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Local and regional drivers of the African coffee white stem borer (*Monochamus leuconotus*) in Uganda

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Abstract

1 The African coffee white stem borer (CWSB) *Monochamus leuconotus* is a destructive pest of Arabica coffee in Africa. Documentation on outbreaks, spatiotemporal development and the relationship with different environmental conditions and coffee production system is limited.

2 To underpin effective control measures, we studied aspects of local and regional pest drivers in Eastern Uganda.

3 At the local scale, we (i) characterized the temporal development of CWSB and explored associations with environmental and shade-related indicators. During two growing seasons and on 84 coffee plots, we recorded CWSB incidence/infestation and microclimate on an altitudinal gradient and different shading systems. The bimodal rainfall, altitude and shade affected CWSB development through their effect on minimum temperature.

4 At the landscape level, we (ii) analyzed the spatial pattern of CWSB. Data on CWSB were collected on 180 plots. Pest incidence showed a spatial arrangement varying by districts. A possible relationship with human movement and the landscape context contributing to pest spread is suggested.

5 CWSB control measures should be synchronized with the bimodal rainfall patterns and an emphasis should be given to identifying and limiting pathways of pest spread from highly infested to new areas.

Keywords Arabica coffee, climate change, microclimate, *Monochamus leuconotus*, shade-grown coffee, spatial autocorrelation.

Introduction

Stem borers of the Cerambycidae family are severe pests of Arabica coffee (Waller *et al.*, 2007; Egonyu *et al.*, 2015). They have become more important with respect to the banning of dieldrin insecticide and poor management of coffee plantations. Studies of the bioecology of the important coffee stem borer *Xylotrechus quadripes* in southeast Asia and India underpin recommendations for its sustainable management (Giddegowda Venkatesha & Dinesh, 2012; Thapa & Lantinga, 2016). The African coffee white stem borer (CWSB, *Monochamus leuconotus*) is similarly destructive on Arabica coffee in Africa (Waller *et al.*, 2007; Jonsson *et al.*, 2014). Although up to 80% of infested coffee farms in eastern and southern Africa have been reported, few studies have focussed on this (Kutywayo *et al.*, 2013; Egonyu *et al.*, 2015).

Early instars of CWSB ring bark the plants, affecting the vascular transport system so that heavily-affected young trees may die (Schoeman *et al.*, 1998; Rutherford & Phiri, 2006; Vega *et al.*, 2006). Because the pest develops inside the trunk, it is difficult to control. There are few economically-effective chemicals and management is limited to laborious stem treatments

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such as manual removal (Vega *et al.*, 2006; Egonyu *et al.*, 2015). More recently, research has sought alternatives such as plant resistance (Egonyu *et al.*, 2015), biological control (Karanja *et al.*, 2010) and pheromones for trapping systems (Murphy *et al.*, 2008), although these are in their early stages. Nevertheless, any control method requires an understanding of the bioecology of a pest, as well as its inter-relationships within the production agroecosystem.

The life cycle of CWSB and its reproductive and feeding behaviour has been studied both in the laboratory and field. Females insert eggs under the bark of a coffee stem. After hatching, early-instar ringbarking stages feed on phloem and cambium tissue, whereas the late-instar wood boring stages create galleries in the coffee stems. In total, there are seven larval stages, which are followed by pre-pupal and maturation periods. The adults emerge by making circular exit holes. The duration of the life cycle varies between one and half and two years, depending on the environmental conditions (Knight, 1939; Tapley, 1960; Gichuhi *et al.*, 2017). There are only limited data available, however, for CWSBs regarding spatiotemporal development, outbreaks, and their relationship with environment and shade management. Similar to other insect pests, CWSB is expected to expand its altitude and latitude limits in response to climate change, as well as through changed development patterns and inter-generational timing (Porter *et al.*, 1991; Kutywayo *et al.*, 2013; Bjorkman & Niemela, 2015). CWSB responds to shade and higher infestation is observed in shaded compared with sun-exposed coffee. The shade effect on CWSB is also altitude dependent. Some studies report it to be most pronounced at altitudes between 1511–1605 m a.s.l. (Jonsson *et al.*, 2014) and others at higher altitudes (> 1700–2000 m a.s.l.) (Liebig *et al.*, 2016). The effect is assumed to be a result of differences in microclimate. The interaction between shading and changed climate in the future is a trade-off in the broader context of adaptation to climate change. In coffee agroecosystems, shade is often seen as an option for adaptation to future climates (Lin, 2007). It is therefore important to determine whether and how shading and other environmental and temporal aspects affect the abundance of CWSB.

