



Research Article

The impact of climate, local habitat, surrounding landscape and management on coffee wilt disease and Armillaria root rot on Arabica coffee in its native range

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ABSTRACT

Climate change is predicted to lower yields through increased disease pressure. Yet, we often lack insights into how climate affects disease dynamics, and how we can manage the environment to reduce the impact of climate change. This knowledge gap is especially prominent for stem and root diseases that concern smallholder farmers in low-income countries. To provide insights into the patterns and drivers of stem and root diseases, and how they will be affected by climate change, we surveyed the prevalence and incidence of a major stem (coffee wilt disease; *Gibberella xylarioides*) and root disease (Armillaria root rot; *Armillaria mellea*) attacking Arabica coffee in 58 sites in southwestern Ethiopia, and simultaneously recorded climatic, habitat, spatial and management variables. Coffee wilt disease was found in all but four sites, and the incidence of coffee wilt disease was positively affected by temperature and soil moisture, negatively affected by coffee density and lower in sites with a more forest-like shade tree species composition. Armillaria root rot was found in 29 out of 58 sites. While none of the factors explained the prevalence of Armillaria root rot, Armillaria root rot incidence was, in contrast to coffee wilt disease, negatively affected by temperature. Armillaria root rot was positively affected by soil moisture and surrounding forest cover. Canopy cover affected the two diseases through opposing direct and indirect pathways, resulting in non-significant total effects. Neither of the two diseases was affected by coffee structure index (reflecting e.g. pruning), the proportion of coffee berry disease resistant cultivars, or each other's presence. Overall, our findings shed light on the patterns and drivers of stem and root diseases, and provide management guidelines to reduce the devastating impact of these diseases for smallholder farmers.

Introduction

Climate change poses a major threat to global crop production, not only directly by affecting crop growth and yield but also indirectly by increasing pest and disease levels (Juroszek & von Tiedemann, 2011; Skendzić et al., 2021). Understanding the relationship between climate, management and disease pressure is thus important for developing farming practices in a changing climate (Ayalew et al., 2024a; Gagliardi et al., 2021). We particularly lack insights into the relationship between climate, management and disease pressure for stem and root diseases, even though they can have large impacts on plant health and

productivity (Singh et al., 2018). This knowledge gap is especially concerning for smallholder farmers in low-income countries, as these diseases directly threaten their livelihoods. By establishing the link between climate, management and disease dynamics for often-ignored pathogens in often-ignored regions, we can develop sustainable ecologically-informed strategies to reduce crop losses by pests and diseases under climate change for smallholder farmers.

As global temperatures increase and precipitation patterns shift, the incidence and severity of plant diseases are likely to change as infection, colonization, sporulation, and dispersal of pathogens may be either favoured or hindered (Singh et al., 2023). Moreover, pathogens can

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rapidly evolve to changing climatic conditions, in contrast to many (perennial) crops (Burdon & Laine, 2019). Understanding the relationship between climate and disease levels in natural and agricultural systems may enable us to predict the impact of climate change on crop diseases and develop effective ecologically-informed strategies to reduce crop losses by diseases under climate change (Zhang et al., 2023). Agroforestry can be leveraged as a climate-smart and sustainable agricultural system where agricultural crops such as coffee and cacao are cultivated under a canopy of shade trees (Altieri & Nicholls, 2004; Perfecto et al., 2014). Shade trees within agroforestry modify the microclimate by buffering extreme temperatures and increasing humidity, though they may reduce dew formation compared to open areas (Dobhal et al., 2024; Kemppinen et al., 2024). The shaded microclimate may reduce environmental stress on the understory plants, thereby enhancing crop growth and reducing disease levels. For example, Mensah et al. (2022) and Wagner (2022) reported shade enhanced resilience to drought and heat stress in East African coffee systems, and López-Bravo et al. (2012) showed that shaded coffee systems had a lower severity of coffee leaf rust compared to unshaded monocultures in Latin America.

Local, spatial and management factors such as canopy cover, plant density, the composition of shade tree species, surrounding forest cover and pruning can play an important role in reducing diseases levels in agricultural systems (Juroszek & von Tiedemann, 2011; Schroth et al., 2000; Tschamntke et al., 2011). For example, managing the canopy cover by shade trees can regulate microclimatic conditions such as temperature and soil moisture (Tschamntke et al., 2011), and plant density can affect disease transmission (Sseremba et al., 2021). The diversity of shade tree species in coffee and cacao agroforests not only enhances biodiversity but also supports natural pest control mechanisms through increased predator and parasitoid abundance (Bisseleua et al., 2013; Burger et al., 2022; Stüber et al., 2021) and improves soil health (N'Guessan Diby, 2024). From a spatial perspective, the surrounding forest cover can act as a buffer, providing habitat for beneficial organisms that suppress pest populations and diseases (Ratnadass et al., 2012). Finally, pruning of the crop can enhance airflow and sunlight penetration (Beer et al., 1998; Gagliardi et al., 2021), which in turn reduces humidity levels, which can inhibit pathogen dispersal and spore germination (Avelino et al., 2004; Finch-Boekweg et al., 2016). Together, these integrated practices have the potential to create a resilient agricultural system that enhances the health and productivity of crops under climate change. Beyond local, spatial and management factors, interactions between co-occurring plant pathogens may also intensify disease incidence or alter transmission dynamics (Susi et al., 2015; Zhou et al., 2023). In some cases, one pathogen may indirectly favor another by weakening the host, thereby increasing host susceptibility (Abdullah et al., 2017). As two examples, co-infection by *Fusarium aglaonematis* and *Fusarium elaeidis* in *Aglaonema modestum* led to an increased incidence of stem rot disease (Zhang et al., 2022), and *Fusarium oxysporum* f. sp. *medicaginis* and *Rhizoctonia solani* co-infections caused more severe disease in alfalfa than either pathogen did alone (Fang et al., 2021). These interspecific interactions among pathogens sharing the same host highlight the importance of considering pathogen interactions in integrated disease management strategies.

Arabica coffee is attacked by a diverse community of fungal pathogens, and several reports have warned that climate change might increase the incidence and severity of these diseases (Groenen, 2018; Pham et al., 2019). In southwestern Ethiopia, coffee wilt disease (tracheomycosis) and Armillaria root rot rank among the most destructive fungal diseases (Adugna et al., 2009). Coffee wilt disease, caused by *Fusarium xylarioides* (asexual form; sexual form: *Gibberella xylarioides*), is endemic to Africa, attacks coffee plants at all growth stages, and eventually kills the infected plant (Adugna et al., 2009; Zhang et al., 2023). This soil-borne pathogen invades through the roots, colonizing the xylem vessels and disrupting water transport (Flood, 2023; Rutherford, 2006). The resulting vascular blockage induces wilting, defoliation and

necrosis in wood below the bark, and in advanced stages the coffee plant dies (Fig. 1b) (Flood, 2023; Peck & Boa, 2024). The fungus produces asexual conidia on dead leaves and ascospores within root and stem bark of infected shrubs (Zhang et al., 2023). The most reliable way to detect the disease is to scrape off the stem bark; internally, brown or blue-black discoloured bands are seen on the exposed wood of the stem. In addition, these trees cannot be easily pushed over and uprooted as opposed to coffee trees that have died from root rot disease (*Armillaria mellea*) (Adugna et al., 2009; Zewdie et al., 2020). The intravascular nature of the infection poses challenges for natural and chemical treatments, and the disease causes substantial production losses of up to 80 % in plantations and, in some instances, complete loss in smallholder farms. Typical management actions include uprooting and burning infected material, as well as other sanitary measures such as (i) avoiding wounding the stems during weeding and cultivation of the coffee, (ii) avoiding shrubs with wilting symptom during pruning, and (iii) regularly disinfecting pruning shears (Adugna et al., 2009; Flood, 2023). Coffee wilt disease is currently confined to central and eastern Africa (Flood, 2023).

