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Research article

Contrasting coffee leaf rust epidemics between forest coffee and semi-forest coffee agroforestry systems in SW-Ethiopia

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HIGHLIGHTS

- Coffee leaf rust infection (CLR) was higher for the semi-forest (SFC) than forest coffee system (FC).
- CLR reduced gradually from the beginning of dry season November through the main rainy season July for both coffee systems.
- Hhigher CLR in the SFC were partly explained by low crown cover and high human impact.

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ABSTRACT

Ethiopian Arabica coffee is produced in different agroforestry systems which differ in forest management intensity. In forest coffee systems (FC), coffee shrubs grow naturally in the understory of Afromontane forests with little human intervention, whereas in semi-forest coffee systems (SFC) thinning of the canopy and removal of the understory is applied. Coffee leaf rust (CLR) disease is a growing concern for coffee agroforestry, but to what extent infection pressure is affected by management intensity is poorly known. Here we assessed CLR infection through time across FC and SFC systems in SW-Ethiopia. CLR infection was significantly higher for SFC, with a gradual reduction of this difference during the beginning of dry season (November) through main rainy season of (July). Our findings also demonstrated that CLR infections were significantly lower in the FC system as compared to SFC system in both years 2015/16 and 2020/21. The higher CLR infection was partly explained by lower crown cover and higher human impact. We expect that reduced wind speed and droplet penetration under closed canopies and reduced human-facilitated spore dispersal are the dominating mechanisms behind lower CLR infection in FC systems, yet lower coffee density in FC may also play a role. Overall, our results indicate that although higher management intensity still generally results in higher total yields per hectare, proportionally larger losses due to CLR infection can be expected. Therefore, introducing more coffee genetic diversity, screening resistant coffee varieties and increasing canopy cover in the SFC will mitigate the CLR disease pressure and guarantee the sustainability of higher yields of the system in the future. Also, lower yields in the FC will be rewarded through providing price premiums so that farmers instantly get a higher price for their lower yield, guaranteeing livelihoods.

1. Introduction

Ethiopia is a leading producer of Arabica coffee (*Coffea arabica* L.) in Africa and the sixth largest producer in the world, producing 7.7 million bags (60 kg bag) of Arabica coffee beans in 2016–2017 (CSA, 2018). The total land area covered by coffee cultivation in Ethiopia is estimated to be over 700,000 ha (CSA, 2018). The cultivation, processing and exporting of Arabica coffee beans is the backbone of the Ethiopian economy, accounting for 5% of the GDP and 25% of the employment (Worku and Astatkie 2010). The crop contributes to 41% of the foreign exchange earnings and delivers an important source of revenue for about 15–16 million people (Chala et al., 2011; Hailu et al., 2015).

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In Ethiopia, coffee is cultivated under four different management types, namely forest coffee (FC), semi-forest coffee (SFC), home garden coffee and plantation coffee (Wiersum et al., 2008; Labouisse et al., 2008). FC and SFC systems together account for 44% of the total coffee production in the country (Zeru et al., 2009; Kufa 2012). In the FC system, coffee shrubs grow naturally in the understory of Afromontane evergreen forests with little to no human intervention. Coffee yields are low reaching around 50 kg of green coffee ha^{-1} yr^{-1} (Wiersum et al., 2008). The SFC system encompasses human intervention through the manipulation of the canopy layer, and the removal of shrubs and the herbaceous understory, to reduce interspecific competition and increase coffee yield (Labouisse et al., 2008). Furthermore, the canopy layer is more open than in the FC system due to the selective thinning of emergent trees (Aerts et al., 2011). Both wild coffee plants and local landraces are cultivated, and depending on the intensity of the forest management, yields range from 100 to 300 kg ha^{-1} yr^{-1} (Wiersum 2010).

Current coffee yields across Ethiopian agroforestry systems are lower than their actual potential. One of the major causes is the occurrence of diseases such as coffee leaf rust (CLR), which is known to result in yield losses of up to 20–25% (Zeru et al., 2009; Chala et al., 2011). CLR is caused by the fungal pathogen *Hemileia vastatrix* Berk. & Broome (Pucciniales, Basidiomycota) (Aime 2006). *Hemileia vastatrix* is a hemicyclic fungus producing urediniospores, teliospores and basidiospores. Urediniospores are dikaryotic asexual spores, and represent the most important (if not the only) source of inoculum (Fernandes et al., 2009). Urediniospores initiate infections that develop into lesions which produce more urediniospores. These newly formed spores re-infect coffee leaves as long as environmental conditions are suitable, by which the disease rapidly spreads (Talhinhas et al., 2017). In Ethiopia, CLR was initially described in 1934 (Sylvain 1958) and its occurrence has been increasing from 12.96% in 1999 to 36% in 2009 (Zeru et al., 2009). The incidence of CLR has been observed to range from 32.2 % in the SW highlands near Berhane-Kontir to 96% in Herenna in the SE of Ethiopia (Zeru et al., 2009). Chala et al. (2011) reported incidences ranging between 7.9 % and 31.1 % in the Bonga and Yayu regions, respectively.

It is known that shading of the coffee shrubs can influence CLR occurrence in various ways (Talhinhas et al., 2017). For example, increased canopy closure reduces urediniospore dispersal due to reduced wind velocity, making shaded coffee less susceptible to CLR infection (Avelino et al., 2004; Boudrot et al., 2016). Shade can furthermore decrease CLR occurrence through its negative effect on fruit production, which is, in turn, associated with reduced leaf receptivity to the pathogen (López-Bravo et al., 2012). At low rainfall intensity and duration, a dense canopy may also provide a barrier against CLR through preventing water droplets from reaching the coffee canopy, reducing spore liberation and dispersal (Avelino et al., 2004). On the other hand, the reduced amount of light reaching the coffee canopy under shaded conditions has been reported to favor urediniospore germination (Avelino et al., 2004; López-Bravo et al., 2012). Shade also increases soil moisture levels and buffers ambient temperatures, both reducing the latency period of CLR and favoring urediniospore germination and fungal penetration of the leaves (Avelino et al., 2004; Rodrigues et al., 2014). Coffee planting density can also affect CLR infection, largely through similar processes as those involved in canopy closure effects. For instance, high planting density limits the number of fruits per individual tree, due to increased intraspecific competition, and may thus decrease susceptibility to CLR (Avelino et al., 2004). High planting density, on the other hand, has also been reported to increase CLR infection as a high number of trees in closely spaced plantations increase CLR urediniospore interception (Avelino et al., 2004; Ehrenbergerová et al., 2018). Finally, also human disturbance may impact CLR infection levels. When infected coffee leaves are touched by humans (through the movement of farmers and laborers), spores can be further dispersed across the coffee plantations, thus spreading CLR infection (Rountree and Guido 2016). Apart from humans, CLR spores could also be dispersed by wind and rain, insects and wildlife (Aime, 2006). Since the FC and SFC management types in Ethiopia differ in the percentage canopy closure, coffee shrub density and human disturbance, CLR infection levels can be expected to differ between both management types. However, considering the potential for either a net positive or negative effect of both high shade levels (prevalent in FC) and high coffee planting density (prevalent in SFC), predicting which management type is most prone to CLR infection is difficult. So far both management types have not been systematically compared in terms of CLR infection levels.