Many previous studies have shown contradictory results with respect to shading effects on coffee pests and diseases because they were site-specific (Allinne *et al.*, 2016; Boudrot *et al.*, 2016). In the present study, we therefore compared CWSB abundance along altitudinal gradients and coffee shading systems. The altitudinal gradient covers a range of environments and, moreover, it allows potential responses to climate change to be estimated (Hodkinson, 2005). At the local scale, we (i) aimed to characterize the temporal development of CWSB to explore associations with environmental (altitude) and shade-related indicators. At the landscape level, we (ii) explored the spatial pattern of CWSB to discuss further spatially relevant factors related to pest abundance.

Materials and methods

Study area

The present study was conducted in seven districts that produce Arabica coffee in the Mt Elgon area of eastern Uganda (Fig. 1). The area, dominated by smallholder agriculture, has an altitude of 1000–2200 m a.s.l. We sampled three altitude ranges: low (< 1400 m a.s.l.), mid (1400–1700 m a.s.l.) and high (> 1700 m a.s.l.). The area has bimodal rainfall with peaks in March/April and October/November and is dry in December to February. At high altitudes, the rainy season is prolonged. Annual rainfall is 1200–1800 mm, with a mean temperature in the range 18–23 °C, depending on altitude (Hijmans *et al.*, 2005). Smallholders grow coffee with varying shade-tree species and density, with bananas or with no shade. They grow traditional varieties, including SL 14, SL 28 and Nyasaland.

Plot selection and characterization

We selected sites based on a survey made in 2014 (Liebig *et al.*, 2016). In brief, along the three altitude ranges, we created typologies of shading systems using descriptors of the vegetation structure. Table 1 shows which shade-related descriptors were used, as well as how they were characterized (see also Supporting information, Appendix A).

We collected data from 35 plots in the 2014/2015 and 49 plots in 2015/2016 season to characterize the temporal development of CWSB and its association with altitude and shade-related indicators [objective (i)]. Plot size ranged between 0.03 and 0.5 ha. Farmers usually prune attacked stems during the dry season and stump plots that were heavily attacked. Stumping is a pruning technique leading to the removal of all the foliage by cutting the trunk at 30 cm from the ground. We discarded any plots that were completely stumped in the first season but conserved those that were sparingly pruned for the second season. We considered data of the plots for each year as independent (Avelino *et al.*, 2006, 2007), giving a total of 84 plots. We installed temperature data loggers (Thermochron® iButtons® DS1923; Maxim Intergrated, San Jose, California) on a subset of 27 plots (three replicates for each shading system by three altitudes). We installed two screened loggers (Holden *et al.*, 2013) on each plot at the height of 1.50 m, and set them to record each hour during the 2015/2016 season.

For the spatial analysis [objective (ii)], we selected 180 plots (including the 49 plots used for the plot scale study) in the seven coffee-producing districts of Mt Elgon. We allocated each plot to one of the three shade systems and the appropriate altitude class (see Supporting information, Appendix B1).

Data collection

Data on the temporal development of CWSB at plot scale (i). We collected data in two growing seasons from 2014/2015 and 2015/2016. Plots were heterogeneous in structure and size. Per plot, we systematically selected 5–15 coffee bushes representing the shading system of the whole plot. We avoided bushes that were too old (> 30 years) or too young (< 5 years) and also those on plot borders to avoid boundary effects. We sampled a total of 767 coffee bushes in both years.

We examined all stems up to 2 m above the collar level of each bush for CWSB infestation. Stem borer damage differs depending on the life stage of the insect (see supporting information, Appendix C). New infestations, visible by the typical ringbarking

