Multi-scale mosaics in top-down pest control by ants from natural coffee forests to plantations

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Abstract. While top-down control plays an important role in shaping both natural and agricultural food webs, we lack insights into how top-down control effects vary across spatial scales. We used a multi-scale survey of top-down control of coffee pests and diseases by arboreal ants to examine if colony location creates a small-scale mosaic in top-down control around trees and if the strength of that control varies between sites at the landscape scale. We investigated pest and disease levels on coffee shrubs at different distances from shade trees with and without a *Crematogaster* spp. ant colony in 59 sites along a coffee management intensity gradient in southwestern Ethiopia. Within sites, ants significantly suppressed herbivory and coffee leaf rust at distances less than 10 m from nesting trees. Top-down control varied between sites, with stronger top-down control of free-feeding herbivory near ant colonies at sites with lower management intensity and stronger top-down control of a skeletonizer at sites with higher canopy cover. We conclude that the strength of top-down control by ants is highly heterogeneous across spatial scales, as a consequence of the biology of the predator at the small scale and herbivore density or changes in herbivore–ant interactions at the landscape scale.

Key words: ants; biological pest control; Coffea arabica*; coffee leaf rust;* Crematogaster *sp.; Ethiopia; herbivory;* Leucoplema dohertyi*;* Leucoptera *sp.; scale-dependence.*

Introduction

Top-down control of populations of species at lower trophic levels is an important mechanism that shapes communities in both natural and agricultural ecosystems (Hunter and Price 1992). For example, a recent meta-analysis showed that many herbivorous insects are strongly regulated by predators (Vidal and Murphy 2018), and top-down control is a common management strategy in agroecological farming (Médiène et al. 2011). However, in the same way as there is variation across space in abiotic factors that regulate the distribution and abundance of species (Kearney and Porter 2004), there is often spatial variation in top-down control with significant impacts on populations and communities (Gripenberg and Roslin 2007). Thus, while it is important to understand whether there are top-down effects in different systems (Mäntylä et al. 2011, Vidal and Murphy 2018), we also need insights about how top-down effects vary spatially and which mechanisms underlie such variation (Gripenberg and Roslin 2007).

Spatial mosaics in top-down control can be present at different spatial scales and many different mechanisms can shape such variation. At smaller scales, it could be the variation in abundance of the predator that causes gradients in top-down control. One obvious reason for spatial variation in predator presence could be the distribution of colonies to which the predator returns regularly (e.g., foxes, owls, ants; Atlegrim 2005). Another and often linked mechanism has to do with how top-

down control varies along gradients in environmental variables or management over larger spatial scales. For example, the top-down effects of birds on herbivorous arthropods may vary with the density (Böhm et al. 2011) or diversity of host plants in the canopy (Bereczki et al. 2014). The environment could influence the abundances of the herbivore and predator, as well as the interactions between them (Mumma et al. 2019). Overall, we need studies that identify the multi-scale patterns and drivers of top-down control (Maron et al. 2014).

Ants (Hymenoptera: Formicidae) are abundant in many different ecosystems around the world. They are mostly predatory and often forage on plant-feeding insects in natural and agricultural systems, but often rely on more than one food source and may complement predation with tending sap-feeding insects for honeydew (Wielgoss et al. 2014). From the plant's perspective the ants can thus have both positive and negative effects, even if net benefits seem to be most common (Clark et al. 2016). Many ants have colonies around which they forage. By having a fixed point in the landscape to return to, there is a large chance that there will be some spatial patterning in their interactions with other organisms in the surrounding area. The top-down control by ants may also vary at larger spatial scales. For example, it has been shown that *Azteca* spp. ants are efficient predators of the coffee berry borer (*Hypothenemus hampei*), but also that this effect varies along a gradient of coffee management intensity (Morris et al. 2015, Aristizábal and Metzger 2018).

We aimed to assess spatial variation in the impact of top-down control of ants on herbivores both in relation to distance from their colonies and along a management gradient that modifies the environment across larger spatial scales. To this aim, we focused on a system of tree nesting *Crematogaster* spp. ants that are commonly found in forests and coffee agroforests in southwestern Ethiopia. We asked the following questions: (1) Does ant colony location create small-scale mosaics in the strength of top-down control? (2) Do ant colony density, environmental, and management variables across a landscape create large-scale mosaics in the strength of top-down control? We approached these questions by studying ant colony distribution and the biological pest control potential of *Crematogaster* ants on coffee pests and diseases at 59 sites along a coffee management gradient. In each 2-ha site, we surveyed pest and disease levels on coffee shrubs at multiple distances from one tree with and one without an active ant nest. Moreover, we surveyed the density of trees with ant colonies.