Armillaria root rot is caused by *Armillaria mellea* (Ayalew et al., 2024c; Zewdie et al., 2020). Armillaria root rot is a globally distributed, soil-borne fungal pathogen that causes the rotting of roots, which in time kills the coffee plant (Ayalew et al., 2024c; Zewdie et al., 2020). A coffee shrub infected with Armillaria root rot shows symptoms of yellowish leaves, die-back, and cracking of the stem at the collar region (Fig. 1c) (Roux & Coetzee, 2016). The infected shrub has black threadlike rhizomorphs in the cracked stem, which are particularly easy to see during the wet season, and a diseased shrub can be easily pushed over and uprooted (Girma et al., 2001), allowing for easy identification of the disease in the field. Armillaria root rot spreads primarily through root-to-root contact between trees (Adugna et al., 2009; Waller et al., 2007) and growth is closely linked to soil moisture conditions (Gezahgne et al., 2004). The pathogen can persist in root pieces within the soil for extended periods and the presence often goes unnoticed until coffee canopies wilt and succumb to the disease. Typical management actions include sanitary measures, and promptly uprooting and burning infected trees (Waller et al., 2007). Armillaria root rot is not only a primary pathogen, but also a secondary pathogen on stressed trees and a saprophyte on dead trees (Wargo & Shaw, 1985). The disease is particularly problematic in areas where native forests have been cleared to establish plantations, with tree mortality often concentrated around stumps and large woody debris left after cutting (Waller et al., 2007). The mycelium can survive saprophytically in residual woody roots after cutting of trees and can remain buried in the soil to serve as inoculum for infection of the next crop (Redfern & Filip, 1991). After the host plant has died, the pathogen can survive as a saprophyte. Depending on environmental conditions, stump size, and other factors, Armillaria species may survive for decades in stumps. Management of Armillaria root rot is often unsuccessful due to the persistence of fungal inoculum in roots, stumps, and soil.

In southwestern Ethiopia, Arabica coffee *Coffea arabica* grows wild, and natural populations are characterized by a high genetic diversity (Anthony et al., 2001). Within the same landscape, coffee is cultivated along a broad gradient of management intensity, ranging from coffee growing with little management in the natural forest to smallholder farms and a few larger commercial plantations (Ayalew et al., 2024a; Zewdie et al., 2020). Arabica coffee is the region's major agricultural commodity, providing a livelihood income for millions of people (Moat et al., 2017). Arabica coffee is attacked by a diverse community of fungal pathogens, and several reports have warned that climate change might increase the incidence and severity of these diseases (Groenen, 2018; Pham et al., 2019).

Our overarching aim was to identify the patterns and drivers of stem and root diseases on Arabica coffee. For this, we surveyed the prevalence and incidence of a major stem (coffee wilt disease) and root disease (Armillaria root rot) attacking Arabica coffee in 58 sites across

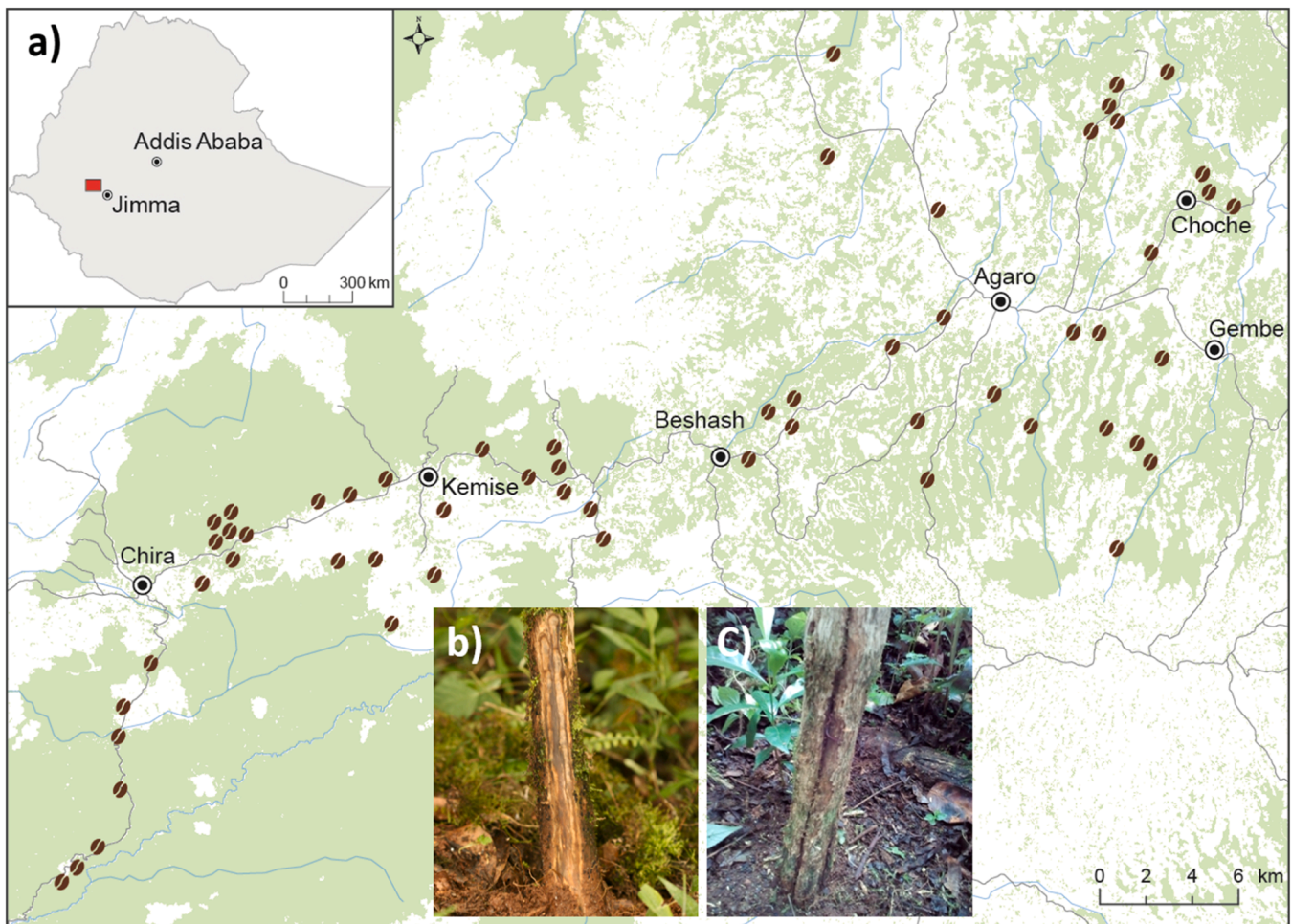


Fig. 1. Overview of the study location and system. The inset in panel a) shows the location of the study area (red rectangle) in Jimma zone in southwestern Ethiopia. The 58 sites (coffee beans) are plotted on the map of the study area. The gray and green background colours represent open and forested areas, respectively. The photos in the bottom right show characteristic damage by the two major coffee fungal diseases: b) the characteristic brown or blue-black discoloured bands that are seen on the exposed wood of a coffee wilt disease infected stem when the bark is scraped off, as caused by *Gibberella xylarioides*, and (c) the typical black threadlike rhizomorphs in the cracked stem caused by *Armillaria root rot* (*Armillaria mellea*) (photos credits: Beyene Zewdie).

southwestern Ethiopia along a broad environmental and climatic gradient. In each site, we recorded aspects of the climate (mean soil temperature, soil temperature variability and soil moisture), local habitat (canopy cover, coffee density and shade tree composition), spatial context (surrounding forest cover) and management (coffee structure index and proportion of coffee berry resistant coffee cultivars relative to coffee shrubs of local or wild origin). We then used structural equation modelling to address the following questions:

- i. What are the direct and indirect effects of climatic, habitat, spatial and management variables, as well as *Armillaria* root rot incidence, on coffee wilt disease incidence?
- ii. What are the direct and indirect effects of climatic, habitat, spatial and management variables, as well as coffee wilt disease incidence, on *Armillaria* root rot prevalence and incidence?