To further complicate CLR infection predictions across management types, both altitude of cultivation and soil characteristics are also known to influence CLR occurrence (Talhinhas et al., 2017). Increasing altitude has been reported to decrease CLR incidence in Honduras (Avelino et al., 2006), Rwanda (Bigirimana et al., 2012) and Ethiopia (Daba et al., 2019), whereas CLR epidemics development was found to be negatively affected by increasing soil nutrient levels and pH (Avelino et al., 2006; Toniutti et al., 2017). On the other hand, a recent study conducted in the central Peruvian Amazon found no significant effect of soil properties on CLR incidence (Ehrenbergerová et al., 2018).

The percentage share of these two-production system is more than 50% in this area and our study has focused on two systems only, i.e. FC and SFC. The main reason is that we aimed at studying differences across the reference situation on the one side (i.e. FC), and what is actually a degradation phase of the natural forest (i.e. SFC) on the other side. The two other coffee management systems (plantation and home garden) are completely artificial and are so different from the forest coffee systems, that we did not include these. In this study, we assessed CLR infection (measured by CLR incidence, severity and prevalence) at 68 sites across both FC and SFC systems in the native Arabica coffee range in the Jimma region of SW Ethiopia. As CLR is known to have a pronounced annual cycle with infection peaking during coffee collection at the onset of the dry season (Daba et al., 2019), we assessed CLR infection across four time points in two years, which are essential for developing effective disease management strategies. Our specific objectives were to:

1) Assess temporal changes in CLR incidence, severity and prevalence across different years;
2) Quantify the effects of coffee forest management system (FC vs. SFC) on temporal variation in CLR incidence, severity and prevalence; and
3) Identify the mediating role of canopy closure (shading), human disturbance, altitude, and soil characteristics on CLR incidence, severity and prevalence.

2. Materials and methods

2.1. Study area

We conducted our research in the Gera and Mana districts of the Jimma zone (Oromia Region) in Southwestern Ethiopia (7°46′N, 36°0′E) (Figure 1). The Jimma zone is one of the chief coffee producing regions of Ethiopia (Geeraert et al., 2019). The area features both mosaic landscapes with small fragmented coffee forests surrounded by cropland, home gardens, pasturelands, riverine wetland and human settlements, and large relatively undisturbed natural coffee forest areas. Annual average rainfall is 1595 mm. The yearly average maximum and minimum air temperatures are 25.9 °C and 11.2 °C, respectively (Kufa 2012). The study area has three main seasons. From October to January is the long dry season when coffee harvesting and processing takes place. From February to May is the first (short) rain season, which is the main period for coffee flowering and early fruit development. The season is followed by the main rain season, from June to September (Moat et al., 2017).

Gera and Mana districts were selected purposively since these two study areas are the most important coffee producing districts of the SW-Ethiopia. During our study we used Stratified disproportionate sampling design considering these two production systems. We selected two study areas (Garuke and Fetche) with SFC systems in the Mana district, and two areas with FC systems (Afalo and Kacho) in the Gera district (Figure 1). All plots were selected randomly through walking in the coffee forest and

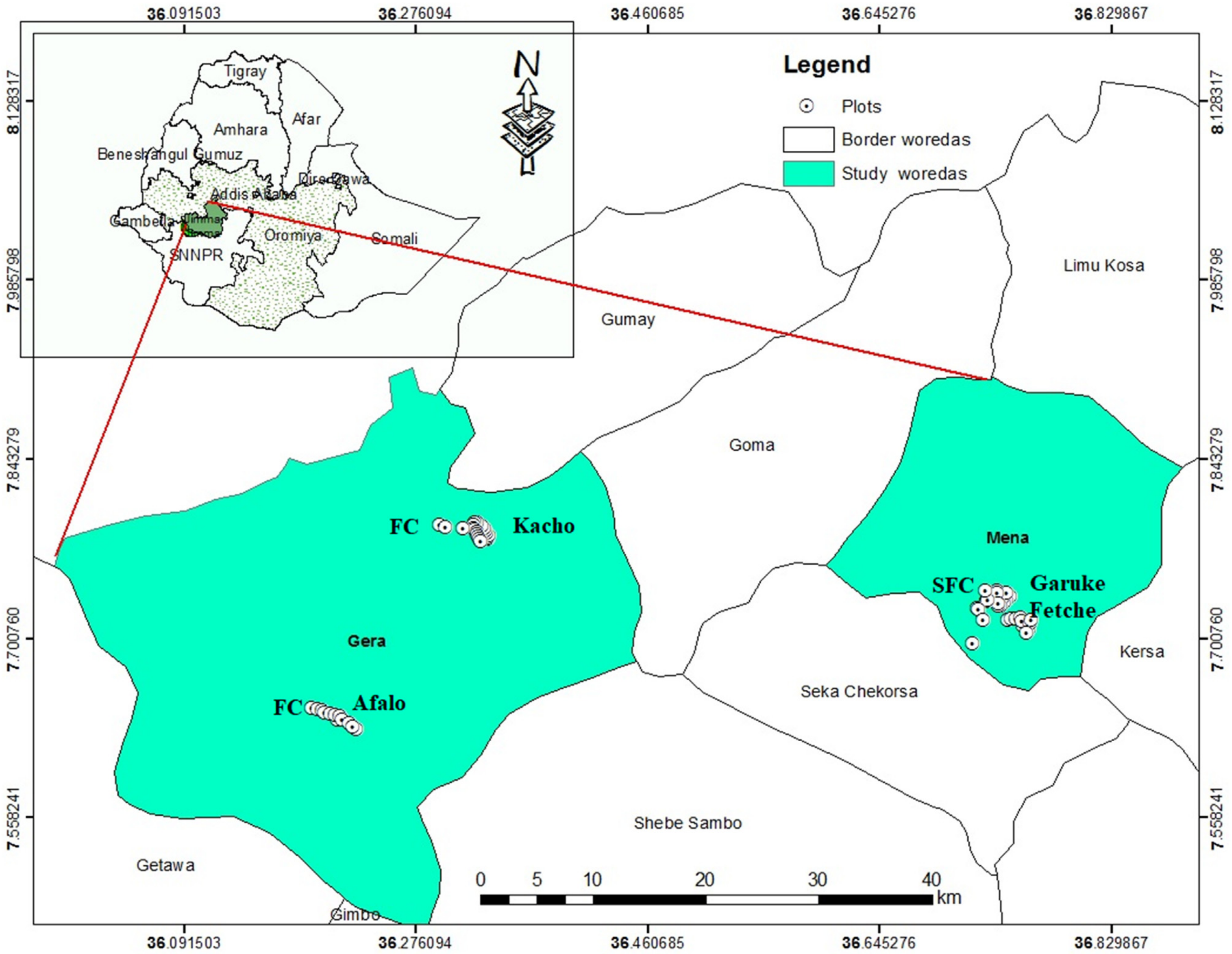

Figure 1. Map of the study sites in the Mana and Gera districts in Southwestern Ethiopia. Forest coffee (FC) systems were located in the Gera district (32 study sites), whereas the semi-forest coffee (SFC) systems were located in the Mana district (36 study sites).

randomly selecting a point that served as the SW corner of the plot that was established. Across these four study areas, a total of 68 plots of 20 m × 20 m were established across 21 forests (36 plots in the Mana district, 32 plots in the Gera district), at least 50m from the forest edge to account for edge effects. Twenty-five SFC plots were located in Garuke, 11 SFC plots in Fetche, 20 FC plots in Kacho and 12 FC plots in Afalo (Figure 1). Altitude of the study sites are in the range of 1766 m. a.s.l - 2308 m. a.s.l.

