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Coffee variety outweighs associated tree identity in shaping disease incidence and fruit load in a large-scale Ugandan Robusta agroforestry system

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Article

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Abstract

Robusta coffee in Uganda is traditionally cultivated under agroforestry systems, yet farmers increasingly question whether certain tree species exacerbate disease risks or negatively impact coffee productivity. Consequently, we assessed the effects of associated tree identity, spatial arrangement, and coffee variety on major coffee diseases and fruit loads, based on a cross-sectional field survey in the Kaweri Coffee Plantation, Uganda's largest Robusta coffee estate. Four dominant associated tree species—Mugavu (*Albizia coriaria*), Jackfruit (*Artocarpus heterophyllus*), Bark-cloth fig (*Ficus natalensis*), and Avocado (*Persea americana*)—were selected across multiple Robusta varieties. Three major foliar diseases, *i.e.* coffee wilt disease (CWD), coffee leaf rust disease (CLR), and Brown-eye spot (BES) were monitored during the rainy season, when disease pressure peaks. Disease incidence was extremely high for CLR and BES, approaching 100%. Coffee variety was the strongest predictor of leaf CLR and BES incidence. By contrast, fruit load depended on complex interactions among tree species, tree–coffee distance, and coffee variety. Notably, fruit load per branch increased significantly near Mugavu, while other tree species had neutral or negative effects. The relation between CLR and fruit load also varied among varieties. Our findings highlight the need for Robusta breeding programs to consider agroforestry conditions and tree–disease interactions, rather than relying on single-trait selection. Moreover, associated tree diversity, density, and spatial arrangement—as well as broader ecological factors such as soil fertility and biodiversity—likely modulate diseases and productivity, and should be integrated into future agroforestry recommendations.

Introduction

Coffee is traditionally cultivated in agroforestry systems across tropical regions, accounting for about 60% of global coffee production (Koutouleas et al. 2022). Associated trees are a major component of coffee agroforestry systems (CAS), providing multiple ecosystem services such as carbon sequestration, water conservation, soil fertility enhancement, income diversification, and improved coffee quality (Cerdán et al. 2012; Lasco et al. 2014; Wright et al. 2024). They also influence the regulation of pests and diseases by various mechanisms, including the promotion of natural enemies and parasitoids, improved efficiency of entomopathogens, physical obstruction or resource dilution for pathogens and pests, disruption of pest life cycles, and allelopathic effects (Schroth et al. 2000; Cerda et al. 2020; Piato et al. 2020; Rodriguez-Gallo et al. 2024). However, adverse effects related to shading provided by associated trees are also reported on pests and diseases (Avelino et al. 2018; Schroth et al. 2000; Staver et al. 2001). In addition, the benefits of various associated trees on coffee fruit load remain also debated. Global comparisons between agroforestry and monoculture systems often show no clear advantage (Wright et al. 2024), and lower fruit loads have even been reported in wild coffee agroforests under excessive shading (> 50%) (Broeckhoven et al. 2025; Haggar et al. 2011).

The effects of associated trees are dependent on tree species, age, density and management within the system (Avelino et al. 2020; Nantongo et al. 2025) but also on tree and leaf traits (Avelino et al. 2023). Yet, comprehensive evaluations of individual CAS components remain scarce in Robusta CAS (Nantongo et al. 2025) contrary to Arabica, and most assessments are restricted to simple comparisons with monocultures (Broeckhoven et al. 2025). The shading capacity of a tree increases with its age, size, and planting density; differences in shade provision are expected among tree species (Piato et al. 2020). Globally, associated trees have been shown to regulate coffee diseases more effectively than insect pests (Ayalew et al. 2022). A disease survey performed in the Uganda's largest coffee estate, Kaweri Coffee Plantation, showed a negative correlation between increasing shade tree diversity and damages caused by the pests *Xylosandrus compactus* and *Epicampoptera andersoni*, as well as with the pathogens *Hemileia vastatrix* and *Cercospora coffeicola* (Nanjego et al., 2024b). However, adverse effects were observed for other pests, and neither tree species or coffee variety were considered (Nanjego et al., 2024b). Yet, some tree species can exacerbate pest problems: in Ugandan Robusta CAS, *Albizia chinensis* (Osbeck) Merr. was associated with higher infestations of the black coffee twig borer (*X. compactus*) (Bukomeko et al. 2018), and *Maesopsis eminii* Engl., a commonly used associated tree, was identified as a reservoir of this pest (Kagezi et al. 2019).

Unraveling the complexity of associated tree–coffee–disease interactions is critical for sustaining Robusta CAS productivity, especially in Uganda where Robusta accounts for 80% of national coffee production, and nearly all Robusta is cultivated under CAS (Nantongo et al. 2025). The present study evaluates in Kaweri Coffee Plantation the relationships between dominant associated tree species integrated into Robusta CAS and the incidence of major coffee diseases—namely coffee leaf rust (CLR, *Hemileia vastatrix*), brown-eye spot (BES, *Cercospora coffeicola*), and coffee wilt (CWD, *Fusarium xylarioides*)—and their association with coffee fruit load, during the rainy season, considered as the peak for many coffee diseases. We hypothesized that (i) associated trees and distance to trees can influence coffee diseases, (ii) coffee varieties influence coffee diseases, (iii) the response of Robusta coffee depends of interactions between the identity of trees and coffee varieties, and (iii) fruit load of a coffee variety is impacted by associated tree species and distance.

Materials and methods

Study site

The study was carried out from October to November 2023 at Kaweri Coffee Plantation, MaduduSub-County, Mubende District, Central Uganda (00°36'N, 31°24'E; Fig. 1). This period corresponds to the second rainy season (September–November), with a monthly rainfall averaging 200–300 mm, November being the wettest month of the year. The total annual rainfall averaging distributed over the two rainy seasons (March–May and September–November) was 938.8 mm in Kaweri Coffee Plantation for 2023 The second rainy season is characterized by strong rains compared to the first one with rising rainfall. Fungal pathogens responsible for coffee foliar diseases are generally related to high humidity and favored by extreme events, and peaks of foliar diseases are consequently observed during or after rainy seasons (Lu et al. 2022). Mean temperatures range from 13–14°C (minimum) to 26–28°C (maximum) (Najjuma et al. 2021). Kaweri Coffee Plantation (2,512 ha, of which 1,626 ha are planted with Robusta coffee and 25% natural tropical rainforest) was selected because of its long-standing coffee production, consistent management practices, and diverse tree cover. The plantation management is considered as intensive, i.e. with a frequent weeding, pruning of coffee shrubs once a year, two rounds of organic fertilizer application per year, and watering of coffee shrubs in extreme dry season as reported by section managers (for more details, see Table S1). Consequently, the study site allowed to capture disease incidence and fruit load patterns under realistic farming conditions in a long-term agroforestry system, which inherently limits experimental control but increases ecological relevance. The plantation is divided into five sections (Luwunga, 354 ha; Nonve, 342 ha; Kyamutuma, 344 ha; Kitagweta, 348 ha; and Kitemba, 312) which were treated as field replicates (Fig. 1). Coffee variety was identified from plantation records. Soil properties were determined for each section (Table S2), revealing similar characteristics (PERMANOVA, $P = 0.1747$). The coffee varieties are from three different origins, i.e., open pollinated-1 (Op1) representatives of the different Robusta production areas in Uganda, 4 coffee lines (clone A: 1s/2, B:0 1s/3, D: 1s/6, F: 257/32) and one hybrid (clone C: combination of clones 1s/2, 1s/3, and 1s/6). These were entirely planted between 2001 and 2004 (Pinard et al. 2016). However, there were also open-pollinated-2 (Op2), probably deriving from open-pollinated-1 and coffee lines. The Op2 shrubs were harboring different traits from mother lines. The coffee varieties were initially distributed to Ugandan farmers in the 1980s for their high fruit loads, good bean and cup quality, and relatively high field resistance to CLR and BES, while resistance to CWD was not taken into account (Musoli et al. 2008) (for more details, see Table S3)