Materials and methods

Description of the study area

The study was conducted in Goma and Gera districts in Jimma zone, southwestern Ethiopia (7°37'–7°56' N and 36°13'–36°39'E) from April 2018 to June 2019 (Fig. 1a). The landscape has a varied topography, and the elevation of our study sites ranges from 1500 to 2200 m.a.s.l. The

climate is warm and humid with a mean daily minimum and maximum temperature of 12.0 and 26.4 °C, respectively (Zignol et al., 2023). Rainfall in the area is unimodal, with a mean annual rainfall between 1500 and 2000 mm. The climax vegetation is moist Afromontane forest with mostly evergreen trees such as *Pouteria adolfi-friederici*, *Olea welwitschia*, *Prunus africana*, *Syzygium guineense*, *Schefflera abyssinica*, and *Ficus sur* (Friis et al., 2010), and the landscape is currently a mosaic of primary and secondary forests, smallholder coffee farms, a few large coffee plantations, annual crop and grazing fields, and human settlements (Koelemeijer et al., 2021; Zewdie et al., 2020). The region is part of the indigenous distribution of Arabica coffee and is of major importance for coffee production (Ayalew et al., 2022; Burger et al., 2022).

Coffee in southwestern Ethiopia is grown under the shade of trees along a wide gradient of management intensities (Zewdie et al., 2022). This gradient includes coffee grown with little or no management under a dense, species-rich canopy of native forest trees; smallholder farms where shade tree species typical of the natural forest are less common and less dense; and, finally, commercial plantations characterized by lower tree diversity and canopy cover (Hundera et al., 2013; Tadesse et al., 2014). Farmers in our study area do not apply fungicides, and thereby heavily rely on natural disease control and other agricultural practices such as pruning (Ayalew et al., 2022; Stüber et al., 2021). The larger coffee plantations, and to some degree also the smallholder farms with high management intensity, employ coffee cultivars resistant to

coffee berry disease caused by the fungal pathogen *Colletotrichum kahawae*. These cultivars are not known to have cross-resistance or cross-susceptibility to other fungal diseases (Daba et al., 2019).

Assessment of coffee wilt disease and Armillaria root rot

To assess the patterns and drivers of coffee wilt disease and Armillaria root rot, we selected 58 coffee farms (hereafter “sites”) across the study area (Fig. 1a). Each site was separated by at least 1 km to ensure spatial independence. These sites were previously selected to encompass a range of environmental and management gradients (Zewdie et al., 2020). Within each site, we established a 50 × 50 m plot, and within each plot, we recorded the proportion of coffee shrubs with coffee wilt disease and Armillaria root rot symptoms on a single date between July to August 2019. To distinguish between coffee wilt disease and Armillaria root rot, we followed established field diagnostic protocols. Coffee wilt disease was identified by scraping the stem bark with a knife and looking for characteristic brown or blue–black discoloured bands in the exposed wood (Girma et al., 2001). Armillaria root rot was diagnosed by inspecting the root collar and lower stem for black, threadlike rhizomorphs, particularly visible during the wet season, and by checking whether infected shrubs could be easily pushed over or uprooted. For coffee wilt disease, which was present in nearly all sites, we then calculated the incidence as the proportion of infected shrubs out of the total number of coffee shrubs per site. For Armillaria root rot, which was present in only roughly half of the sites, we created two variables: i) the prevalence (presence-absence) of Armillaria root rot, and ii) the incidence, which was calculated as the proportion of infected shrubs out of the total number of coffee shrubs per site for the subset of Armillaria root rot-infected sites.

Recording climatic variables

We recorded soil temperature and moisture at each site from August 2018 to July 2019. Soil temperature was recorded using iButtons (model DS1921G-F5, Maxim Integrated, San Jose, CA, USA) and moisture was measured using a portable soil moisture probe (SM150, Delta-T Devices Ltd., UK). The iButtons were wrapped in parafilm and plastic to avoid water damage, and placed 5 cm belowground near the stem of a coffee shrub, for a total of three coffee shrubs per site. The iButton was set to record every three hours. For each site, we calculated the annual average of daily mean temperature as well as the annual temperature variability. The annual temperature variability was calculated as the annual average of the daily standard deviation. Soil moisture was recorded during the dry seasons of 2018 and 2019 (February to March). At each occasion, we took three recordings 10 cm away from the stem of the coffee shrub, for a total of three coffee shrubs per site. Recordings were then averaged to obtain a yearly site-level estimate, which was then averaged across the two years. Given the large microtopographic variation across the landscape, we preferred in situ measurements over interpolation of coarse-resolution satellite derived gridded data, which are less suited to capture fine-scale variation in soil water availability. A strong and statistically significant correlation between the two years ($r = 0.81$, $p < 0.001$; Fig. S1) supports the notion that relative differences in soil moisture conditions among sites are consistent ensuring that this metric is well capturing the rank order of the sites.

Recording habitat, spatial and management variables

To characterize the habitat, spatial and management variables associated with each site, we measured canopy cover, coffee density, shade tree composition, surrounding forest cover, coffee structure index and the proportion of coffee cultivars resistant to coffee berry disease. Canopy cover was estimated from canopy photos taken from above the coffee shrubs at the centre of the plot and each of the quadrants. Canopy cover was then estimated as the mean of the percentage of pixels covered

by canopy after binarizing the five photos using the ImageJ software v. 1.50i (Schneider et al., 2012). Coffee density was counted in the 30 × 30 m inner plot. For tree species composition (a site-by-species matrix of all woody species), we performed a non-metric multidimensional scaling (NMDS) ordination with two dimensions ($K = 2$, stress = 0.224) using the metaNMDS function in the R package *vegan* (Oksanen et al., 2020). We extracted the site scores from the analysis and used the NMDS axis 1 as a predictor variable representing shade tree species composition in the analysis (see Zewdie et al., 2022 for further details on the methodology). Sites with low values of NMDS scores were characterized by forest species such as *Schefflera abyssinica*, *Teclea nobilis*, *Syzygium guineense*, *Polyscias fulva*, and *Olea welwitschii*, whereas sites with high values of NMDS scores were characterized by high abundances of *Cordia africana*, *Croton macrostachyus* and *Acacia abyssinica*. We estimated the percentage of forest in the surrounding landscape for each site using a 1 km radius using ArcMAP version 10.6.16.1 (ESRI, 2018). To characterize pruning of the coffee shrubs at each site, we used the coffee structure index, which was previously developed for the same set of sites to characterize the physical characteristics of growth of coffee shrubs that results from a different intensity of pruning practices (see “coffee structure index” in Zewdie et al., 2020). The coffee structure index is a continuous metric 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 coffee berry disease (CBD) resistant cultivars in the plot was estimated based on interviews with the farmers (Ayalew et al., 2024b). The proportion of CBD resistant cultivars ranged from 0 (only wild genotypes or local landraces) to 1 (only CBD resistant cultivars). We were unable to include tree age in our analysis due to the lack of reliable age estimates and the fact that the coffee shrubs can be several decades old in both the forests and smallholder farms. See Table S1 for detailed information on the environmental characteristics of our study sites.