Previous research in this area has shown that the average crown cover in the FC study sites is around 88% (Hundera et al., 2013). Dominant tree species include *Syzygium guineense, Prunus africana, Olea welwitschii, Schefflera abyssinica,* and *Ilex mitis* (Hundera et al., 2013). For the SFC locations, the average crown cover is around 61%, with *Albizia gummifera, Albizia schimperiana, Croton macrostachyus* and *Millettia ferruginea* as the dominant tree species (Hundera et al., 2013). Overall in Ethiopia, coffee shrub density is significantly higher in the SFC (450 plants ha^{-1}) system than in the FC system (270 plants ha^{-1}) (Wiersum et al., 2008; Aerts et al., 2013), while the tree/shrub density is lower in the SFC system (133 trees ha^{-1} for stems > 2m high) compared to the FC system (625 trees ha^{-1}) (Aerts et al., 2011). Furthermore, in the latter, coffee shrubs are maintained through pruning, stumping and removal of epiphytes. Planting density was fairly constant across all plots within one management type in our study, making it impossible to separate planting density effects from other management type effects on CLR infection. More specifically, we observed, on average, eighteen and eleven coffee shrubs per plot in the SFC and FC systems, respectively. No application of pesticides, herbicides or chemical fertilizer occurs in either of the two management types.

2.2. *Data collection*

Three CLR infection measures, namely incidence, severity and prevalence, were surveyed in our study, and were recorded four rounds for each plot, for two years through 2015/16 and 2020/21. CLR infection measures were evaluated in November (beginning of the dry season), January (main dry season), April (beginning of the short rainy season) and July (beginning of the main rainy season) for both years, following the protocol of Chala et al. (2011) and Daba et al. (2019). At each time point, five coffee shrubs of even age were randomly taken from each plot. For each plant, three pairs of branches, each pair representing the upper, central and bottom canopy layers of the coffee plant were carefully chosen and marked with a tag to evaluate the three CLR infection measures (Daba et al., 2019).

CLR incidence was determined as the proportion of diseased leaves per branch. CLR severity was determined as the average proportion of sporulating lesion area per leaf across all leaves of the sampled branch, using the visual scale established by Kushalappa and Chaves (1980). CLR incidence and severity from all six branches were averaged per shrub and afterward averaged across all five shrubs, resulting in CLR infection measures at the plot level. CLR prevalence was calculated as the proportion of plants diseased by CLR per plot (Daba et al., 2019), and can also be understood as a measure of plant scale incidence.

In each plot, four soil samples were taken at the first time point at a depth of 0–10 cm and pooled. Samples were sieved, and oven dried for 24 h at 80 °C. Each soil sample was subsequently analyzed for acidity (pH), Cation Exchange Capacity (CEC), plant available phosphorus (P), and content of calcium (Ca), magnesium (Mg), potassium (K), nitrogen (N), soil carbon (C) and organic matter (OM) following standardized procedures (Reeuwijk 2002).

Four different forms of human disturbance were assessed for each plot, including grazing, wood harvesting, tree cutting and slashing of undergrowth. The magnitude of the disturbance was recorded for each plot on a scale from zero to three for grazing and wood harvesting, based on visual assessment, where zero represents absence and three indicates the highest effect. For tree cutting and grazing, impact was scored as absent (0) or present (1) (Senbeta and Denich 2006; Hundera et al., 2013). Using this information, we constructed a single combined ‘human impact’ indicator by summing the four different measures (grazing, wood harvesting, tree cutting and slashing) and dividing the resulting number by the maximum value possible ($3+3+1+1=8$). The resulting human impact indicator was bound between 0 (no human impact) and 1 (maximum human impact). Crown cover (percentage canopy closure) was estimated for each plot with hemispherical photographs using SVS 3.0 (stand visualization system, Forest Service, Portland, OR).

2.3. Statistical analyses

To avoid multicollinearity, we first performed a Principal Component Analysis (PCA) on all soil variables. The PCA are largely build from soil variables pH, Ca, Mg, K, P, N, C, OM, and CEC. During dimensional reduction eigenvalues greater than 1 was considered and as a result the two axes were retained in the final model. From this PCA, we retained the first two axes for further analyses, which together contain 76.3% of the total variation. PCA axis 1 is mainly negatively correlated with OM, C, N, Ca, Mg and K content and pH, while PCA axis 2 is mainly negatively correlated with CEC, pH and P and K content (Table 1).

Table 1. Results of the principal components analysis (PCA) on all soil variables. Eigenvalues explained variation and variable loadings for the first two PCA axes.

	PCA1	PCA2
Eigenvalue	4.6	2.27
Explained variation (%)	51.1	25.2
Loadings		
pH	-1.8	-1.19
CEC (cation exchange capacity)	0.25	-1.81
Ca	-2.12	-0.21
Mg	-1.79	-0.81
K	-1.12	-1.66
P	-0.27	-1.28
N	-2.08	0.87
C	-2.07	0.97
OM (organic matter)	-2.07	0.97

We then used generalized linear mixed effects models (GLMMs) to evaluate differences in the three monitored CLR infection measures (CLR incidence, severity and prevalence) across both management systems and the four time points. Since the three response variables present fraction data, the GLMM models were constructed using beta distributions with logit link function (with maximum likelihood approximation). Since relative limits 0 and 1 are not suitable in a beta distribution, all CLR infection measures (Y) were converted as follows: $Y' = \frac{Y\times(N-1)+0.5}{N}$, with N meaning the sample size (Cribari-Neto and Zeileis 2009). Plot identification was involved as a random intercept since all CLR infection measures were measured consecutively through time. Forest ID was furthermore involved as a second random intercept, while management system (FC vs. SFC), crown cover, the human effect indicator, soil PCA axes 1 & 2, altitude, years (2015/16 and 2020/21), time point (November, January, April and July) and the interaction between year, time points and management type were included as fixed factors/covariates. Final models were obtained after step-by-step model reduction based on Akaike's information criteria (AIC). Note that before model building, collinearity among predictors was evaluated using variation inflation factors, with a cut off level of 3 (Zuur et al., 2010).

We also performed Mann-Whitney U tests to compare altitude, crown cover, the human effect indicator and the soil PCA axes between FC and SFC systems. Since several of these variables differed between both management types, we reran all previously described GLMM models, excluding management type (and its interaction with time), to evaluate the effects of the other variables, independent of management type. All GLMM models were run with the ‘glmmTMB’ R package (Magnusson et al., 2017) in R 3.3.3 (R Development Core Team, 2017). Pairwise comparisons between factor levels were carried out using Tukey Tests.