MATERIAL AND METHODS

Study system

We conducted the fieldwork in the Gomma and Gera districts in Jimma zone, Oromia region, southwestern Ethiopia (7°37′–7°57′ N; 36°13′–36°37′ E, Fig. 1a) from January to March 2019. The landscape has a varied topography, and altitude of our study sites ranges from 1,500 to 2,200 m above sea level. The mean annual temperature is 20°C, while precipitation ranges from 1,500 to 2,000 mm. The climax vegetation in this region is moist Afromontane forests, but nowadays substantial parts of the landscape are open agricultural fields with small-scale subsistence agriculture. Coffee is grown under the shade of trees along a wide gradient in management intensity from plantation systems owned by companies, to smallholder coffee stands located adjacent to their homes, to little-managed coffee in the forest understory harvested by smallholder farmers living far away from the sites (Zewdie et al. 2020). Some of these coffee plants are of wild origin and the Ethiopian forests hold much of the genetic diversity for Arabica coffee (Davis et al. 2018). In general, farmers rely on natural pest control and no pesticides are used, except for occasional use of herbicides by the wealthiest farmers (Zewdie et al. 2020). We focused on four of the major pest and disease problems on coffee leaves in Ethiopia: free-feeding herbivory, coffee leaf skeletonizer, leaf miners, and coffee leaf rust (Fig. 1e–h). Coffee leaf rust might be dispersed by ants or be indirectly affected by the presence of ants via interactions with other species (e.g., Vandermeer et al. 2009 describe how rust is affected by an intricate ant–hemipteran–hyperparasite interaction). Colonies of arboreal ants of the genus *Crematogaster* (Fig. 1d) are found in both forests and shade coffee plantations. To the best of our knowledge, it appears that a colony consists of a single large carton nest hanging on the outside of the trunk, often above 3 m. Little is known about the frequency, distribution, or ecology of these arboreal ants, as well as how many and which species they belong to. Based on preliminary studies of morphological characters of workers, 102 out of the 106 examined colonies appeared to be from a single morphospecies.

Data collection

We visited 59 coffee growing sites, which represent a wide management gradient. The sites were established in a previous project including data on site characteristics in a 50 × 50 m central plot (Zewdie et al. 2020). We counted all ant colonies in a circular area of 2 ha including the central plot and assumed that the management and environmental variables collected in the 50 × 50 m plot are representative for the whole 2 ha area (Fig. 1b). For each tree with a colony, we recorded tree species identity, tree height, height of the ant nest, and nest size (width × height).