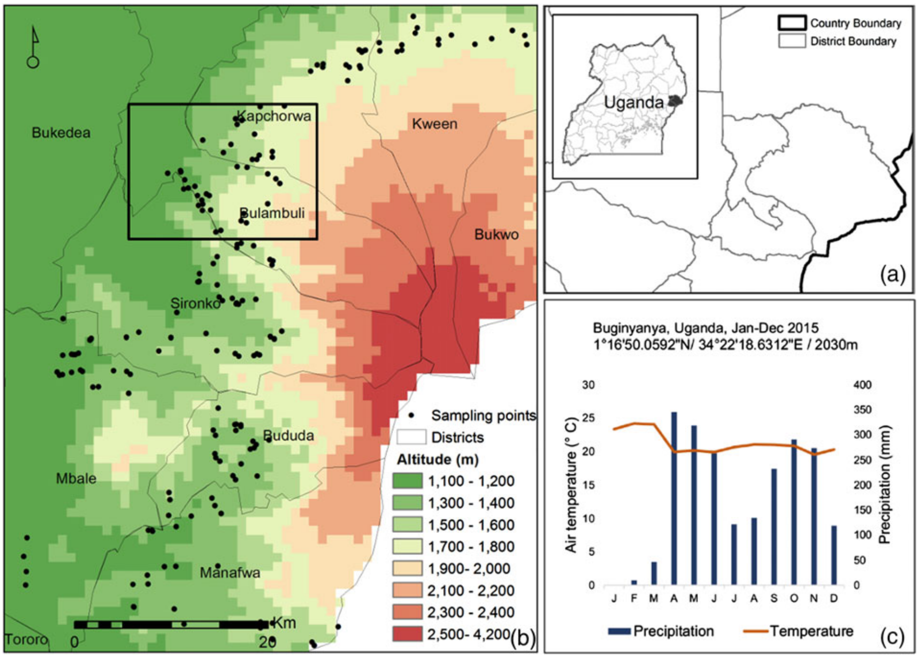

Figure 1 (a) Location of study area within Uganda. (b) Location of the sampled plots within the study area. The squared area contains plots used for assessing the temporal development of coffee white stem borer (CWSB) and associations with altitude and shade-related indicators at plot scale [objective (i), season 2014/2015 and 2015/2016]. Spatial distribution of CWSB at landscape scale [objective (ii), season 2015/2016] used all of the sites shown. (c) Monthly mean temperature (mean of daily dry bulb temperature) and accumulated precipitation from January to December 2015. [Colour figure can be viewed at wileyonlinelibrary.com].

Table 1 Characteristics of the coffee-shading systems

	Coffee-open canopy (CO) ($n = 54$)	Coffee-banana (CB) ($n = 44$)	Coffee-tree (CT) ($n = 46$)
Coffee density (coffee ha^{-1})	2255 ± 125^a	2094 ± 127^a	2095 ± 112^a
Banana density (bananas ha^{-1})	29 ± 17^a	1496 ± 105^b	278 ± 82^c
Shade tree density (trees ha^{-1})	63 ± 6^a	49 ± 6^a	146 ± 16^b
Shade tree species richness[a]	2.8 ± 0.2^a	2.7 ± 0.2^a	6 ± 0.4^b
Canopy closure (%)[b]	21 ± 1.4^a	28 ± 1.4^b	48 ± 2^c

[a]The total tree species richness was 37, of which 69% were indigenous to the area. *Cordia africana* and *Ficus* spp. accounted for 50% of tree species abundance.

[b]Canopy closure indicates the average plot shade estimated using a spherical crown densiometer (Forestry Suppliers, convex model A) (Lemmon (1957)) at four random positions within the plot. Data are the mean ± SE. Means within rows with different letters indicate significant differences (one-way analysis of variance, $P < 0.05$). Clustering was based on a total of 148 plots, which were sampled in May 2014. In 2015, 22 additional plots were included and classified retrospectively. CB, coffee-banana system; CO, coffee-open system; CT, coffee-tree system. These plots were used for assessments of coffee white stem borer.

phase, are characterized by frass on the bark surrounding the entry hole. Older damage (barked areas and entry holes) has no frass, whereas exit holes, from which adults have emerged, all are circular and larger than entry holes. The number of orthotropic stems per marked coffee bush was counted and damage was recorded for each stem.

We monitored four times in 2014/2015 (June, August, October, and December) and eight times in 2015/2016 (February, March/April, May/June, July, September and November of 2015, as well as January and February of 2016). We derived two plot-based indices of pest infestation. CWSB incidence was the number of bushes showing any signs of infestation as a proportion of the total number of bushes sampled in each plot. The rate of new infestation was the difference between the number of new entry holes of two consecutive dates as a proportion of the total number of stems and sampled bushes per plot.

Data on the spatial distribution of CWSB at landscape scale (ii). We established cross-shaped transects of 15 coffee bushes through the center of each plot, using the same criteria as described above, to score the presence of signs of CWSB. CWSB incidence (i.e. the number of bushes showing any signs of infestation as a proportion of the total number of bushes sampled in each plot) was calculated. We sampled in February to April 2016, corresponding to the activity peak of early-instar ringbarking (Appendix C, supporting information).

Statistical analysis

Data on the temporal development of CWSB and associations with altitude and shade-related indicators at plot scale (i). We analyzed seasonal development of CWSB graphically, plotting the rate of new infestation against a sampling date. We analyzed the effect of altitude and shading (main effects, tested individually and in interaction) on CWSB incidence (maximum annual infestation value per plot) using a generalized linear model with a Poisson error structure. We tested model suitability and goodness of fit with the Akaike information criterion (AIC) and the likelihood ratio test. We then used post-hoc pairwise comparisons on the interaction terms. We used a three-step procedure to analyze associations between maximum CWSB incidence, altitude and the four descriptors of shading. Because the relationships were not linear, we transformed each input variable using hierarchical clustering (see Supporting information, Appendix B2). We then used multiple correspondence analysis as a precursor to profile clustering, using only the first dimensions to stabilize the clustering (Husson *et al.*, 2010). A combination of principle component methods and hierarchical clustering was used to describe similarities and differences between individuals with respect to a set of variables from a multidimensional dataset. We extracted monthly means of minimum and maximum temperatures from the hourly data and applied a linear mixed-effects model with the plot ID as the random factor. We assessed goodness of fit with AIC and R^2 for the mixed models.

