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ORIGINAL PAPER

Contrasting effects of shade level and altitude on two important coffee pests

Mattias Jonsson · Ijala Anthony Raphael · Barbara Ekbom · Samuel Kyamanywa · Jeninah Karungi

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Abstract The diversity and abundance of natural enemies of insect pests is often higher in agroforestry plantations than in sun-exposed monocultures, and it is often assumed that this will lead to improved pest suppression. The effect that incorporating trees in cropping systems will have on pest populations, however, also depends on the habitat requirements of the pests themselves. In Eastern Uganda, we studied how shade level (full >50 trees per acre, moderate 21–50 trees per acre, and low 0–20 trees per acre) and altitude (high 1,717–1,840 m.a.s.l. and low 1,511–1,605 m.a.s.l.) influenced the abundance of the white stem borer *Monochamus leuconotus* and the coffee berry borer *Hypothenemus hampei*. We found that the effect of shade trees differed between the two pest species. The coffee berry borer was more common on sun-exposed plantations, whereas the white stem borer was more common in shaded plantations. Furthermore, the effect of shade level on the white stem borer depended on altitude, with the differences between shade levels being most pronounced in plantations at low altitudes. This implies that the impact of agroforestry on pest regulation both under current conditions and in a global warming scenario will be highly context dependent; it will depend on the identity of the most important pests in the area, and on environmental factors such as altitude.

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M. Jonsson (✉) · B. Ekbom
Department of Ecology, Swedish University of Agricultural Sciences, P.O. Box 7044, 750 07 Uppsala, Sweden
e-mail: mattias.jonsson@slu.se

I. A. Raphael · S. Kyamanywa · J. Karungi
School of Agricultural Sciences, Makerere University, P.O. Box 7062, Kampala, Uganda

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Key message

- We studied how agroforestry influenced infestations of two key coffee pests in Uganda: the coffee berry borer and the white stem borer.
- Agroforestry decreased incidence of coffee berry borers, but increased white stem borers.
- The effect of agroforestry on the white stem borer was larger at low altitudes.
- The overall impact of agroforestry on pest regulation will therefore be context dependent; it will depend on the identity of the most important pests in an area, and on environmental factors such as altitude.

Introduction

Tropical deforestation is one of the most important drivers of loss of biodiversity and associated ecosystem services (Foley et al. 2005). The restoration of tree cover via the adoption of agroforestry, i.e., the practice of mixing trees and crops, may mitigate the negative effects of deforestation, and can complement the protection of pristine forest ecosystems (Tscharntke et al. 2011). However, it remains unclear to what extent agroforestry management practices, which partially utilize exotic tree species and generally apply a short tree rotation, can restore ecosystem services that have been compromised by deforestation.

It is often argued that agroforestry plantations provide more effective pest control services than crop monocultures, because plantations with trees are likely to host a higher biodiversity and more complex food webs (Vandermeer et al. 2010). This assumption largely builds on the fact that crop polycultures tend to be less damaged by pests than monocultures (Letourneau et al. 2011), either because pests are less likely to find and remain on their host plant and/or because natural enemies are provided a more favorable environment (Root 1973). Indeed, agroforestry plantations often have a higher abundance and diversity of natural enemies compared to crop monocultures (Perfecto et al. 2003; Borkhataria et al. 2012), pest predation may be higher (Perfecto et al. 2004; Karp et al. 2013), and pest abundances sometimes decrease (Teodoro et al. 2009). Thus, there is evidence that agroforestry in some cases has strong beneficial effects on pest regulation. However, such outcomes are not universal. The presence of trees may enhance some pest problems, for example if the trees act as a resource for the pests, if they provide a more suitable microclimate for pests, or if they modify the nutritional conditions or water availability for the crop which in turn benefit the pests (Rao et al. 2000; Schroth et al. 2000; Sileshi and Mafongoya 2003).

