ethiopia) and one of medium quality (from Brazil), and one high quality robusta sample (from Indonesia), were used as the controls (Fig. 3). The evaluation was blind, i.e. the name and origin of the samples was unknown to the judges. The evaluation revealed that stenophylla has a complex flavour profile (Supplementary Tables 1–3), natural sweetness (Supplementary Table 3), medium-high acidity, fruitiness, and good body, as in higher quality Arabica (Fig. 3; Supplementary Figs. 1 & 2; Supplementary Table 1). When asked if the four samples represented Arabica, 81% of the (15) judges said 'yes' for stenophylla, compared to 98% for Arabica from Ethiopia, 44% for Arabica from Brazil, and 7% for robusta from Indonesia (Fig. 4; Supplementary Table 4). Despite the high Arabica-like percentage score for stenophylla, 42% of the judges identified the sample as something new; 58% did not (Fig. 4; Supplementary Table 4). The difference in the scores for the Ethiopia vs. Brazil samples, do not infer substantive differences in intrinsic quality. Arabica cultivated in Brazil can attain high quality; Ethiopian-grown Arabica can be of lower quality.

Three judges from a fifth panel, using the sensory protocol and scoring system of the Specialty Coffee Association (SCA), identified the sample of stenophylla from Sierra Leone (sample (5)) as Arabica-like. The panel leader awarded a (consensus) specialty score (SCA) of 80.25. Specialty coffee refers to high quality Arabica, and requires a score of 80 points or higher. This was remarkable, given the size of the sample (10g), crudeness of processing and lack of either domestication or pre-farm selection (i.e. the sample was from wild plants, selected at random). Positive attributes conferred by the panel using the SCA protocol included: a fragrance [i.e. the smell of the dry, ground coffee] reminiscent of washed African Arabica, close to a Rwandan profile, and other characteristics associated with quality Arabica, including sweetness and fruit driven acidity (E. Chodarcevic pers. comm.).

Across the two protocols, the judges identified a complex range of tasting notes[22] for stenophylla (Supplementary Table 3), including those popular or desirable in high quality Arabica, including: stone fruit (peach), soft fruits (blackcurrant, mandarin), honey, light black tea, jasmine, spice, floral, chocolate, caramel, nuts, English candy, and elderflower syrup. Negative notes were given by some judges, e.g. fermented, medicinal, soup (Supplementary Table 3), although the main negative attributes were not pronounced (Fig. 3), or significant in a statistical test (Supplementary Table 1). Further details of the sensory analyses are given in Supplementary Information.

These results provide the first credible sensory evaluation for stenophylla coffee, from which we are able to: (1) corroborate historical reports of a superior taste (see above); (2) demonstrate a complex and desirable flavour (aroma and taste); and (3) reveal a flavour profile analogous with high quality Arabica coffee.

The sensory similarity with Arabica is surprising, and remarkable, because stenophylla does not have a close phylogenetic relationship with Arabica[23,24]; populations of indigenous Arabica and stenophylla occur on opposite sides of the African continent, separated by a distance of c. 4,800 km (Fig. 1); the environmental requirements of these two species are very different (Fig. 2); and their seed (coffee bean) chemistry is not the same[25,26], although some of the key chemical constituents are shared.

Trigonelline and sucrose, two coffee aroma precursors, are suggested as among the main chemical constituents relating to consumer preference for Arabica[27]. Levels of trigonelline in stenophylla are similar to Arabica, and both species have considerably greater amounts than robusta; the sucrose content of stenophylla is reported to be greater than robusta, but less than Arabica[27]. Kahweol, a diterpene of high pharmacological interest and with anti-inflammatory properties, is present in considerable amount in Arabica and stenophylla, but is almost entirely absent in robusta[26]. The seed chemistry of stenophylla populations from Sierra Leone and Ivory Coast are broadly the same[28] but with some clear differences. For example, Sierra Leone stenophylla has a caffeine content of 0.9–1.9 % dry matter basis (dmb), which falls within the range of Arabica (0.6-1.9% dmb)[25], whereas those from Ivory Coast are higher (2.05–2.64%) [25,27].

