Influence of shaded systems on Xylosandrus compactus infestation in Robusta coffee along a rainfall gradient in Uganda

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Abstract
1 We investigated the relationship between characteristics of coffee shade systems and coffee pest infestation by the black coffee twig borer Xylosandrus compactus Eichhoff. The pest deprives Uganda of $40 millions annually, yet its control remains inadequate.
2 The present study considered three rainfall zones in Central Uganda and 50 coffee plots that were randomly selected from each rainfall zone. Data were collected on X. compactus infestation and key shade indicators: canopy cover, tree-species densities, diameter at breast height (DBH) and ratio of coffee to banana.
3 Cluster analysis revealed two coffee shade systems: a matured shade tree (MST) system and a young poly-culture (YPC) system. Xylosandrus compactus infestations were significantly less in the MST system than in the YPC system and significantly less in the low rainfall zone than in the high rainfall zone. An increase in the density of Carica papaya and Albizia chinensis significantly reduced and increased X. compactus infestation, respectively. A higher average DBH of individual trees and a higher density of trees that exude sap significantly lowered X. compactus infestation.
4 Suppressing X. compactus infestation requires bigger trees, a high density of sap-exuding trees and no Albizia chinensis. Further research should aim to investigate X. compactus flight activity and microclimate influencing X. compactus population dynamics.

Keywords Alternative hosts, black coffee twig borer, coffee agroforestry systems, diameter at breast height, East Africa, ecological pest control, tree sap, Xylosandrus compactus.

Introduction
The black coffee twig borer also known as Xylosandrus compactus Eichhoff (Coleoptera: Scolytidae) has severely affected Uganda’s coffee industry for more than a decade (Kagezi et al., 2014). By 2012, X. compactus had spread to 68% of Robusta coffee (Coffea canephora) farms in Uganda, where it infested 40% of coffee trees per farm and killed 8.6% of twigs (Kagezi et al., 2013c). Xylosandrus compactus mostly infests Robusta coffee, constituting over 70% of coffee produced in Uganda, which is the world’s second largest producer of Robusta coffee (Egonyu et al., 2015; UCDA, 2012). The pest costs Uganda US$ 40 millions of foreign exchange annually and thus there is an urgency for effective control mechanisms (Kagezi et al., 2013a; Kagezi et al., 2013c).

The phytosanitary control of pruning and burning infested twigs requires large investments in labour and time that are unaffordable to most smallholder farmers. Chemical control is ineffective because X. compactus remains concealed in the galleries that it bores inside coffee twigs (berry bearing branches) where chemicals cannot reach (Peña et al., 2011). Biological control still requires knowledge on the biology and ecology of X. compactus, as well as opportunities for the mass rearing of its natural enemies (Egonyu et al., 2015). However, designing coffee agroforestry systems (CFS) that suppress X. compactus infestation offers a potential alternative to X. compactus pest control that relies on ecological principles.

Generally, ecological pest control increases with habitat complexity: the extent and configuration of noncrop vegetation.
(Bianchi et al., 2006; Tscharntke et al., 2011; Iverson et al., 2014). Habitat complexity controls pests through ecological mechanisms, such as resource availability (Ratnadass et al., 2012), although their effectiveness in CAFS depends on pest and crop characteristics, as well as their configuration, namely shade systems and their constituent tree characteristics (Staver et al., 2001; Silesi et al., 2008; Gidion et al., 2014). For generalist pests such as *X. compactus* (Greco & Wright, 2015), infestation increases with plant diversity (Veres et al., 2013), although the relationship between *X. compactus* infestation and tree characteristics such as identity (species), size (diameter at breast height; DBH), density and configuration (shade systems) of agroforestry trees remains poorly understood (Kagezi et al., 2015).

Furthermore, *X. compactus* infestation, similar to other arthropod infestations, likely varies with climatic conditions (Jaramillo et al., 2009; Jaramillo et al., 2011). Therefore, current ecological solutions should consider insights into future climatic changes and how such changes might influence *X. compactus* dynamics (Teodoro et al., 2008; Avelino et al., 2011; Oliver et al., 2015).