Statistical analysis

We used structural equation modelling (SEM) to investigate the direct and indirect effects of climatic, habitat, spatial and management variables, as well the effect of the other pathogen species, on coffee wilt disease and Armillaria root rot, respectively, using the *psem* function in the *PiecewiseSEM* package (Lefcheck, 2016). Structural equation modeling is a powerful statistical approach that combines multiple predictor and response variables into a single framework to analyse complex relationships among a set of interconnected variables. In structural equation modeling, paths are used to represent hypothesized causal relationships between variables, with some variables acting as predictors in one path and as responses in another. This approach allows the exploration and quantification of both direct and indirect causal relationships between response and predictor variables (Lefcheck, 2016; Shipley, 2009). Total effects are the sum of direct and indirect effects and were estimated using the *semEff* package (Murphy, 2022). Statistical analyses were conducted in R v. 4.1.3 (R Core Team, 2020).

Using a priori knowledge of the study system, we constructed initial conceptual models of cause–effect relationships based on hypothetical pathways supported by the literature, separately for coffee wilt disease and Armillaria root rot (Fig. 2). To achieve normality of residuals, the incidences of coffee wilt disease and Armillaria root rot were log-transformed. Because of the intrinsic correlations between mean soil temperature, temperature variability and soil moisture, we assumed correlated errors between those variables (Fig. 2, double-headed arrows). Correlated errors describe a relationship between variables that is not presumed to be causal or unidirectional. Models were evaluated with a d-separation test to examine whether significant non-hypothesized independent paths were missing, and the overall model fit was tested with Fisher’s C statistic. A Fisher’s C test that produces a high p-value indicates that the proposed model is a good fit for the data and would likely not benefit from the inclusion of unspecified relationships

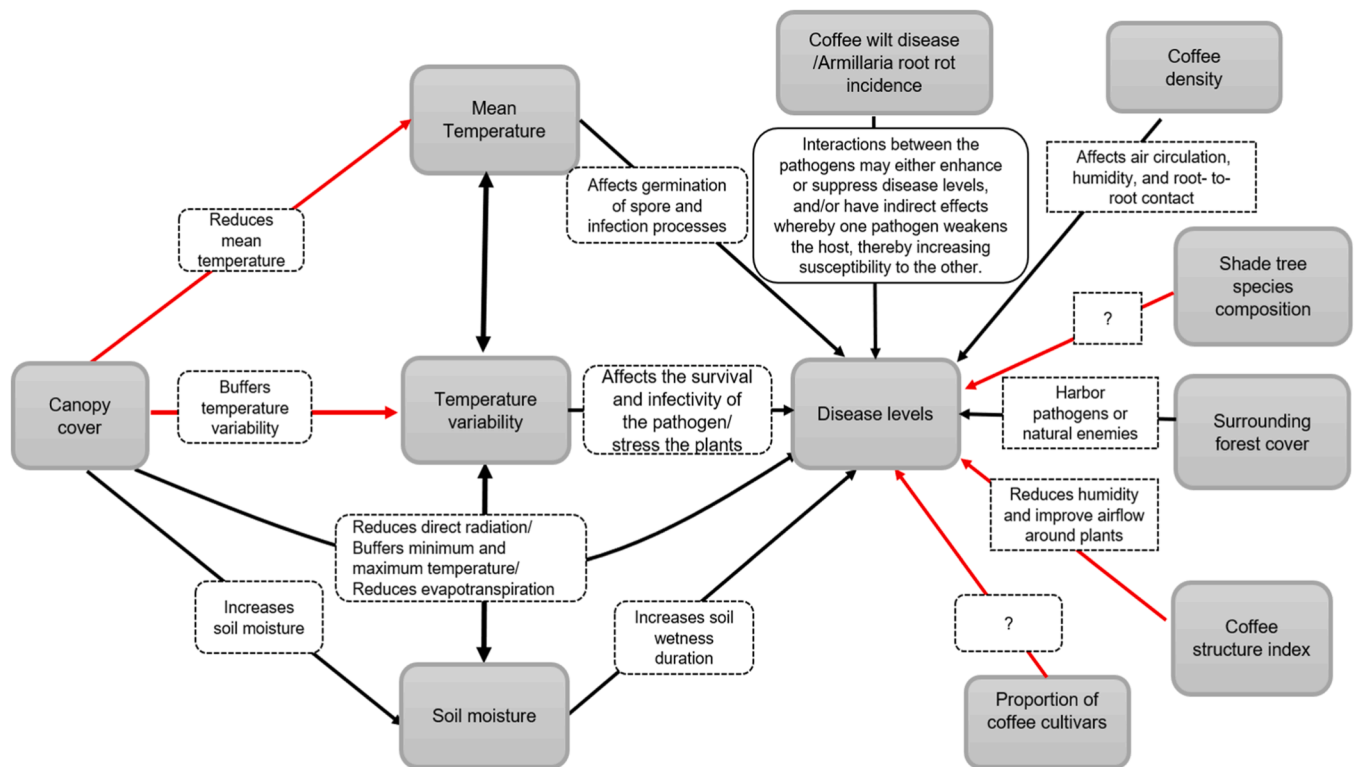


Fig. 2. Hypothesized path diagram of the direct and indirect effects of canopy cover and climate on coffee wilt disease and Armillaria root rot. Expected mechanisms behind the hypothetical pathways are shown in white boxes and are discussed in further detail in the Discussion section. Expected positive and negative relationships are presented with black and red arrows, respectively. Black double headed arrows represent correlations between climatic variables.

(Lefcheck, 2016; Shipley, 2009).

Results

The effect of canopy cover on local climate

Canopy cover lowered mean soil temperature and temperature variability, and increased soil moisture (Fig. 3 and Fig. 4a-c).

Coffee wilt disease

Coffee wilt disease was present in 54 out of 58 sites. The incidence of coffee wilt disease was affected by climate and habitat variables, but not by spatial and management variables (Fig. 3). Of the climatic variables, the incidence of coffee wilt disease was positively affected by mean temperature and soil moisture, but was not affected by temperature variability (Fig. 3 and Fig. 4d, e). Of the local habitat characteristics, coffee wilt disease was negatively affected by coffee density (Fig. 4f), and was less common in sites with a more forest like shade tree species composition (Fig. 2 and Fig. 4g). While canopy cover had no direct effect on coffee wilt disease, it indirectly affected coffee wilt disease through two opposing pathways: canopy cover decreased coffee wilt disease by lowering the mean temperature, and increased coffee wilt disease by increasing soil moisture, resulting in a non-significant total effect (β : 0.09; 95 % bootstrap CI [-0.12, 0.31]) (Fig. 3). Surrounding forest cover, coffee structure index, the proportion of CBD resistant cultivars and Armillaria root rot incidence did not affect coffee wilt disease incidence (Fig. 3).