The reported mean annual temperature for stenophylla is 25–26°C, and mean total annual rainfall 1,500–2,650 mm per year[1,29]. Our modelled climate data for stenophylla was congruent with these observed data, with a mean annual temperature of 24.9ºC, and mean total annual rainfall of 2,288 mm per year (Fig. 2). The mean annual temperature and mean total annual rainfall of stenophylla, is slightly and considerably higher (respectively), than wild and cultivated robusta[8,9], and modelled robusta and Liberica, although the ranges for these values are similar (Fig. 2; Supplementary Table 6). The mean temperature reported and modelled, for Arabica is 19.0ºC (18–20ºC)[5,6] and 18.7ºC (Fig. 2), respectively; and for stenophylla 25.8ºC (25.5ºC/26ºC)[1,29], and 24.9ºC, respectively (Fig. 2). These data infer that stenophylla has a much higher temperature tolerance than Arabica, with a mean annual temperature difference of 6.8ºC for recorded data, and 6.2ºC for modelled data. Total mean annual rainfall for stenophylla is higher than Arabica, but even at higher temperatures the rainfall requirements can be equivalent, as reported[1,29] and as demonstrated here (Fig. 2; Supplementary Table 6). Arabica cannot be cultivated successfully in the locations where stenophylla either occurs in the wild or was once cultivated in Upper West Africa; only robusta and Liberica can be used as crop plants in these areas[1], confirming both published [5,8] and modelled (Fig. 2; Supplementary Table 6) climate data.

In the analysis (Fig. 2) the number of data points for stenophylla is far fewer than Arabica, robusta and Liberica, owing to the rarity of this species and paucity of field data (see Methods). This will influence the density of the datapoints for stenophylla, but changes to the climate envelope for this species are likely to be negligible if further data points were to be added (as demonstrated in Fig. 2). A T-test for temperature and rainfall for stenophylla vs. the other three species (via their data points) gives p-values of 1.117e-08 for temperature and 0.0458 for precipitation. The temperature profile is highly significant, whereas precipitation is not, compared to the other coffee species. The precipitation P-value is what we would expect, i.e. not substantially different across the four species. Like Arabica, stenophylla experiences a distinctly seasonal climate over its native range, with a marked three to four month dry season (November to March/April)[1].

These findings open the way for substantially broadening the temperature range for farming high quality (and thus higher value) coffee, and the possibility for market differentiation in the specialty coffee sector, via the reestablishment of stenophylla coffee. In the longer term, this species could have critical utility in coffee plant breeding, especially for climate resiliency. To ensure a commercially acceptable taste, the production of interspecies hybrids has so far relied on back-crossing with Arabica. In the case of breeding for heat and drought tolerance, initial and repeated backcrossing to Arabica (to ensure sensory quality) would likely weaken climate resiliency attributes[30]. Interspecies hybridization using stenophylla, and backcrossing using this species would alleviate this limitation, as it has the required sensory traits and ability to withstand elevated temperatures, and may have drought tolerance attributes. Drought tolerance has been attributed[29,31,32] or implied[33-35] for stenophylla, but so far this has not been properly tested. Stenophylla is an amenable breeding partner. Interspecies crosses with Liberica have been confirmed[1], as have those with robusta, *C. psedozanguebariae* and *C. congensis*[36]. The diploid hybrid *C. stenophylla* × *C. liberica* shows marked vegetative vigour and an accelerated growth rate (A.P.D, J.H., D.S. pers. observ.). Conversion of diploid (2n = 2x = 22) hybrids to the tetraploid (2n = 4x = 44) state would be required to restore or improve fertility[15,37]. Over its natural range, and in cultivation, stenophylla demonstrates substantial phenotypic diversity[1,20], and the potential for considerable inter-population genetic diversity[1].

Efforts are now required to safeguard the future of the species in the wild and *ex situ*, and to evaluate its full potential as a climate resilient high-value crop species and breeding resource.