3. Results

Coffee management type, time, year and their interaction significantly affected all the three CLR infections measures (incidence, severity and prevalence) (Table 4). Overall, CLR incidence was significantly higher for SFC than FC. In the first year, interestingly, the extent of this difference was not consistent through time, with a gradual reduction of the difference from the beginning of dry season (November 2015) to the main rainy season (July 2016). While CLR incidence was more than six times higher for SFC (58.3%) than FC (8.4%) in the beginning of dry season during November 2015, this difference was strongly reduced during the main rainy season by July 2016 (3.9% vs. 0%) (Table 2, Figure 2A). Consequently, although both SFC and FC plots showed a gradual reduction in CLR incidence through time, this reduction was

Table 2. Results of the generalized linear mixed effect models (GLMM) on the CLR infection measures after model reduction. Beta-coefficients and test statistics (z) for each pairwise factor contrast (Tukey tests) for all retained factors. Model parameters (beta coefficients) and test statistics are also provided for the retained covariates (N = 272).

Coefficients		CLR Incidence		CLR Severity		CLR Prevalence	
		beta	z	beta	z	beta	z
Management type	FC–SFC	-1.99	-18.47***	-1.72	-11.87***	-2.91	-15.77***
Time	Nov–Jan	0.62	5.10***	0.51	5.06***	0.68	3.76**
	Jan–Apr	1.31	9.37***	1.08	9.06***	1.34	7.39***
	Apr–Jul	0.48	3.09*	0.31	2.26	0.53	2.98*
Management type*Time	Nov: FC-SFC	-3.00	-17.36***	-3.25	-17.49***	-3.41	-11.53***
	Jan: FC-SFC	-2.46	-13.37***	-2.20	-11.74***	-2.59	-9.44***
	Apr: FC-SFC	-1.73	-7.92***	-1.03	-4.69***	-3.35	-11.34***
	Jul: FC-SFC	-0.76	-3.29**	-0.41	-1.81	-2.28	-8.17***
PCA1		-	-	-	-	-0.36	-1.96*
PCA2		-0.22	-2.21*	-	-	-0.56	-3.46***

Significance: *: 0.05 ≥ *P*-value >0.01; **: 0.01 ≥ *P*-value >0.001; ***: 0.001 ≥ *P*-value. CLR = coffee leaf rust, FC = forest coffee, SFC = semi-forest coffee.

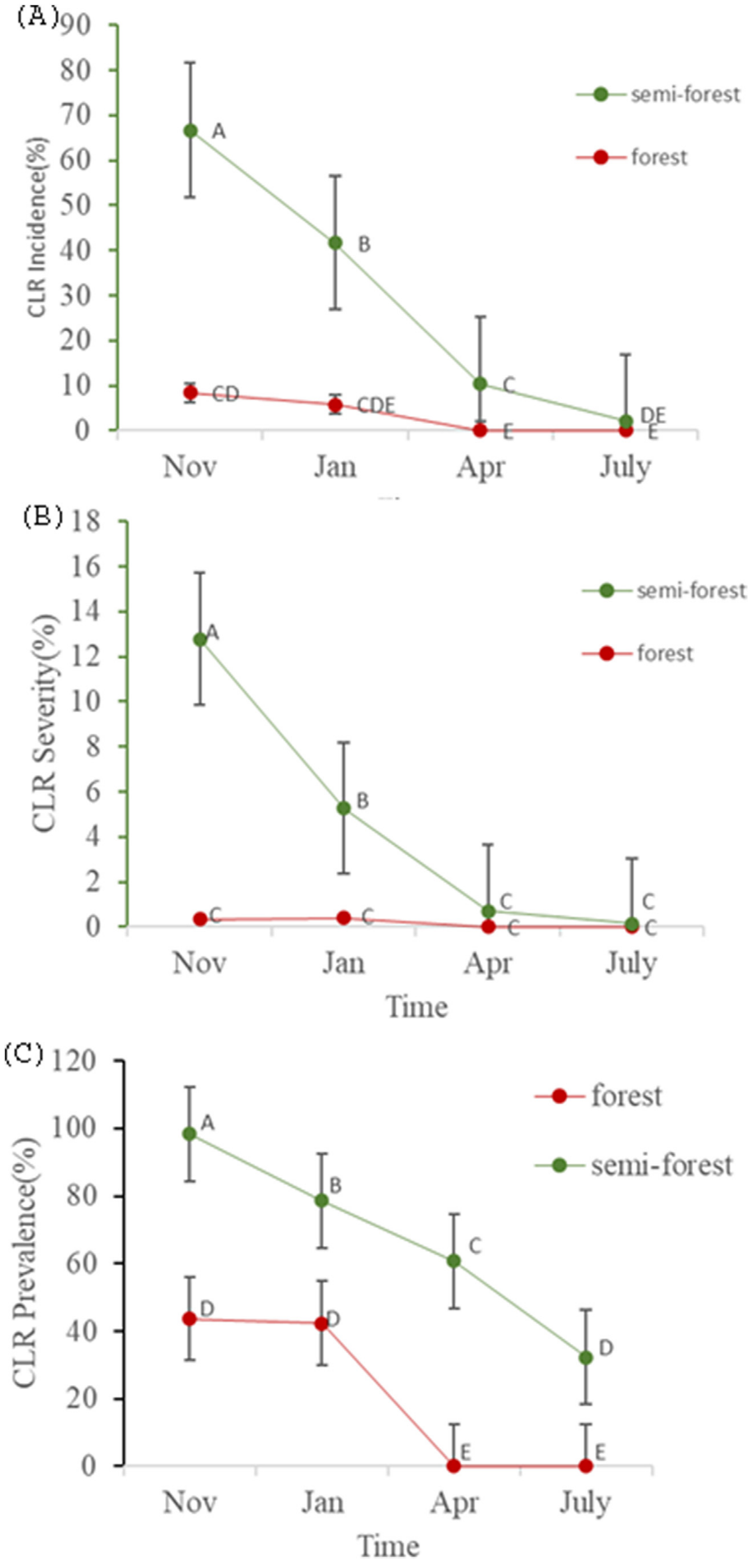

Figure 2. Changes in coffee leaf rust 2015/16 (CLR) incidence (A), severity (B) and prevalence (C) (mean and confidence intervals) through time for both the forest (FC) and semi-forest coffee (SFC) management types.