Armillaria root rot

Armillaria root rot was present in 29 out of 58 sites. The climatic, habitat, spatial and management variables, as well as the incidence of

coffee wilt disease, could not explain the site-level incidence of Armillaria root rot (Fig. S2). However, the incidence of Armillaria root rot in the subset of sites where it was present was strongly affected by climate and surrounding forest cover (Fig. 5 and Fig. 6). Of the climatic variables, the incidence of Armillaria root rot was negatively affected by mean temperature, and positively affected by soil moisture (Fig. 5 and Fig. 6a, b). Of the local habitat characteristics, coffee density and shade tree composition did not affect Armillaria root rot incidence. While canopy cover had a direct negative effect on Armillaria root rot incidence (Fig. 6c), it also indirectly and positively affected Armillaria root rot by lowering the mean temperature and increasing soil moisture, resulting in a non-significant total effect (β : -0.22; 95 % bootstrap CI [-0.47, 0.05]) (Fig. 5). Surrounding forest cover positively affected Armillaria root rot incidence (Fig. 6d), while coffee structure index, the proportion of CBD resistant cultivars and the incidence of coffee wilt disease did not affect Armillaria root rot incidence.

Discussion

We investigated the direct and indirect effects of microclimate, habitat, spatial and management variables on coffee wilt disease and Armillaria root rot on Arabica coffee in its native distribution in southwestern Ethiopia. While it is often stated that climate change will worsen disease levels (Ayalew et al., 2024c; Jaramillo et al., 2011), our findings show that responses to temperature are strikingly different between two major fungal diseases attacking coffee in its native distribution: higher mean temperatures were related to higher incidence of coffee wilt disease, but lower incidence of Armillaria root rot. Our finding of coffee wilt disease incidence increasing with soil mean temperatures appears to contrast with Zhang et al. (2023), who reported optimal growth of *Fusarium xylarioides* arabica strains at lower temperatures (18–22 °C) as compared to higher temperatures (25–28 °C), at which robusta strains grow best. However, when inspecting the range of

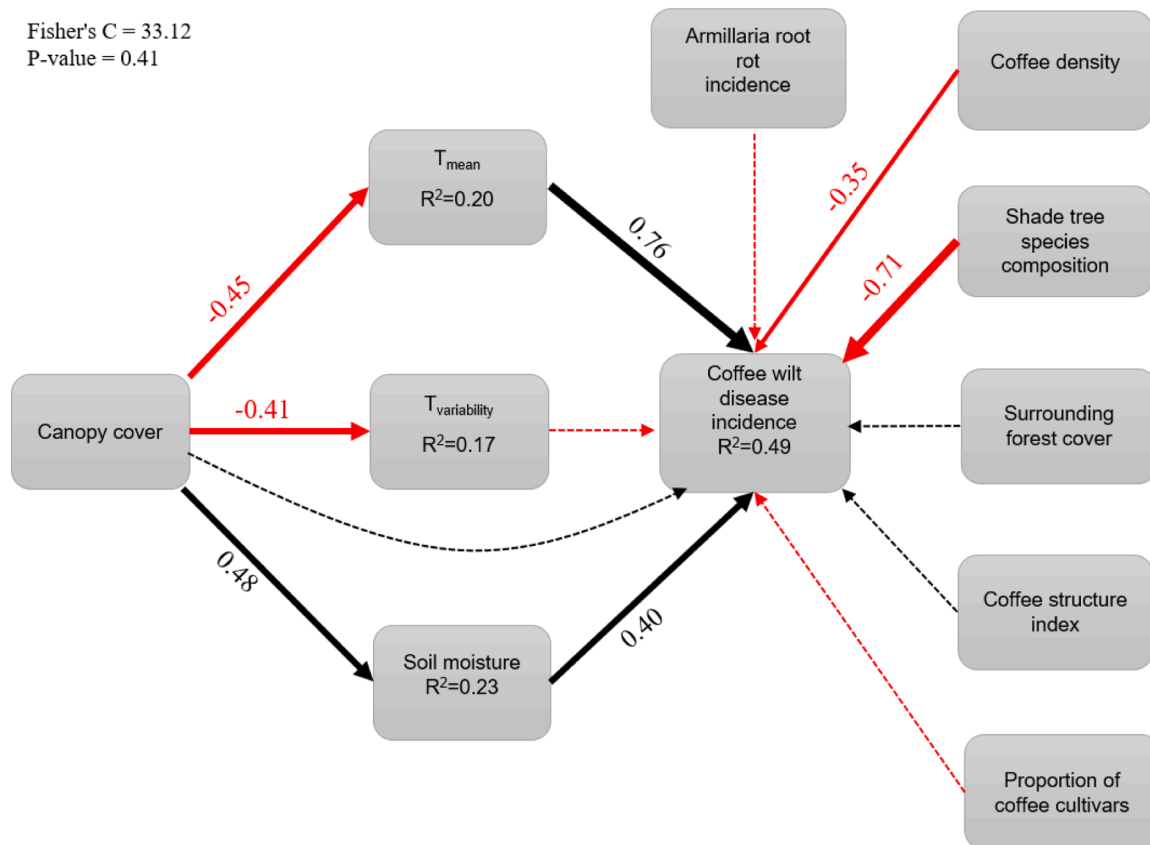


Fig. 3. Structural equation model showing the direct and indirect effects of local climate, habitat, spatial and management variables, as well as the incidence of Armillaria root rot, on the incidence of coffee wilt disease (caused by *Gibberella xylarioides*) on Arabica coffee in southwestern Ethiopia. Positive and negative relationships are presented with black and red arrows, respectively. Numbers on arrows are standardized regression coefficients, arrow thickness scales with the strength of the relationship, and R^2 -values are reported below response variables. Solid and dashed arrows represent significant ($P < 0.05$) and non-significant relationships ($P > 0.05$), respectively.

temperatures of our study sites (e.g. x-axis in Fig. 4d, with a minimum site-level temperature of 16.5 °C and maximum of 20 °C), it is apparent that most of our study sites are within the optimal range reported by Zhang et al. (2023), even though methodological differences might make a direct comparison difficult (e.g. we measured soil, not air temperature). Taken together, while our study indicates that climate change might lead to increased coffee wilt disease incidence in Ethiopia and other coffee-producing regions in Africa, and potentially facilitate the spread of the disease into coffee growing regions previously free from coffee wilt disease, there might well be a maximum temperature after which coffee wilt diseases incidence would start to decline. Conversely, Armillaria root rot incidence decreased with increasing mean temperatures, suggesting that cooler conditions are more conducive to its development. Although the impact of temperature on Armillaria root rot has not been investigated previously on coffee, studies in woody plants suggest that higher soil temperatures can inhibit Armillaria growth (Munnecke et al., 1976; Rishbeth, 1978). We thus expect that the disease pressure by Armillaria root rot will decrease with climate change, unless new heat-adapted strains evolve or colonize the area. While there is currently no documented evidence of heat-adapted Armillaria strains affecting coffee or other crops, soilborne pathogens in other systems have demonstrated the capacity to adapt to changing climatic conditions (Delgado-Baquerizo et al., 2020; Peng et al., 2023). Thus, while our findings suggest a likely reduction in Armillaria risk under warming, continued monitoring is warranted to detect potential shifts in pathogen behavior or range. In contrast to the different responses to temperature, both diseases were positively affected by soil moisture, which is a common response for wilt and root rot fungi. Consistent with our findings, Peck and Boa (2024) reported that coffee wilt disease thrives under

moist soil conditions that facilitate infection and spread. Similarly, Armillaria species are known to increase in incidence with higher soil moisture, which facilitates their colonization of host roots (Kubiak et al., 2017). Notably, we detected this pattern using soil moisture data based on only two single-point dry-season soil measurements (2018 and 2019), which will not fully capture seasonal or interannual variability. However, the soil moisture measurements correlated strongly between the two years, suggesting a consistency in rank-order among the sites for soil moisture. As the same time, disease development is a long-term process and our reliance on short-term climate data and disease measurements might represent a limitation, as highlighted by the long-term study by Musoli et al. (2008), which showed low coffee wilt disease levels four years after plot establishment, with severe outbreaks appearing only after nearly a decade. Hence, we encourage future studies to incorporate multi-year climate data to better capture temporal disease dynamics. Overall, the contrasting temperature responses of coffee wilt disease and Armillaria root rot make it more difficult to take management actions. For example, lowering the mean temperature is expected to reduce coffee wilt disease, but increase Armillaria root rot. In contrast, lowering soil moisture might be an effective management strategy for both fungal diseases.

