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RESEARCH PAPER

Impact of climate and management on coffee berry disease and yield in coffee's native range

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A R T I C L E I N F O

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A B S T R A C T

Climate change might increase plant diseases, reduce crop yields and threaten the livelihoods of millions of smallholder farmers globally. It is thus important to understand the relationships between climate, disease levels and yield to improve management strategies for sustainable agroforestry in a changing climate. One of the major threats to coffee production in Africa is the coffee berry disease (*Colletotrichum kahawae*). To investigate the effects of climatic and management variables on coffee berry disease (CBD) incidence and yield, we recorded minimum and maximum temperature and relative humidity, as well as CBD and yield, along a broad environmental and management gradient in southwestern Ethiopia during two consecutive years. CBD was affected by several climatic and management variables. For example, CBD incidence increased with minimum temperature during the fruit expansion stage, and decreased with minimum temperature during the endosperm filling stage. CBD incidence was negatively affected by the proportion of resistant cultivars, whereas the coffee structure index (pruning) had no effect on disease incidence. Coffee yield decreased with increasing minimum temperature during the flowering period in 2018 and maximum temperature during the fruit developmental period in 2019. Coffee yield was negatively affected by canopy cover and positively affected by the coffee structure index in both years. Our findings highlight that CBD and yield were affected by different climatic and management variables. Yet, managing for low disease levels and high yield is practically difficult due to season-dependent effects of several climatic variables. One way to break the correlation of climatic variables between seasons might be to take advantage of differences among shade trees in the presence or timing of leaf drop. To reduce CBD incidence, using resistant cultivars is an effective strategy, but this might threaten the wild coffee genetic reservoir.

Introduction

Climate change is threatening global crop production by increasing temperature, shifting rainfall, and increasing climate variability (Abbass et al., 2022; Anderson et al., 2020). These threats may come from effects of a changing climate on crop physiology or increased disease outbreaks (Abbass et al., 2022). Understanding the relationship between climate, disease incidence levels and crop yield would enable us to develop effective ecologically-informed strategies to reduce crop losses by pests and diseases under climate change (Altieri & Rosset, 1996). One system where it might be relatively easy to modify the linkage between macroclimate and microclimate (i.e., the climate experienced by the crop) is agroforestry, where shade-tolerant crops such as coffee and cacao are cultivated under shade trees (Avelino et al., 2020; Schroth et al., 2000). These shade trees have a strong impact on the microclimate, and farmers manipulate canopy cover to influence plant physiology, pest and disease dynamics and crop yield (Ayalew et al., 2022; Gagliardi et al., 2021). It is thus important to understand the relationship between microclimate, canopy cover, disease levels and yield to improve management strategies for sustainable agroforestry in a changing climate.

Climatic and environmental factors, as well as crop management, may affect the incidence and severity of diseases (Avelino et al., 2020; Zewdie et al., 2020). Within agroforestry systems, shade trees modify the microclimate by buffering the temperature and amount of light that

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reaches the coffee canopy, which may affect disease levels on understory crops (Avelino et al., 2020; Gagliardi et al., 2021). The effects of shade on microclimatic conditions in agroforestry systems may either promote or inhibit pathogen growth and disease spread, depending on the characteristics of the pathogen (Akoutou Mvondo et al., 2022; Avelino et al., 2020; Motisi et al., 2019). As an example of a study where a plant disease increased with shade, López-Bravo et al. (2012) reported that the incidence of coffee leaf rust, which is caused by *Hemileia vastatrix*, was higher in shade grown coffee due to a lower maximum temperature and a higher leaf wetness, which stimulated uredospore germination and infection. Moreover, Motisi et al. (2022) reported that shade may promote CBD by reducing the latent period of the pathogen. As an example of a study where a plant disease decreased with shade, Bedimo et al. (2008) found that shade trees lower the incidence of CBD as shade cover reduces rain intensity and thereby limits splash dispersal of the pathogen. The climatic conditions favoring or disfavoring disease development might also shift during the growing season due to changes in leaf or fruit ontogeny (Kremer et al., 2016). Management intensity and the use of disease-resistant cultivars are also important in explaining disease levels (Mouen Bedimo et al., 2007). For example, pruning of the canopies of both crops and shade trees increases aeration and sunlight infiltration within the crop's canopy, resulting in dryer leaf and fruit surfaces, which often negatively affects pathogen dispersal and spore germination (Schroth et al., 2000).

Crop yield can be influenced by a range of factors, including climate conditions, crop management practices, and pests and diseases (Haggar et al., 2011; Liliane & Charles, 2020). As an example of a direct effect of climate on crop physiology, Craparo et al. (2015) reported a 137 kg ha^{-1} reduction in Arabica coffee yield per 1 °C rise in minimum temperature in Tanzania. Management practices, such as reducing or increasing canopy cover, pruning of the understory crops, and fertilization, may further affect crop yield (Haggar et al., 2011). Importantly, different stages of the plant's life cycle require different climatic conditions (Piao et al., 2019). Understanding the effect of climatic variables on key plant life stages, such as flowering and fruit development, will help improve current farming practices and can improve resilience to climate change (Cannell, 1985; Craparo et al., 2015).

Southwestern Ethiopia is considered the center of origin of Arabica coffee (*Coffea arabica*) where coffee is grown along a broad gradient of management intensity, ranging from forest coffee systems, where naturally regenerated coffee is grown with little or no management, to commercial plantations, where coffee cultivars that are selected for disease resistance and improved yield are grown under a more open canopy with more intensive management practices (Zewdie et al., 2021). Coffee berry disease (CBD), caused by the fungal pathogen *Colletotrichum kahawae* (Glomerellales: Glomerellaceae), is one of the most destructive diseases of Arabica coffee in Africa, including Ethiopia (Garedew et al., 2017; Hindorf & Omondi, 2011). In Ethiopia, CBD has been responsible for average yield losses between 24 % and 30 %, and losses may reach up to 100 % during years favourable to the disease in some areas of Ethiopia (Alemu et al., 2016; Van der Graaff & Pieters, 1983). The pathogen mainly attacks green berries during the fruit expansion stage (c. 8 to 16 weeks after flowering), causing dark sunken lesions (Hindorf & Omondi, 2011; Motisi et al., 2022). Weather conditions such as temperature, relative humidity and rainfall, as well as management and host resistance, play an important role in CBD development (Motisi et al., 2022; Mouen Bedimo et al., 2008).