Data on the spatial distribution of CWSB at landscape scale (ii). We analyzed and mapped the spatial pattern of CWSB distribution in the whole Mt Elgon region in a two-step process. We first analyzed the spatial autocorrelation among sites. We used semi-variograms to visualize the extent of spatial autocorrelation and how it behaved over distance. We then fitted an empirical variogram using least squares. Next, we modelled the spatial distribution of CWSB in relation to the altitude and geographical coordinates. We used a generalized additive model with a negative binominal error distribution to accommodate the nonlinear relationships between the predictors and response variables (Hastie & Tibshirani, 1990). Incorporating the geographical coordinates enabled the model to account for spatial autocorrelation (Dormann *et al.*, 2007; Miller, 2010) and to model CWSB distribution dependent on altitude for each level of the shade systems. We plotted the additive effects of altitude, location and shade on the predicted CWSB infestation with confidence intervals. We mapped the CWSB predictions for the entire region on a 1-km grid based on altitude and geographical location.

Software and packages. We used R software (R Foundation for Statistical Computing, Austria) with RSTUDIO, version 0.99.903 (Rstudio, Boston, Massachusetts) and specific packages for data analysis: 'FactorMineR' (Lê *et al.*, 2008), 'lsmeans' (Lenth, 2015), 'lme4' (Bates *et al.*, 2014), 'spdep' (Bivand *et al.*, 2015), 'geoR' (Ribeiro & Diggle, 2001), 'mgcv' (Wood, 2001), 'ggplot2' (Wickham, 2010) and 'raster' (Hijmans, 2013). We used ARCMAP (ESRI, 2011) to produce the maps. We used the 90-m resolution digital elevation model of the shuttle radar topography mission and the administrative borders from the Data.Ug database (http://maps.data.ug/).

Results

Temporal development of CWSB and associations with altitude and shade-related indicators at plot scale (i)

Temporal development of CWSB. The temporal pattern of CWSB is shown in Fig. 2. In both seasons, the number of new entry holes increased after the onset of the two rainy seasons, showing infestation peaks in the periods from December to February for both seasons, and from May to July for the second season (2015/2016). The CWSB incidence was affected by the altitude range, coffee shading system and the interaction between the two predictors (Fig. 3). Overall, the CWSB incidence was highest in coffee-tree system systems, although this effect was expressed most at high altitudes.

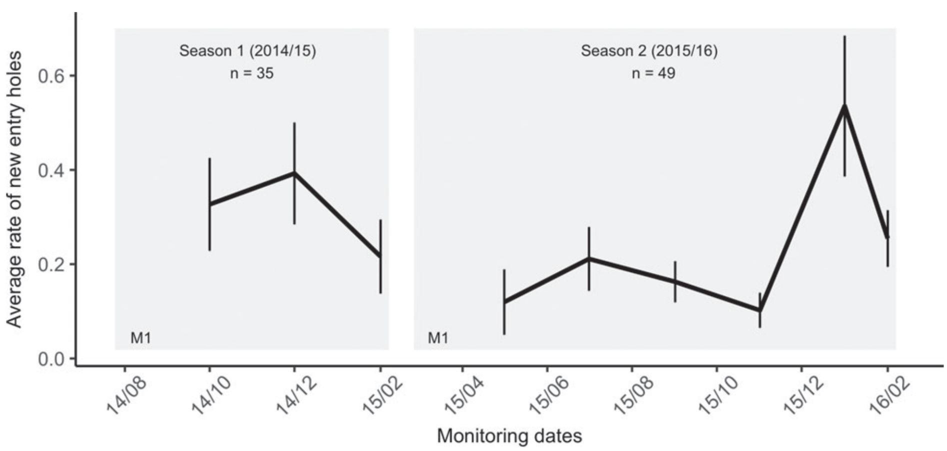

Figure 2 Seasonal development of coffee white stem borer. The rate of increase in the number of new entry holes. Means with standard errors are plotted. Because the rate is the difference of two consecutive dates, means starting from the second monitoring are shown. M1 refers to the first monitoring date of each season. The mean number of entry holes per plot (relative to the total number of stems/total of sampled bushes) of the first date was 0.85 for the 2014/2015 season and 0.83 for the 2015/2016 season, respectively.