The effect of canopy cover on disease levels involved a complex set of opposing direct and indirect effects, where the identity and sign of the pathways differed between the two diseases. Thus, while canopy management was related to important climatic drivers of disease dynamics, its net impact on both coffee wilt disease and Armillaria root rot was non-significant. Canopy cover affected coffee wilt disease through two opposing pathways: by lowering the mean temperature, canopy cover reduced disease incidence, and by increasing soil moisture, it increased

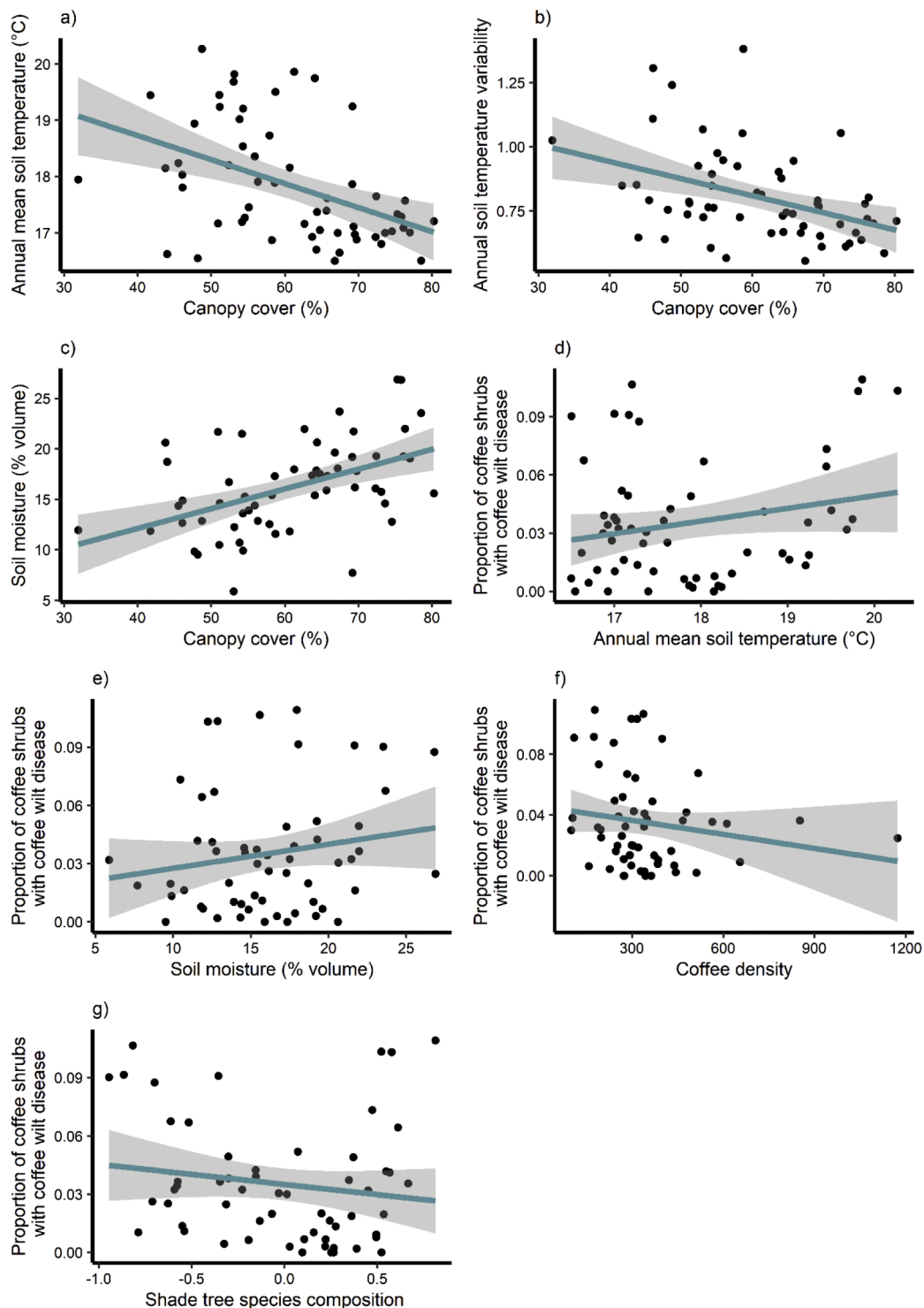


Fig. 4. The effect of local climate, habitat, spatial and management variables on the incidence of coffee wilt disease (caused by *Gibberella xyloarioides*) on Arabica coffee in southwestern Ethiopia in the rainy season of 2019. Shown are the relationships between canopy cover and (a) annual mean soil temperature, (b) annual soil temperature variability and (c) soil moisture, as well as the relationships between coffee wilt disease incidence with (d) annual mean soil temperature, (e) soil moisture, (f) coffee density and (g) shade tree species composition. The black circles represent the proportion of infected coffee shrubs with coffee wilt disease at the site-level, and the blue trend line represents the model-predicted relationship. Shaded areas represent the 95 % confidence interval. Only significant relationships are shown.

disease incidence. In contrast to coffee wilt disease, canopy cover had a negative direct effect on Armillaria root rot. Yet, the indirect effects of reducing mean temperature and increasing soil moisture, that both are positive for Armillaria, resulted in a non-significant total effect of canopy cover on Armillaria root rot. The negative direct effect of canopy

cover on Armillaria root rot incidence might be due to the fact that several sites with lower canopy cover were recently opened up, leaving many fresh stumps that serve as substrate for Armillaria. Indeed, previous studies have shown that dead woody material, particularly tree stumps and large logs, can serve as a persistent inoculum source for