Methods

The sensory analysis was undertaken using two different protocols, for five samples, comprising four species: (1) a high quality (specialty) Arabica coffee, farmed in Sidamo, Ethiopia; (2) a medium quality Arabica, farmed in Sul de Minas, Brazil; (3) a high quality robusta, farmed on Flores Island, Indonesia; (4) stenophylla, maintained on Reunion Island (Mascarene Islands), but originally from eastern Ivory Coast; and (5) stenophylla, collected from the wild in eastern Sierra Leone[1]. Samples (1) to (4) were evaluated using a protocol developed by CIRAD (Centre de Coopération Internationale en Recherche Agronomique pour le Développement), derived from the European standard ISO 6668 and 13299 (https://www.iso.org/standard/44609), and hereafter referred to as the CIRAD protocol. Sample (5) was evaluated using the Specialty Coffee Association (SCA) protocol and scoring system (https://sca.coffee/research/protocols-best-practices), and sensory terminology of the SCA Coffee Taster's Flavor Wheel[22], with modifications due to small sample size. Further details of the two protocols are given in Supplementary Information. Four independent sensory panels were used for the CIRAD protocol evaluation, including 15 panel members (judges). A total of 15 variables were scored (10 points each; 150 points in total). Scores from each of the 15 judges were combined (Supplementary Tables 1 & 2), and an analysis of variance (ANOVA) was applied to the scores, followed by a Tukey test (HSD for Honest Standard Deviation) for comparison of means (XLSTAT 2021, Addinsoft). Additional commentary, e.g. tasting notes, sweetness, and negative characteristics were also requested (Supplementary Table 3). In addition to the CIRAD protocol, the panel were asked four questions: (1) Is this Arabica coffee (yes/no)? (2) Is this robusta coffee (yes/no)? (3) Is this coffee new (yes/no)? (4) Could this coffee be commercialized (yes/no)? Yes/no responses (0/1) for the four questions were totalled to provide a percentage score (Fig. 4; Supplementary Table 4).

The SCA protocol (https://sca.coffee/research/protocols-best-practices) was undertaken using a single panel, with three judges, and by applying a consensus cupping score (an overall score awarded by the panel leader), based as closely as possible on the SCA scoring system. Four other species (Arabica, Liberica, *C. brevipes* and *C. montekupensis*) were assessed alongside the stenophylla (sample (5), although they were not included in the analysis or scoring. Full details of the sensory protocols are given in Supplementary Information.

For the distribution map and climate envelope analysis we used a dataset of 1,324 ground point records, derived from a coffee occurrence database (herbarium specimens and *in situ* observation)[4,15], comprising 711 records for Arabica, 297 for Liberica, 304 for robusta, and 20 for stenophylla. *In situ* observation data (615 records) were only for wild Arabica in Ethiopia[4], otherwise all specimens are vouchered by herbarium specimens (verifications by A.P.D.). All ground point data were georeferenced (if not already available), manually checked for geolocation accuracy (1 km^2 or less), and corrected if necessary. Fig. 1 was produced in ArcGIS Pro 2.6.1 (ESRI, Redlands, CA[38]), using background and country data from Natural Earth (https://www.naturalearthdata.com/). For Fig. 2 we resampled all specimen data to remove duplicates within 1km of each other, reducing the total number of records used from 1,324 to 586 (193, 182, 199, 12, respectively for each species). R[39] was used to sample specimen data against all Bioclim variables[40] from the CHELSA dataset[41] (Supplementary Table 6). We originally selected four Bioclims for our analysis (Bio1 = Annual Mean Temperature; Bio4 = Temperature Seasonality; Bio12 = Annual Precipitation; Bio15 = Precipitation Seasonality) to represent the main abiotic determinants of coffee species distribution[4], simplifying to Bio1 and Bio12 for demonstration purposes (Fig. 2). Scatter and density plots were plotted using R[39] and using the ggplot2[42] and ggpubr packages[43]. For validation purposes, our modelled temperatures and rainfall for Arabica and robusta (Fig. 2) were compared against published data for cultivated coffee, and were found to fall within reported ranges[5,6,8,9]. We agree that temperature ranges given for the native range of coffees is often reported as too high[9], especially when comparing wild and farmed coffee, but did not find any marked discrepancies in our analysis and observations. Temperature range data for cultivated Liberica is limited and unreliable, at present. To test for significances, we used a standard T-test in R[39] to ascertain whether the climate results for stenophylla could be a sample of the other coffee species.