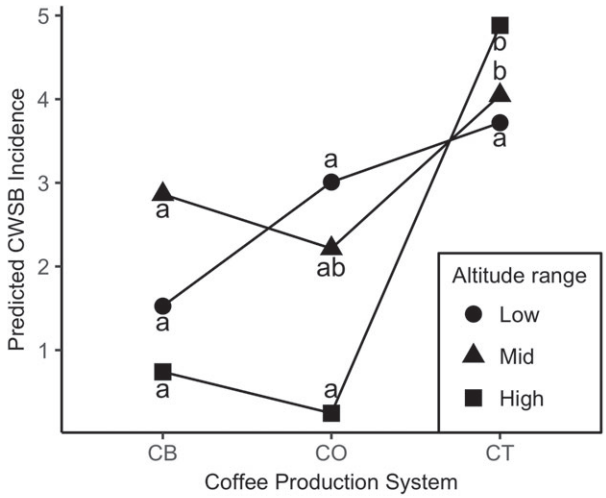

Figure 3 Least-squares means of predicted probability of coffee white stem borer (CWSB) incidence (back-transformed by inverse-link function to the original response scale) based on the fitted generalized linear model (GLM) model testing the interaction between altitude category and coffee system. Differences between coffee systems are indicated by different letters (Tukey-type comparisons of GLM parameters, $P < 0.05$, tested separately for each altitude category). CB, coffee-banana system; CO, coffee-open system; CT, coffee-tree system. The interaction was significant ($P < 0.001$).

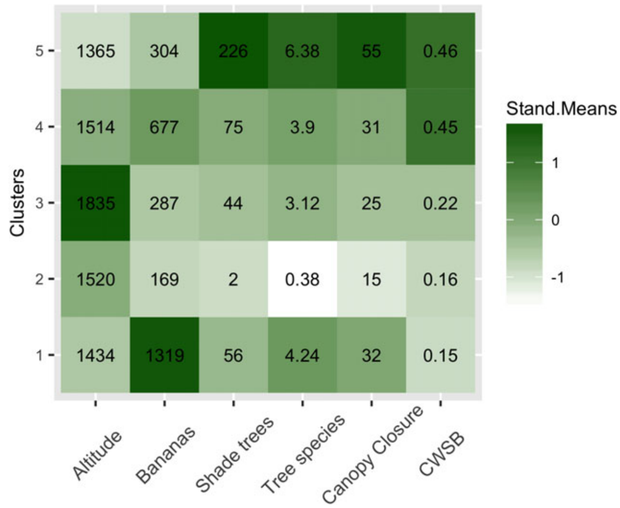

Figure 4 Clusters based on hierarchical classification showing cluster means for input variables. The mean values of the input variables are shown within the squares, and the standardized means are shown by colours. For example, cluster five showing the highest coffee white stem borer (CWSB) incidence are related to high numbers of shade trees, tree species and canopy closure. Bananas, banana density (mats ha^{-1}); Shade trees, shade tree density (trees ha^{-1}); Tree species, shade tree diversity; Canopy closure, percentage of sky hemisphere obscured by shade canopy; CWSB, CWSB incidence (proportion of infested bushes). [Colour figure can be viewed at wileyonlinelibrary.com].

Associations with altitude and shade-related indicators. The multiple correspondence analysis showed a significant association between maximum CWSB incidence, altitude and the four descriptors of shading (banana density, shade tree density, shade tree species richness and canopy closure). The leading six components, which explained 66.8% of the variance, were subsequently used in a hierarchical classification (Fig. 4). The clustering indicates that CWSB incidence is related to shade tree quantity and diversity. The two clusters with the highest incidences (45% and 46% of infested bushes on average, respectively) are related to high numbers of shade trees, tree species and canopy closure, whereas cluster two, with the second lowest mean CWSB incidence (16%), shows the lowest values for those shade-related variables. In addition, cluster three shows the relationship for CWSB incidence and altitude. Individuals of this cluster with a moderate CWSB incidence show intermediate values for shade indicators and a high average altitude. The first cluster has the lowest CWSB incidence (15%) despite a relatively high shade tree density, canopy cover and shade tree diversity. It is notable for its a high density of banana mats.

Canopy minimum air temperature showed a significant interaction between altitude, shade system and month ($P < 0.001$), whereas, for the maximum temperature, only the main effects were significant ($P < 0.001$) (Fig. 5). At high altitudes and consistently over time, coffee-tree systems showed significantly higher minimum canopy air temperatures (least-squares mean = 14.7 °C) compared with the other systems [coffee-banana system = 13.9 °C and coffee-open system = 13.1 °C]. For low and mid altitudes, there were no differences between systems, although only between months. Coffee-open systems had the highest maximum canopy air temperatures at all altitudes.