The retail value of coffee was recently estimated to US$ ~90 billion, making it one of the most valuable tropical crops (Jaramillo et al. 2011). Coffee is traditionally grown under shade trees, but during recent decades, sun-exposed plantations have been promoted and become popular in many coffee-producing countries, e.g., in East Africa (Willey 1975; Beer et al. 1998). However, sun-exposed coffee monocultures often require high levels of inputs of nutrients and pesticides to maintain high levels of yield (Willey 1975), and therefore the recently growing demands for organic and fair-trade coffee have resulted in a revival of shade-grown coffee. The importance of shade-grown coffee is likely to increase further as shade trees may help mitigate some of the detrimental effects of climate change on coffee production (Lin et al. 2008; Jaramillo et al. 2009, 2011). A better understanding of how agroforestry practices influence pest problems in coffee is, therefore, urgently needed.

Along the slope of Mt. Elgon in Uganda, we studied how shade level and altitude influenced the abundance of two of the most destructive coffee pests in the region: the coffee berry borer *Hypothenemus hampei* (Ferrari) (Coleoptera: Curculionidae) and the white stem borer *Monochamus leuconotus* (Pascoe) (Coleoptera: Cerambycidae (Rutherford and Phiri 2006). It has been shown that biological control of the coffee berry borer is more effective in forested coffee plantations (Karp et al. 2013; Railsback and Johnson 2013), and that abandoned coffee plantations may have lower coffee berry borer abundances compared to managed coffee agroforests with lower levels of shade (Teodoro et al. 2008). Recently, Jaramillo et al. (2013) found higher coffee berry borer infestations in a sun-exposed coffee plantation compared to a shaded one. Other studies, however, failed to show an influence of shade on coffee berry borers (Soto-Pinto et al. 2002), and some older observations even indicate that excessive shade may increase coffee berry borer attack rates (Willey 1975). The white stem borer has been little studied, but it has been observed to be more common close to shade trees (Rutherford and Phiri 2006). It was recently proposed that research is needed to explore if agroforestry can be an effective way of managing the stem borer (Kutywayo et al. 2013). Based on these observations, we hypothesized that the abundance of coffee berry borers would decrease with the level of shade, whereas white stem borer abundance would increase. Recent modeling of climate change scenarios suggests that the problems of both pests are likely to increase in many parts of Africa (Jaramillo et al. 2009, 2011; Kutywayo et al. 2013). To simulate global warming in the next 15–50 years, we studied the effect of shade on the pests at two different altitudes.

Materials and methods

Study species and study site

The coffee berry borer *H. hampei* and the white stem borer *M. leuconotus* are both native to Africa and are considered among the most important coffee pests in the region (Hillocks et al. 1999; Rutherford and Phiri 2006; Jaramillo et al. 2009). The coffee berry borer is the most destructive insect pest on coffee in the world (Damon 2000; Jaramillo et al. 2006). Very high levels of infestation by the coffee berry borer have been reported, including in East African countries such as Uganda 80 % and Tanzania 90 % (Vega 2004). The white stem borer has been documented to cause yield losses of 25 % in sub Saharan Africa where over 80 percent of coffee farms are affected (Rutherford and Phiri 2006).

Female coffee berry borers make galleries into the coffee seed, and infested berries can be recognized by the round entrance holes close to the apex of the berries (Rutherford and Phiri 2006). Economic losses are caused by adults and progeny directly through their feeding activities, by making attacked berries more vulnerable to disease infection and further pest attack, and by causing young berries to fall prematurely (Damon 2000). White stem borer females oviposit under the bark of the lower part of the stem of the coffee tree, and beetle larvae feed and develop under the bark. Large adult emergence holes on the lower part of the tree indicate stem borer attack.

Other diagnostic symptoms of stem borer infestation include rings on the stem where the bark has been eaten by the larvae, and the presence of ‘frass’ on the ground next to the stem. Young trees are especially susceptible to stem borer damage, and trees <2 years are often killed. Older trees are less likely to be killed but often give poor coffee yields when they are under stem borer attack.