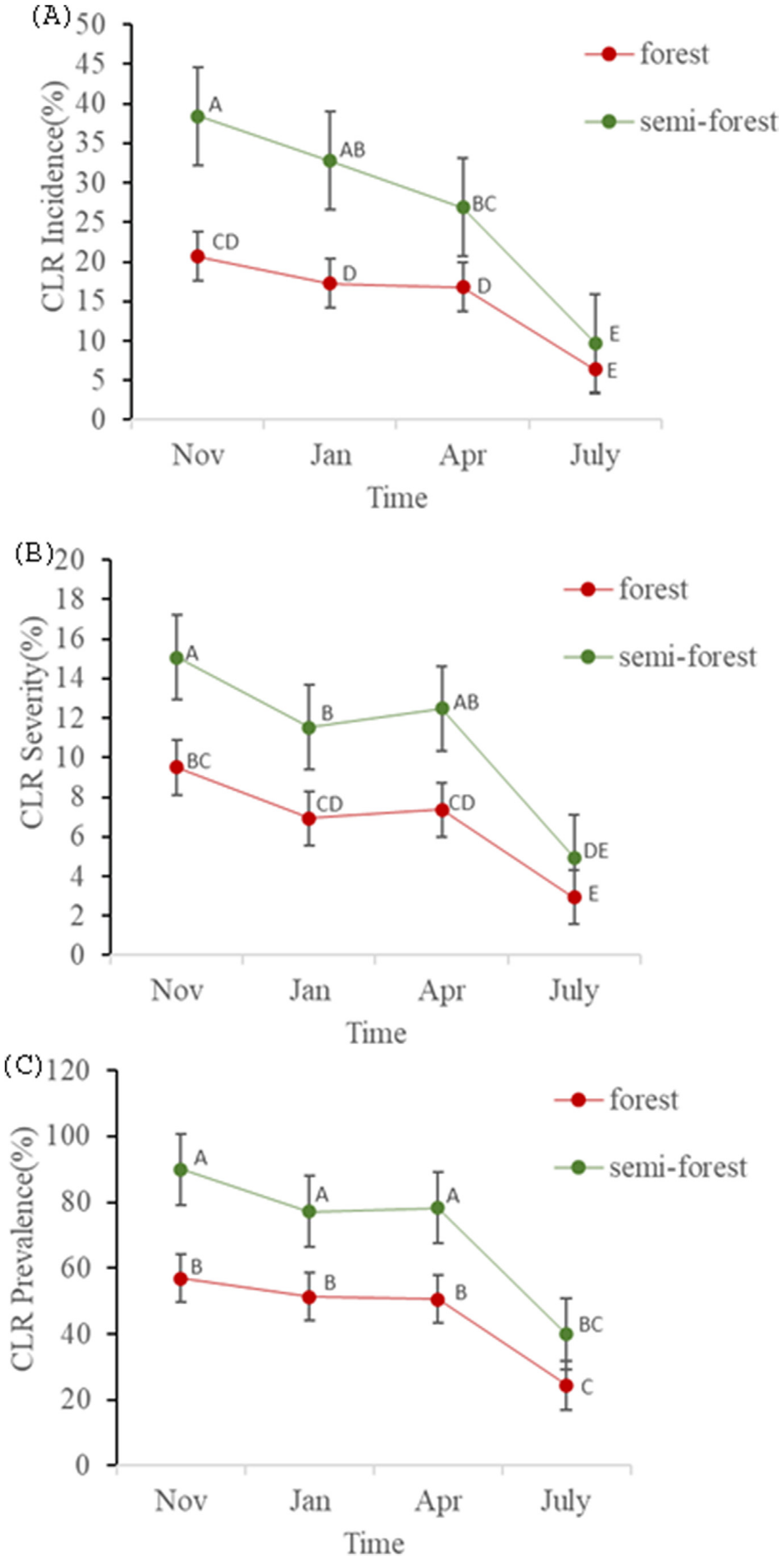

Figure 3. CLR intensity of 2020/21, CLR incidence(A); CLR severity(B) and CLR Prevalence (C) were significantly influenced with year, time and coffee production system in SW-Ethiopia.

much more pronounced for SFC plots, although CLR incidence fell to zero only for FC (Figure 2A).

The results for CLR severity were largely identical to those for CLR incidence (Table 2, Figure 2B). However, unlike for CLR incidence, the difference in CLR severity observed in November 2015 between SFC (12.4%) and FC (0.4%) disappeared completely by July 2016 (0.2%), since CLR severity disappeared almost completely for SFC (Table 2, Figure 2B). CLR prevalence also followed the overall patterns observed for CLR incidence. However, unlike CLR incidence, the initial difference in CLR prevalence between SFC (98.3%) and FC (43.7%) in November 2015, remained pronounced in July 2016 (32.3% vs. 0%) (Table 2, Figure 2C). In other words, the gradual reduction in CLR prevalence through time was not faster for FC than SFC, in contrast to CLR incidence and severity (Table 2, Figure 2C). Similar to the previous year 2015/16, the CLR incidence recorded for the second year 2020/21 was significantly highest for SFC system during the beginning of dry season in November and the incidence became the lowest in the FC system during the main rainy season of July 2020/21 (Figure 3A). Also, significantly the highest CLR severity was recorded in the SFC system during the beginning of dry season November 2020/21 (Figure 3B). The CLR severity was not statistically significantly differ from the severity recorded in the SFC system during the short rainy season of April 2020/21. Correspondingly, the CLR prevalence was observed to be highest in the SFC system during the beginning of dry season in November for the year 2020/21 (Figure 3C) while the lowest CLR prevalence was recorded in the FC system during the main rainy season of July (Figure 3C). Year*time*management type interaction influenced both CLR infections (incidence and severity) (Table4; Figure 4 A & B). For both years 2015/16 and 2020/21 CLR incidence was observed to be the highest in the SFC system through the beginning of dry season November (Figure 4A). However, the incidence recorded in the SFC system in the year 2015/16 during the main dry season of January was not statistically different from incidence recorded in the SFC system in the year 2020/21 during the beginning of dry season November (Figure 4A). For both years 2015/16 and 2020/21 the CLR incidence became the lowest in the FC system in the main rainy season of July (Figure 4A). However, this incidence was not statistically different from the incidence recorded in the FC system during the main dry season of January, short rainy season of April and in the SFC system during the main rainy season of July (Figure 4A). CLR incidence recorded in the SFC system in the year 2020/21 during the main rainy season of July was not statistically different between the incidence recorded in the FC system in the same year during the main rainy season of July (Figure 4A). The CLR incidence observed in the SFC system during the beginning of dry season November was 6.95 time greater than the incidence recorded in the FC system for the year 2015/16 in the same season. Similarly, CLR incidence recorded in the SFC system in the year 2020/21 during the beginning of dry season November was 1.86 times greater than the incidence recorded in the FC