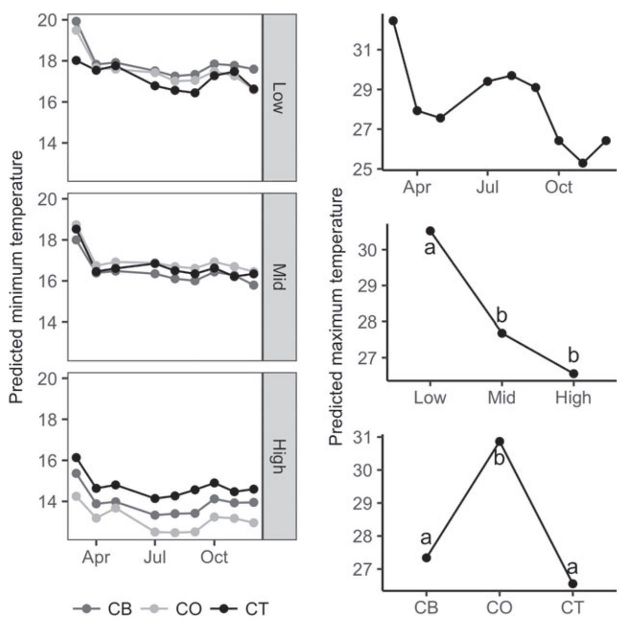

Figure 5 Minimum canopy air temperature (left) showing the second-order interaction between altitude, coffee system and month. CB, coffee-banana system; CO, coffee-open system; CT, coffee-tree system. ($P < 0.001$) (for detailed data, see Supporting infromation, Appendix B3). Maximum canopy air temperature (right) showing the main effects of month of the year, altitude and shade system ($P < 0.001$). Differences between altitudes and coffee systems are indicated by different letters (Tukey-type comparisons of generalized linear mized model parameters, $P < 0.05$).

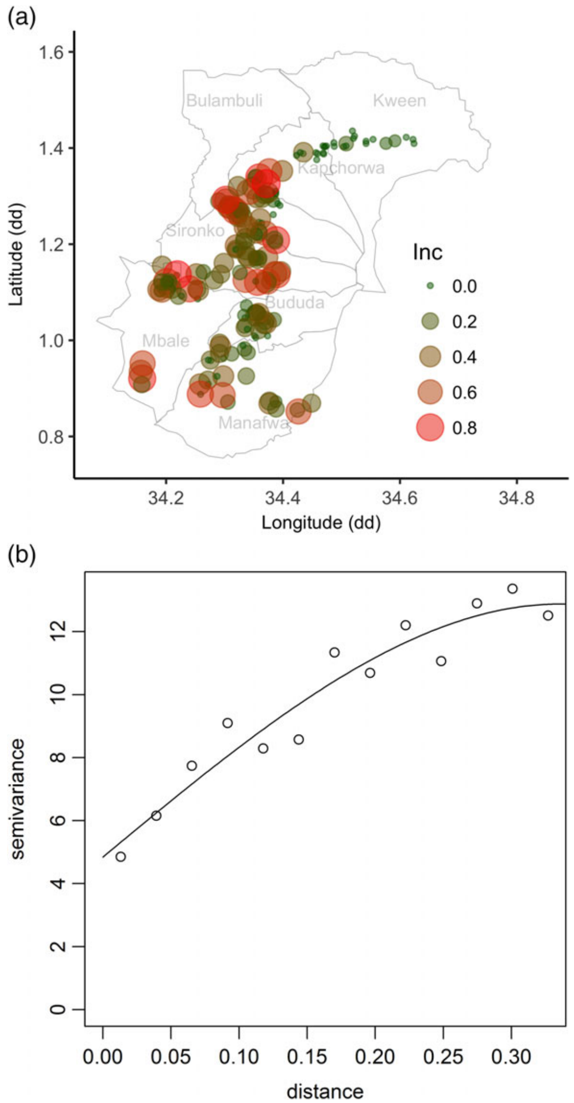

Figure 6 (a) Coffee white stem borer (CWSB) incidence according to geog raphical location. (b) Spatial dependency of CWSB incidence. Semivariance is the mean square deviation, which is plotted against the distance (km*100) between points. [Colour figure can be viewed at wileyonlinelibrary.com].

Spatial distribution of CWSB at landscape scale (ii)

Analysis of spatial autocorrelation. There were high incidences of CWSB in the districts of Kapchorwa and Bulambuli and lower incidences around Kween and Bududa (Fig. 6a), with significant spatial autocorrelation (Moran I coefficient, $P < 0.05$). The semi-variogram (Fig. 6b) shows a nugget effect between the degree and range of the spatial autocorrelation, indicating that the spatial structure only explained part of the variability in the CWSB incidence. Spatial autocorrelation decreased with distance and reached a plateau at approximately 25–30 km.

Influence of altitude and geographical coordinates distribution on CWSB. Generalized additive models were used to describe the effect of altitude, geographical location and coffee shading system on CWSB incidence. The model showed a significant effect of both predictors, altitude (by coffee shading system) and geographical location, on CWSB incidence (Table 2). The response curve for CWSB with respect to dependence on altitude for each level of the coffee shading system is shown in the Supporting information (Appendix D). There are no differences in CWSB response for the different systems below an altitude of approximately 1700 m a.s.l.; however, above this altitude, the model estimated a slightly higher CWSB response in coffee-tree systems, whereas no differences were estimated for the other systems.