Experimental design

Four tree species frequently associated with Robusta coffee shrubs by farmers due to their roles for ecosystem services (*e.g.*, soil fertility, insecticidal activities, food and feed) were selected, *i.e.* Mugavu (*Albizia coriaria* Welw. ex Oliv), Jackfruit (*Artocarpus heterophyllus* Lam), Bark-cloth fig (*Ficus natalensis* Hochst), and Avocado (*Persea americana* Mill) (Buyinza et al. 2015; Cerda et al. 2020). For each section of Kaweri coffee plantation, three to six individuals of each associated tree species were chosen as replicate units. Overall, 24 Mugavu (*Albizia coriaria* Welw. ex Oliv), 21 Jackfruit (*Artocarpus heterophyllus* Lam), 21 Bark-cloth fig (*Ficus natalensis* Hochst), and 19 Avocado (*Persea americana* Mill) trees (85 associated tree replicates in total) (Table S3). The density of associated trees in Kaweri Coffee Plantation is relatively heterogeneous, resulting from the site's historical management (remaining trees from deforestation, scatter tree planting by farmers). Consequently, from each associated tree selected, a transect direction was set to avoid any effects of other surrounding trees. Three coffee shrubs were sampled along the transect at different distances (3–5 m, 10–12 m, 20–22 m). A total of 255 shrubs were assessed. All associated trees were georeferenced to allow long-term monitoring (Fig. 1).

Coffee disease survey

On each shrub, twelve primary branches were sampled across three canopy levels (top, middle, bottom), selecting one branch per orientation (N, S, E, W) (Olango et al. 2024; Segura et al. 2004). Two approaches were used to estimate incidence as detailed in Madden et al (2007), depending on the biology of pathogens. For CWD, which is a vascular wilt and killing coffee plants, incidence was first recorded as whole-shrub incidence, i.e., presence / absence per shrub based on early-stage symptoms (leaf curling, yellowing) before shrub mortality (Musoli et al. 2008; Girma et al. 2010). The second approach was applied to the three diseases CLR, BES, and CWD, and corresponds to the leaf disease incidence, calculated as the proportion of symptomatic leaves per branch. Average fruit load per branch was estimated at ripening stage as the mean of berries across the 12 branches.

Data curation

Twenty-three shrubs were excluded: nine lacked leaves, and fourteen belonged to underrepresented variety–tree combinations (e.g., only one replicate for clone D under *F. natalensis*), and clone H was represented by four replicates with *P. americana*, two with *A. coriaria*, one with *A. heterophyllus*, and none with *F. natalensis*. Overall, 222 coffee shrubs were used for the statistics.

Statistical analyses

Differences in soils and tree traits were estimated by PERMANOVA using adonis3 function from the GUniFrac package v.1.8 (Chen et al. 2023), and principal component analysis of tree traits using fviz_pca_biplot function from factoextra package v.1.0.7 (Kassambara and Mundt, 2020). Generalized linear mixed models (GLMMs) were used to analyze disease incidence and average fruit load per branch. Incidence at the whole coffee shrub level was analyzed for CWD with binomial regression. Coffee leaf disease incidence was considered as a proportion at the branch level (number of infected leaves / total number of leaves). Consequently, beta regression was identified as the most appropriate model type. Because Beta regression models require values strictly between 0 and 1, incidence values equal to 1 were adjusted to 0.999, and a zero-inflation term was incorporated. Coffee diseases are not equally distributed within coffee shrub canopy (Nanjego et al. 2024a). Consequently, for BES and CWD, the top portion of shrubs was analyzed; for CLR, the lower portion (Alvarado-Huamán et al. 2020; Peck & Boa, 2024; Silva et al. 2016). Associated tree species, distance, and their interaction were included as fixed effects and locked for all models. The traits of associated trees were not included in the models because canopy, tree height and diameter of the trunk was highly related to tree species (for more details, see Figure S1). Nested random effect accounting for section, associated tree replicates and shrubs effect were added. A model selection was applied, first based on AICc, and secondly on correct assumptions of residual distribution and homoscedasticity. Variables and interactions were incrementally added in fixed, zero inflation and dispersion terms. Competing models were compared using dredge function from the Mumin package v1.48.11 (Bartoń, 2025). Model residuals were assessed with the DHARMa package v0.4.7 (Hartig, 2024), testing residual distribution (Kolmogorov–Smirnov), dispersion, and zero inflation. Finally, type II ANOVA was performed on selected models to detect significant portions of variance explained by each variable. Marginal means and contrasts were computed using marginaleffects package v0.31.0 (Arel-Bundock et al. 2024). Predictions were generated on duplicated datasets, creating one copy for each combination of focal values using counterfactual grids. This approach allows broader combinations of non-focal variables. The only exception concerns the estimation of the slope between disease incidence and fruit load, for which predictions were computed on the empirical grid (i.e., the original data). This choice was made to avoid biologically unrealistic combinations of leaf-level disease incidence.

Results

Coffee shrub disease incidence

Across the plantation, the incidence of CLR and BES approached 100% of coffee shrubs, and 50% for CWD (Fig. S2). Shrub disease incidence was assessed for CWD to evaluate potential interactions with CAS characteristics. Selected model had 4 parameters (AICc = 316.7) and good residuals (Table S5, Fig. S3). Coffee variety significantly influenced CWD incidence (Table 1). Interaction between distance from associated trees and tree species showed a near-significant effect (Table 1). Pairwise slope analyses indicated that shrub CWD incidence slightly but significantly increased with distance from *F. natalensis* (slope = 0.02; confidence intervals, $CI_{95\%}$ = 0.01 to 0.04; z = 3.05; P = 0.002) and a tendency increased with distance from *P. americana* (slope = 0.02; $CI_{95\%}$ = -0.01 to 0.037; z = 1.76; P = 0.079) (Fig. 2A). Variety comparisons revealed significantly higher shrub CWD incidence in varieties clones A (estimated marginal means, EMMs = 0.68; $CI_{95\%}$ = 0.52 to 0.84) and Op2 (EMMs = 0.68; $CI_{95\%}$ = 0.50 to 0.86) compared with varieties clones C (EMMs = 0.37; $CI_{95\%}$ = 0.20 to 0.55) and Op1 (EMMs = 0.27; $CI_{95\%}$ = 0.06 to 0.49). The varieties Clones B and F did not differ significantly from other varieties (Fig. 2B).