Designing CAFS that suppress *X. compactus* requires knowledge on how shade systems, constituent trees and their characteristics influence *X. compactus* infestation along a climatic gradient. The present study (i) used shade indicators to characterize coffee plots into shade-based systems along a rainfall gradient; (ii) examined the influence of shade systems and rainfall on *X. compactus* infestation; and (iii) determined the effect of density, size and sap exudation of selected trees species on *X. compactus* infestation. Based on the above objectives, the study tested the hypotheses that: (i) coffee shade systems of Central Uganda are heterogeneous; (ii) coffee shade systems and rainfall zones influence *X. compactus* infestation; (iii) tree density of selected tree species influence *X. compactus* infestation; (iv) tree size influences *X. compactus* infestation and; (v) density of sap-exuding trees influence *X. compactus* infestation.

**Materials and methods**

**Site description**

The study covered the greater Luweero region of Central Uganda (between 31°E, 32°E and 0.5°N, 1.3°N) with an area of approximately 9000 km². The greater Luweero region receives a bimodal rainfall with peaks in March to May and October to November. Annual rainfall varies from 700 mm in the North up to more than 1300 mm in the South (Lwasa et al., 2011; Funk et al., 2012). Consequently, the rainfall gradient was divided into three zones: a high rainfall zone (>1300 mm), a moderate rainfall zone (1100–1300 mm) and a low rainfall zone (<1100 mm). Across the rainfall gradient, most of the Robusta coffee is grown in CAFS. The present study used this rainfall gradient as a proxy for a climatic gradient to generate insights into possible climate change effects on *X. compactus* infestation in Robusta coffee. The coffee systems are rain-fed and on small land (<2.5 ha) holdings; their age is mixed such that it ranges from 5 years to more than 60 years on the same farm/plot.

**Data collection**

Fifty coffee (*Coffea robusta*) farming households were randomly selected within each of the three rainfall zones. From each household, if a farmer had more than one plot, we studied one coffee plot that was chosen randomly. For each selected plot, (i) plot area was measured using a Global Positioning System satellite receiver and shade cover by trees as canopy closure (%) was measured using a densiometer (Bellow & Nair, 2003); (ii) the number of coffee shrubs, number of banana plants and number of coffee plants infested by *X. compactus* per plot were counted; (iii) all tree species were identified by local name in Luganda (Language of Central Uganda) and the corresponding botanical name via a tree identification guide of Katende et al. (1995); and (iv) DBH for all trees (DBH > 10 cm) and tree density for each species were measured. Although pest damage assessment was a one-time survey conducted from September to November in 2015, it was timed during fruit maturation for coffee and shortly after pest-population peak period that runs from May through to August (Egonyu et al., 2016) so that we captured the maximum possible damage of the year.

**Statistical analysis**

The study characterized coffee plots into shade systems using hierarchical cluster analysis (CA) (Ward, 1963) that divided coffee shade systems into groups based on four shade indicators: (i) shade cover measured as percentage canopy closure (%) per farm; (ii) ratio of coffee to banana per farm; (iii) shade tree density per farm; and (iv) average DBH per tree on the farm. Furthermore, *X. compactus* infestation was measured as a proportion (between 0 and 1) of infested coffee plants to total number of coffee plants per plot. CA was based on ‘mclust’ package of R statistical software (Fraley et al., 2012; R Core Team, 2015). The influence of rainfall zones, shade systems, DBH, density of the dominant tree species and density of sap exuding trees on *X. compactus* infestation was modelled using the generalized linear model with a negative binomial error term for over dispersed count data via the ‘MASS’ package of R statistical software (Venables & Ripley, 2002; R Core Team, 2015). The inflection points were calculated from model equations as points on the model curves at which the second derivative of the curve functions were equal to zero.

**Results**

**Influence of coffee-shading systems and rainfall zones on *X. compactus* infestation**

Cluster analysis based on four shade indicators revealed two clusters, referred to here as shade systems: (i) the young poly-culture (YPC) coffee shade system [smaller trees and a low ratio (6:1) of coffee to banana] and (ii) the matured shade tree (MST) system [bigger trees and a high ratio (15:1) of coffee to banana] (Fig. 1). The shade systems showed no significant (*P > 0.05*) differences in the percentage of canopy closure and tree density but the YPC had significantly (*P > 0.001*) smaller trees and a lower coffee to banana ratio than MST (Table 1). The YPC systems were evenly distributed across rainfall zones, whereas the MST systems largely occurred in moderate and lower rainfall zones. However, no significant (*P > 0.05*) association between shade systems and rainfall zones was found.
Table 1: Characteristics of coffee agroforestry systems clusters generated by Ward’s method (n = 145) in the Greater Luweero region of Central Uganda

| Coffee-agroforestry systems                  | Clustering variables |
|---------------------------------------------|----------------------|
| Young poly-culture                          | Canopy closure (%)   |
| system (n = 111)                            | Mean ± SD            |
| Matured shade system (n = 34)               |                      |
| Shade-tree density (trees ha\(^{-1}\))       | 110.0 ± 91.5\(^a\)  |
| Coffee : banana ratio                       | 5.9 ± 6.6\(^a\)     |
| Mean DBH per tree (cm)                      | 22.1 ± 8.2\(^a\)    |