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Author contributions

A.P.D., D.M., J.M., J.H. and D.S. designed the experiments; A.P.D., D.M., J.M. and D.S. provided the data; A.P.D., D.M. and J.M. analysed the data; A.P.D., J.H. and J.M. wrote the first draft, and D.M. and D.S. provided additional text and editing.

Competing interest statement

The authors declare no competing interests.

Data and materials availability

All data is available in the manuscript, in Supplementary Information, or from published sources.

Supplementary Information

Supplementary Figs. 1, 2
Supplementary Text
Supplementary Tables 1–6 [tabulated spreadsheet]

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Figure legends

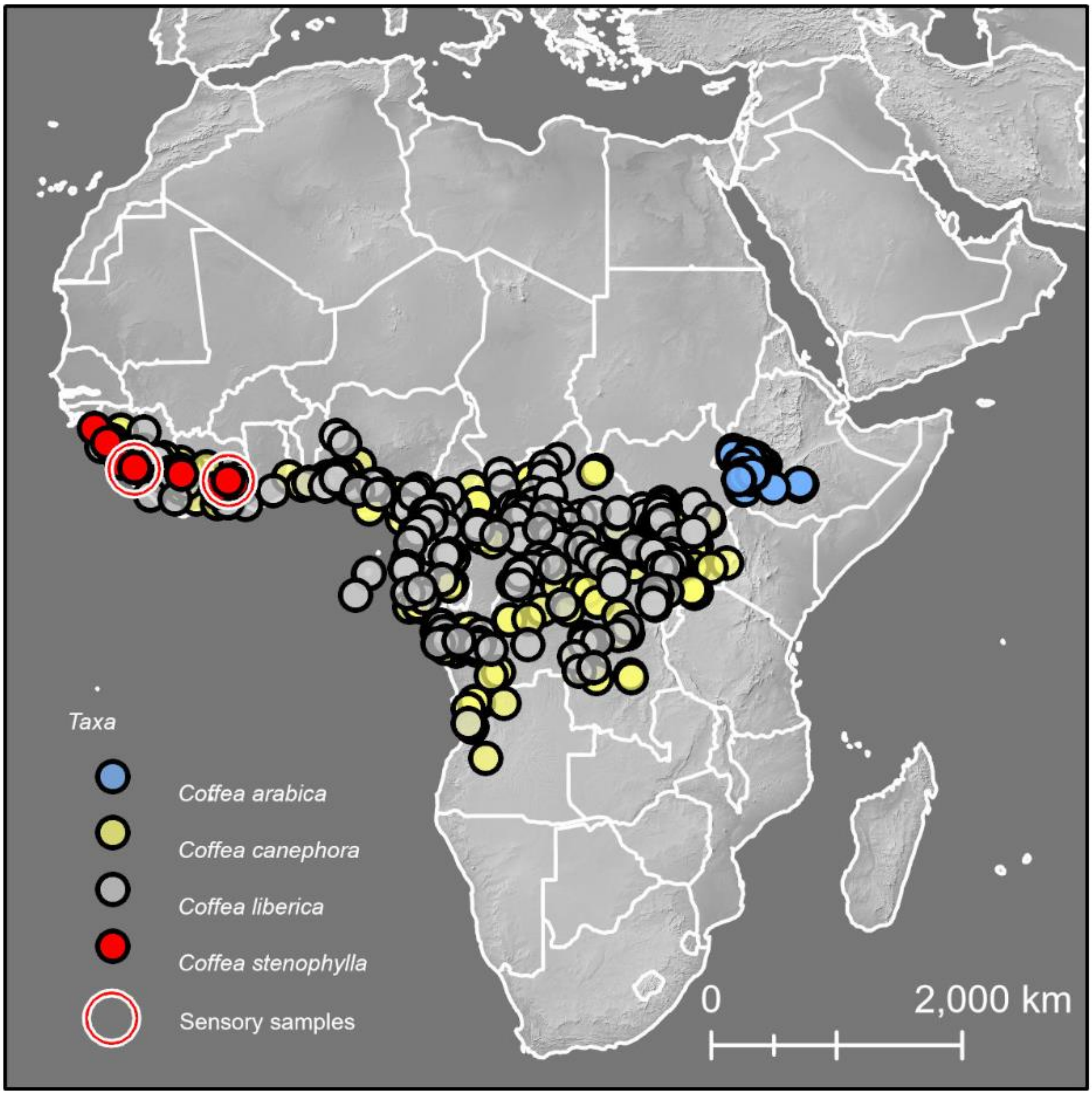

Fig. 1. Distribution map of wild locations for Arabica (*C. arabica*), **robusta** (*C. canephora*), **Liberica** (*C. liberica*) and **stenophylla** (*C. stenophylla*) **coffee**. Location of sensory (cupping) samples for stenophylla coffee, circled. See Methods for further details.