Table 1
Impact of agroforestry system characteristics on CWD whole-shrub incidence (Type II Wald ² test)

χ				
Disease	**Variables**	**χ^2**	**Df**	**Pr(>χ^2)**
CWD	Tree species	1.30	3	0.73
	Distance	1.88	1	0.17
	Coffee variety	10.95	5	0.05 *
	Tree species:Distance	7.28	3	0.06

Coffee leaf disease incidence

No correlation was detected among leaf incidence across canopy portions, except a weak negative association between CLR and BES on lower portions (▯ = -0.077) (Fig. S11). The leaf CWD incidence did not show any association with our variables (Table S7). For BES and CLR, selected model had respectively 5 and 7 parameters (Tables S6 and S7). Based on AICc, BES first rank model had good residuals (Table S6, Figs. S5 and S7), but only the third CLR rank model met correct assumption of residuals (Table S8, Figs. S6 and S7). The Incidence patterns were largely driven by coffee variety for both CLR and BES (Table 2). In addition to its effect on CLR absence (zero-inflation terms), coffee variety was a significant predictor of branch-level CLR incidence intensity (Table 2). Moreover, CLR incidence was weakly influenced by distance from associated trees (Table 2). By contrast, neither leaf BES nor CWD incidence intensity was affected by distance or coffee variety (Table 2). The (log) number of leaves per branch strongly predicted incidence dispersion for BES, and CLR (Table 2), with higher leaf counts reducing variability in incidence.

Table 2
Impact of agroforestry system characteristics on leaf disease incidence (Type II Wald ² test)

χ					
Disease	**Term**	**Variables**	**χ²**	**Df**	**Pr(>χ²)**
BES	Fixed	Tree species	2.01	3	0.57
		Distance	0.15	1	0.70
		Tree species:Distance	2.50	3	0.48
	Zero inflation	Coffee variety	139.09	5	< 2e-16 ***
	Dispersion	log(Leaf total count)	32.82	1	1e-8 ***
CWD	Fixed	Tree species	1.86	3	0.60
		Distance	0.19	1	0.66
		Tree species:Distance	0.98	3	0.81
CLR	Fixed	Tree species	3.41	3	0.33
		Distance	3.20	1	0.07
		Coffee variety	49.01	5	< 2e-16 ***
		Tree species:Distance	2.96	3	0.40
		Coffee variety:tree species	15.56	15	0.41
	Zero inflation	Coffee variety	42.66	5	< 2e-16 **
	Dispersion	log(Leaf total count)	123.34	1	< 2e-16 ***

CLR exhibited the highest leaf incidence (Fig. 3). Clone A showed significantly lower leaf CLR incidence (EMMs = 0.14; $CI_{95\%}$ = 0.10 to 0.16) compared to other varieties, particularly clone C (EMMs = 0.33; $CI_{95\%}$ = 0.27 to 0.38). The Leaf BES incidence was generally low, ranging from clone C (lowest: EMMs = 0.02; $CI_{95\%}$ = 0.01 to 0.03) to Op2 (highest: EMMs = 0.12; $CI_{95\%}$ = 0.10 to 0.14). CLR was the only disease whose incidence declined with increasing distance from associated trees (slope = -0.002; $CI_{95\%}$ = -0.004 to 0; z = -1.74; P = 0.08) (Fig. 4).

Average coffee fruit load per branch

The selected model had 12 parameters and was the first AIC ranked model (Table S9). Residuals were correct except homoscedasticity assumption was not perfectly met for this model (Figs. S9 and S10), however other models had also this issue, so we choose to keep this one based on AICc. Average fruit load was strongly associated with coffee variety, as well as leaf CLR incidence and BES incidence (Table 3). The variety Clone A displayed the highest fruit load (92 berries/branch; $CI_{95\%}$ = 69 to 115), while the varieties clones C (46 berries; $CI_{95\%}$ = 35 to 57) and Op2 (48 berries; $CI_{95\%}$ = 34 to 63) produced the lowest (Fig. 5). Average fruit load relationship with distance from associated trees varied depending on coffee variety and shade tree species. More precisely, the varieties clones F (slope = 1.0; $CI_{95\%}$ = 0.1 to 1.8; z = 2.26; P < 0.01) and Op1 (slope = 2.7; $CI_{95\%}$ = 1.8 to 3.7; z = 5.5; P < 0.0001) showed more berries per branch further from associated trees, whereas the varieties clones B (slope = -0.8; $CI_{95\%}$ = -1.4 to -0.3; z = -3.1; P < 0.001) performed better closer to trees (Fig. 6). For associated tree identity proximity to *A. coriaria* increased fruit loads, with berry number decreasing by 1.2 per meter away from the tree ($CI_{95\%}$ = -1.8 to -0.7; z = -4.55; P < 0.0001). In contrast, fruit loads per branch rose with distance from *F. natalensis* (+ 1.5; $CI_{95\%}$ = 0.9 to 2.126.6; z = 5.1; P < 0.0001) (Fig. 6). Relation between disease incidence and average fruit load varied by variety. The leaf BES incidence was associated with a loss of 62 berries at 100% incidence ($CI_{95\%}$ = -103 to -20; z = -2.9; P < 0.01). With BES berries loss was the most important for the variety clone C (slope = -302; $CI_{95\%}$ = -439 to -166; z = -4.3; P < 0.0001) (Fig. 7). The CLR incidence was paradoxically positively associated with fruit load, with a predicted gain of 28 berries at 100% incidence ($CI_{95\%}$ = 12 to 43; z = 3.5; P < 0.001). The variety clone A benefited most CLR incidence (slope = + 117; $CI_{95\%}$ = 71 to 162; z = 5.1 P < 0.0001), while clone C was the most negatively affected (slope = − 35; $CI_{95\%}$ = -66 to -3; z = -2.13; P = 0.03) (Fig. 7). CWD incidence showed a relationship with average fruit load only on 3 two coffee varieties. The fruit load of coffee variety Op2 was negatively associated (slope = − 303; $CI_{95\%}$ = -416 to -189, z = -4.5; P < 0.0001) while positively associated for Clone C and Op1 (slope = 134; $CI_{95\%}$ = 76 to 192, z = 4.5; P < 0.0001) and (slope = 313; $CI_{95\%}$ = 80 to 546, z = 4.5; P < 0.001). These diseases incidence to average fruit load slopes should be interpreted cautiously, since extreme incidence values were rare (Fig. 7). Consequently, models may overestimate effects at the highest levels.