The management and environmental variables include the landscape variables distance to forest, percentage of tree cover within a buffer of 1 km radius, altitude, and slope, and the local variables canopy cover, number of trees, tree species richness, coffee density, proportion of non-coffee shrubs to coffee, and Coffee Structure Index (Appendix S1: Table S1). Canopy cover was calculated
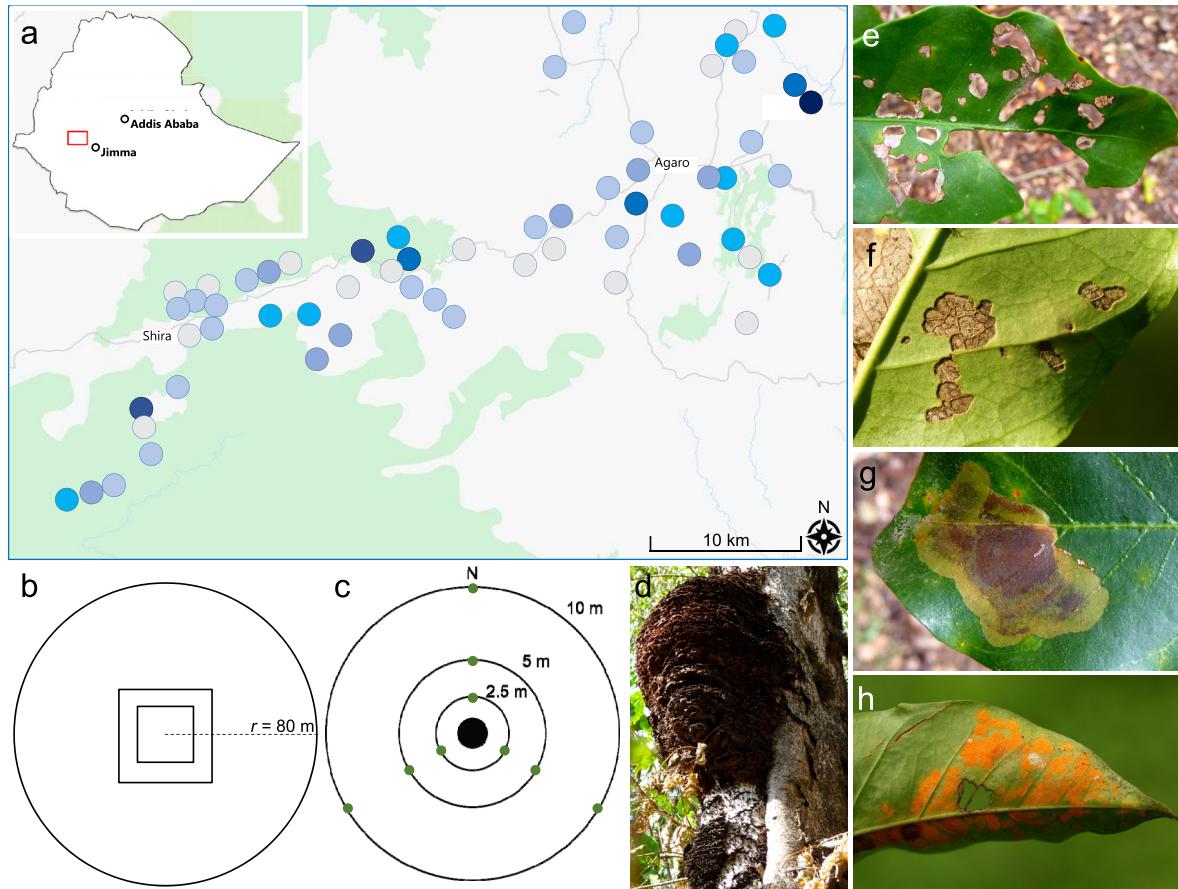
FIG. 1. Overview of the study location, study species, and experimental design. (a) Map over study area in southwestern Ethiopia (inset) with all study sites indicated using a color scheme indicating the number of found ant colonies from white (0 colonies) to dark blue (6 colonies). Green denotes forests or areas with a dense canopy of shade trees for coffee management and yellow open agricultural land. (b) Circular plot site of 2 ha with the 30 × 30 m and 50 × 50 m central plots indicated, (c) a selected tree with the location of the nine examined coffee shrubs (green dots) at different distances from the tree. At each site, one tree with an ant colony and one tree without an ant colony were investigated. (d) Nest of *Crematogaster* sp. in a shade tree. We studied the following coffee pests and diseases: (e) free-feeding insect herbivory, (f) coffee leaf skeletonizer (*Leucoplemadohertyi*), (g) leaf miners (the most common are coffee blotch miner *Leucoptera meyricki* [depicted here] and serpentine leaf miner *Chryphiomystis aletreuta*), and (h) coffee rust (*Hemileia vastatrix*). Photo credits: Moritz Stüber.

based on five canopy pictures taken above the coffee shrubs and calculated using the software ImageJ (Version 1.51; Abramoff et al. 2004). Coffee Structure Index (CSI) is an index representing management intensity, ranging from low (1) to high (3). It was calculated using a cluster analysis on a number of measures including height, number of main stems, and bearing branches on 16 coffee shrubs in each plot (for details see Appendix S1: Section S1; Zewdie et al. 2020).