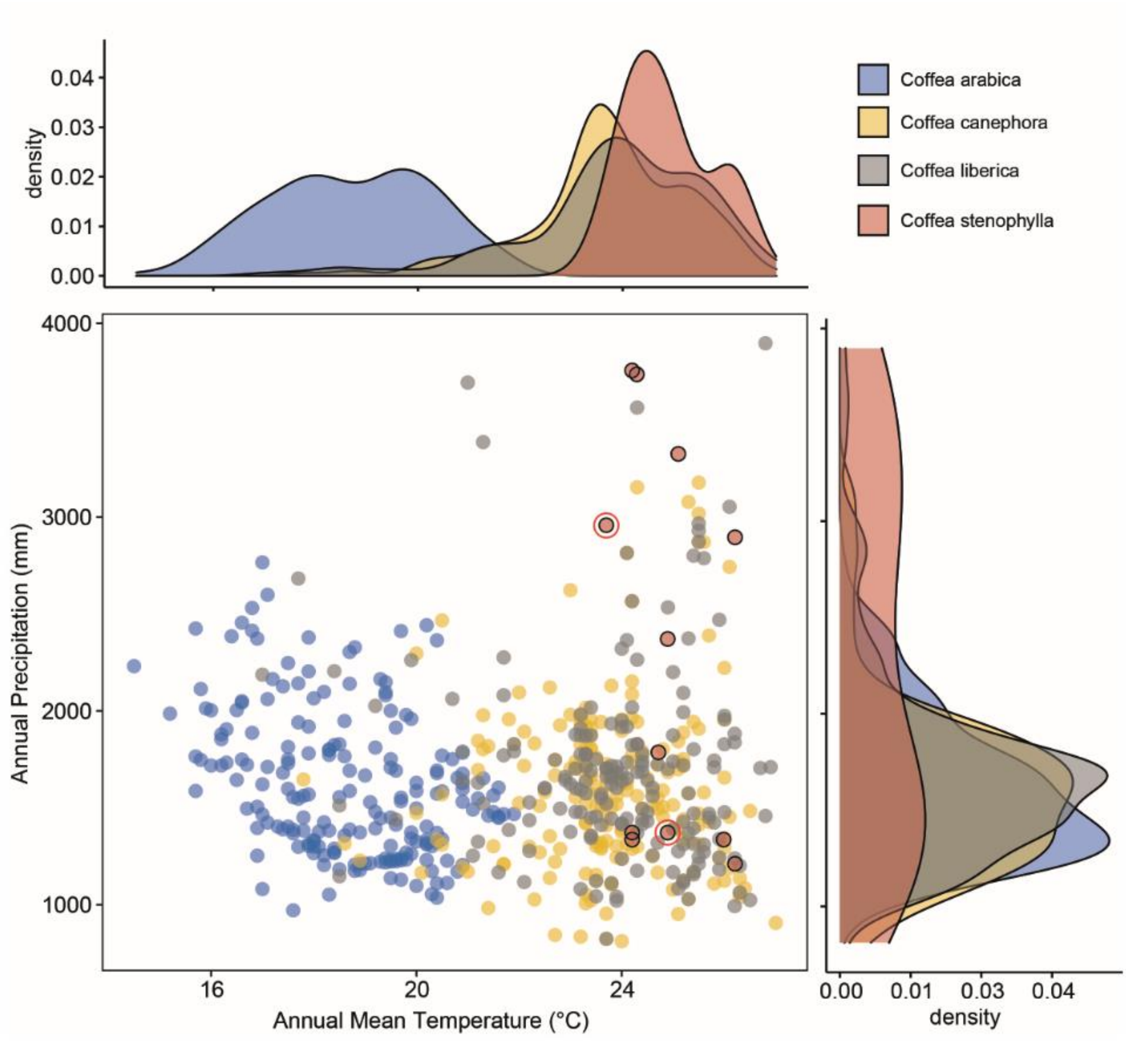

Fig. 2. Scatter and density plots of modelled annual mean temperature vs. total mean annual precipitation. Mean values in parentheses. Arabica (*C. arabica*; 18.7 °C/1,614 mm), robusta (*C. canephora*; 23.7°C/1,601 mm), Liberica (*C. liberica*; 23.9 °C/1,699 mm) and stenophylla (*C. stenophylla*; 24.9°C/2,288 mm). Stenophylla data points black-outlined for single (small) and double data points (large). Location of sensory (cupping) samples for stenophylla coffee, circled (upper circle for Sierra Leone, lower for Ivory Coast). See Methods for further details.