Means within a row with different lowercase letters indicate significant differences according to the Mann–Whitney test (P < 0.001). DBH, diameter at breast height.

The low rainfall zone had a lower mean infestation of *X. compactus* than the high and moderate rainfall zones and the MST systems had a lower mean *X. compactus* infestation than the YPC system (Table 2). The negative binomial model confirmed a significant influence of both rainfall zones and shade systems on the proportion of coffee shrubs infested by *X. compactus* (Fig. 2 and Table 3). Transitioning from high to low rainfall zone decreased the expected log count of *X. compactus*-infested coffee shrubs by 3.8639, implying a 98\% reduction in the proportion of coffee shrubs infested by *X. compactus*. Transitioning from YPC to MST systems also reduced the expected log count of *X. compactus*-infested coffee shrubs by 1.8568, implying a 84\% reduction in the proportion of coffee shrubs infested by *X. compactus*. Although both rainfall zones and shade systems significantly influenced *X. compactus*, their interaction was not significant.

Regarding shade indicators that defined the shade systems, DBH per tree was significantly and negatively correlated with *X. compactus* infestation (Table 4). The negative binomial model confirmed that DBH per tree significantly influences *X. compactus* infestation (Fig. 3 and Table 5). A one unit change in average tree DBH reduces the expected log count of *X. compactus*-infested coffee shrubs by 0.02915, implying a 2.9\% reduction in the proportion of coffee shrubs infested by *X. compactus*. From the equation of the curve shown in Fig. 3, the theoretical average DBH of individual trees that would significantly reduce *X. compactus* infestation is 46.1 cm.

Table 2: Average proportion of coffee plants infested by *Xylosandrus compactus* according to rainfall zones and agroforestry systems in the Greater Luweero region of Central Uganda

| Rainfall zones     | Average plot area (ha) | Mean *Xylosandrus compactus* infestation |
|--------------------|------------------------|----------------------------------------|
| High rainfall (> 1300 mm) | 0.440 ± 0.404 | 0.385 ± 0.245 |
| Moderate rainfall (1100–1300 mm) | 0.531 ± 0.421 | 0.359 ± 0.208 |
| Low rainfall (900–1100 mm)     | 0.303 ± 0.212 | 0.099 ± 0.015 |

Table 3: Coffee shade systems and *X. compactus* infestation

| Coffee shade systems | Average infestation |
|----------------------|---------------------|
| YPC                  | 0.430 ± 0.313       |
| MST                  | 0.440 ± 0.284       |

Figure 1: Grouping coffee-farms based on their shade indicators in the Greater Luweero region of Central Uganda. The dendrogram shows clustering by Ward’s method and number of clusters determined by the Beale index; YPC is Young Poly-Culture shade system and MST is Mature Shade Tree shade system. The individual divisions of dendrogram represents coffee farms/plots.

Figure 2: Negative binomial model examining individual effects of rainfall zones and agroforestry systems on proportion of coffee plants infested by *Xylosandrus compactus* (n = 122) in the Greater Luweero region of Central Uganda. The interaction was not significant and hence is not shown.

Influence of agroforestry tree-species density and their sap exudation on the proportion of coffee plants infested by black coffee twig borer

The density of some agroforestry tree species, notably *Albizia chinensis* and *Carica papaya*, significantly (P < 0.001) influenced the proportion of *X. compactus*-infested coffee plants (Table 6). A unit increase in density of *A. chinensis* was associated with a 0.2916 increase in the expected log count of coffee plants infested by *X. compactus*, implying a 34\% increase in the proportion of coffee shrubs infested by *X. compactus*. A unit increase in density of *C. papaya* decreases the expected...
implies a 2.7% decrease in the proportion of coffee shrubs did not significantly influence DBH, diameter at breast height.

\[ x = \frac{\text{Residual deviance}}{\text{Degrees of freedom}} \]

The constant is mean count at log scale at high rainfall and for young poly-culture. Ratio of residual deviance to degrees of freedom

\[ P < 0.01. \]

\[ **P < 0.001. \]

Constant is mean count at log scale at high rainfall and for young poly-culture. Ratio of residual deviance to degrees of freedom = 1.215. High rainfall zone and young poly-culture are the reference categories for the variables rainfall zones and agroforestry systems, respectively.