In each site where ants were present, we selected one tree with a colony and enough coffee shrubs below in all directions and distances and one reference tree, if possible, of the same species and size as the ant colony tree. We selected nine coffee shrubs around both the ant colony tree and the reference tree, respectively; three shrubs at each of the approximate distances 2.5, 5, and 10 m spread out in three directions (Fig. 1c). The coffee shrubs at 10 m from the reference trees were always

>20 m away from an ant colony tree. From each coffee shrub, we collected the following response variables: (1) level of free-feeding herbivory, (2) incidence of skeletonizing damage by the coffee leaf skeletonizer, (3) incidence of leaf-mining damage by the leaf miners (several species pooled), and (4) incidence of coffee rust infestation. For free-feeding herbivory we visually estimated the percentage eaten by insects on 10 leaves of the branch tip (except for the two youngest leaves) on each of three randomly selected branches for each coffee shrub. For the other three response variables we noted the presence or absence of each on the same leaves. In total, we surveyed 90 leaves per distance (2.5, 5, and 10 m) at each ant colony and reference tree. While *Crematogaster* ants are known to form a mutualistic relationship with scale insects, we only observed interactions of ants and scale insects at four of the study sites. We did not further analyze these sparse data.

Statistical analyses

We compared the level of damage by each of the four pests and diseases as functions of trees with vs. without ant colony and distance to the respective tree (2.5, 5, 10 m) and their interaction in four separate generalized linear mixed effect models using the functions lmer and glmer in the lme4 package in R 3.5.3 (R Core Team 2019). To account for the design of the study and non-independence of coffee shrubs, we included site and shade tree ID as random effects. We used a binomial distribution for coffee rust, skeletonizer, and leaf miner damage and a Gaussian distribution for free-feeding herbivory damage. To assess the level of statistical significance, we used the function Anova with Type II sum of squares in the car package, with subsequent post-hoc tests using the emmeans package.

To explore if any site characteristics were related to the variation in ant colony abundance among sites, we used generalized linear models with the number of ant colonies per site as the response variable and the following predictor variables: distance to forest, proportion of forest cover/dense tree cover in a 1 km radius, slope, altitude, canopy cover, tree species richness, coffee density, proportion of non-coffee to coffee shrubs, and CSI. Number of trees was highly correlated with number of tree species ($r = 0.71$) and was therefore not included in the analyses. We used a quasi-Poisson distribution because of slight over-dispersion and evaluated the residual plots. The final model was obtained by backward model selection using a threshold value of $P < 0.1$ (Crawley 2013).

We tested if there was any difference in the frequency distribution between the tree species with ant colonies and the overall tree species composition in the sites using a chi-square goodness of fit test. In this test, we pooled tree species with fewer than 1% of the total number of trees into one category to denote rare species.

To evaluate if the variation in top-down pest control of *Crematogaster* ants among sites was related to management and environmental variables we ran a new set of generalized linear models (GLM), separately for (1) free-feeding herbivory, (2) skeletonizer, (3) leaf miners, and (4) coffee rust. As response variable, we calculated a Pest Control Index for each site and pest to represent ant top-down control efficiency as the log odds-ratio of the pest level around the ant colony tree and the reference tree for the coffee shrubs growing closest to the trees (2.5 m; Rita and Komonen 2008), according to the following equation:

$$\text{Pest Control Index} = \log\left(\frac{A\left(N_{\text{Pest}}/N_{\text{Leaves}}\right)}{R\left(N_{\text{Pest}}/N_{\text{Leaves}}\right)}\right) \quad (1)$$

where $A\left(N_{\text{Pest}}/N_{\text{Leaves}}\right)$ denotes the number of infested leaves on coffee shrubs surrounding the ant colony tree divided by all examined leaves, and R the same value for the coffee leaves surrounding the reference tree. A Pest Control Index below zero corresponds to a lower pest damage around the ant colony tree than around the reference tree. This index was calculated separately for each pest or disease species. In the models we used the following predictor variables: proportion of surrounding forest/tree cover, altitude, canopy cover, tree species richness, CSI, colony density in the plot, and size of the nest.