Table 3
Impact of agroforestry system characteristics and coffee diseases on coffee fruit load (Type II Wald ² test)

χ				
Type	**Variables**	**χ^2**	**Df**	**Pr(>χ^2)**
Fruit load	Shade tree species	1.13	3	0.77
	Distance	3.18	1	0.07
	Coffee variety	166.06	5	< 2e-16 ***
	CLR incidence	19.63	1	< 2e-16 ***
	BES incidence	39.34	1	< 2e-16 ***
	CWD incidence	2.40	1	0.12
	Tree species:Distance	97.55	3	< 2e-16 ***
	Coffee variety:Distance	84.47	5	< 2e-16 ***
	Coffee variety:CLR incidence	49.27	5	< 2e-16 ***
	Coffee variety:BES incidence	68.31	5	< 2e-16 ***
	Coffee variety:CWD incidence	110.49	5	< 2e-16 ***

Discussion

This study assessed the contribution of three major components of Robusta coffee agroforestry systems—associated tree species, coffee variety, and the spatial distance of shrubs relative to associated trees—to disease and fruit load during the rainy season (peak of symptoms of many foliar coffee diseases) (Lu et al., 2022). Three key insights emerged: (i) coffee variety was the main determinant of leaf disease incidence for CLR and BES, (ii) associated tree species and proximity influenced both disease (CLR and CWD) and fruit load, and (iii) significant interactive effects shaped complex outcomes between disease pressure and fruit load.

Despite intensive management at Kaweri Coffee Plantation, shrub disease incidence was extremely high, reaching nearly 100% for CLR and BES, and over 30% for CWD. Leaf incidence levels, however, varied markedly: CLR, caused by *Hemileia vastatrix* Berk. et Br., exhibited the highest incidence, consistent with its status as the most damaging coffee disease globally (Berny Mier y Teran et al. 2025), whereas BES and CWD remained relatively mild. High leaf CLR incidence aligns with increasing reports of outbreaks linked to climate change and genotype-by-environment interactions (Berny Mier y Teran et al. 2025). Conversely, the comparatively low leaf CWD incidence, even in clones previously identified as susceptible (Pinard et al. 2016), may reflect the long-term decline in epidemic intensity since the early 2000s (Musoli et al. 2008; Zhang et al. 2023) and the rigorous sanitation practices (routine rouging) implemented at

Kaweri. Any signs of early CWD infection can lead to premature removal of coffee shrub. A negative correlation between leaf CLR and BES incidence was observed on lower branches, likely reflecting their contrasting ecological requirements: BES development relies on light for cercosporin biosynthesis, whereas CLR incidence is influenced by reduced spore wash-off by rain (Avelino et al. 2018). At the whole-tree scale, co-occurrence of *H. vastatrix* and *C. coffeicola* is frequently reported in productive coffee, where heavy fruit load both promotes rust (Lopez-Bravo et al. 2012) and induces nutritional imbalances that exacerbate BES (Barbosa Junior et al. 2019; da Silva et al. 2019). While pathogen synergy is well documented in Arabica (Avelino et al. 2018), this pattern may differ in Robusta, which is less susceptible to CLR than Arabica (Guerra-Guimarães et al. 2023). Future research using abundance–occupancy frameworks could help determine whether exclusion thresholds exist between *H. vastatrix* and *C. coffeicola* across canopy strata (Strauss et al. 2019). Disease incidence at both the leaf and shrub levels was primarily driven by coffee variety, highlighting the central role of host genetics in plant-pathogen interactions. Clone A combined high tolerance to multiple diseases with the highest average fruit load per branch, confirming its agronomic value. Such varietal contrasts emphasize the importance of breeding programs that integrate resistance traits without compromising productivity. Associated tree effects were more nuanced. Overall, associated tree identity and distance had limited influence on disease regulation, only distance from *F. natalensis* was strongly positively correlated with CWD incidence at the shrub level. Leaf CLR incidence showed a small negative correlation with distance to associated tree. This pattern corroborates previous findings on the context-dependent role of shade in foliar disease complexes (Avelino et al. 2018; Ayalew et al. 2022). Surprisingly, leaf BES incidence was unaffected by tree proximity, despite reductions previously observed under 35 to 65% shading (Staver et al. 2001; Souza et al. 2015). Fruit production was far more impacted by associated trees, with an increase average fruit load per branch at proximity to *A. coriaria*, aligning with farmer preferences in Arabica systems (Sebuliba et al. 2023) and consistent with this species' contributions to soil fertility, nutrient cycling, and water-use efficiency (Dossa et al. 2008; Kobusinge et al. 2025). These results echo earlier findings that moderate shading (41–65%) can increase Robusta yield compared to full sun, although declines may occur in young trees or specific clones beyond ~ 30% shading (Piato et al. 2020; Venancio et al. 2020). Varietal responses to associated tree were heterogeneous, with clone B performing better under proximity to trees, while others (e.g., Op1) declined. These findings highlight that associated tree–variety interactions, rather than associated tree alone, could determine mean fruit load per branch outcomes. Disease–fruit load relationships were also variety-dependent. The leaf BES incidence was generally associated with reduced mean fruit load per branch, except in clone F, where a paradoxical increase was observed. Conversely, leaf CLR incidence showed a positive association with mean fruit load in some clones, likely reflecting short-term physiological trade-offs (Avelino et al. 2006; Costa et al. 2006). Finally, leaf CWD incidence showed a negative association with mean fruit load only with Op2 variety while other variety were either positively or not associated. Differences in mean fruit load between clones are likely due to phenological discrepancies; however, our sampling design did not allow us to quantify this effect. Such contrasting patterns underscore the complexity of host–pathogen–environment interactions in Robusta systems.

Our results demonstrate that while coffee variety remains the principal determinant of disease incidence, complex interactions with shade tree species and spatial arrangement strongly influence average fruit load per branch. The positive contribution of *A. coriaria* to fruit production highlights the potential of carefully selected shade trees in enhancing productivity. Nevertheless, the results also highlight adverse effects of shade trees on coffee health, in line with previous concerns highlighted in coffee systems (Avelino et al. 2018; Staver et al. 2001). Future agroforestry design and breeding programs should jointly integrate varietal resistance, shade tree identity, and spatial configuration to optimize both disease management and productivity resilience. Given the adaptive capacity of pathogens such as *H. vastatrix* to overcome varietal resistance (Várzea et al. 2023), multi-trait strategies that combine genetic resistance with ecological regulation are essential. The selection of a long-term commercial coffee plantation with mature Robusta coffee shrubs and associated trees increases the ecological relevance of patterns observed, but further investigations should expand to additional shade tree species abundant in Kaweri (e.g., *Markhamia lutea* (Benth.) K.Schum., *Spathodea campanulata* P.Beauv., *Melia azedarach* C. Linnaeus) to better understand their potential contributions to disease regulation and fruit load. Furthermore, establishing multi-season monitoring of disease incidence and fruit load would provide better insights into how climatic variability affects tree–coffee–pathogen interactions in agroforestry systems, as precipitation regimes have a significant impact on all components of the agroecosystem (Wang et al., 2015; Nambaziira, 2022). On-farm management of shade trees must also be considered, as farmer practices will ultimately determine the balance between the benefits and drawbacks of shade in Robusta coffee agroforestry systems (Buyinza et al. 2023, 2024). A more holistic approach, integrating above- and belowground biotic interactions, will be critical to harness the full potential of these complex systems (Nantongo et al. 2025).

Declarations

Ethics approval and consent to participate.

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Competing interests.

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Author Contribution

K.R., H.S., J.N.S., A.K.T., S.Y.A. - conceptualized and led the study; K.R., G.M., R.V. - Data analysis, S.M. - supported in data collection, varieties nomenclature, secondary data sourcing; P.F., F.B. – Project Coordination; K.R., H.S., G.M., J.N.S., A.K.T., S.Y.A. - Initial manuscript; All authors approved the final manuscript. This manuscript is part of the first author's PhD work.