We investigated the effects of climate and coffee management intensification on CBD and yield in the center of origin of Arabica coffee. For this, we recorded daily minimum and maximum temperature, relative humidity, incidence of CBD and coffee yield in 58 sites in southwestern Ethiopia. These sites were located along a broad environmental and management gradient, and were surveyed for two consecutive years (2018 and 2019). More specifically, we addressed the following questions:

i What is the effect of minimum and maximum temperature, relative humidity, canopy cover, coffee structure index (reflective of pruning) and the proportion of CBD-resistant cultivars on CBD incidence?
ii What is the effect of minimum and maximum temperature, relative humidity, canopy cover, coffee structure index (reflective of pruning) and CBD incidence on coffee yield?

Materials and methods

Study system

The study was conducted in Gomma and Gera districts (7°37'–7°56' N and 36°13'–36°39' E) in southwestern Ethiopia (Fig. 1A), which is considered the center of origin of Arabica coffee *Coffea arabica* (Anthony et al., 2001). The monthly mean minimum and maximum temperatures are 12.0 °C and 26.4 °C, respectively (Zignol et al., 2023). Rainfall follows a unimodal pattern and varies between 1500 and 2000 mm, with the main rainy season from May to September. The landscape consists of a mixture of natural and secondary moist tropical forests, smallholder coffee agroforestry, a few commercial coffee plantations, and fields with annual crops and grazing lands (Zewdie et al., 2022).Within the landscape, coffee is growing along a broad gradient of management intensity (Schmitt et al., 2010). This management gradient starts with coffee growing with little or no management in diverse natural forests with a dense canopy cover, no pruning and no fertilizer use, and ends with commercial plantations characterized by a low diversity of shade tree species, low canopy cover, use of improved coffee cultivars, and herbicide and fertilizer use (Hundera et al., 2013; Tadesse et al., 2014; Zewdie et al., 2022) (see Appendix A: Fig. S1). Pesticides and fungicides are not used in our study area to control coffee diseases or pests, and coffee is harvested by hand in all production systems (Ayalew et al., 2022). In Ethiopia, most smallholder coffee farms are less than 0.5 hectare (Kufa et al., 2008; Mekuria et al., 2004).

Arabica coffee in Ethiopia often flowers 10 days after sporadic heavy rains during the dry season in February or March (Dubale & Shimber, 2000; van der Graaff, 1981). The period from flowering to mature berries takes c. 7-8 months, when the berries go through several developmental stages, including the (i) pinhead stage (4–7 weeks after flowering), (ii) fruit expansion stage (8–16 weeks), endosperm filling stage (17–24 weeks), endosperm hardening stage (25–32 weeks), and ripening stage (33–35 weeks) (Cannell, 1985; Mulinge, 1970; Fig. 1B). While coffee regenerates naturally in the natural forest, the commercial plantations are dominated by cultivars bred for quantitative resistance against CBD (Hundera et al., 2013; Zewdie et al., 2022). For more details on the life-history of the diseases, see Appendix A: Text S1a.

Site selection and environmental variables

We selected a total of 58 sites from Gomma and Gera districts along a management gradient ranging from little or no management in the natural forest to commercial plantations (Fig. 1A). Within each site, we had previously established a 50 × 50 m plot, and further divided the plot into 10 × 10 m grid cells. We labelled 16 coffee shrubs at the intersections of the central 30 × 30 m grid cells (for more details on site selection, see Zewdie et al. 2020). The elevation of the study sites ranged from 1506 m to 2159 m a.s.l. To characterize site-level management, we focused on three variables: (i) canopy cover, (ii) coffee structure index and (iii) the proportion of coffee cultivars resistant to CBD. Canopy cover was estimated from pictures taken from five different locations in each 30 × 30 m plot. Each plot was divided into four quadrants, and photos were taken from the centre of the plot and from the centre of each of the four quadrants. From the photos, canopy cover was calculated using ImageJ software v. 1.50i (Schneider et al., 2012). To characterize pruning of the coffee shrub, we used the previously developed 'coffee structure index' (Zewdie et al., 2020). This metric was calculated using architectural attributes measured on 16 coffee shrubs per site: (a) the