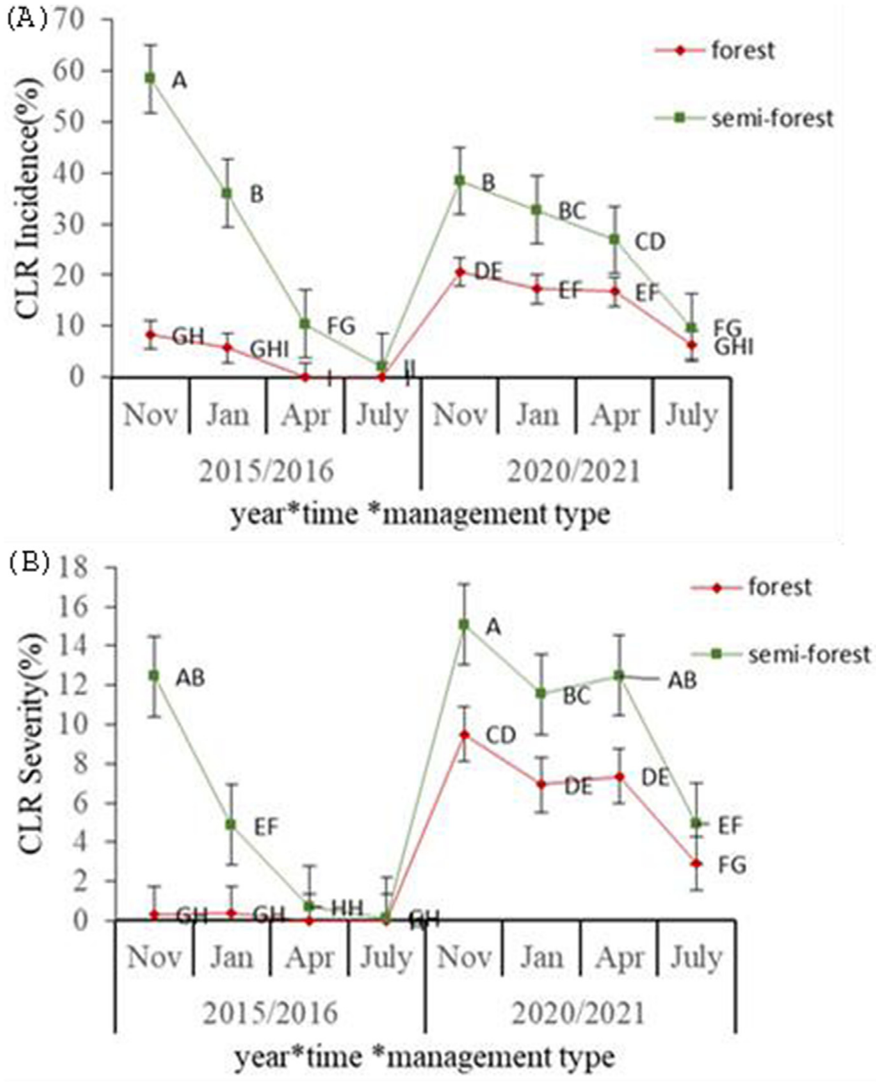

Figure 4. CLR Intensity CLR incidence, CLR Severity as influenced by the interaction of year*time and management type in SW-Ethiopia.

system (Figure 4A). Similarly, the highest CLR severity was recorded in 2020/21 during the beginning of dry season November in the SFC system which was not statistically different from the severity recorded in the year 2015/16 during the beginning of dry season November in the SFC (Figure 4B). The severity recorded in the SFC in the year 2020/21 during the main dry season of January and short rainy season of April was not statistically different from severity recorded in the SFC in the year 2015/16 during the beginning of dry season November (Figure 4B). The lowest CLR severity was recorded in the FC in the year 2015/16 during the main rainy season of July. However, this severity was not statistically different from the severity recorded in the same year during the beginning of dry season November, main dry season of January, short rain season of April in the FC system and short rainy season of April and main rainy season of July in the SFC system. CLR severity recorded in the year 2020/21 during the main rainy season of July in the SFC system was not statistically different from the severity recorded in the FC system in the same year during the main rainy season of July (Figure 4B). CLR severity recorded in the SFC system in the year 2015/16 during the beginning of dry season November was 37.7 times greater than the severity recorded in the FC system in the same year in the same season while the severity recorded in the SFC system in the year 2020/21 during the beginning of dry season November was 1.86 times greater than the severity recorded in the FC

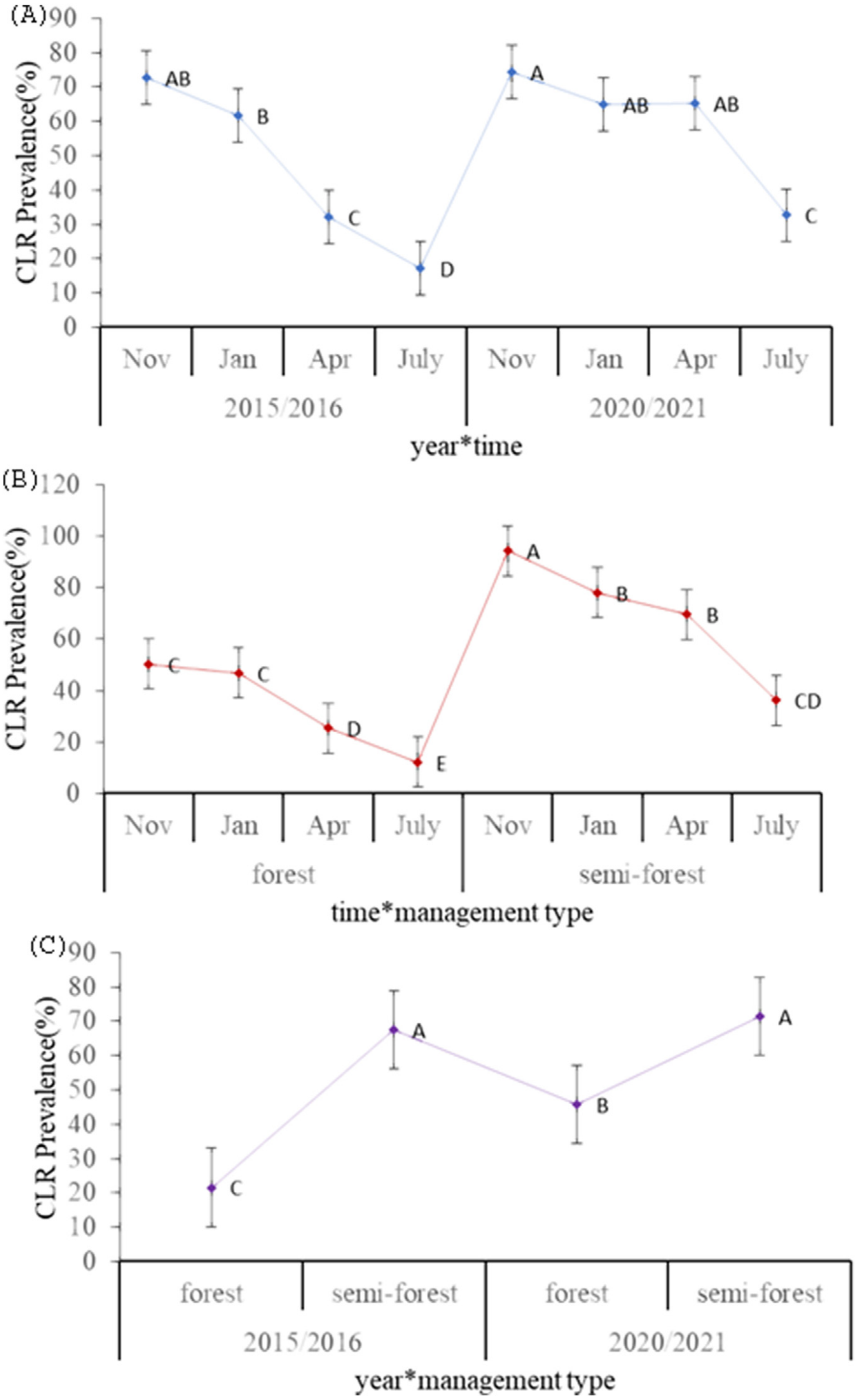

Figure 5. CLR prevalence as influenced by the interaction of year*time (A), time*management (B) and year*management (C) in SW-Ethiopia.

Table 3. Results of the generalized linear mixed effect models (GLMM) on the CLR infection measures, excluding management type. Beta-coefficients and test statistics (z) for each pairwise factor contrast (Tukey tests) for all retained factors. Model parameters (beta coefficients) and test statistics are also provided for all covariates (N = 272).