Maps based on the models of altitude and geographical location show that the highest infestations are predicted at altitudes below 2000 m a.s.l. (Fig. 7). We predict a high risk in the districts of Kapchorwa and Bulambuli, as well as the lowlands of Mbale and Manafwa, and a lower risk in Bududa and Kween.

Discussion

In the present study, we show that the development of the African coffee white stem borer is controlled by the bimodal rainfall, as well as by altitude and shade through their effect on minimum temperature. Pest incidence showed a spatial arrangement varying in accordance with geographical location.

Temporal development of CWSB and associations with altitude and shade-related indicators at plot scale (i)

Temporal development of CWSB. African coffee white stem borer phenology and its link with the bimodal rainfall pattern is in agreement with previous studies (Knight, 1939; Tapley, 1960). The peaks can be attributed to the phenological stages where new entry holes were bored (see supporting information, Appendix C). There were more attacks in the second rainy season (October/November 2015/2016) than in the first rainy season (March/April 2015/2016). Growers implement control measures during the post-harvest (dry) season that reduce residual infestation to low levels. A higher infestation at the start of the second rainy season in October might result from less time spent on pest management during the harvest season (see supporting information, Appendix B4). Moreover, the duration of the CWSB life cycle varies with latitude and altitude (Waller *et al.*, 2007), enabling the pest to coordinate its life cycle with conducive environmental conditions (Gichuhi *et al.*, 2017). The identification of CWSB adults emerging in synchrony with the rainfall patterns suggests that control measures might be focused on the start of the two rainy seasons. Control options that aim to prevent oviposition such as smoothing the stem bark (the females lay eggs under the bark scales), wrapping or insecticide banding (de Villiers *et al.*, 1973; Egonyu *et al.*, 2015) should be synchronized with the bimodal rainfall pattern. Once the larvae have penetrated the bark, preventative control options are inefficient. Inadequate timing might explain why those methods have remained inconclusive (Murphy *et al.*, 2008; Egonyu *et al.*, 2015).

Associations between CWSB, altitude and shade-related indicators. CWSB infestation is highest in coffee systems with high shade tree density and diversity (Murphy *et al.*, 2008;

Jonsson *et al.*, 2014; Liebig *et al.*, 2016). Poikilotherms depend on ambient temperatures (Bale *et al.*, 2002); therefore, the modification of thermal environment by shade is a possible mechanism. Altitude drives CWSB populations (Waller *et al.*, 2007), although it is only decisive in connection with other factors of the agroecosystem. The interactive effect of altitude and the coffee system on minimum temperatures might be key for CWSB at high altitudes. Where mean atmospheric temperatures are too low (the optimum is 25 °C; Schoeman *et al.*, 1998; Gichuhi *et al.*, 2017), increased minimum temperatures in shaded systems (i.e. coffee-tree system) appear to enable CWSB establishment. This could be important for CWSB adults during the reproductive and oviposition phases, as well as the early larval stages. At lower altitudes with favourable mean atmospheric conditions, minimum temperatures are not a limiting factor. Accordingly, differences in CWSB infestation and minimum temperature between systems are negligible. African coffee white stem borer probably prefers shaded habitats to allow it more flexibility with respect to regulating its body temperature. Interactions between the macroclimate and abiotic or biotic factors create a complex thermal landscape. The resulting local microclimate is heterogeneous in space and time and has a decisive effect on the bioecology of insects (Hodkinson, 2005; Sears *et al.*, 2011). The ecological importance of microclimates is more important in mountain habitats than it is for habitats at lower altitudes. Variability in radiation, atmospheric pressure and interactions with local factors create habitats for insects, regardless of the mean air temperature (Hodkinson, 2005; Mani, 2013). Ecologically relevant microenvironments have not been studied sufficiently and their relevance remains understated (Potter *et al.*, 2013; Sunday *et al.*, 2014; Stigter, 2015). The impact of spatial variability and interactions with the local environment on pests and diseases is essential for understanding agricultural systems and the development of integrated pest management strategies (Dormann *et al.*, 2007; Sciarretta & Trematerra, 2014). This is especially relevant for the analysis of potential future climate effects on pest dynamics in tropical mountain areas.

Other shading mechanisms are possible, such as light level. Females appear to prefer darkness for oviposition, although CWSB is not generally attracted by light (Knight, 1939; Schoeman *et al.*, 1998; Gichuhi *et al.*, 2017). Shade trees are unlikely alternative hosts for CWSB because only some wild Rubiaceae species are known to host it (Dufpy, 1957).