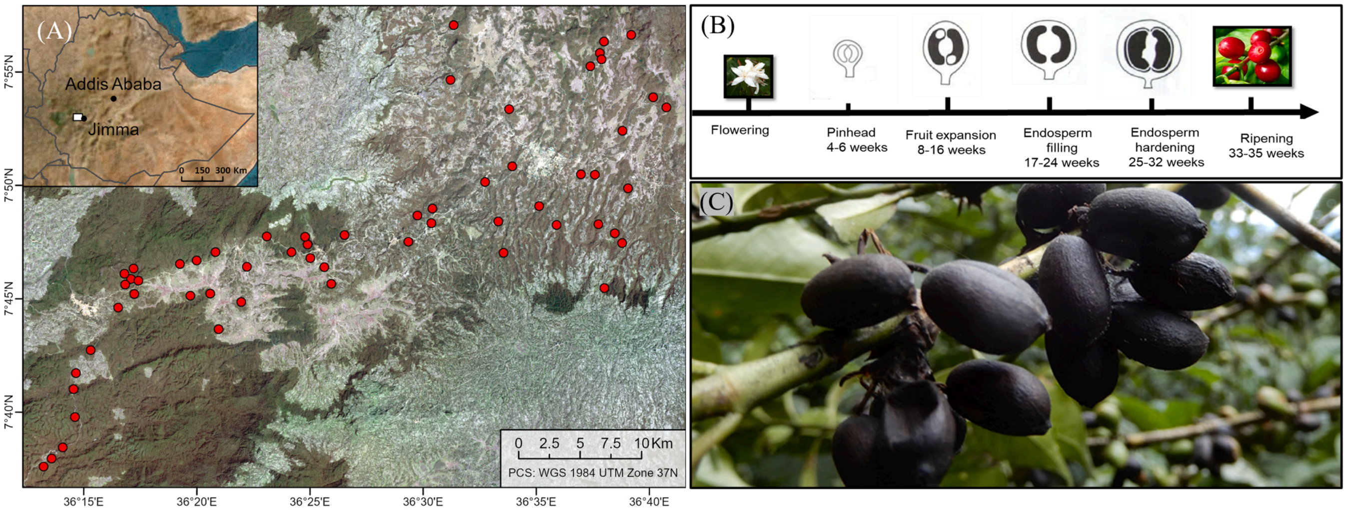

Fig. 1. Overview of the study area and system. Panel **A** shows a map of the study area, with the 58 study locations as red circles. The gray and green background colors on the map represent open and forested areas, respectively, and the inset shows the location of the study area (white rectangle) in southwestern Ethiopia. Panel **B** illustrates the developmental stages of Arabica coffee from flowering to maturation: flowering, pinhead stage, fruit expansion stage, endosperm filling stage, endosperm hardening stage and ripening stage (modified from Cannell 1985). Panel **C** shows a photo of berries blackened after infection by coffee berry disease (photo credit: Biruk Ayalew).

number of primary and secondary orthotropic and plagiotropic shoots, (b) the number of plagiotropic shoots, (c) the shrub's basal stem diameter at knee height, (d) average of two perpendicular diameters of the ground projection of the canopy of the coffee, and (e) the proportion of coffee height with plagiotropic shoots. We used these measurements to do a cluster analysis with a K-means clustering technique on the five attributes (see Appendix A: Text 1b). We then found a continuous index ranging from 1 to 3, with 1 representing no pruning, and 3 representing extensive pruning characteristic of plantations (Zewdie et al., 2020). The proportion of CBD-resistant cultivars in the 30 $\times$ 30 m plot was estimated based on interviews with the farmers. The proportion of CBD-resistant cultivars ranged from 0 (only wild genotypes or local landraces) to 1 (only CBD-resistant cultivars). The average canopy cover was 61 $\pm$ 11 % ($\pm$ SD), the average coffee structure index was 2.2 $\pm$ 0.5, and the average proportion of CBD-resistant cultivars was 0.5 $\pm$ 0.4. The coffee structure index was negatively related to canopy cover and coffee shrub density, but positively related to CBD-resistant cultivars, fertilizer and herbicide use, as well as soil and water conservation (see Appendix A: Fig. S2).

Assessment of CBD and yield

We assessed CBD and coffee yield in the wet season (July – August) for two consecutive years (2018–2019) in each of the 58 sites. On each of the 16 coffee shrubs per site, we recorded CBD (i.e., the proportion of infected berries out of the total number of surveyed berries) from three plagiotropic branches, one each at the lower, middle and upper part of the coffee shrub (see Zewdie et al. 2022 for further details on the methodology). The proportion of infected berries was averaged at the shrub level, and is henceforth referred to as CBD incidence. Coffee yield was assessed on the 16 coffee shrubs in each of the 58 sites following the standard described in Zewdie et al. (2022) in both 2018 and 2019 (see Appendix A: Text S1c for a detailed description of yield assessment). Importantly, our survey approach allowed us to assess patterns across broad environmental and management gradients across two years. At the same time, such large-scale approach does naturally not allow to capture high-resolution temporal relationships between climate and disease dynamics at each location, and, hence, it complements detailed studies conducted within single or few sites (Motisi et al., 2019, 2022).

Temperature and relative humidity

Air temperature and relative humidity were monitored in all 58 sites from February 2018 to August 2020 using iButton (model DS1921G-F5, Maxim Integrated, San Jose, CA, USA) and LASCAR dataloggers (LASCAR El-USB-2, UK), respectively. (see Appendix A: Text S1d for further details). For each site, we calculated the monthly average of the daily minimum temperature, daily maximum temperature, and daily mean relative humidity (hereafter, minimum temperature, maximum temperature, and relative humidity, respectively). As mean temperature had a strong correlation with minimum and maximum temperature, and the literature reports that CBD and Arabica coffee are particularly sensitive to minimum and maximum temperatures (Craparo et al., 2015; Nutman, 1970), we did not include mean temperature in the models (see Appendix A: Figs. S3–S5 for a correlogram of the remaining predictor variables for CBD incidence and yield). The average minimum and maximum temperature and relative humidity from flowering to berry development (i.e. February to July) were 13.4 °C, 24.0 °C and 81.6 % in 2018 and 14.2 °C, 24.3 °C and 83.7 % in 2019, respectively. As the effect of climatic variables on disease incidence and yield might differ between berry developmental stages, we averaged the minimum and maximum temperature, and relative humidity, for time periods corresponding to relevant developmental stages, which differ between disease incidence and coffee yield. For modeling disease incidence, we followed Mulinge (1970), and used the stages of fruit expansion (March–April), endosperm filling (May-June) and endosperm hardening (July) (Fig. 1B). For coffee yield, we used the stages of flowering (February-March) and fruit development (April–July) (Craparo et al., 2015).

Statistical analyses

All analyses were conducted in R v. 4.1.0 (R Core Team, 2020). Generalized linear (mixed) models were fitted using the functions *lm* and *glmer* in the base R-package and *lme4*, respectively (Bates et al., 2015; R Core Team, 2020), and we used the *MuMIn* package (Barton, 2009) for model selection. Model assumptions such as the distribution of residuals and model dispersion were validated with the *DHARMa* (Hartig & Lohse, 2020) and *sjPlot* packages (Lüdecke et al., 2020). Model plots with 95 % confidence intervals were generated using the function *ggpredict* from the package *ggeffects* (Lüdecke, 2018) and plotted using the *ggplot* function from the *ggplot2* package (Wickham et al., 2016).