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Data Availability

The datasets generated and analyzed during the current study are available, jointly with R codes, in a permanent GitHub repository, https://github.com/GhMathis/Robusta_shade_tree.

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Figures

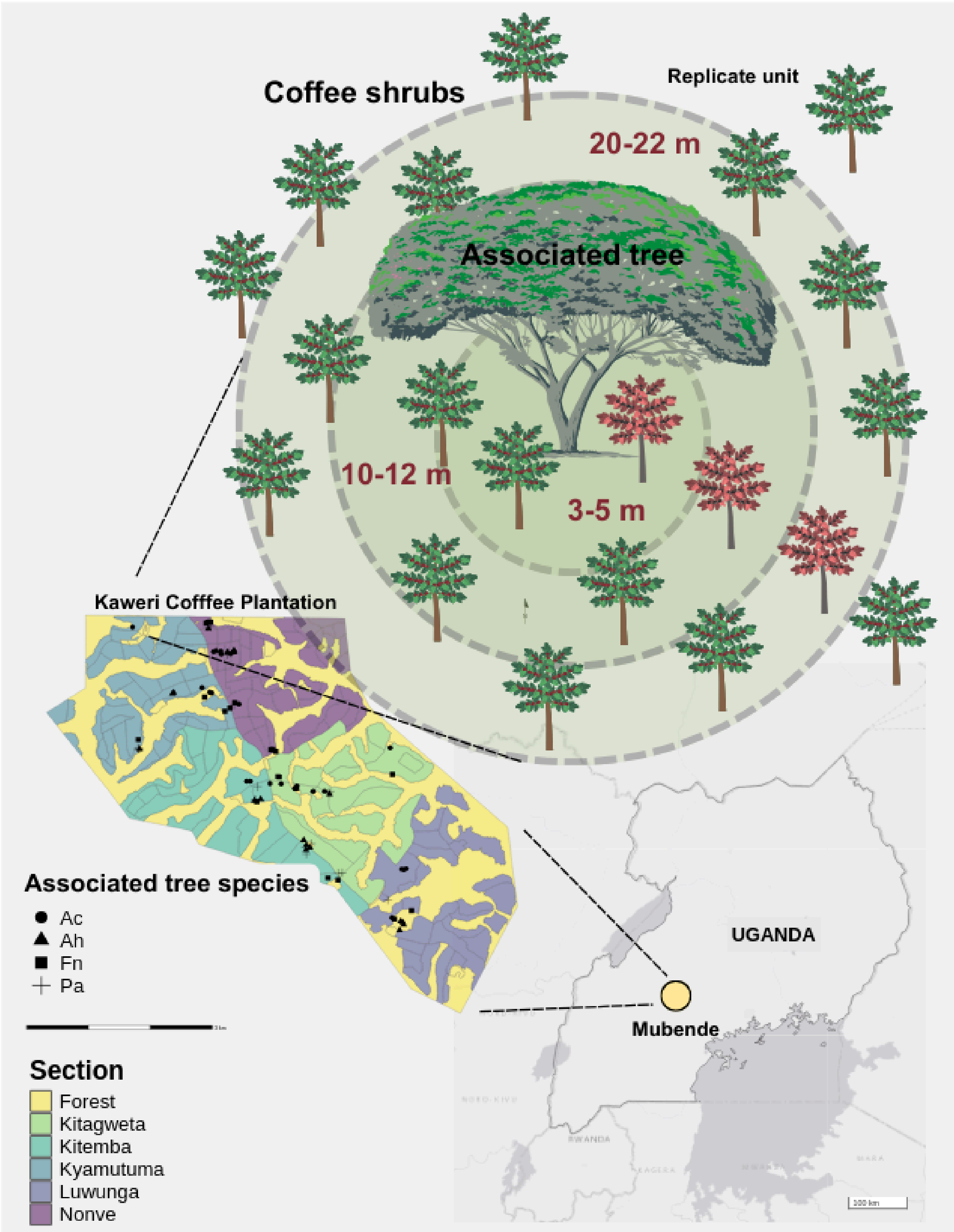

Figure 1

Map of Uganda indicating Mubende district (yellow circle) where Kaweri Coffee Plantation is located. Map of Kaweri Coffee Plantation with the location of associated trees selected for the study, defining a replicate unit with surrounding coffee shrubs. The associated trees were distributed in the five sections of Kaweri Coffee Plantation. Scheme of a replicate unit, composed by an associated tree species and three coffee shrubs (red shrubs) selected according a random direction, and three distances, 3-5 m, 10-12 m, 20-22 m from the associated tree.

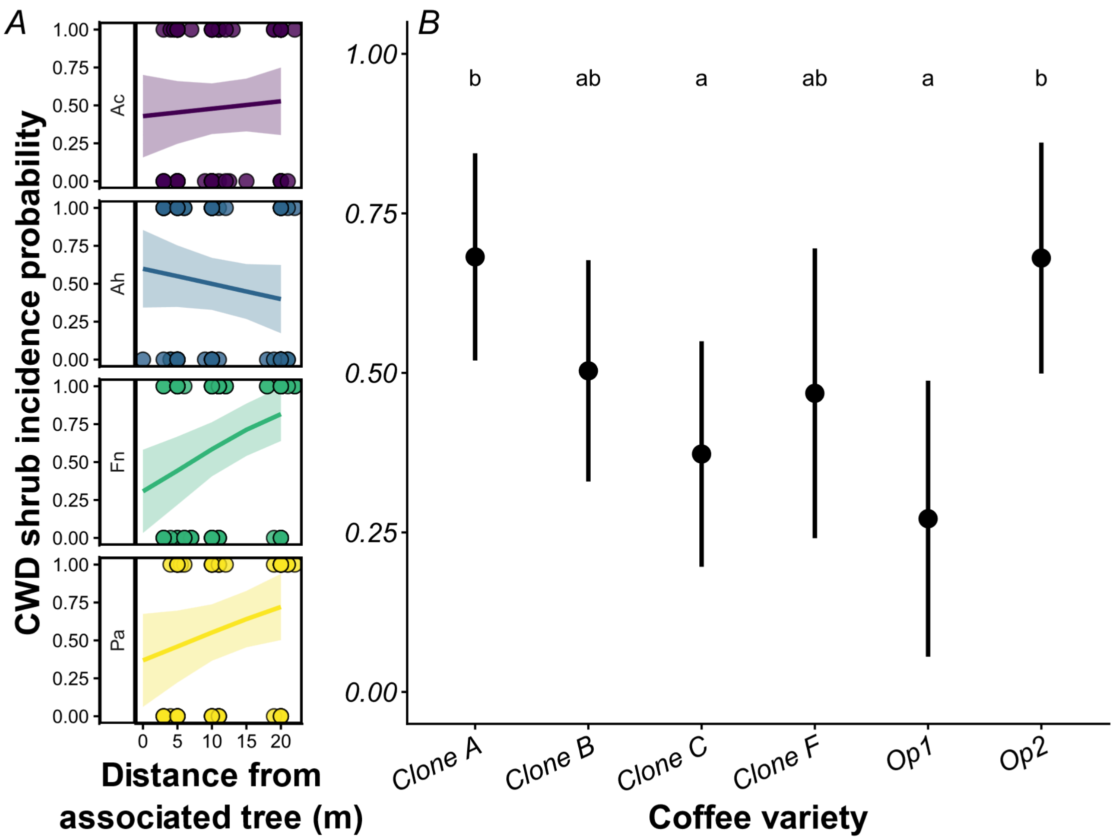

Figure 2

(A) Interaction between CWD incidence and distance from associated tree species. Full lines represent the estimated incidence probabilities of CWD, with their confidence interval at 95%. Points show true values of incidences. (B) Effect of coffee varieties on incidence probabilities of CWD, with mean values and confidence intervals at 95%. The names of coffee varieties are listed as follows Op1, Op2, clone A, clone B, clone C, clone F. *Ficus natalensis* (*Fn*), *Albizia coriaria* (*Ac*), *Persea americana* (*Pa*), and *Artocarpus heterophyllus* (*Ah*).