The study was conducted in the Mt. Elgon area, in the Manafa District of Eastern Uganda with a total area of 532.6 km^2. The study covered the villages of Soono, Sitira, Matokota, and Majanja in the parishes of Soono and Bukokho in the Bumbo sub-county, which border the Mt. Elgon national Park. The area has fertile volcanic soils, an average rainfall of 1,500 mm/year, an altitude of about 1,500–1,900 m.a.s.l., and average temperatures range from 17 to 22 °C (EcoTrust 2012). The economic activity in the area is purely agricultural with crops grown including Arabica coffee, maize, bananas, beans, millet, and potatoes. Coffee is grown under sun-exposed conditions and under varying levels of shade provided by different tree species, notably *Acacia* spp. (Fabaceae), *Albizia coriaria* Welw. ex Oliver (Fabaceae), *Calliandra* spp. (Fabaceae), *Cordia millenii* Bak. (Boraginaceae), *Croton macrostachyus* Hochst. Ex Delile (Euphorbiaceae), *Erythrina abyssinica* Lamarck ex de Candolle (Fabaceae), *Ficus* spp. (Moraceae), *Gliricidia* spp. (Fabaceae), *Grevillea robusta* A. Cunn (Proteaceae), *Inga* spp. (Fabaceae), *Leucaena leucocephala* (Lam.) de Wit (Fabaceae), *Maesopsis eminii* Engl. (Rhamnaceae), *Markhamia lutea* (Benth.) K. Schum (Bignoniaceae), *Persea americana* Mill. (Lauraceae), *Premna angolensis* Gürke (Verbenaceae), and *Sesbania sesban* (L.) Merr. (Fabaceae) (EcoTrust 2012).

Experimental design

The study was conducted at 30 coffee plantations that differed in shade level and altitude. Plantations were categorized as having either full shade, moderate shade, or low shade, and to be located at either high (1,717–1,840 m.a.s.l.) or low (1,511–1,605 m.a.s.l.) altitude. Five plantations were selected for each combination of shade level and altitude, and each plantation was used as a replicate in the analysis (plantations were located 0°51.371′–0°52.821′N and 34°25.678′–34°26.465′E). Plantations with full shade had >50 trees per acre, moderate shade 21–50 trees per acre, and low shade 0–20 scattered trees per acre without canopy contributing to shade. Shade levels were further characterized using light intensity measured with a Foot candle meter (Model 3413F) following the guidelines of Bellow and Nair (2003). Temperature and relative humidity were measured using a Thermo-hygrometer pen model 3402. All microclimatic variables were measured at three locations in each plantation between 11:00 and 12:00 h on two dates each month between March and August 2012. The microclimate differed among plantations, with the ones with highest shade having an average temperature of 26.3 °C, moderate shade 27.4 °C, and low shade 28.3 °C. Mean light intensities were 3,606, 1,404, and 470 foot candles, and relative humidities were 51.7, 52.5, and 52.9 %, respectively. The microclimate also differed with altitude, with plantations at the highest altitude having an average temperature of 27.0 °C and the low altitude 27.9 °C, light intensity being 1946 and 1706 light candles, and relative humidity 53.0 and 51.8 %, respectively. It has been predicted that mean temperatures will increase with ~1 °C in Eastern Africa in the next 15–50 years depending on climate change scenario (Hulme et al. 2001). Thus, by comparing the above altitude levels, we simulate global warming during this time scale.

Data collection

The infestation levels of coffee berry borers and white stem borers were estimated during 12 visits to each plantation at fortnightly intervals from March to August 2012. At each plantation and sampling round, 10 trees were sampled by zigzag movement to cover the entire field. Two branches were randomly selected for each of the ten trees per farm, and berries with and without coffee berry borer entry holes were counted to estimate proportion of berries infested. The same trees were closely examined at the lower trunk up to 0.6 m above the collar level of the main stem for signs of stem girdling, fresh frass and exit holes of white stem borers. White stem borer infestation was estimated as the proportion of trees with signs of attack.

Data analysis

To analyze the data, we performed generalized linear mixed effects models (GLMM’s), with binomial error structure using the glmer function in the lme4 package in R 2.14.0 (R Development Core Team 2011). For both white stem borer and coffee berry borer infestation, the fixed model included shade level (three levels) and altitude (two levels) and the interaction between these variables, and the random model included sampling date to account for repeated measures of the plantations. Over dispersion was detected in both models, and therefore an observation level vector was also added to the random models (Bolker et al. 2009). To compare the effect of different shading levels on means, Tukey contrasts were used with the glht function in the multicomp package in R 2.14.0. When only the main effect of shade was significant in the GLMM, we used the interaction averaging argument to compare shade levels averaged over interaction terms. When a significant interaction between shade level and altitude was detected in the GLMM, we compared all combinations of shade and altitude levels.