To investigate the effect of temperature, relative humidity, canopy cover, coffee structure index and the proportion of CBD-resistant cultivars on CBD incidence, we modelled the proportion of infected berries out of the total number of berries surveyed on each coffee shrub (binomial distribution, logit link) as a function of the ecologically-relevant bioclimatic variables, canopy cover, coffee structure index and proportion of resistant cultivars using generalized linear mixed-effects models. We retained shrubs and sites without disease in a given year in the models because there was high turnover between years (indicating the absence of dispersal limitation at the site level), and to be able to compare a similar set of shrubs and sites between years. Notably, exclusion of sites without disease (n = 19 and 8 in 2018 and 2019, respectively) resulted in no or very minor changes in the results (results not shown). To account for the non-independence of the sixteen coffee shrubs within each site, we included 'site' as a random effect. We conducted similar models for coffee yield per hectare, where we assumed a Gaussian distribution with identity link. Models were constructed separately for each year.

We used an information-theoretic approach for model selection to determine the most important explanatory variables using the *dredge* function in the package *MuMIn* (Barton, 2009). This procedure generates a complete set of sub-models with all possible combinations of the predictor variables. We used Akaike's information criterion corrected for small sample sizes (AICc) to identify the set of best models (i.e. all models within a distance of 2 ΔAICc units of the model with the lowest AICc). We then calculated the AIC weight (w_i), which reflects the probability that a given model is the best model within the set of candidate models. When several models competed with the best model (i.e., multiple models with ΔAICc < 2), we applied a procedure of multi-model inference. We then averaged their effect sizes across all the models in the set of best models, using w_i as a weighting parameter (i.e., model averaging) (Burnham & Anderson, 2002). We reported the parameter estimates obtained through conditional averaging. The relative variable importance (RVI), which reflects the importance of a particular variable in relation to all other variables, was calculated as the sum of w_i of every model including this variable.

Results

Coffee berry disease

CBD infected on average 13.6 ± 1.10 % (± SE) and 12.8 ± 0.9 % of the berries in 2018 and 2019, respectively. In both 2018 and 2019, CBD incidence was affected by several climatic and management variables (Figs. 2 and 3; Table 1 and see Appendix A: Tables S1–S6). Of the climatic variables, disease incidence was higher when minimum temperature was high during the fruit expansion stage from March to April (Fig. 3A, Table 1) and was lower when minimum temperature was high during the endosperm filling stage from May to June in both years (Fig. 3B, Table 1). Disease incidence increased with minimum and maximum temperature during endosperm hardening in July in 2018 and 2019, respectively (Fig. 3C, D, Table 1). In 2019, but not in 2018, disease incidence decreased with the maximum temperature during the fruit expansion and endosperm filling stages (Table 1, see Appendix A: Fig. S6B–D). The effect of relative humidity differed between the two years, with a negative relationship between disease incidence and relative humidity during the endosperm filling stage from May to June in 2018 (Fig. 3E, Table 1), and a positive relationship during the endosperm hardening stage in July 2019 (Fig. 3F). Of the management variables, disease incidence was negatively affected by the proportion of resistant cultivars in both years (Fig. 3H, Table 1), whereas canopy cover negatively affected disease incidence only in 2019 (Fig. 3G, Table 1).

Coffee yield

Coffee yield was on average 1316 ± 201 (± SE) and 855 ± 114 kg ha^{-1} in 2018 and 2019, respectively. In both 2018 and 2019, coffee yield was affected by several climatic and management variables (Figs. 4 and 5; Table 2 and see Appendix A: Tables S7–S10). In 2018, but not in 2019, yield was lower in sites with higher minimum temperatures during the flowering stage from February to March (Fig. 5A, Table 2). In 2019, but not in 2018, yield decreased with higher maximum temperatures during the fruit development period from April to July (Fig. 5B, Table 2). In 2019, yield decreased with increasing relative humidity during the

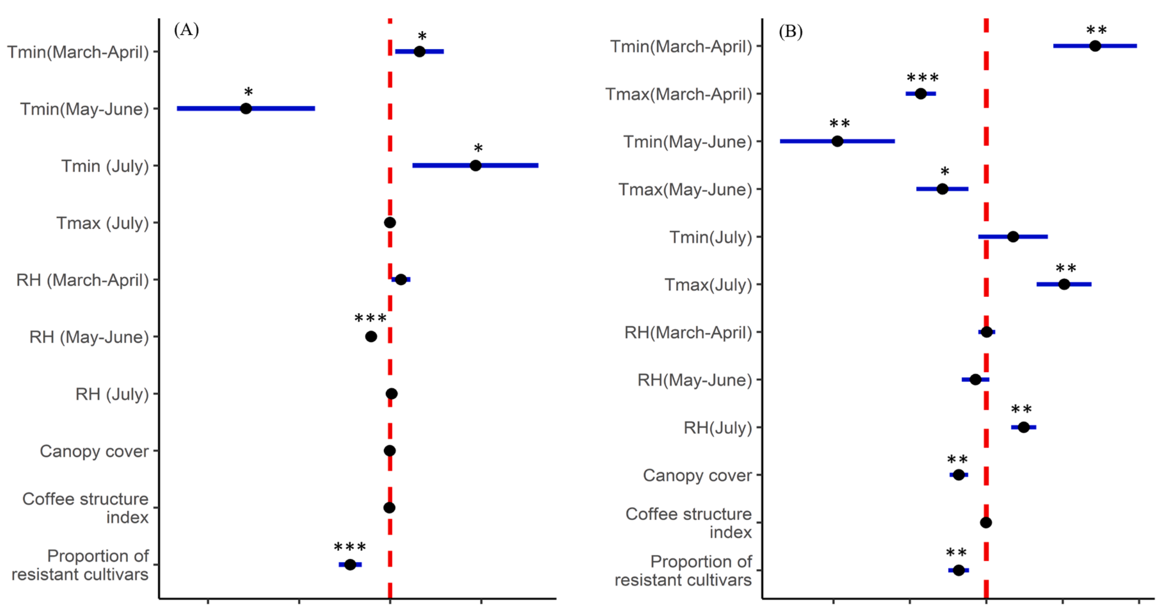

Fig. 2. The effect of climatic and management variables on coffee berry disease incidence in (A) 2018 and (B) 2019. Shown are standardized parameter estimates obtained from averages across the best competing models (ΔAICc < 2). The full set of predictor variables consisted of minimum temperature, maximum temperature and relative humidity (separately for the periods March-April, May-June, and July), as well as canopy cover, coffee structure index, and proportion of resistant cultivars. Circles and error bars represent standardized parameter estimates and corresponding 95 % CI. The vertical dashed line centered on zero indicates no effect. For details of the set of best competing models and relative variable importance, see Appendix A: Tables S1–S6.