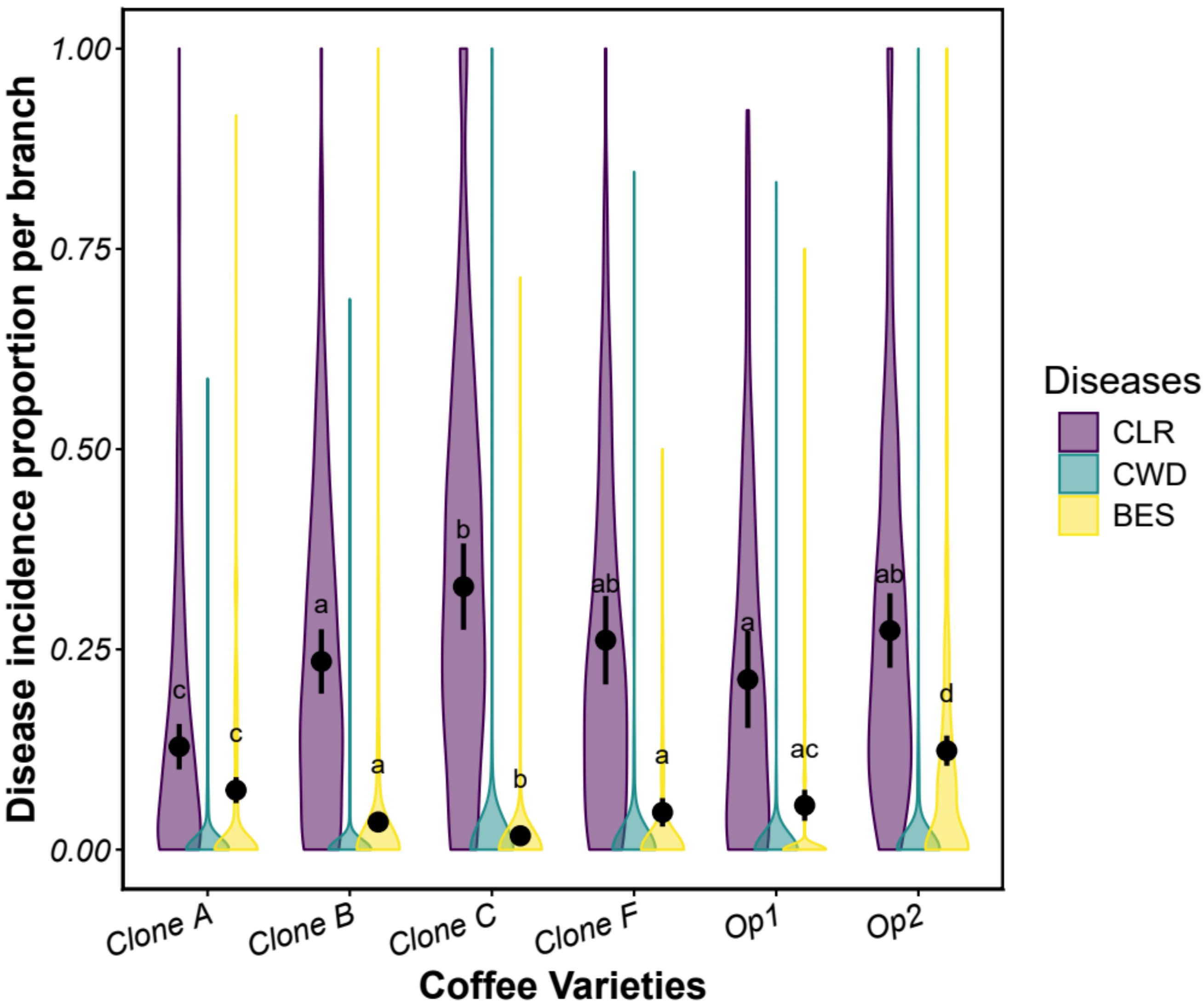

Figure 3

Incidence of leaf diseases (CLR, CWD, and BES) across six coffee varieties.The violin plots illustrate the distribution of disease incidence proportion across branch. Black circular dots and vertical bars represent the estimated mean incidence and 95% confidence interval. Because coffee variety was not identified as a significant predictor for CWD, estimated means are omitted for this disease; only the raw distribution density is shown for comparative purposes. Lowercase letters (a–d) denote statistically significant differences between coffee varieties within a specific disease category. These letters should not be used to compare different diseases against one another. The names of coffee varieties are listed as follows Op1, Op2, clone A, clone B, clone C, clone F