Table 1 Results from a generalized linear mixed effects model (GLMM) testing the effects of shade level and altitude on white stem borer infestation

Parameter	Estimate	SE	z	Pr(>|z|)
(Intercept)	1.064	0.191	5.570	<0.001
Moderate shade vs. low shade	−0.535	0.247	−2.167	0.030
High shade vs. low shade	−0.998	0.244	−4.087	<0.001
Low vs. high altitude	0.357	0.254	1.403	0.161
Moderate shade × low altitude	−1.773	0.355	−4.990	<0.001
High shade × low altitude	−1.222	0.353	−3.457	<0.001

SE standard error of parameter estimates, *z* z-score testing whether the parameter estimate is significantly different from zero, *Pr*(\|z\|) probability of the observed z-score being greater than the critical value

Table 2 Results from a generalized linear mixed effects model (GLMM) testing the effects of shade level and altitude on coffee berry borer infestation

Parameter	Estimate	SE	z	Pr(>|z|)
(Intercept)	2.753	0.160	17.202	<0.001
Moderate shade vs. low shade	0.213	0.105	2.030	0.042
High shade vs. low shade	0.418	0.106	3.930	<0.001
Low vs. high altitude	0.073	0.104	0.701	0.484
Moderate shade × low altitude	0.137	0.149	0.919	0.358
High shade × low altitude	0.116	0.152	0.764	0.445

SE standard error of parameter estimates, *z* z-score testing whether the parameter estimate is significantly different from zero, *Pr*(\|z\|) probability of the observed z-score being greater than the critical value

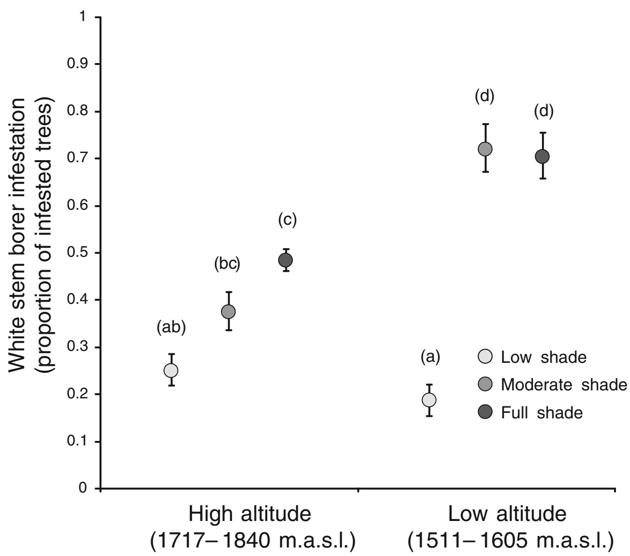

Fig. 1 Average proportion (±SE) of coffee trees infested by white stem borers in coffee plantations with different shade levels and altitudes. Plantations with full shade had >50 trees per acre, moderate shade 21–50 trees per acre, and low shade 0–20 scattered trees per acre without canopy contributing to shade. There was a significant main effect of shade and a significant interaction between shade level and altitude in the GLMM (Table 1). Different letters above each combination of shade level and altitude indicate significant differences according to the Tukey contrasts