### Table 4

| Factors                          | Coefficient | SE    |
|----------------------------------|-------------|-------|
| Constant                         | -0.8505***  | 0.2198|
| Moderate rainfall                | 0.1021      | 0.3053|
| Low rainfall                     | -3.8639***  | 0.3355|
| Matured shade-tree system        | -1.8568**   | 0.6536|
| Moderate rainfall: matured shade-tree system | 0.4741   | 0.7548|
| Low rainfall: matured shade-tree system | 1.1070   | 0.8528|

**P < 0.01.

***P < 0.001.

Constant is mean count at log scale at high rainfall and for young poly-culture. Ratio of residual deviance to degrees of freedom = 1.215. High rainfall zone and young poly-culture are the reference categories for the variables rainfall zones and agroforestry systems, respectively.

### Table 5

| Factor                      | Coefficient | SE    |
|-----------------------------|-------------|-------|
| Constant                    | -0.659004***| 0.189708|
| Average DBH per tree        | -0.029148*  | 0.007375|

**P < 0.5.

***P < 0.001.

Constant is mean count at log scale at high rainfall and for young poly-culture. Ratio of residual deviance to degrees of freedom = 3.7. The constant refers to a theoretical scenario of no tree species intercropped with coffee. DBH, diameter at breast height.

### Discussion

The present study found a 98% higher \textit{X. compactus} infestation in the high compared with the low rainfall zone. The higher rainfall zone has a higher humidity that favours the growth of ambrosia fungi such as \textit{Fusarium solani} (Mart.) associated with \textit{X. compactus} and other beetles of the \textit{xyleborini} tribe (Atkinson & Equihua-Martinez, 1986). The low rainfall zone has a higher temperature, which probably inhibits the growth of ambrosia beetle symbionts that are sensitive to temperature (Six & Bentz, 2007). This further implies that, in future climate scenarios with a warmer temperature in Uganda (Funk \textit{et al.}, 2012), Robusta coffee in currently suitable areas will likely become less prone to \textit{X. compactus} infestation as a result of higher temperatures and lower humidity. However, coffee in more humid areas in the future scenario will likely become more prone to \textit{X. compactus} infestation. Unfortunately, the humid areas in the future scenario might coincide with areas that Bunn \textit{et al.} (2015) predicted to become those that are most suitable for Robusta coffee based on future climate change scenarios of the Intergovernmental Panel on Climate Change. However, precise predictions of \textit{X. compactus} response to future climate change scenarios still require knowledge of thermal tolerance for \textit{X. compactus} and its various ambrosia symbionts.

Our classification of shade coffee systems reveals considerable heterogeneity that would otherwise be hidden if we adhered to any other pre-defined classification, such as that of Toledo and Moguel (2012), which amalgamates all studied farms as traditional poly-culture systems. The difference of 84% \textit{X. compactus} infestation between YPC systems and MST systems resulted from a significant difference in the average DBH of agroforestry trees. Possibly, smaller tree canopies are closer to the coffee canopy, providing a relatively more humid environment around coffee branches and hence supporting more \textit{X. compactus} infestation.

Table 3

| Factors                          | Coefficient | SE    |
|----------------------------------|-------------|-------|
| Constant                         | -0.8505***  | 0.2198|
| Moderate rainfall                | 0.1021      | 0.3053|
| Low rainfall                     | -3.8639***  | 0.3355|
| Matured shade-tree system        | -1.8568**   | 0.6536|
| Moderate rainfall: matured shade-tree system | 0.4741   | 0.7548|
| Low rainfall: matured shade-tree system | 1.1070   | 0.8528|

Table 4 Correlations between proportions of coffee plants infested by \textit{Xylosandrus compactus} with shade indicators used to characterize coffee-agroforestry systems of the Greater Luweero region of Central Uganda

| Shade indicators                  | Correlation coefficient |
|-----------------------------------|-------------------------|
| Canopy closure (%)                | -0.010                  |
| Shade-tree density (trees ha⁻¹)   | -0.129                  |
| Coffee : banana ratio             | -0.036                  |
| Average DBH per tree (cm)         | -0.337***               |

***P < 0.001.

DBH, diameter at breast height.