Small-scale mosaic of top-down control up to 10 m from ant colonies

Free-feeding herbivory was reduced on coffee shrubs close to trees with colonies of *Crematogaster* ants, but no such effect was detected around reference trees (interaction effect between distance and ant vs. reference tree, $P < 0.001$, Appendix S1: Table S2). On average, about 2% of the leaf surface was damaged by free-feeding herbivores at 2.5 m from an ant colony tree, while 4% was damaged at 2.5 m from a reference trees, whereas free-feeding herbivory levels were similar at a distance of 10 m from the ant colony and reference trees (Fig. 2a). Also, at 5 m, there was a significant but smaller reduction. The damage by skeletonizing insects was lower at both 2.5 and 5 m from trees with ant colonies compared to reference trees. At a distance of 2.5 m, 30% vs. 44% of the leaves had signs of attacks by the skeletonizer, respectively. The difference between damage around ant colony trees and reference trees was very small and non-significant at 10 m from the respective trees (41% vs. 45%, Fig. 2b; Appendix S1: Table S2). The incidence of leaf miners did not seem to be affected by the presence of ants (Fig. 2c; Appendix S1: Table S2). The incidence of coffee leaf rust infestation showed a similar pattern, as free-feeding herbivory and the incidence of skeletonizer damage, with a lower incidence on coffee shrubs at both 2.5 and 5 m from trees with ant colonies (~30%) compared to levels at reference trees (~40%; Fig. 2d; Appendix S1: Table S2).

Top-down control variation across landscape

Ant colonies were found in 44 of the 59 plots with a maximum of six colonies in one plot and an average of 1.6 ant colonies per plot (i.e., a density of 0.82 colonies/ha; further data on characteristics of the nests and trees harboring the nests are shown in Appendix S1: Table S3). The distribution of the number of ant colonies per site followed a Poisson distribution, which implies that there was not a strong clustering or overdispersion (Appendix S1: Fig. S1). Yet, the number of ant colonies decreased with higher altitude and management intensity (Appendix S1: Table S4). There seemed to be preferred and non-preferred tree species for the ants to nest in, since the frequency distribution of trees with colonies differed from the overall frequency distribution of tree species ($\chi^2 = 40.2$, df = 20, $P = 0.005$, Appendix S1: Fig. S2).
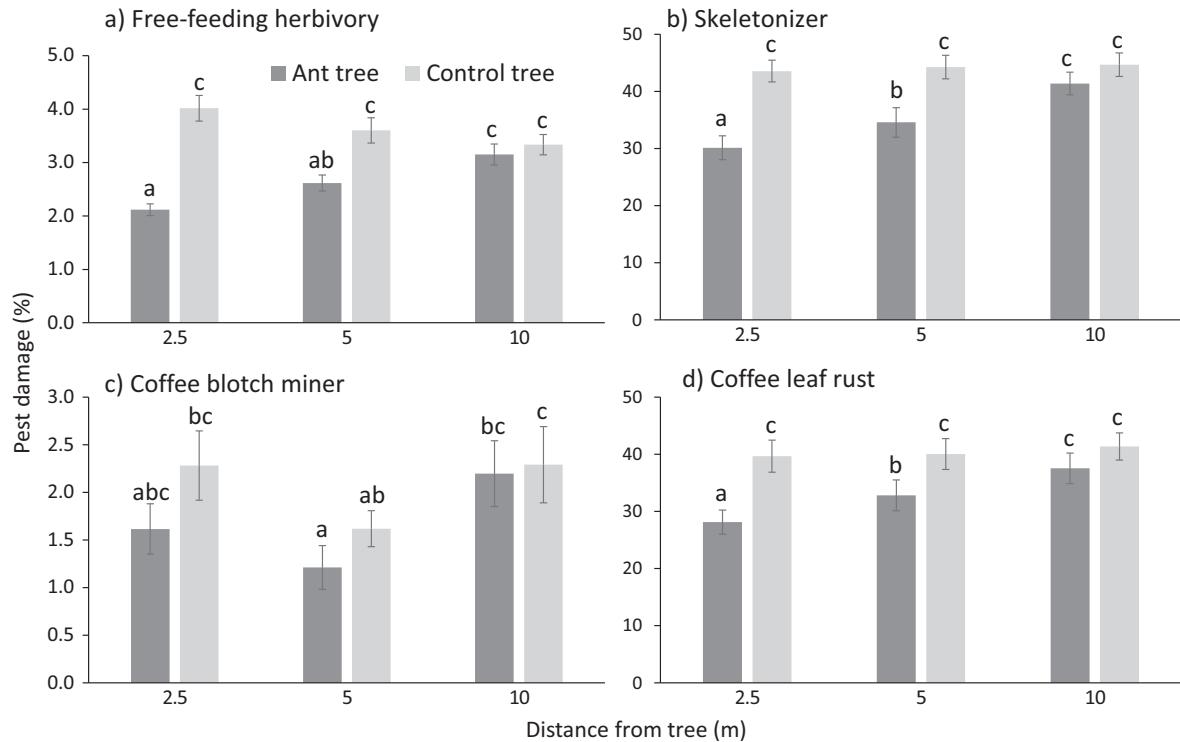
Fig. 2. Level of pest damage on coffee shrubs at different distances from trees with and without an ant colony for (a) free-feeding herbivory (b) skeletonizer (c) leaf miners, and (d) coffee rust. Values denote the percentage of a leaf that is eaten by free-feeding herbivores and the incidence of attacked leaves for the other three pests/diseases. The interaction between distance and ant tree vs. reference tree was significant ($P < 0.001$) in a, b, and d (see Appendix S1: Table S2). Different lowercase letters above bars denote significant differences ($P < 0.05$) from pairwise post-hoc tests. $N = 44$ sites.