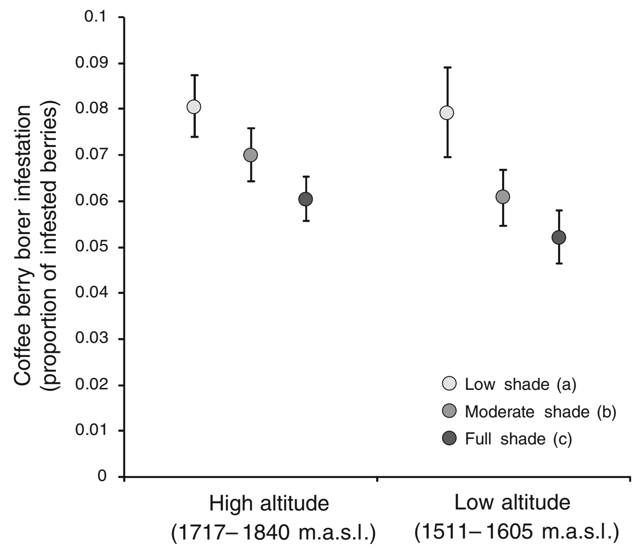

Fig. 2 Average proportion (±SE) of coffee berries infested by coffee berry borers in coffee plantations with different shade levels and altitudes. Plantations with full shade had >50 trees per acre, moderate shade 21–50 trees per acre, and low shade 0–20 scattered trees per acre without canopy contributing to shade. There was a significant effect of shade level only in the GLMM (Table 2). Different letters after the shade labels indicate significant differences according to the Tukey contrasts

Results

The proportion of coffee stems that showed signs of attack by white stem borers ranged from 0.21 to 0.78 for the different plantations, and the proportion of coffee berries attacked by coffee berry borers varied between 0.05 and 0.12. Arcsin square-root transformed proportions of stem borer and coffee berry borer infestations were uncorrelated with each other ($r = -0.064$, $P = 0.224$).

There were significant effects of shade level on the proportion of coffee trees with signs of white stem borer attack, and this effect was dependent on altitude (Table 1; Fig. 1). Multiple comparisons of means with Tukey contrasts revealed that, at high altitude, the most shaded sites had significantly higher attack rates by white stem borers than the most sun-exposed plantations ($z = -4.087$, $P < 0.001$), but there were no significant differences between the other shade levels (moderate vs low: $z = -2.167$, $P = 0.253$, full vs moderate: $z = -1.918$, $P = 0.391$) (Fig. 1). Similarly, there was a significant difference between full shade and low shade at low altitude ($z = -8.690$, $P < 0.001$). However, at low altitude, there was also a significant difference between moderate shade and low shade ($z = -9.033$, $P < 0.001$), but there was no difference between full and moderate shade ($z = 0.352$, $P = 0.999$).

The proportion of coffee berries attacked by the coffee berry borer was negatively affected by shade level, but there was no influence of altitude or the interaction between shade level and altitude (Table 2; Fig. 2). Tukey contrasts showed that there were significant differences between all shade levels (full vs. low shade: $z = 6.283$, $P < 0.001$; full vs. moderate shade: $z = 2.551$, $P = 0.029$; moderate vs. low shade: $z = 3.776$, $P < 0.001$).

Discussion

In accordance with our hypothesis, we found essentially opposite effects of shade trees on two key coffee pests across 30 coffee plantations in Eastern Uganda. Coffee berry borers were significantly less common in more shaded coffee plantations, whereas the abundance of white stem borers increased with increasing level of shade. The positive effect of shade on white stem borer infestation was even more pronounced at plantations located at lower altitudes. For the individual farmer, this implies first that the impact of shade tree management on the overall yield losses to pests will depend on the identity of the pest species of most concern and of the altitude of a particular plantation. It furthermore suggests that the impact of shade trees on pest control under a warming climate may be pest dependent. Jaramillo et al. (2009) suggested that increased use of shade trees may help mitigate the effects of climate change on coffee berry borer pest pressure. In contrast, the fact that we found that shade had a particularly strong positive effect on white stem borers at lower (warmer) altitudes suggests that an increased use of shade trees in a warmer climate may increase the severity of this important pest during the next 15–50 years.

Coffee berry borer

Our work supports recent papers suggesting that provision of shade trees is likely to be an effective way of managing coffee berry borers (Teodoro et al. 2008; Jaramillo et al. 2009, 2011; Jaramillo et al. 2013; Karp et al. 2013), but contradicts studies that either failed to show an effect of shade (Soto-Pinto et al. 2002), or indicated that excessive shade may increase borer problems (Willey 1975). Together, this suggests that shade tree provision is an effective approach to manage coffee berry borers in many situations but that this may not be the case at all locations or shade levels. For example, it is possible that shade trees may increase coffee berry borer problems at warm locations that otherwise experience temperatures above the optimum for the borer (Jaramillo et al. 2009).