Figure 3 The relationship between tree size (DBH) and predicted \textit{Xylosandrus compactus} infestation of coffee systems in the Greater Luweero region of Central Uganda based on predictions using the model in Table 5. The curve equation is \( y = 6 \times 10^{-9}x^4 - 2 \times 10^{-6}x^3 + 0.0002x^2 - 0.0149x + 0.5168 \) with \( r^2 = 0.999 \) and the inflection point is 46.1 cm.

![Figure 3](image-url)

log count of \textit{X. compactus}-infested coffee plants by 0.0273, implying a 2.7% decrease in the proportion of coffee shrubs infested by \textit{X. compactus}. The density of the rest of tree species did not significantly influence \textit{X. compactus} infestation.

Although not significant in the model, a trend is noticeable: tree species exuding copious sap when injured (Table 6) influenced \textit{X. compactus} infestation negatively, whereas trees that do not exude copious sap influenced \textit{X. compactus} infestation positively. The negative binomial model confirmed that the combined density of sap exuding trees significantly influenced \textit{X. compactus} infestation (Fig. 4 and Table 7). A unit increase in the density of sap exuding trees per farm decreases the expected log count of \textit{X. compactus}-infested coffee plants by 0.003467, implying a 0.35% reduction in the proportion of coffee shrubs infested by \textit{X. compactus}. From the equation of the curve shown in Fig. 4, the theoretical density of sap exuding trees that would significantly reduce \textit{X. compactus} infestation is 281 trees ha⁻¹, even though this is four times higher than recommended tree density of 70 trees ha⁻¹.

Table 5 Generalized linear model with a negative binomial error term showing the influence of agroforestry tree size on infestation by \textit{Xylosandrus compactus} in the Greater Luweero region of Central Uganda

| Factor                      | Coefficient | SE    |
|-----------------------------|-------------|-------|
| Constant                    | -0.659004***| 0.189708|
| Average DBH per tree        | -0.029148*  | 0.007375|

**P < 0.5.

***P < 0.001.

Ratio of residual deviance to degrees of freedom = 3.7. The constant refers to a theoretical scenario of no tree species intercropped with coffee. DBH, diameter at breast height.
Table 6 Generalized linear model with a negative binomial error term showing influence of tree species on proportion of coffee plants infested by black coffee twig borer in agroforestry systems of the Greater Luweero region of Central Uganda

| Factors                  | Number of plots | Tree abundance (n) | Sap Exudation | Coefficient | SE  |
|--------------------------|-----------------|--------------------|---------------|-------------|-----|
| Constant                 | 0               | 0                  | —             | −1.347***   | 0.283 |
| Albizia chinensis        | 22              | 67                 | No            | 0.292*      | 0.131 |
| Carica papaya            | 82              | 226                | Yes           | −0.027*     | 0.013 |
| Albizia zygia            | 36              | 56                 | No            | 0.027       | 0.046 |
| Markhamia lutea          | 82              | 433                | No            | 0.011       | 0.007 |
| Maesopsis eminii         | 100             | 446                | No            | 0.008       | 0.010 |
| Mangifera indica         | 113             | 451                | No            | 0.007       | 0.010 |
| Ficus ovata              | 34              | 57                 | Yes           | 0.008       | 0.048 |
| Canarium schweinfurthii  | 14              | 20                 | No            | 0.004       | 0.095 |
| Artocarpus heterophyllus | 108             | 388                | Yes           | −0.001      | 0.008 |
| Ficus natalensis         | 128             | 741                | Yes           | −0.007      | 0.008 |
| Albizia coriaria         | 137             | 865                | No            | −0.009      | 0.008 |
| Spathodea campanulata    | 28              | 51                 | Yes           | −0.016      | 0.023 |
| Milicia excelsa          | 25              | 39                 | No            | −0.048      | 0.060 |
| Ficus mucuso             | 13              | 22                 | Yes           | −0.083      | 0.071 |

*P < 0.5.  
***P < 0.001.
Ratio of residual deviance to degrees of freedom = 1.282. The constant refers to a theoretical scenario of no tree species intercropped with coffee.