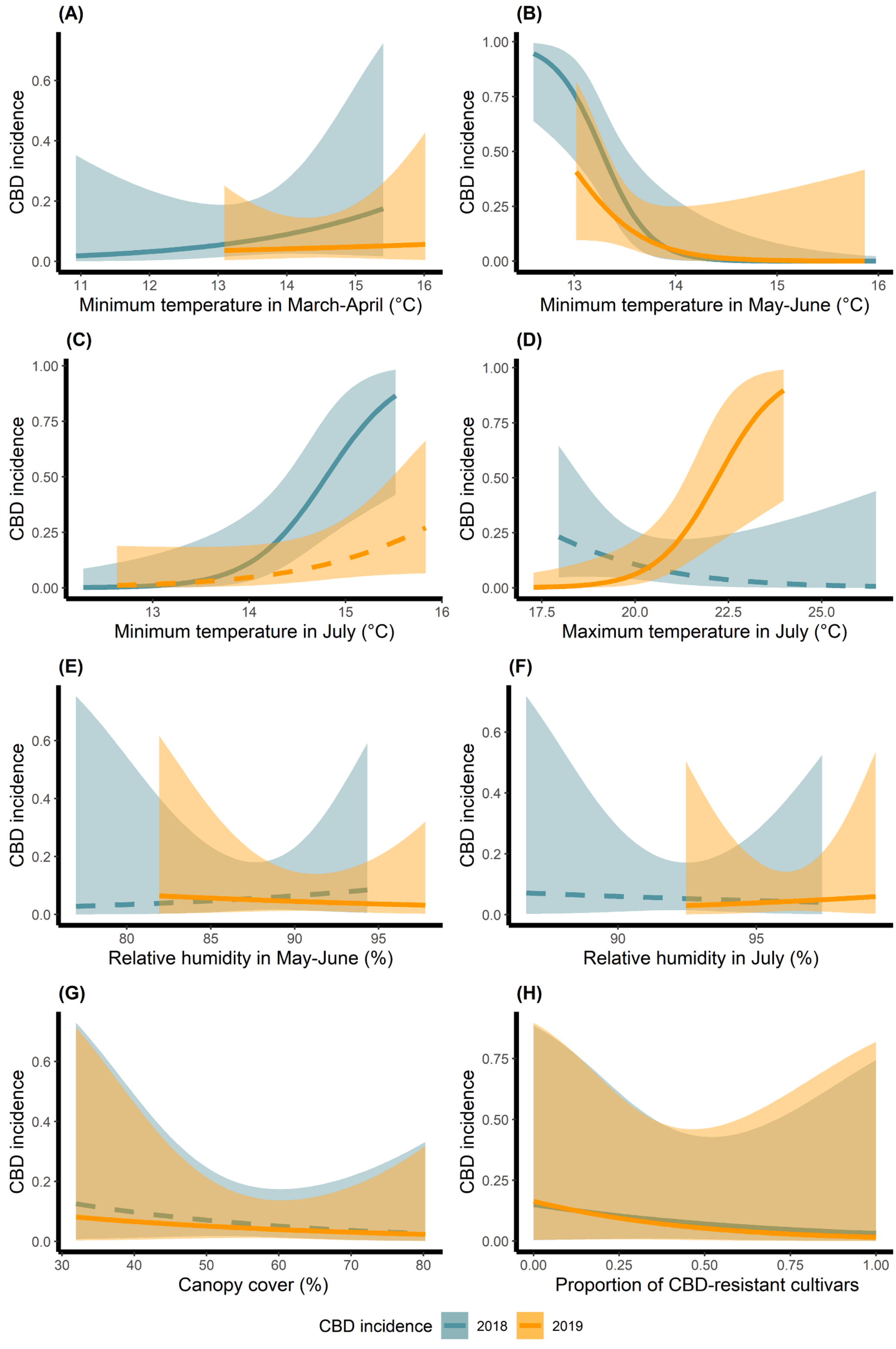

Fig. 3. The effect of climatic and management variables on coffee berry disease incidence in 2018 (in blue) and 2019 (in orange). The solid lines represent the predicted relationships of disease incidence with (A) minimum temperature during the fruit expansion stage in March-April, (B) minimum temperature during the endosperm filling stage in May-June, (C) minimum temperature during the endosperm hardening stage in July, (D) maximum temperature during the endosperm hardening stage in July, (E) relative humidity during the endosperm filling stage in May-June, (F) relative humidity during the endosperm hardening stage in July, (G) canopy cover, and (H) proportion of resistant cultivars. The blue and orange solid trend lines represent the predicted relationships for 2018 and 2019, respectively. Shaded areas represent the 95 % confidence interval. Significant relationships have solid lines ($P < 0.05$), and nonsignificant relationships dashed lines. For a visualization of the relationships in the raw data, see Appendix A: Figs. S7 and S8. The predicted effects were calculated using the function *ggpredict* from the package *ggeffects* (Lüdecke, 2018).

Table 1
The effect of climatic and management variables on CBD incidence in 2018 and 2019. Shown are model-averaged (conditional) parameter estimates (β) and P-values of the set of best competing models (delta AICc < 2). Shown are first those variables that are included in the set of best competing models in both years, as followed by variables included in the set of best competing models in 2019. For standard errors of the parameter estimates, test statistics, the full set of statistical models and relative variable importance (RVI), see Appendix A: Tables S1–S6.