There was stronger top-down control of free-feeding herbivory by *Crematogaster* ants in sites with the following three characteristics: lower number of colonies, lower altitude, and less intensive management (i.e., lower CSI; Appendix S1: Table S5a). The strongest pattern was for management intensity, where sites with low values (i.e., little management) had strong top-down control (negative values on the *y*-axis; $P = 0.008$, Fig. 3a). When plotting free-feeding herbivory at 2.5 m separately for ant colony trees and reference trees, there was a declining trend of the herbivory at the reference trees with increased management intensities not seen at the coffee close to ant colony trees (Fig. 3c). The top-down control of the skeletonizing insect increased with more tree cover in the surrounding area ($P = 0.006$, Fig. 3b; Appendix S1: Table S5b), even if the absolute level of skeletonizer incidences was lower in those sites (Fig. 3d). The top-down control of coffee leaf rust at the site level was not related to any management or environmental variables and variation in top-down control across the landscape for leaf-miners was not analysed, since it was non-significant in the within-site analysis.

DISCUSSION

All ecosystems are characterized by interacting species, including species that prey on organisms at lower

trophic levels. Here we demonstrate how such effects can vary spatially at several scales. Using a system with arboreal ants in shade-grown coffee, we show that damage by some herbivorous pests was significantly reduced by ants, a difference not seen any longer at 10 m from the ant colony. At a larger spatial scale, across tens of kilometers, there was also variability in the efficiency of top-down control by *Crematogaster* ants. For example, damage by free-feeding herbivores was reduced more in little managed coffee systems. Thus, the top-down control of ants on coffee herbivores displays a heterogeneous pattern across spatial scales, with possible implications for the overall interaction network. However, coffee yields are probably not much affected because of a combination of low nest densities and limited local spatial extent of top-down control.