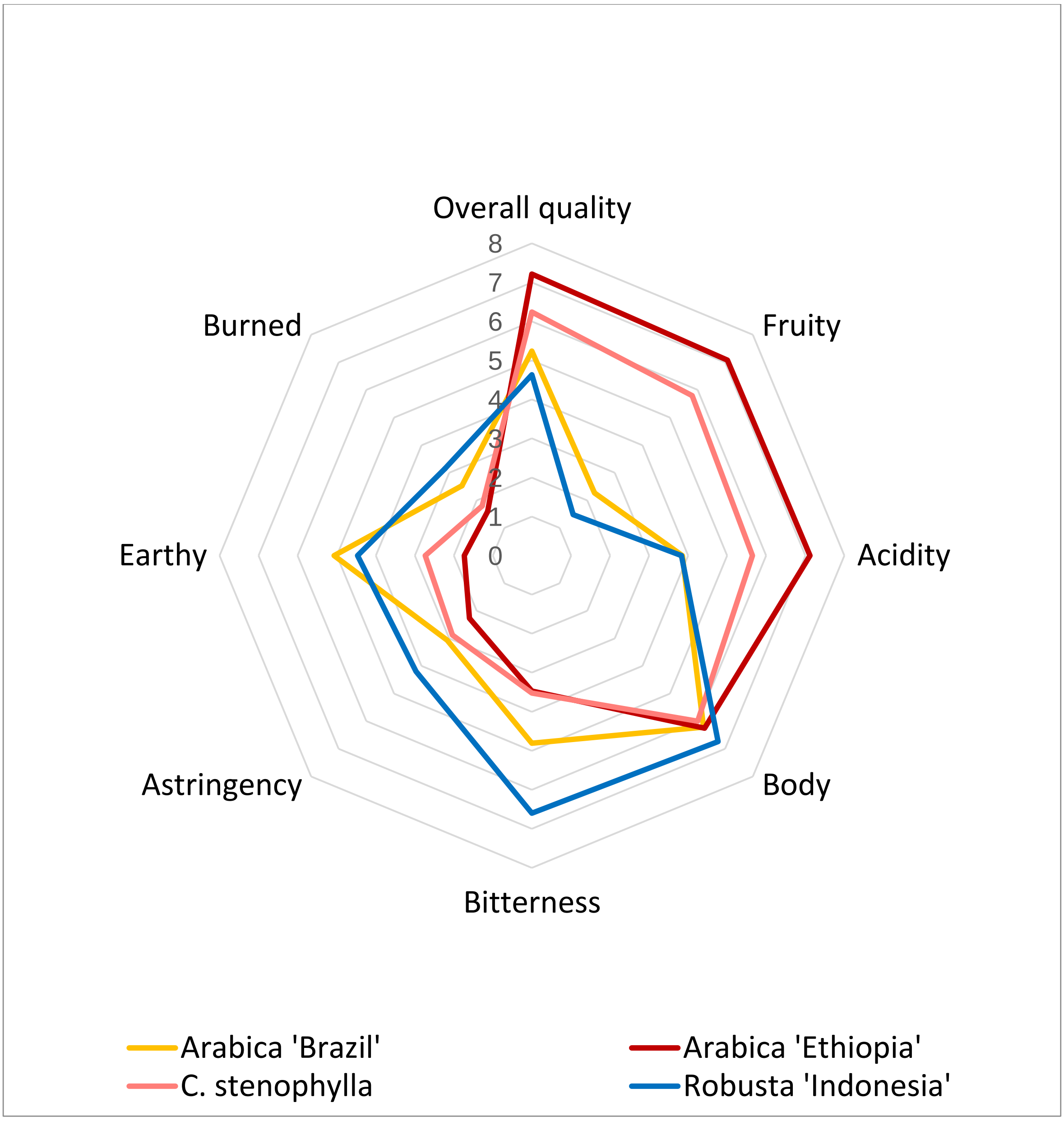

Fig. 3. Radar graph for sensory (flavour) profile using a light roast, for stenophylla, Arabica and robusta coffee. Graph based on results of CIRAD sensory protocol evaluation (see Methods, Supplementary Informaton, and Supplementary Table 1). The first four criteria (clockwise from the top (overall quality, fruity, acidity and body) are positive for coffee quality, the other four (bitterness, astringency, earthy and burned) are usually negative.