Predictor variables	2018	2019
Minimum temperature (March-April)	β = 2.04 *P* = **0.05**	β = 3.56 *P* = **0.008**
Minimum temperature (May-June)	β = -7.92 *P* = **0.04**	β = -4.87 *P* = **0.008**
Minimum temperature (July)	β = 5.69 *P* = **0.05**	β = 1.71 *P* = 0.10
Maximum temperature (July)	β = -0.20 *P* = 0.77	β = 2.55 *P* = **0.004**
Relative humidity (March-April)	β = 1.11 *P* = 0.13	β = 0.10 *P* = 0.88
Relative humidity (May-June)	β = -1.05 *P* = **<0.001**	β = -0.66 *P* = 0.12
Relative humidity (July)	β = 0.54 *P* = 0.49	β = 1.23 *P* = **0.002**
Canopy cover	β = -0.34 *P* = 0.53	β = -0.89 *P* = **0.002**
Coffee structure index	β = -0.39 *P* = 0.57	β = -0.11 *P* = 0.74
Proportion of CBD-resistant cultivars	β = -2.19 *P* = **<0.001**	β = -0.90 *P* = **0.007**
Maximum temperature (March-April)	–	β = -2.14 *P* = **<0.001**
Maximum temperature (May-June)	–	β = -1.58 *P* = **0.03**

flowering period and increased with increasing humidity during the fruit development period (Fig. 5C, D, Table 2), whereas humidity had no effect on coffee yield in 2018. Of the management variables, yield was positively affected by coffee structure index and negatively affected by canopy cover in both 2018 and 2019 (Fig. 5E, F, Table 2), whereas CBD incidence negatively affected yield only in 2018 (Fig. 5G, Table 2).

Discussion

We investigated the effects of climate and management on CBD incidence and coffee yield along a management gradient in Arabica coffee's native range in southwestern Ethiopia. Both CBD and coffee yield were affected by several climatic and management variables. Some of the climatic variables, as well as the proportion of resistant cultivars, were consistent between years in explaining CBD incidence, whereas management and canopy cover were consistent between years in explaining coffee yield. Strikingly, for both CBD incidence and yield, the effect of climatic variables strongly differed among developmental stages from flowering to endosperm hardening. CBD incidence explained coffee yield in only one of the two years. Our findings identify climatic and management variables as important in shaping disease incidence and yield, which provides tools for developing sustainable, climate-resilient management strategies.

CBD was affected by both climatic and management variables, with a consistent imprint of minimum temperature and the proportion of resistant cultivars between years. Importantly, the effect of minimum temperature differed between the berry developmental stages, with a positive relationship during fruit expansion from March to April, and a negative relationship during endosperm filling from May to June. The positive relationship between high minimum temperatures and CBD incidence during the fruit expansion stage might be due to high minimum (night) temperatures creating favorable conditions for *C. kahawae* germination, which might be particularly important during the fruit expansion stage when coffee berries are highly susceptible to disease since the coffee skin is soft and easily penetrated by the fungus (Garedew et al., 2017; Mulinge, 1970; Nutman, 1970). Our finding of a positive relationship between minimum and maximum temperature and CBD during endosperm hardening contrasts with the findings of Garedew et al. (2017), Mouen Bedimo et al. (2012),who found no relationship between climatic conditions and CBD incidence during this stage. The effect of relative humidity differed between developmental stages and between years. As most studies have focused on the effect of climate variables averaged across the year, or climatic variables for a single developmental stage, stage-dependent effects of climatic variables on

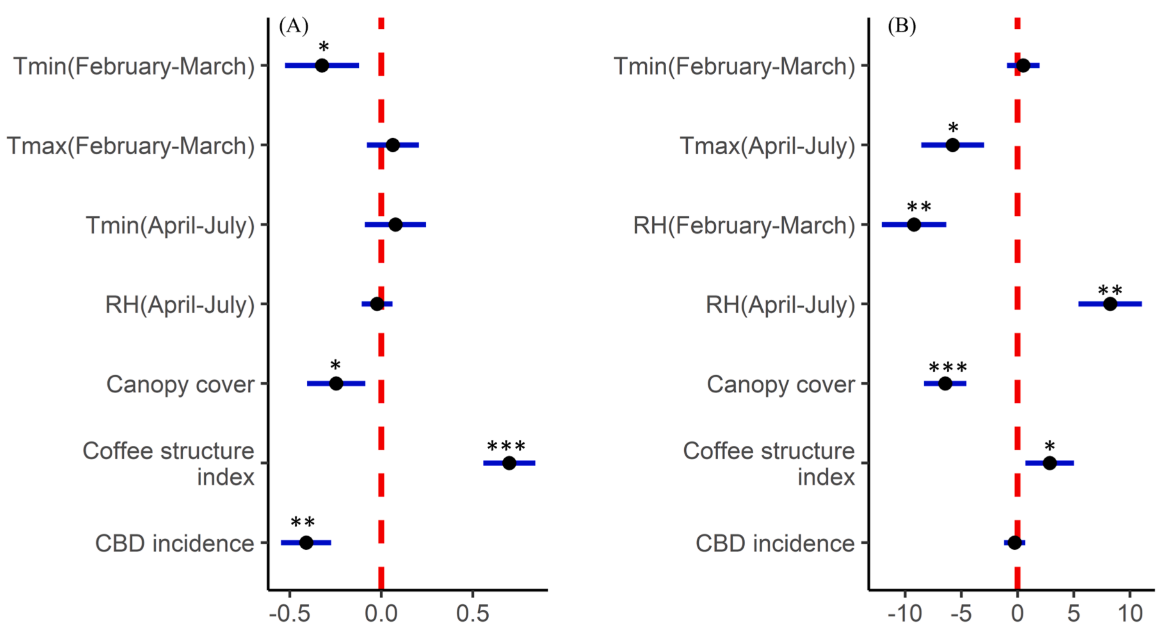

Fig. 4. The effect of climatic and management variables on coffee yield ha-1 in (A) 2018 and (B) 2019. Shown are standardized parameter estimates obtained from averages across the best competing models (ΔAICc < 2). The full set of predictor variables consisted of minimum temperature, maximum temperature and relative humidity (separately for the periods February-March and April–July), as well as canopy cover, coffee structure index, and coffee berry disease incidence. Circles and error bars represent standardized parameter estimates and corresponding 95 % CI. The vertical dashed line centered on zero indicates no effect. For details of the set of best competing models and relative variable importance, see Appendix A: Tables S7–S12.