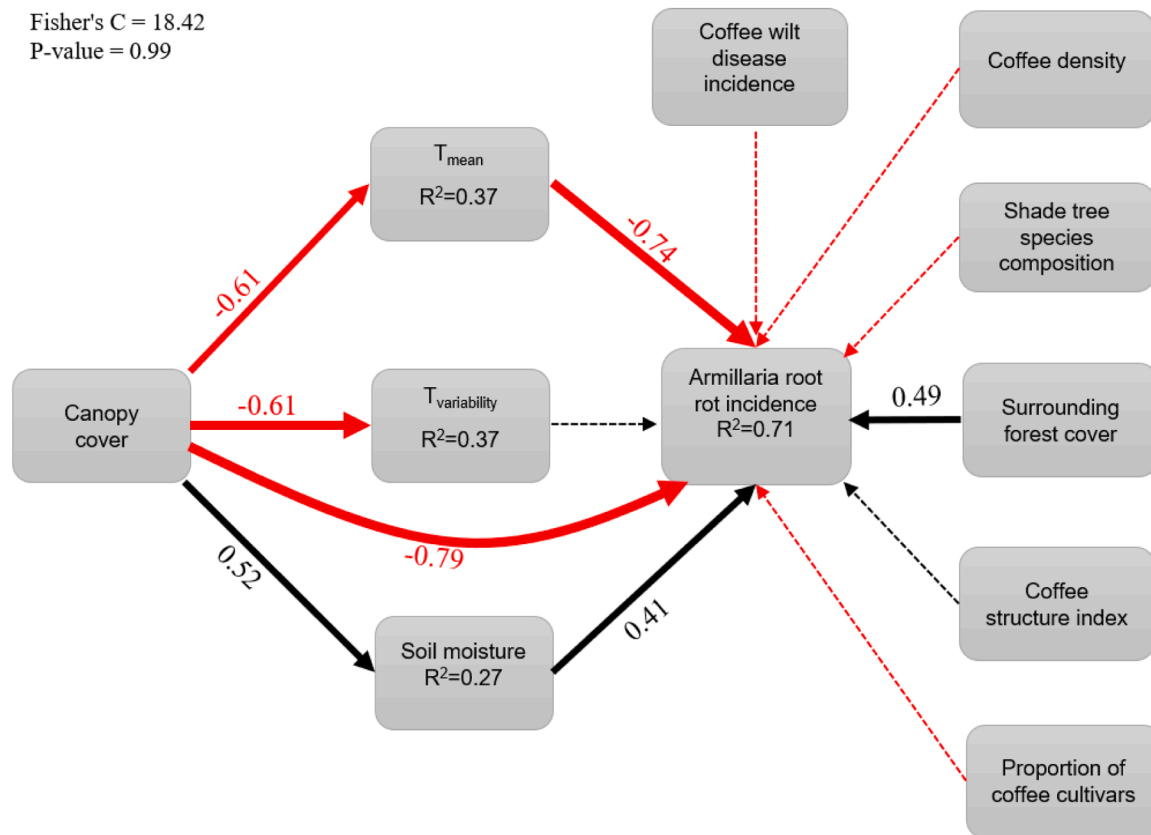


Fig. 5. Structural equation model showing the direct and indirect effects of local climate, habitat, spatial and management variables, as well as the incidence of coffee wilt disease, on the incidence of Armillaria root rot (caused by *Armillaria mellea*) on Arabica coffee in southwestern Ethiopia. Positive and negative relationships are presented with black and red arrows, respectively. Numbers on arrows are standardized regression coefficients, arrow thickness scales with the strength of the relationship, and R^2 -values are reported below response variables. Solid and dashed arrows represent significant ($P < 0.05$) and non-significant relationships ($P > 0.05$), respectively.

Armillaria root rot (Wargo & Shaw, 1985 ; Redfern & Filip, 1991). We therefore speculated that Armillaria is – in addition to climate – also limited by substrate, and that by removing canopy cover quickly, farmers unintentionally create ample substrate for Armillaria. However, we did not detect a significant relationship between the presence of dead wood and Armillaria incidence across a subset of 30 sites for which dead wood data were available (Text S1). However, we stress that this lack of significance may reflect the limited number of study sites. Additionally, the quality or decay stage of the dead wood, which we did not quantify in detail, could play an important role in modulating its suitability as a substrate. In case dead wood is important, a better management action for reducing shade could be to uproot trees or selectively prune larger branches instead of cutting down entire trees, maintaining some shade while limiting the creation of new substrate for Armillaria. We also suggest that future studies incorporate long-term monitoring after shade tree removal and more detailed assessments of deadwood characteristics to better understand these dynamics. Overall, our findings suggest that modifying canopy cover to reduce coffee wilt disease and Armillaria root rot is complex, and will require further studies into the drivers of, and responses of diseases to, temperature and soil moisture (see management implications below).

Coffee wilt disease responded to coffee density and shade tree composition, whereas Armillaria root rot was influenced by surrounding forest cover, and we detected no effect of management actions, such as pruning and cultivar use, on either disease. While interesting, we are hesitant to interpret the relationship between density and disease levels as causal in our system without further experimental studies. While counterexamples do exist (Brody et al., 1990; Maas et al., 2006), the majority of empirical studies indicate that high plant densities promote

pathogen dispersal by increasing the likelihood that pathogen propagules are deposited on neighbouring susceptible hosts, and promote successful establishment by increasing relative humidity and soil moisture (Burdon & Chilvers, 1982; Café-Filho et al., 2019). The relationship between coffee wilt incidence and shade tree species composition highlights the fact that at least some shade tree species may create microenvironments that either suppress or favor the growth of pathogens, and thereby influence disease dynamics. Such shade tree species specific effects might be due to trait differences among shade tree species that influence the understory microclimate, pathogen dispersal, nutrient cycling and the abiotic and biotic soil characteristics (Avelino et al., 2023; Gagliardi et al., 2021). For example, root exudates or biochemical compounds have been shown to inhibit the growth of *Fusarium oxysporum* (Hao et al., 2010; Were et al., 2022). In the current study, we found that coffee wilt disease was lower in sites characterized by forest tree species, such as *Schefflera abyssinica*, *Syzygium guineense*, *Polyscias fulva*, and *Olea welwitschii*. Overall, these findings emphasize the importance of understanding the functional roles of individual shade tree species in agroforestry systems to inform management strategies aimed at disease suppression.

While Armillaria root rot was not affected by coffee density and shade tree species composition, we found a positive relationship between surrounding forest cover and Armillaria root rot. This supports the idea that forest ecosystems can act as reservoirs for soil-borne pathogens, and that pathogen spillover is more likely at the interface between natural and managed landscapes (Plantegenest et al., 2007; Prospero & Cleary, 2017). As forests harbour the majority of threatened biodiversity within this landscape, there thus seems to be a trade-off between Armillaria disease levels and biodiversity (Hylander et al.,