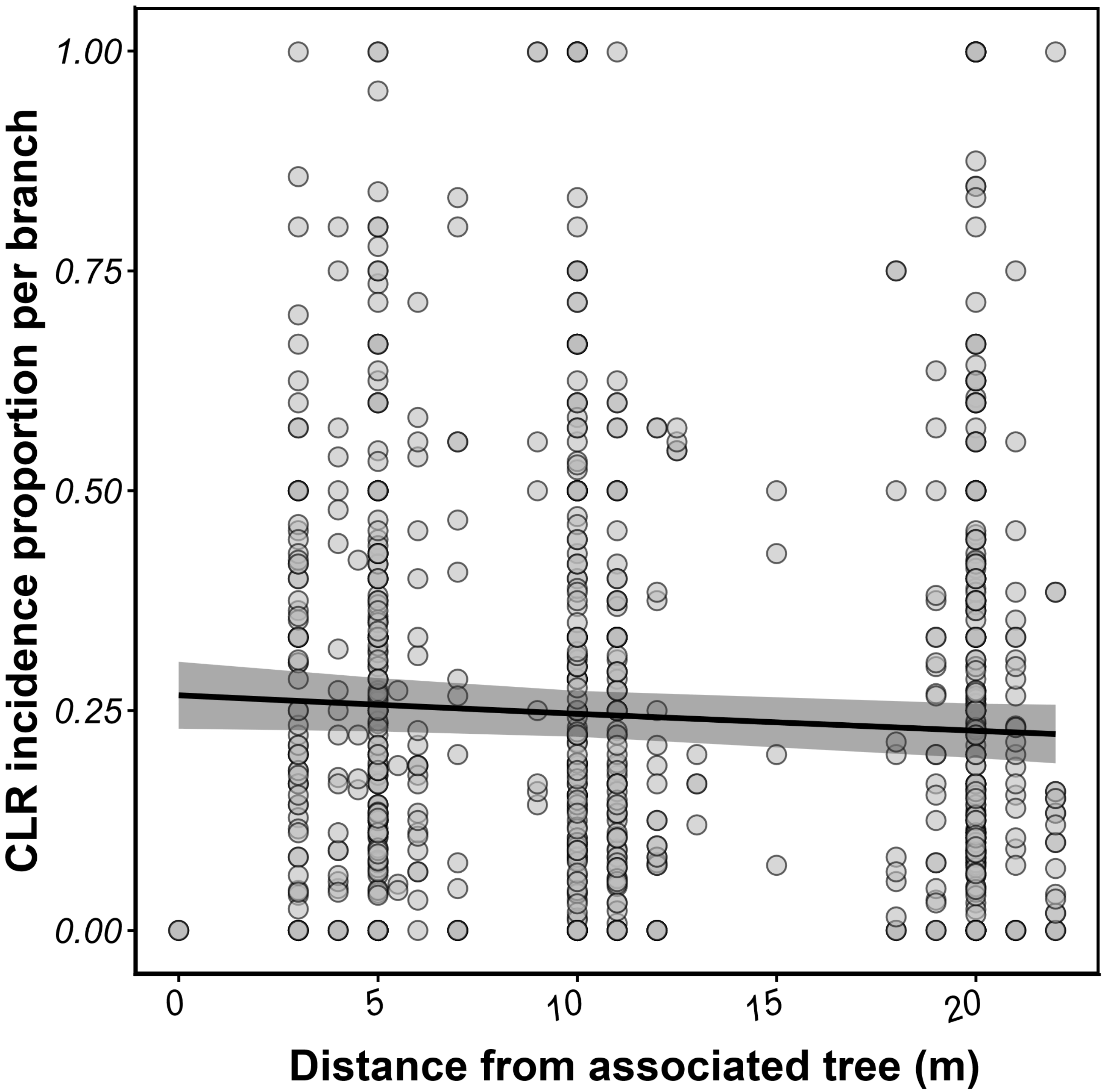

Figure 4

Effect of distance from associated tree species on CLR leaf incidence.

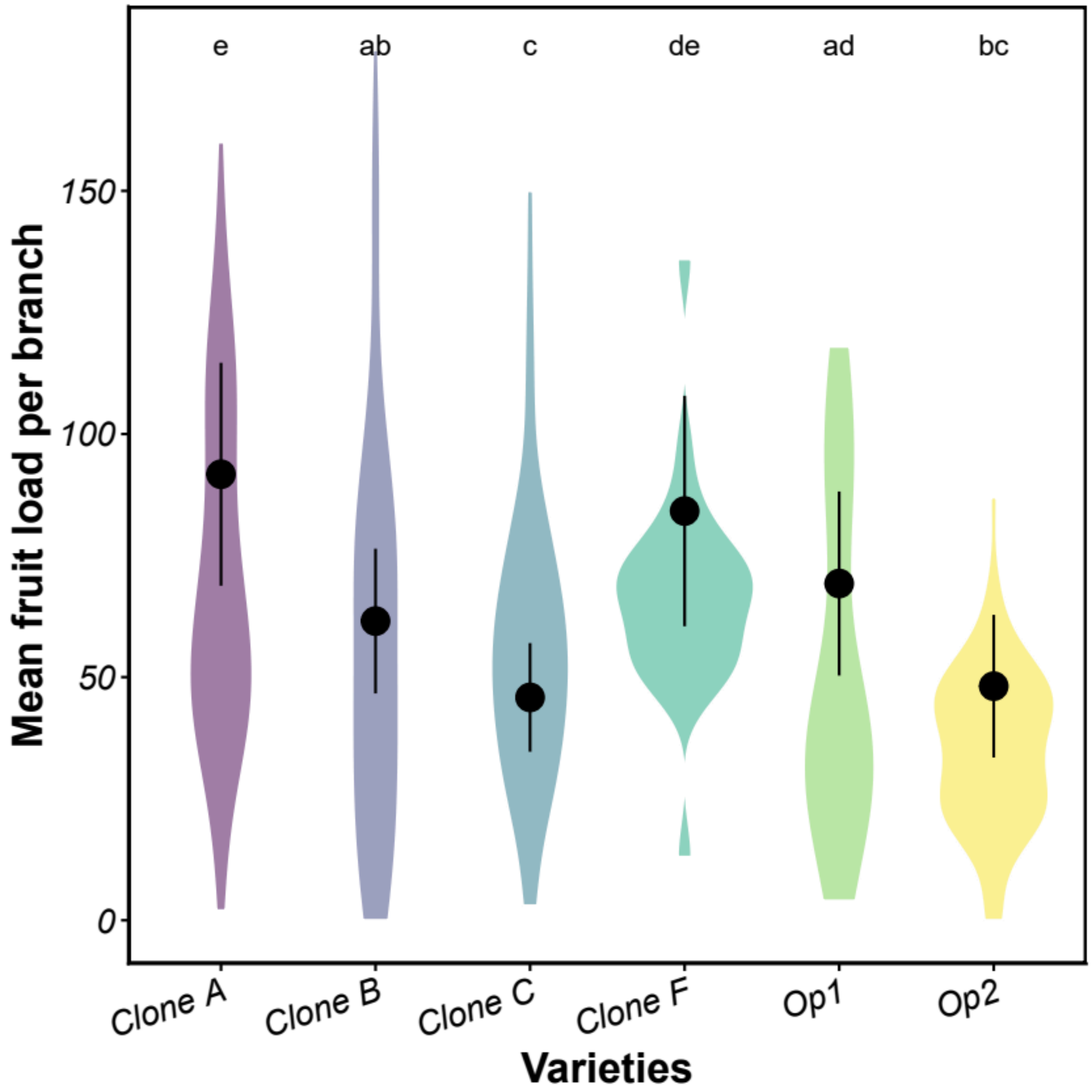

Figure 5

Estimation of coffee mean fruit load per branch depending on coffee variety in the Kaweri Coffee Plantation. The names of coffee varieties are listed as follows Op1, Op2, clone A, clone B, clone C, clone F.