The negative effect of shade on coffee berry borer abundance may be due to both top-down and bottom-up factors. Ants, other hymenopterans (e.g., parasitoids) (Perfecto et al. 1996; Pardee and Philpott 2011), and birds (Karp et al. 2013) have all been shown to benefit from shade tree cover, and they may provide enhanced biological control of the coffee berry borer in shaded coffee plantations. Karp et al. (2013) recently found that forested coffee plantations hosted more predatory birds in Costa Rica than plantations lacking trees, and the damage by coffee berry borers was, therefore, 50 % lower in the forested coffee plantations. Railsback and Johnson (2013) furthermore suggested that introducing trees within coffee farms will be more effective at increasing predation by birds on coffee berry borers than preserving patches of forest. The difference in coffee berry borer abundance between plantations with different shade levels could also have been directly influenced by differences in temperature. The thermal tolerance of the coffee berry borer was determined by Jaramillo et al. (2009). Their work suggested that the maximum rate of increase would be 8.5 % higher for every 1 °C temperature increase within the temperature range recorded in our study. As we found approximately 1 °C difference in mean temperature between each of the three shade levels, it suggests that the most sun-exposed plantations would have had 17 % higher growth rates than the most shaded ones. A similar conclusion was drawn by Jaramillo et al. (2013) when comparing a shaded and sun-exposed coffee plantation at a similar altitude in Nairobi, Kenya. It has also been suggested that the delayed maturation of coffee berries in shaded plantations results in a change in biochemical composition and emission of chemical compounds that make the suitable berries more difficult to locate for ovipositing coffee berry borer females (Jaramillo et al. 2013). Finally, it is possible that trees may help disrupt berry borer dispersal as the berry borers are positively influenced by a high connectivity among coffee plots (Avelino et al. 2012).

White stem borer

We found that coffee plantations under high shade had a significantly higher proportion of trees with symptoms of white stem borer infestation compared to the most sun-exposed plantations, thereby confirming some previous observations that white stem borers are more common close to shade trees (Rutherford and Phiri 2006). Our work thus suggests that agroforestry is an ineffective strategy to manage white stem borers, at least across the altitudes and climatic conditions in our study area. The infestation levels in the shaded plantations were strikingly high, with on average 56 % of the trees infested, compared to 27 % at the most sun-exposed sites. We do not know the mechanism behind the positive effect of agroforestry on white stem borer infestation levels. Natural enemies of the white stem borer include woodpeckers, ants, parasitoids, entomopathogenic nematodes, and fungi (Hillocks et al. 1999; Rutherford and Phiri 2006), but little is known about their respective effectiveness and how they are influenced by shade. As natural enemies in general tend to be more common in shaded plantations, it seems unlikely that the natural enemies of the white stem borer would have been the driver of the positive effect of shade on this pest. Instead, it seems more likely that it would be due to some bottom-up effects such as improved microclimate or more suitable host plants under shade. For example, Kutywayo et al. (2013) found that rainfall had a positive effect on adult emergence of the white stem borer, so it is possible that the increased humidity in shade was beneficial. However, further research is needed to tease apart the mechanisms behind these effects.

Conclusion

Agroforestry practices may increase food security and economic income for smallholder farmers, by enhancing soil conditions, reducing soil erosion, and providing ecosystem goods such as wood, forage, fiber, and fruit (Verchot et al. 2007; Tscharntke et al. 2011). Furthermore, an increased adoption of agroforestry in the future can help mitigate the negative effects of climate change (Lin et al. 2008; Jaramillo et al. 2009). Several studies have shown that pest control services may be enhanced by agroforestry (Vandermeer et al. 2010; Jaramillo et al. 2013; Karp et al. 2013). However, our work cautions that some of the most destructive pest species on coffee such as the white stem borer may in fact increase in abundance in shaded conditions and that these effects may become even stronger under climate change. Therefore, the impact of agroforestry on the overall crop losses to pests will depend on the identity of the most important pest species present and on the ecological context (e.g., altitude) of a particular plantation. A future challenge will be to find ways of minimizing these context-dependent trade-offs while enhancing the benefits of agroforestry practices.

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