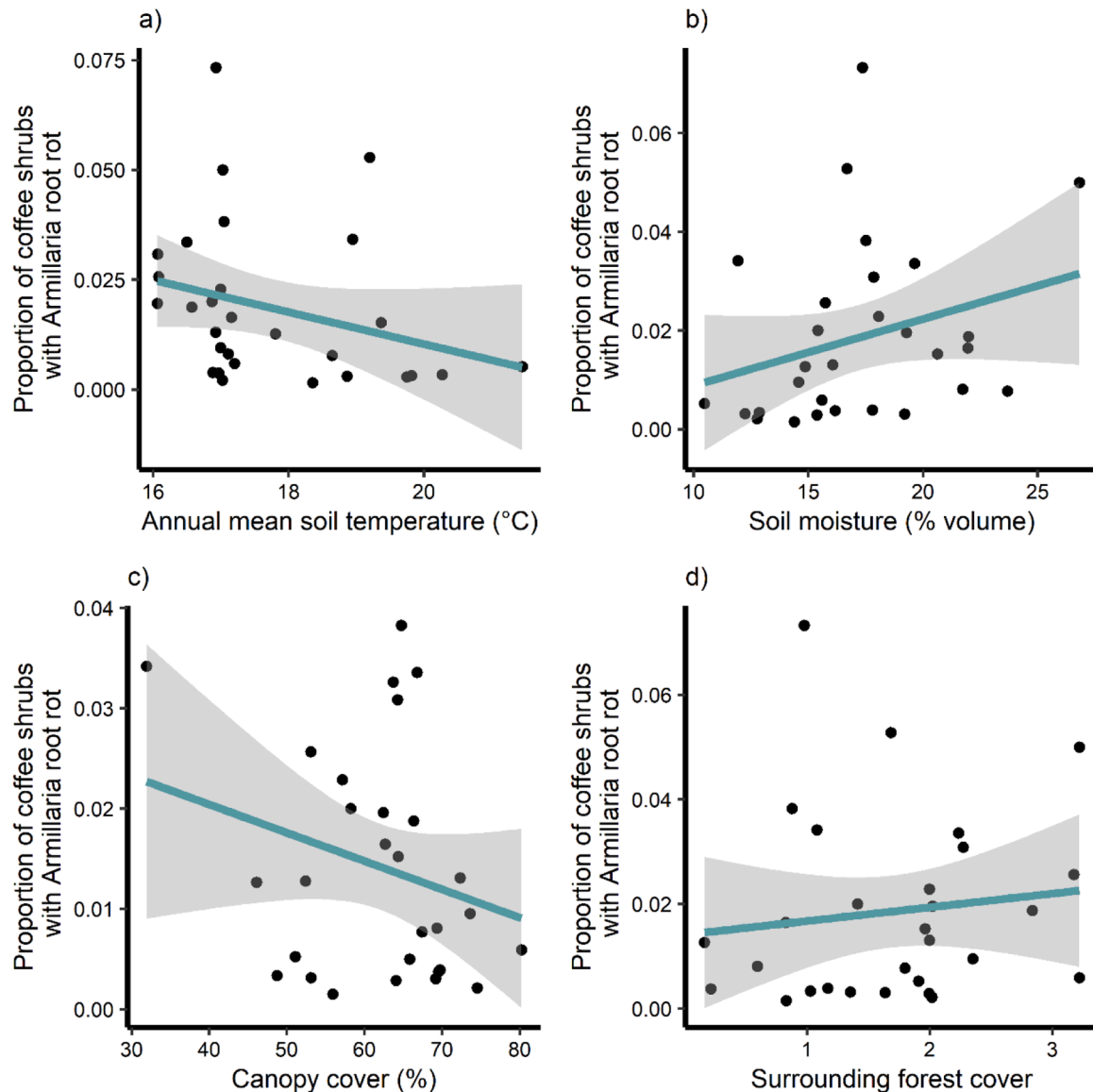


Fig. 6. The effect of local climate, habitat, spatial and management variables on the incidence of *Armillaria* root rot (caused by *Armillaria mellea*) on Arabica coffee in southwestern Ethiopia in the rainy season of 2019. Shown are the relationships between *Armillaria* root rot incidence and (a) annual mean soil temperature, (b) soil moisture, (c) canopy cover and (d) surrounding forest cover. The black circles represent the proportion of infected coffee shrubs with *Armillaria* root rot in the subset of sites where the disease was present, and the blue trend line represents the model-predicted relationship. Shaded areas represent the 95 % confidence interval. Only significant relationships are shown.

2024). Regarding management, we found that pruning and the use of coffee cultivars did not influence coffee wilt disease and *Armillaria* root rot. The absence of a relationship between pruning and *Armillaria* root rot might be because pruning primarily influences aboveground pathogen dynamics, rather than root-associated, soil borne pathogens. However, the absence of a relationship between pruning and coffee wilt disease is surprising, as pruning is known to facilitate the transmission of coffee wilt disease from infected to healthy trees due to the use of non-sterile tools and the creation of wounds (Adugna et al., 2009; Waller et al., 2007). The finding that the proportion of CBD resistant cultivars had no effect on coffee wilt disease and *Armillaria* root rot goes against patterns found for Robusta coffee, where wild populations were often more resistant to coffee wilt disease than cultivated clones (Phiri & Baker, 2009). However, this discrepancy is not very surprising, as most cultivars in our study area have been selected based on their resistance to coffee berry disease, and coffee berry disease is a pathogen with a different infection route and pathogenicity system as compared to coffee wilt disease and *Armillaria* root rot. Nonetheless, our findings provide

important insights into the absence of cross-resistance and cross-facilitation between coffee berry disease on the one hand, and coffee wilt disease and *Armillaria* root rot on the other hand. Although coffee wilt disease and *Armillaria* root rot both have soil-borne phases, our structural equation models revealed no significant association between the incidence of the two diseases. As such, we found no evidence that physiological stress caused by *F. xylarioides* could predispose coffee trees to *A. mellea* infection, or vice versa (Baumgartner et al., 2011). This suggests that, within the studied agroecosystem, these pathogens occupy distinct niches and do not interact during the infection process. At the same time, our study is observational and the analyses were conducted at the site-level. Hence, future studies combining controlled inoculation experiments with longitudinal field monitoring are necessary to validate whether pathogen coexistence changes disease trajectories in coffee systems, as observed in other perennial crops (Bebber et al., 2016; Lamichhane & Venturi, 2015).

Management implications

Our aim was to propose sustainable, climate- resilient solutions to battle two major understudied diseases on coffee on the African continent. Yet, the complex direct and indirect effects of canopy cover, and the opposing responses of the two pathogens to temperature, seem to rule out simple win-win strategies to battle both fungal diseases simultaneously.

From a practical perspective, one way to think about it is to evaluate which disease is most problematic within a certain region, and then take actions that suppress the disease that is causing serious economic damage. For example, if coffee wilt disease is causing major economic damage in one particular region, and Armillaria is absent or at very low levels, our findings suggest two management actions. First, farmers might increase canopy cover to lower mean temperature, alongside drainage practices to avoid an increase in soil moisture. Second, farmers might change the shade tree species composition. For this, we recommend further studies on plant traits and shade tree-mediated disease control. If Armillaria root rot is the most problematic disease in another region, and coffee wilt disease is absent or at very low levels, our findings suggest that it is worthwhile to increase the temperature and reduce soil moisture, which could be achieved by reducing the canopy cover. As discussed above, one way to do this might be to prune the shade trees, as cutting down trees might create resources for Armillaria. Another way to limit Armillaria root rot is to reduce the surrounding forest cover, for example by creating buffer zones. However, it is important to consider the trade-offs between reducing disease levels and removing surrounding forest, as the surrounding forest also contributes to ecosystem services like carbon sequestration, natural biocontrol and conservation. While it would be useful to understand how sites, or entire regions, could avoid infection, we gained very little insights on how to avoid infection of a site by one of the diseases: coffee wilt disease was present nearly everywhere (so we could not test drivers of presence-absence), whereas Armillaria root rot incidence was not related to any of our investigated predictor variables.

If both pathogens are causing damage, we can opt to only change variables that affect a single disease. Regarding temperature and soil moisture, it might be promising to focus on how traits of individual shade tree species, such as leaf shape, rooting depth and canopy architecture, affect daily shade patterns, soil moisture and rainfall interception, and how this in turn affects the dynamics of these fungal diseases (Gagliardi et al., 2021, Staver et al., 2001). At the same time, future studies can delve deeper into the drivers of individual aspects of climatic variables, and their influences on disease dynamics. For example, studies might investigate which specific aspects of temperature the different diseases respond to: while the two diseases responded in different ways to annual temperature, it could be that, for example, one disease is affected by temperature during the rainy season, whereas the other disease is affected by temperature during the dry season. Non-linear relationships and threshold values of both temperature and soil moisture effects might also play a crucial role. If such non-linearities or thresholds exist, perhaps it is possible to find cases in which it is favorable for disease management to open up the canopy to reduce the soil moisture in some sites, but to increase the shade in other sites to reduce temperature. Overall, our findings suggest how we can sustainably manage different aspects of the environment to reduce the impact of two major diseases on Arabica coffee in a changing climate.

Data availability statement

Data will be deposited in the Dryad Digital Repository.

CRediT authorship contribution statement

Biruk Ayalew: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Project administration,

Methodology, Investigation, Formal analysis, Data curation. **Kristoffer Hylander:** Writing – review & editing, Validation, Supervision, Conceptualization. **Beyene Zewdie:** Writing – review & editing, Methodology, Conceptualization. **Francesco Zignol:** Writing – review & editing, Data curation. **Ayco J.M. Tack:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization.

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

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.baee.2025.10.005.

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