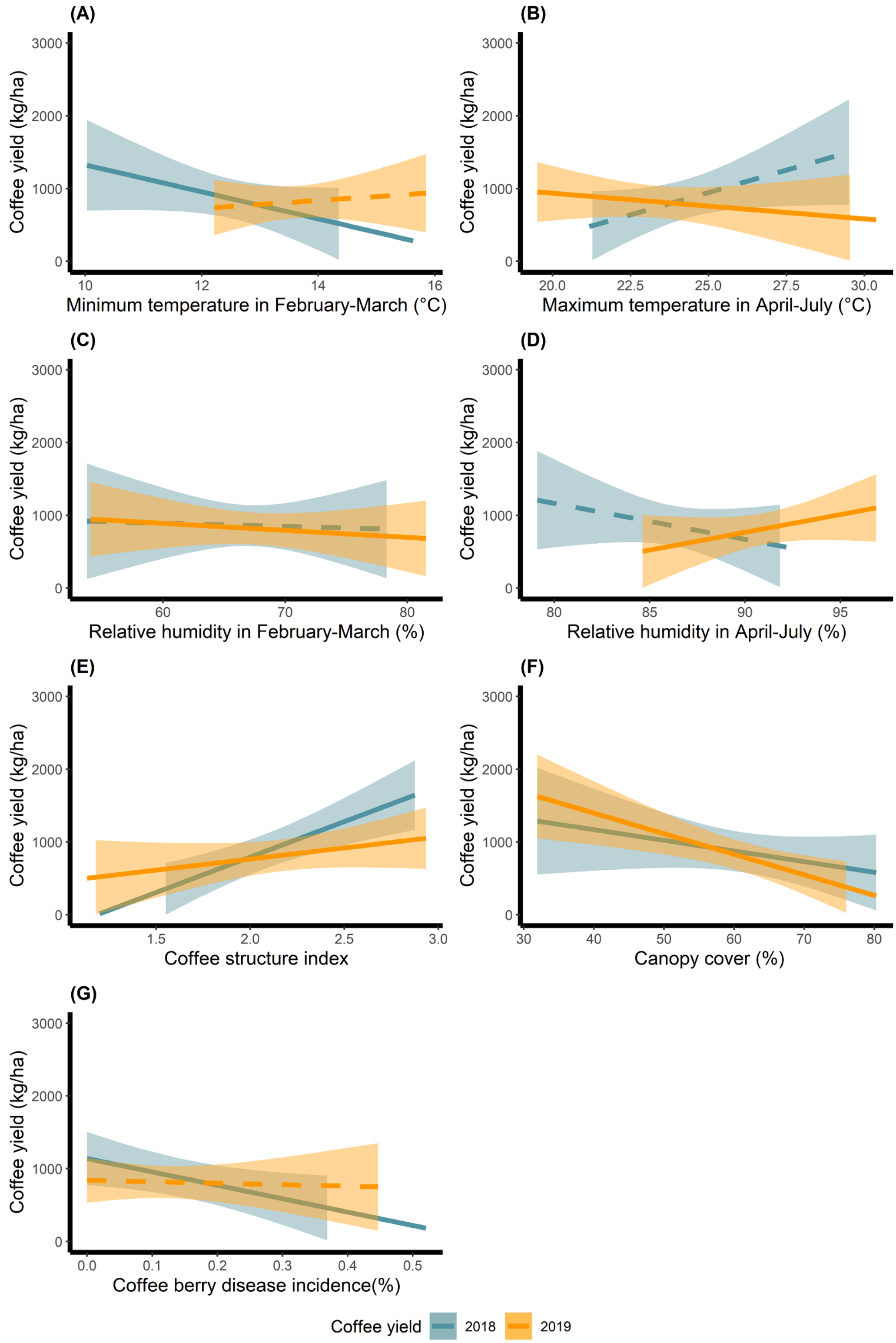

Fig. 5. The effect of climatic and management variables on coffee yield ha^{-1} in 2018 (in blue) and 2019 (in orange). The solid trend lines represent the relationships of coffee yield with (A) minimum temperature during the flowering stage in February-March, (B) maximum temperature during the fruit developmental stage in April–July, (C) relative humidity during the flowering stage in February-March, (D) relative humidity during the fruit developmental stage in April-July, (E) coffee structure index, (F) canopy cover and (G) coffee berry disease incidence. Shaded areas represent the 95 % confidence interval. Significant relationships have solid lines ($P < 0.05$), and nonsignificant relationships dashed lines. For a visualization of the relationships in the raw data, see Appendix A: Figs. S9 and S10. The predicted effects were calculated using the function *ggpredict* from the package *ggeffects* (Lüdecke, 2018).

Table 2
The effect of climatic and management variables on coffee yield in 2018 and 2019 Shown are model-averaged (conditional) parameter estimates (β) and P-values of the set of best competing models (delta AICc < 2). Shown are first those variables that are included in the set of best competing models in both years, as followed by variables included in the set of best competing models in only 2018 and 2019, respectively. For standard errors of the parameter estimates, test statistics, the full set of statistical models and relative variable importance (RVI), see Appendix A: Tables S7–S12.

Predictor variables	2018	2019
Minimum temperature (February-March)	β = -0.36 *P* = **0.04**	β = 2.41 *P* = 0.29
Relative humidity (April–July)	β = 0.30 *P* = 0.28	β = 8.25 *P* = **0.003**
Canopy cover	β= 0.70 *P* = **0.04**	β = -6.44 *P* = **<0.001**
Coffee structure index	β = -0.18 *P* = **<0.001**	β = 3.53 *P* = **0.05**
CBD incidence	β = -0.28 *P* = **0.002**	β = -1.52 *P* = 0.41
Maximum temperature (February-March)	β = 0.25 *P* = 0.16	–
Minimum temperature (April–July)	B = 0.30 *P* = 0.13	–
Maximum temperature (April–July)	–	β = -5.77 *P* = **0.03**
Relative humidity (February-March)	–	β = -9.21 *P* = **0.001**

diseases have not been reported for other agroforestry crops. Of the management variables, the proportion of resistant cultivars, and to a lesser extent canopy cover, were important in shaping CBD incidence, whereas management intensity had no effect on CBD. The negative relationship between the proportion of resistant cultivars and CBD incidence indicates that the use of resistant cultivars is an effective management strategy against CBD (Hindorf & Omondi, 2011; van der Graaff, 1981). The negative relationship between CBD incidence and canopy cover in 2019 is consistent with the finding of Mouen Bedimo et al. (2008), who postulated that shade cover serves as a physical barrier that limits rain intensity, which in turn reduces splash dispersal of the pathogen. Our finding of no effect of management intensity, such as pruning the coffee shrub, on the incidence of CBD contrasts with Mouen Bedimo et al. (2007), Garedew et al. (2017) who reported a negative relationship between management intensity and CBD. This indicates that other management components, such as planting of resistant cultivars and managing shade, are more effective in reducing disease levels than cultural practices such as pruning (Alemu et al., 2021). Taken together, our findings highlight that the relationships of temperature and relative humidity with disease levels fluctuate during the season, and that the proportion of resistant cultivars and canopy cover, but not pruning, could be used as tools for disease management.