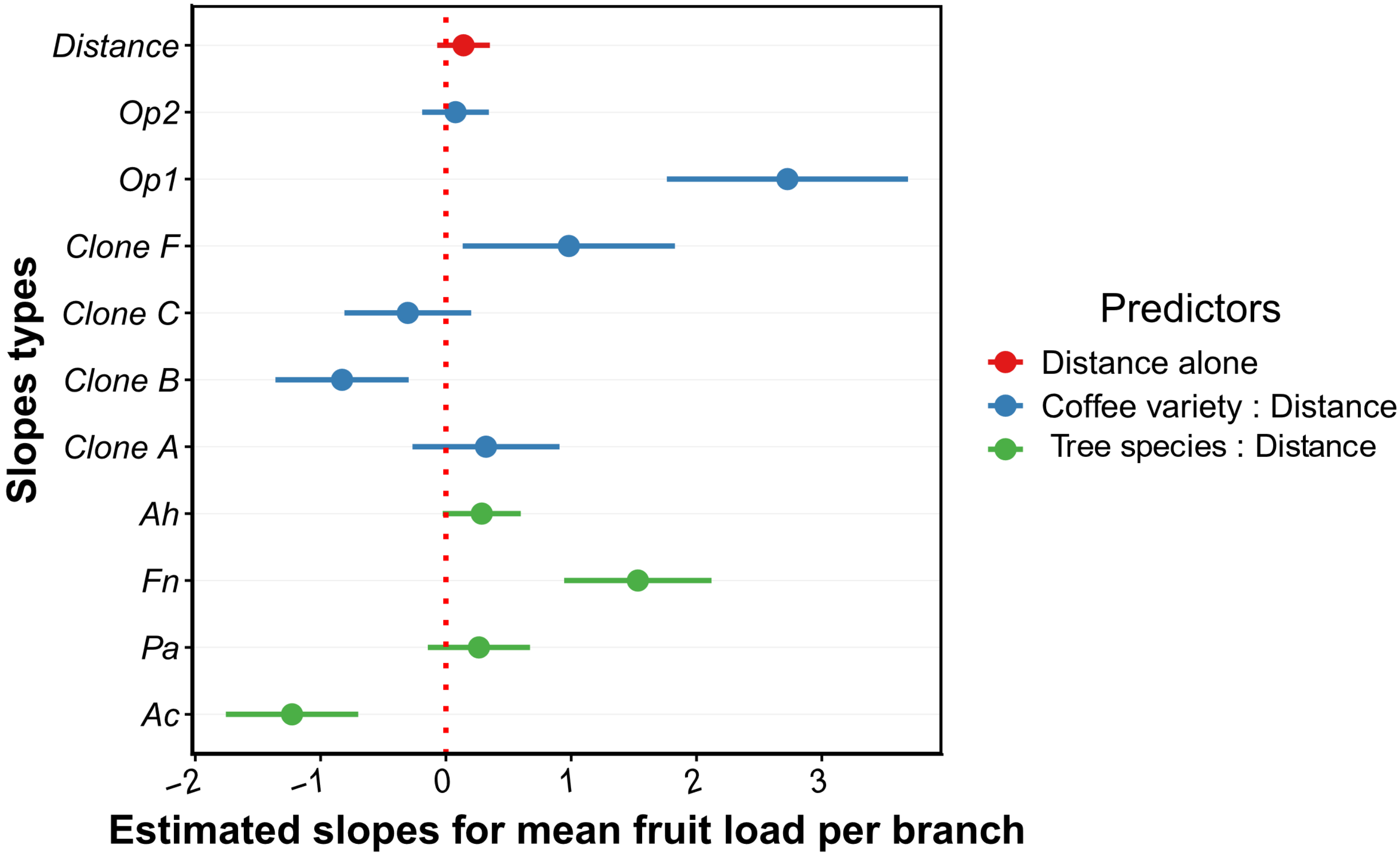

Figure 6

Effect plot of mean fruit load per branch depending on interactions between distance from associated trees and coffee varieties or associated tree species. The names of coffee varieties are listed as follows Op1, Op2, clone A, clone B, clone C, clone F. *Ficus natalensis* (*Fn*), *Albizia coriaria* (*Ac*), *Persea americana* (*Pa*), and *Artocarpus heterophyllus* (*Ah*).

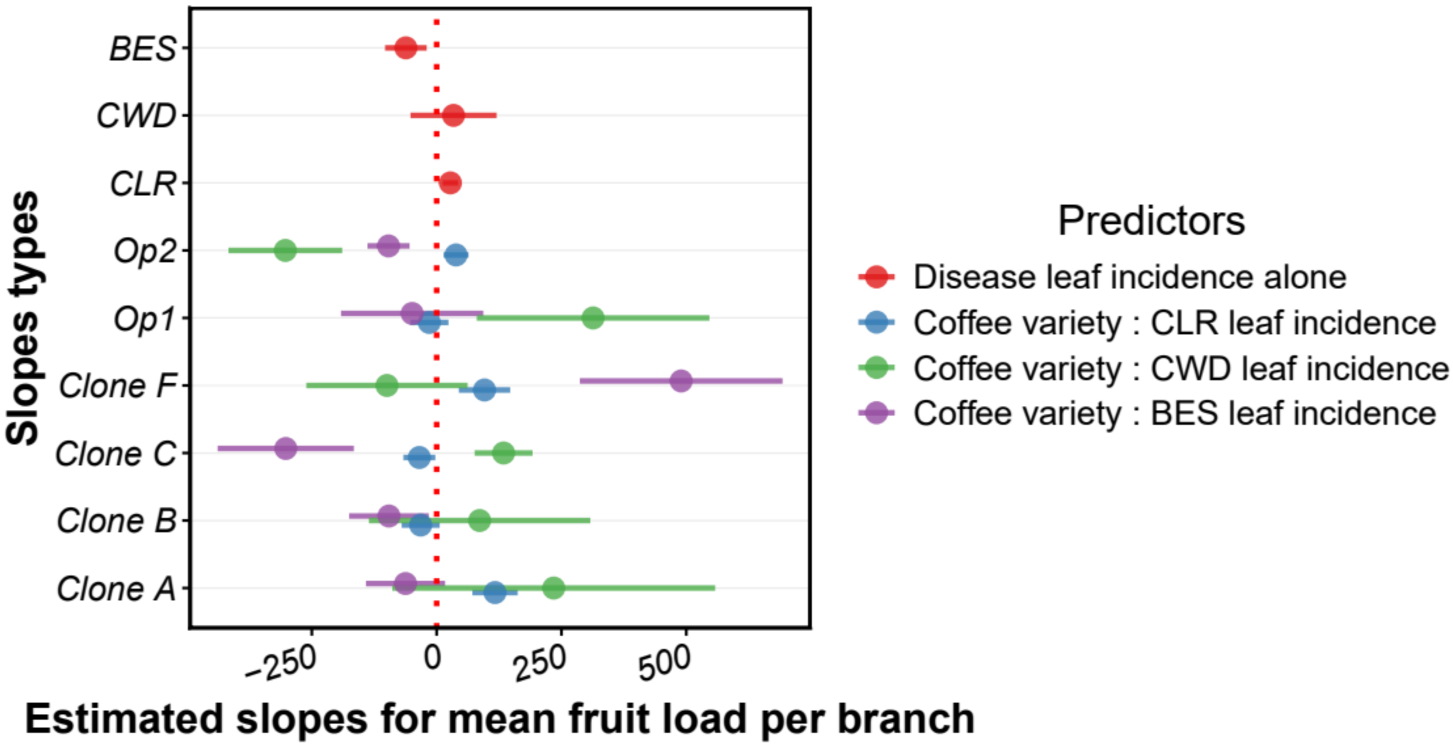

Figure 7

Effect plot of mean fruit load per branch depending on interactions between disease incidence and coffee variety. The names of coffee varieties are listed as follows Op1, Op2, clone A, clone B, clone C, clone F.

Supplementary Files

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- TableS2KisekkaetalDiseaseSurveyKaweri010626supplementary.xlsx
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