Coefficients		CLR Incidence		CLR Severity		CLR Prevalence	
		beta	z	beta	z	beta	z
Time	Nov–Jan	0.73	6.45***	0.77	8.14***	0.68	3.65**
	Jan–Apr	1.42	10.20***	1.23	9.47***	1.43	7.59***
	Apr–Jul	0.70	4.33***	0.40	2.74*	0.49	2.63*
Crown cover		-0.024	-3.51***	-0.02	-3.13**	-0.03	-3.88***
Human impact		0.99	2.05*	1.23	2.66**	1.53	2.61**
PCA1		0.52	1.63	0.60	2.28*	0.40	0.98
PCA2		-0.81	-2.04*	-0.38	-1.34	-1.00	-1.95
Altitude		0.13	1.20	0.056	0.51	0.12	0.92

Significance: *: $0.05 \geq$ *P*-value >0.01; **: $0.01 \geq$ *P*-value >0.001; ***: $0.001 \geq$ *P*-value. CLR = coffee leaf rust.

Table 4. Results of the generalized linear mixed effect models (GLMM) on the CLR infection measures (Incidence, Severity and Prevalence), including coffee management type, time, year and their interactions (N = 544).

		CLR Incidence		CLR Severity		CLR Prevalence	
Term	DF Num	F-Value	P-Value	F-Value	P-Value	F-Value	P-Value
year	1	64.26	0.000	495.560	0.000	57.75	0.000
Time	3	241.89	0.000	107.310	0.000	127.54	0.000
Management type	1	256.08	0.000	112.170	0.001	88.39	0.001
year*Time	3	31.83	0.000	16.470	0.000	15.77	0.000
year*Management type	1	59.12	0.000	0.000	0.957	30.28	0.000
time*Management type	3	84.37	0.000	32.470	0.000	7.24	0.000
year*time*Management type	3	26.91	0.000	16.160	0.000	1.68	0.171

system in the same year in the same season (Figure 4B). Our findings showed that the interaction of year*time, time*management type and year* management type influenced CLR prevalence in SW-Ethiopia (Table 4; Fig 5A, B & C). Our results revealed that year *time interaction influenced CLR prevalence and the highest CLR prevalence (74.17%) was recorded during the beginning of dry season November in the year 2020/21 which was not statistically different from the prevalence (72.63%) recorded in the year 2015/16 during the same season. CLR prevalence (72.63%) recorded in the year 2015/16 during the beginning of dry season in November which was not statistically different between the prevalence (65%) recorded in the year 2020/21 during the main dry season of January and (65.62%) in the short rain season of April (Figure 5A). The lowest CLR prevalence (17.09%) was recorded in the year 2015/16 during the main rainy season of July. However, the CLR prevalence (32.15%) recorded in the year 2015/16 during the short rainy season of April which was not statistically different from the prevalence (32.64%) recorded in the year 2020/21 during the main rainy season of July (Figure 5A). The highest CLR prevalence recorded in the year 2015/16 during the begging of dry season November strongly reduced by 76.46% during the main rain season of July. Similarly, highest CLR prevalence recorded in the year 2020/21 during the beginning of dry season November strongly reduced by 56.14% during the main rain season of July. Time * management type interaction influenced CLR prevalence and the highest CLR prevalence (94.17%) was recorded during the beginning of dry season in November in the SFC system while the lowest CLR prevalence (12.19%) was recorded in the FC system during the main rainy season of July (Figure 5B). The highest CLR prevalence during the beginning of dry season November in the FC system was strongly reduced by 75.77% during the main rain season of July while its prevalence strongly increased by 87.23% in the second year 2020/21 during the beginning of dry season November in the SFC system. Generally, CLR prevalence was observed to be lower in the FC system as compared to SFC system (Figure 5B). Year * management type interaction also influenced CLR prevalence and the highest CLR prevalence was recorded in the SFC system for both years. However, the lower CLR prevalence was recorded in the FC system for both years 2015/16 and 2020/21 (Figure 5C).

Soil variables had a significant effect, independent of management type, on CLR incidence and prevalence, but not on CLR severity (Table 2). Both CLR incidence and prevalence were higher for forests on soils with high CEC, pH, and P and K content (PCA axis 2, Tables 1 and 2). CLR prevalence was furthermore higher for forests on soils with high organic matter content and high C, Ca, Mg and N content (PCA axis 1, Tables 1 and 2).

Compared to FC, SFC was characterized by significantly lower crown cover ($z = 5.8$, $p < 0.001$), soil nutrients (N, P, K, Mg), organic matter, CEC and pH (PCA1: $z = -4.2$, $p < 0.001$; PCA2: $z = -2.5$, $p = 0.014$), and significantly higher human impact ($z = -4.0$, $p < 0.001$), following the Mann-Whitney U tests. Altitude, on the other hand, did not differ significantly between SFC and FC plots ($z = 0.5$, $p = 0.637$). Although these differences between management types were not high enough to cause collinearity problems in the GLMM analyses (VIF <3), crown cover, human impact and altitude did not significantly explain additional variation in any CLR infection measure when management type was included in the model. These models indeed showed significantly higher CLR incidence, severity and prevalence for forests with low crown cover and high human impact (Table 3). Altitude did nonetheless not significantly affect the CLR infection measures, likely due to the relatively limited altitudinal variation between the sampled forests in our dataset (ranging from 1766 to 2308 m. a.s.l.).

4. Discussion

Overall, our study revealed that CLR infection measures were significantly higher in the SFC than in the FC management type. Our results showed that at least part of this difference in CLR infection was caused by the lower crown cover and higher human impact in the SFC management type. Since crown cover reflects the amount of shade, our findings suggest that, overall, the processes that reduce CLR infection under shaded conditions prevail over those that potentially increase CLR infection under these conditions. For example, the reduced wind speed under highly closed canopies in FC likely reduced urediniospore dispersal, consequently hindering CLR infection (Avelino et al., 2004; Boudrot et al., 2016). Additionally, the reduced amount of water droplets reaching the coffee canopy under high canopy closure, at least at light intensity rains, likely also contributed to a reduction of CLR spore dispersal and thus infection (Avelino et al., 2004). Also, shading's negative effect on the number of fruiting nodes per coffee tree might have kept CLR infection levels relatively low (Avelino et al., 2012). Perhaps the lower fruit set in the FC management type increases the plant's fitness and resistance to diseases such as CLR. Indeed, fruit load has been found to be positively correlated to CLR epidemic development (Avelino et al., 2006; López-Bravo et al., 2012; Garedew et al., 2019). The cost of investment in higher reproduction (high yields) is known to reduce vegetative growth which further reduces the plant fitness and its ability to resist pathogen attacks (Creissen et al., 2016). Furthermore, it is also known that high yields reduce the latency period duration of CLR spores (Avelino et al., 2004).

The findings of Merle et al. (2020a) showed that coffee vegetative growth and reproductive period affected CLR development in Costa Rica. As the current study focused only on the effect of human disturbance and crown cover; the questions of host pathogen interaction with vegetative and reproductive phases of the coffee shrubs on CLR infections remains to be studied in SW-Ethiopia. Microclimate conditions have been reported to mediate CLR development in Costa Rica (Merle et al., 2020b). As we did not include microclimate variables in the current study it is vital to identify the role of microclimate on CLR in SW-Ethiopia.