Management is another possible driving factor for the pest. We found a lower infestation in systems shaded by bananas,

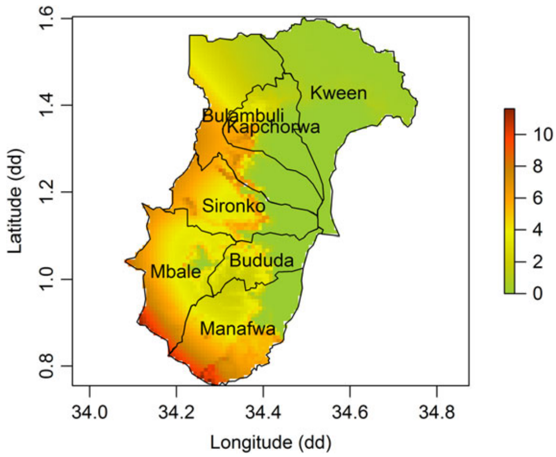

Figure 7 Predicted number of infested coffee bushes per plot (back-transformed data) by geographical location. [Colour figure can be viewed at wileyonlinelibrary.com].

where coffee is better managed than in the other systems. The intercropped system receives more attention and women are also involved in the process, increasing the labour input. Moreover, bananas are sold, which enables farmers to invest more in agronomic inputs (van Asten *et al.*, 2011; Jassogne *et al.*, 2013).

Spatial distribution of CWSB at landscape scale (ii)

Spatial heterogeneity also determines any variation in CWSB infestation, as indicated by both spatial autocorrelation and the incidence map, demonstrating different aggregations at the district level. The effect of altitude is inconsistent. All plots in the Kween district (above 1800 m a.s.l.) had a low infestation, as expected (Hill, 1983), whereas plots in the neighbouring Kapchorwa district at high altitude had a high infestation. The area around Bududa and northern Manafwa, at low and mid altitudes, had a low CWSB infestation. Although altitude does affect CWSB, there must be other factors involved. One potential factor may be the surrounding landscape from which (depending on the species) pests may spill over across both habitats and managed agricultural systems (Tscharntke *et al.*, 2005; Werling & Gratton, 2010). The amount of surrounding land covered by coffee is likely to be important, as is the case for other coffee pests (Avelino *et al.*, 2012; Banks *et al.*, 2013). The flight capacity of CWSB is only up to one mile (1.6 km) (Tapley, 1960). It might therefore benefit from connected coffee growing areas

Table 2 Results of generalized additive model showing approximate significance of smooth terms[a]

	Estimated d.f.	Reference d.f.	Chi squared	*P*
s(altitude) × CB	3.451	4.269	10.747	0.039474*
s(altitude) × CO	3.538	4.383	8.962	0.074417
s(altitude) × CT	2.318	2.823	5.302	0.099687
s(lat, long)	9.898	13.203	36.033	0.000721***
R^2 (adjusted) = 0.305		Deviance explained = 42.3%		*n* = 179
Restricted maximum likelihood = 402.03		Scale est. = 1		

[a]*s*() = coefficients for smooth/spline terms. CB, coffee-banana system; CO, coffee-open system; CT, coffee-tree system. Significance levels: **P* < 0.05, ****P* < 0.001.

because the chances for migration into new coffee fields are increased (Avelino *et al.*, 2012). Moreover, Kween is relatively new to coffee production, having fewer coffee plots and less infestation than the older district Kapchorwa. Coffee was established in Kapchorwa many decades ago and CWSB infestations are widespread. There is spatial autocorrelation up to 25–30 km, which might indicate human intervention. Many of the farmers in the present study use pruned coffee wood for firewood and construction (see Supporting information, Appendix B4). Any trade in the wood risks the spread of pests or diseases to other farms and regions, as for CWSB in Malawi and Zimbabwe (Murphy *et al.*, 2008) as well as coffee diseases, such as coffee wilt disease (*Gibberella xylarioides*) (Baffes, 2006; Belachew, 2016).

Conclusions

CWSB infestation is associated with shade tree density and diversity; however, especially at low altitudes, the removal of trees would increase trade-offs for the mitigation of climate change effects, as well as the provision of tree resources from within-farm trees. Therefore, CWSB control must aim to: (i) remove and eradicate heavily infested stems or preserve infested stems in conjunction with the manual removal of young larvae, (ii) synchronize preventive control actions with the onset of the rainy seasons during adult flight periods; and (iii) at the regional scale, strictly control the movement of coffee wood (e.g. selling wood for firewood or construction) to avoid the dispersal of WSCB to new areas.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix A. Characteristics of production typologies generated by K-means clustering.

Appendix B1. Dataset 2 for spatial analysis. Number of plots per altitude range and system.

Appendix B2. Categories for variables.

Appendix B3. Differences in predicted minimum temperatures between months by altitude and coffee system.

Appendix B4. Stumping activities of farmers based on questionnaire of baseline survey ($n = 148$) described in Liebig *et al.* (2016).

Appendix C. Theoretical **c**offee white stem borer (CWSB) phenology showing overlapping generations of four subsequent years.

Appendix D. Output of the fitted generalized additive model showing the smooth effect of altitude.

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