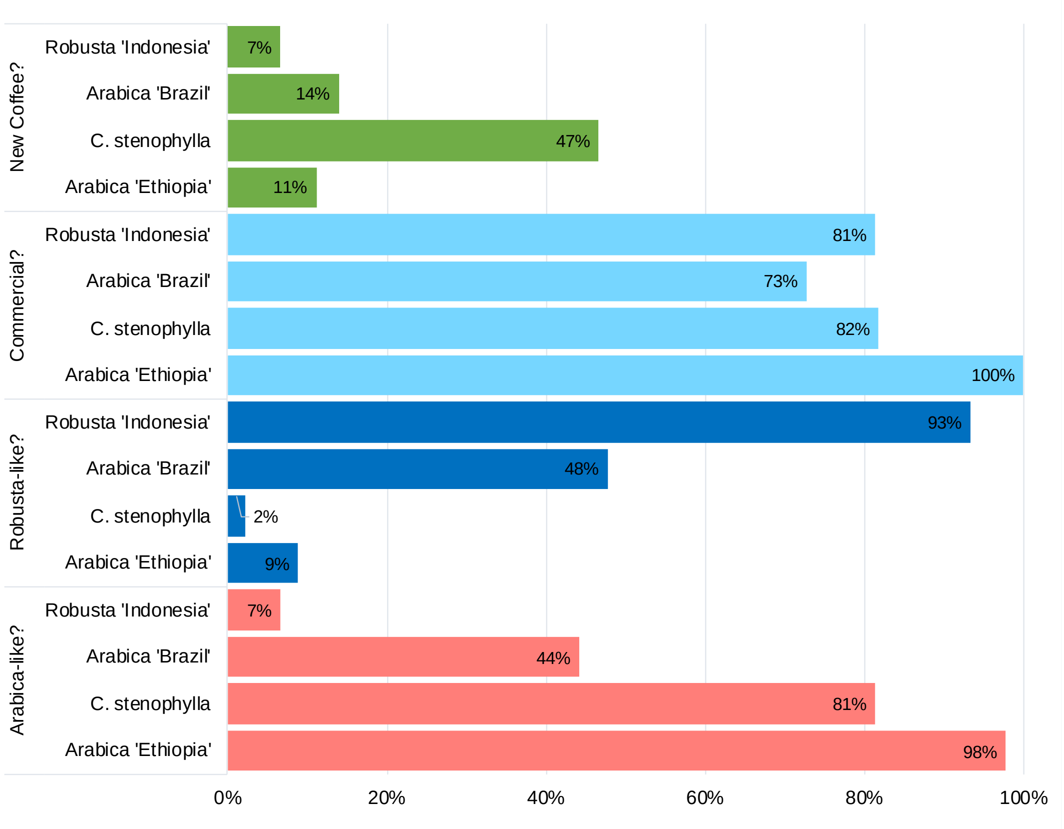

Fig. 4. Yes/no responses to four additional questions. Questions asked, in addition to the CIRAD sensory protocol. From bottom to top: (1) Is this Arabica coffee? (2) Is this robusta coffee? (3) Is this coffee new? (4) Could this coffee be commercialized? Grey shading represents ‘no’ answers. See Methods, Supplementary Information, and Supplementary Table 4.