Similar to CBD, coffee yield was affected by both climate and management, but there was little overlap in the variables that explained disease incidence and yield. While climate affected coffee yield in both years, the climatic drivers of coffee yield varied among years, which contrasted with the consistent imprint of some climatic variables on CBD. For example, increasing minimum temperature and relative humidity during the flowering stage from February to March negatively affected coffee yield. The negative relationship between minimum temperature and yield might be due to higher respiration rates of coffee during warmer nights, which in turn may reduce the amount of assimilates available for growth and yield (DaMatta, 2004). In line with our finding of a negative relationship between high minimum temperature and coffee yield during the flowering stage, Craparo et al. (2015) found that coffee yield decreased with increasing minimum temperature in Tanzania. As another example, and consistent with previous findings in Tanzania (Craparo et al., 2015) and India (Jayakumar et al. 2017), we found a negative relationship between high maximum temperature and coffee yield during fruit development, possibly due to extreme temperatures negatively affecting fruit set and development (Pham et al., 2019; DaMatta, 2004). Of the management variables, canopy cover had a negative effect on coffee yield and management intensity had a positive effect on coffee yield. Our finding of a negative relationship between canopy cover and coffee yield has been reported previously from Ethiopia (Aerts et al., 2011) and other coffee growing regions (Durand-Bessart et al., 2020; Iverson et al., 2019; Jha et al., 2014), and might be due to competition between shade trees and the coffee shrubs for light, water, and nutrients (DaMatta, 2004). Matching our finding of a positive trend between management intensity and coffee yield, Schmitt et al. (2010) found that coffee yield increased with management intensity in southwestern Ethiopia, which might be due to pruning of coffee shrubs, fertilizer use and weeding (Aerts et al., 2011; Schmitt et al., 2010). Even though infection levels were very similar between the years (2018: 13.6 %, 2019: 12.50 %) we found a negative relationship between coffee yield and CBD incidence only in 2018, not in 2019. Taken together, our findings illustrate that the climatic and management drivers of CBD incidence and coffee yield are different, and that the imprint of climatic variables on CBD incidence is more consistent between years. As a future direction, it would be promising to increase the predictive power by incorporating further climatic variables, such as precipitation, which might affect coffee flowering, berry development, yield, and the prevalence of CBD.

Implication for management

Our study highlights several important messages for applied agricultural scientists developing ecologically-informed and climate change-resilient management strategies. First, we found that CBD and yield were affected by a different set of climatic and management variables. Importantly, this implies that it might be possible to design separate management strategies that can reduce disease levels, and increase yield, and that there likely is no strong trade-off between these management strategies. Another key finding was that the relationship between climatic variables, disease and yield differed strongly between the developmental stages from flowering to ripening. While climate change is often presented and modelled as an annual increase in temperature, our findings then emphasize that what truly matters is when during the season the temperature, as well as relative humidity, will change. Finally, while some of the patterns were consistent between years, the inconsistency of some of the patterns between years calls for caution, and the need for long-term studies to unravel why some climatic variables do matter in one year, but not in another.

Importantly, our study focused on an agroforestry system, where it might be possible to modify the linkage between the macroclimate and the microclimate. For example, farmers might modify the shade cover to provide a cooler and more humid microclimate for their crops. Yet, while reducing the minimum temperature can reduce disease levels during the fruit expansion stage, it would increase disease levels during the endosperm filling stage. Measures taken to reduce infection during one period might thus be counteracted by increased infection levels during another period. However, one promising management strategy might be to create seasonal microclimate profiles by purposely selecting shade trees that differ in the presence and timing of leaf drop. While we already know that some shade trees are (semi-)deciduous, and others evergreen, deciduous trees also differ in when they drop their leaves, and we might take advantage of these phenological differences in disease management. Regarding yield, reducing the minimum temperature during the flowering and maximum temperature during fruit developmental stages may help to increase the coffee yield. One low disease-high yield solution might then be to create a microclimate with colder nights in spring, for example by the use of shade trees that drop their leaves during the dry season and only create new leaves by the end of April. While this theoretical solution makes sense in the light of our observational results, we stress that we need experimental studies to validate this suggestion. Our study also illustrates that host genetics, in the form of resistant cultivars, might be more effective in reducing disease levels than managing the microclimate. This highlights that, despite the fact that many of these cultivars have been released several decades ago, their resistance has not been broken by evolutionary changes of the pathogen (McDonald & Linde, 2002). Yet, the use of such improved cultivars within the area of origin of Arabica coffee might threaten the wild coffee genetic reservoir (Labouisse et al., 2008; Zewdie et al., 2023). Taken together, our study demonstrates that insights into the effects of climatic and management variables may help to develop effective ecologically-informed and climate-smart adaptation strategies for reducing disease and increasing yield in agroforestry systems.

CRediT authorship contribution statement

Biruk Ayalew: Conceptualization, Investigation, Resources, Formal analysis, Writing – original draft, Writing – review & editing. **Kristoffer Hylander:** Conceptualization, Investigation, Writing – review & editing. **Girma Adugna:** Conceptualization, Investigation, Writing – review & editing. **Beyene Zewdie:** Resources, Writing – review & editing. **Francesco Zignol:** Data curation, Writing – review & editing. **Ayco J.M. Tack:** Conceptualization, Investigation, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

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