The observed positive effect of human impact through activities such as wood harvesting, tree damage, slashing, coffee planting and grazing on CLR infection in SFC, are potentially linked to increased CLR spore disturbance and liberation. Rountree and Guido (2016) found that CLR incidence is higher close to paths and human settlements than in less traveled areas in coffee plantations. CLR epidemics may increase during, and right after coffee harvest, when people tend to come into contact with coffee plants more frequently (Rountree and Guido 2016). The higher human impact in the SFC management type is furthermore not surprising because the SFC locations in our study area are surrounded by croplands, pasturelands, home gardens and human settlements, thus increasing chances of human impact, independent of management intensity. Alternatively, human impact effects on CLR infection might also be indirect, through increases in coffee yields, and thus CLR susceptibility of the coffee shrubs.

Our results indicated that differences in canopy cover and human impact were not able to fully explain the higher CLR infection in the SFC system, suggesting that other factors are also at play. Planting density is likely partly driving part of the unexplained CLR infection difference between management systems. Indeed, since planting density variation was limited between plots within one management system, we were unable to statistically separate planting density effects from the overall management system effect. Increased host plant uniformity (coffee variety type) in the SFC management type may also play a role. Previous studies have reported that genetic host plant uniformity favors CLR epidemics (Helfer 2014; Toniutti et al., 2017). In SW Ethiopia, farmers have been using a limited number of local landraces for coffee production in SFC systems (Garedew et al., 2019), whereas in FC systems, more genetic diversity might be present. Yet, Aerts et al. (2013) reported only minor differences in coffee genetic diversity between FC and SFC systems. Currently, the CLR infection levels are also increasing in commercial coffee plantations of SW Ethiopia, where intensification is even higher (Amsalu Abera and Amare Teshome, Limu and Goma coffee plantation, personal communication and observations). Furthermore, the long-term co-existence of *C. arabica* and CLR in the more natural FC system, and the presence of antagonists such as the hyperparasite *Lecanicillium lecanii* may play a role in keeping CLR at its lower levels in the more natural FC systems (Vandermeer et al., 2009; Hindorf and Omondi 2011). In this sense, high biodiversity, both at the species level and at the *C. arabica* genetic level could be keeping CLR infection levels low.

All CLR infection measures showed strong seasonal and annual variation in both management systems, with the highest infection levels just after the beginning of dry season (November). The lowest infection levels were recorded at the onset of the main rainy season (July). High CLR infection in the beginning of dry month (November) is probably not only related to water availability during the rainy season (Garedew et al., 2019), but is likely also related to increased spore release due to physical disturbances during coffee harvesting, since November is also the coffee harvesting seasons. High CLR infection levels during the coffee harvesting time were also reported for other countries (Boudrot et al., 2016; Vandermeer et al., 2018) and, our findings are in agreement with the previous work from Ethiopia (Chala et al., 2011). Significantly the highest number of new emerging leaves per branch per coffee shrubs was recorded during dry season (January) for SFC while significantly the highest loses of leaves per branch per coffee shrub were recorded during short rainy season (April) for SFC system (Figure 6). The lower CLR infections recorded during main dry season (January) and short rain season (April) in this study would be partly linked to the loses of infected coffee leaves and new emerging leaves. These findings are similar to the findings of Garedew et al. (2019) reported in Ethiopia. Our results indicated that high pH, Ca, Mg, N, C, organic matter and high CEC, P and K were associated with higher CLR incidence. This is partly in agreement with the findings of Avelino et al. (2006), who reported that an increase in Al and Fe content and a decrease in P content; and to a lesser degree, in Mg,

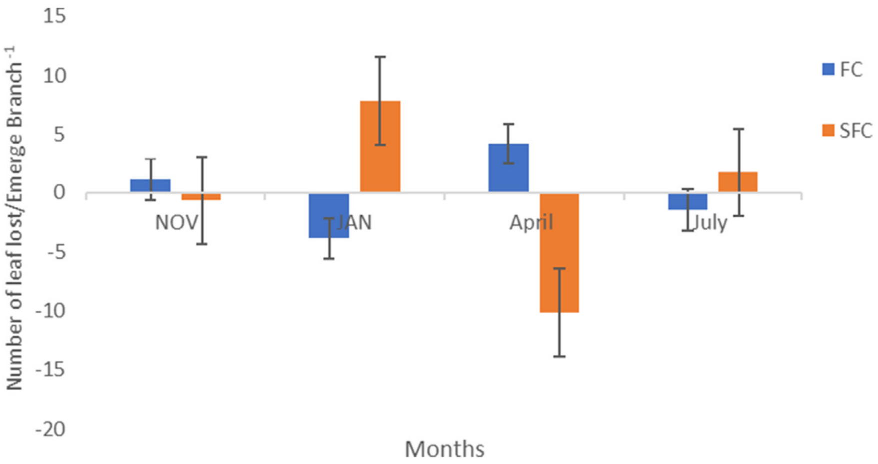

Figure 6. CLR infections were partly linked to the loses of infected coffee leaf and new emerging leaves in SW-Ethiopia.

Zn and Mn content, were associated with increasing CLR incidence. These results were, in turn, linked to increases in soil acidification. On the other hand, a study conducted in Peru revealed that soil properties did not affect CLR incidence (Ehrenbergerová et al., 2018). Because FC systems can be found in the Gera district only, whereas the SFC systems were sampled in the Mana district this may have caused a geographical bias. Yet, both areas are not further than 50 km distant from each other and both areas are characterized by the same potential natural vegetation (Friis et al., 2010; Hundera et al., 2013), suggesting that the soil and macroclimatic conditions are very similar. Furthermore, altitude did not differ significantly between SFC and FC plots ($z = 0.5$, $p = 0.63$). Therefore, we are confident that the differences in CLR infection rates that we established are mainly driven by forest management, and not by geographical or climatological differences.

5. Conclusions

The present study indicates that CLR infection measures increase with increasing coffee management intensity, partly due to lower crown cover and increased human impact in the SFC management type compared to the FC management type. This study complements the research showing negative impacts of coffee management intensity on coffee quality and biodiversity (Senbeta and Denich 2006; Aerts et al., 2011; Geeraert et al., 2019). Overall, our results indicate that although higher management intensity generally still results in higher total yields, proportionally larger losses due to CLR infections can be expected. Therefore, introducing more coffee genetic diversity, screening resistant coffee varieties and increasing canopy cover in the SFC will mitigate the CLR disease pressure and guarantee the sustainability of higher yields of the system in the future. Also, lower yields in the FC will be rewarded through providing price premiums so that farmers instantly get a higher price for their lower yield, guaranteeing livelihoods. Currently, information and awareness about the presence of CLR in SW Ethiopia is largely lacking among the coffee producing farmers, so there is a need to create awareness under the local farmers (Garedew et al., 2019). Further work should also survey CLR infections across wide range of areas in different years, in order to increase robustness of our results. Additionally, future research on CLR disease dynamics and infection levels in Ethiopia should consider the two additional common coffee production systems, plantation coffee and home garden coffee.

Declarations

Author contribution statement

GD, OH, BL and GB: Conceived and designed the experiments.
GD: Performed the experiments.
GD and KH: Analyzed and interpreted the data.
KHG: Contributed reagents, materials, analysis tools or data.
GD, KH, OH, BL and GB: Wrote the paper.

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Data availability statement

Data will be made available on request.

Declaration of interest's statement

The authors declare no conflict of interest.

Additional information

No additional information is available for this paper.

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