Figure 4 Relationship between combined density of sap exuding trees on Xylosandrus compactus infections in coffee agroforestry systems of the Greater Luweero region of Central Uganda. The curve equation is $y = 1 \times 10^{-0.028}x^4 - 8 \times 10^{-10}x^3 + 2 \times 10^{-2}x^2 - 0.0031x + 0.4659$ with $r^2 = 0.9969$ and inflection point of 281 trees ha$^{-1}$.

populations than bigger-taller trees. Additionally, the canopies of bigger trees are too high and possibly out of range for *X. compactus* flight, unlike smaller trees where *X. compactus* can easily fly from and reside in canopies of coffee (in the wet season) and smaller trees (in the dry season). This is plausible because increases in average DBH per tree above 46cm significantly reduce *X. compactus* infestation. Consequently, this present study provides a valuable recommendation on future research effort that should aim to investigate *X. compactus* flight activity and range, as well as its seasonal dynamics as influenced by microclimate and those of its symbionts (i.e. the ambrosia fungi).

Previous studies also suggested that the diversity in shade tree species comprising the shade systems influence *X. compactus* infestation (Kagezi et al., 2013b; Hultman, 2016; Dahlqvist, 2016). We confirmed this hypothesis by demonstrating that a higher density of *A. chinensis* was associated with a higher *X. compactus* infestation, whereas a higher density of *C. papaya* was associated with a lower *X. compactus* infestation. This typically is in accordance with the resource availability hypothesis, where concentrating a resource (increasing pest hosts) increases pest populations, whereas diluting a resource (reducing pest hosts) reduces pest populations (A’Brook, 1968; Root, 1973; Ratnadass et al., 2012). This is further supported by the reduction in pest pressure associated with increasing the density of sap exuding trees that are considered as nonhosts for the pest. Therefore, removing *A. chinensis* from coffee plots and increasing the density of sap exuding trees should reduce *X. compactus* infestations, although this is not without caution: removing one host to a generalist pest such as *X. compactus*, which thrives on many hosts, may not significantly affect their population (Ratnadass et al., 2012). Nonetheless, farmers choosing to eliminate *A. chinensis* should aim to replace it with suitable trees that provide similar ecosystem services and preferably exude sap (Bukomeko, 2017).

Clearly, a higher density of tree species exuding copious sap if injured, such as *Ficus natalensis*, was associated with a lower *X. compactus* infestation compared with the predominance of *A. chinensis* with soft twigs that do not exude copious sap when injured, which results in a high *X. compactus* infestation. When

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X. compactus attempts to bore into a tree-twig with copious sap, the sap will quickly fill up the injured area before X. compactus makes its galleries and thus X. compactus colonization is suppressed (Hara & Beardsley, 1979). However, in that previous study, sap exudation was attributed to plant health and it was proposed that, unlike stressed plants, healthy plants ooze sap if X. compactus injures them and the sap repels X. compactus. The present study found that tree species suppressing X. compactus infestation characteristically exude copious sap regardless of any stress. Therefore, the presence or absence of copious sap exuding from trees upon injury likely differentiates X. compactus hosts from nonhosts.

Xylosandrus compactus infestation is sometimes observed on coffee growing under the shade of nonhost trees, especially at high density; this is probably because the trees form a dense canopy that modifies microclimatic conditions, particularly humidity, and hence this might favour X. compactus infestation (Kagezi et al., 2013b). Therefore, X. compactus-suppressive CAFS must consider canopy density as a key management factor, as well as the ratio of X. compactus-host to nonhost trees, in the development of Integrated Pest Management recommendations for a sustainable control.

Conclusions

In coffee agroforestry systems, X. compactus is influenced by many factors, including rainfall zones and the characteristics of shade systems such as average tree DBH, density of Albizia chinensis and Carica papaya, and density of sap exuding trees. Agroforestry designs intended to suppress X. compactus infestation should therefore allow for the presence of big and tall trees and also increase the density of trees that exude sap upon injury of their twigs (i.e. mimic matured shade systems and integrate them with any existing cultural control). However, the selection of tree species should consider the suitability of such trees for other ecosystem services. Future research should investigate X. compactus flight activity, range and seasonal dynamics, aiming to identify microclimatic variables influencing dynamics of both X. compactus and its symbionts: the ambrosia fungi. This knowledge will greatly help in developing guidelines of X. compactus-suppressive CAFS both now and in the future.

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