We found clear evidence of a top-down effect by arboreal *Crematogaster* ants on both free-feeding herbivores and the skeletonizer. This is consistent with some studies on the predatory effect of ant species on coffee pests (see, e.g., Philpott and Armbrecht 2006, Morris et al. 2015, Aristizábal and Metzger 2018), but contrasts with others that did not find such effects (e.g., Philpott et al. 2008). The different results might indicate that the top-down effect of ants on herbivory is context-specific and depends on the study system and/or the particular ant species (Wielgoss et al. 2014). One mechanism shown to
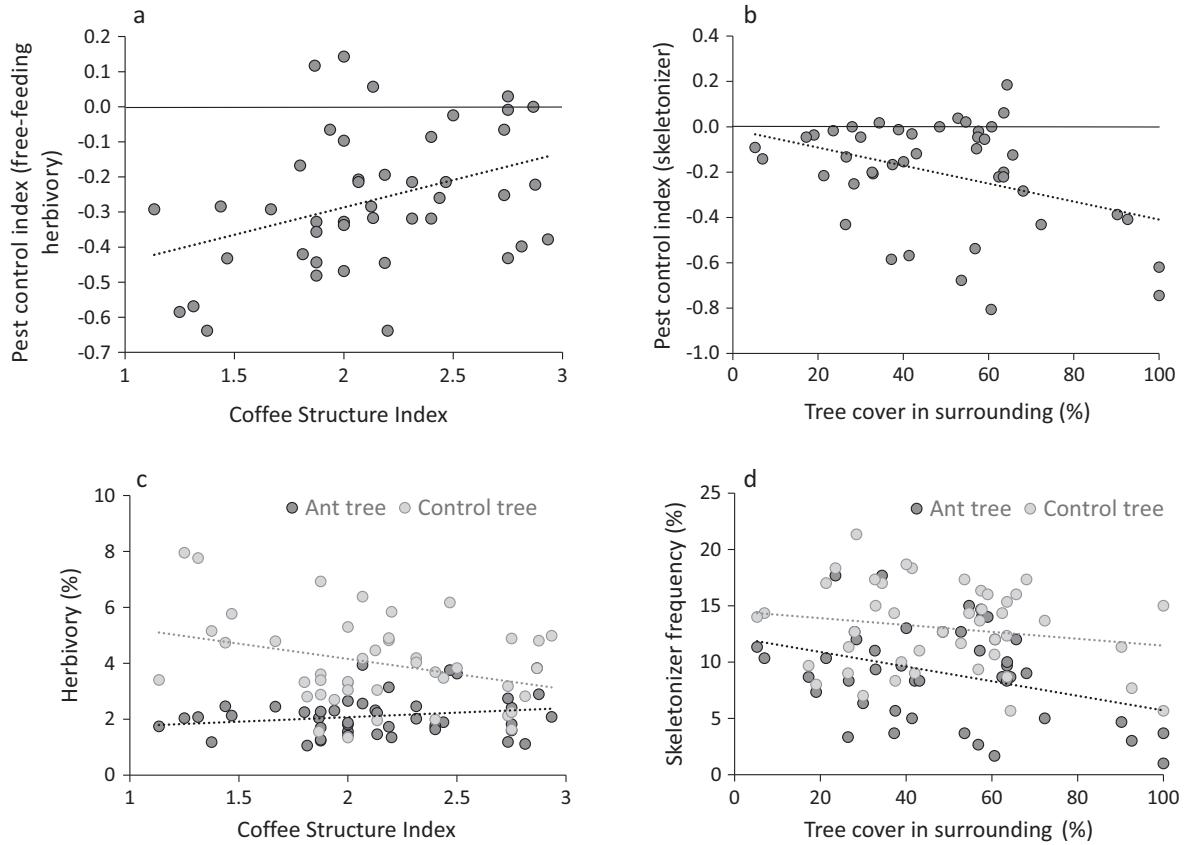
FIG. 3. Pest Control Index for (a) free-feeding herbivory as a function of Coffee Structure Index (an index of management intensity where high values denote more intensive management) and for (b) skeletonizing insects as a function of amount of tree cover in the surroundings (1 km radius). Pest control index is the log-odds ratio between the pest levels at the coffee close to the ant tree and the reference tree. A value below 0 denotes a lower pest level at the ant tree (the zero-line added for clarity). Linear trend lines are superimposed. For statistical interpretation, see Appendix S1: Table S5. Panel c illustrates the percentage free-feeding herbivory at 2.5 m from the ant (dark circles) and reference (light circles) trees as a function of Coffee Structure Index and panel d shows the incidence of the skeletonizer at 2.5 m from the ant (dark circles) and reference tree (light circles) as a function of tree cover in the surroundings.

promote top-down control is when ants that are tending e.g., scale insects for honeydew also suppress free-feeding herbivores when passing across the canopy (Clark et al. 2016). Since we found only occasional presence of scale insects in our study, it is probably not the major mechanism for the suppression of herbivory in our system, but rather a direct effect of predation on caterpillars. *Crematogaster* ants did not seem to have an effect on leaf miners, possibly because they are hidden from the ants within the leaf tissue. Interestingly, the level of coffee rust was also clearly suppressed close to the colonies of *Crematogaster* ants. We tested for such effect because coffee rust is shown to be reduced in sites in Mexico with abundant *Azteca* ants, via an intricate interaction between the rust and a hyperparasite (*Lecanicillium lecanii*), that infect both the rust and a scale insect that is tended by the ants (Vandermeer et al. 2009). However, while rust hyperparasites are also commonly found in the Ethiopian study system, there are no reports that it attacks any other species than the rust

(Zewdie et al. 2020). Thus, the only mechanism we can speculate about is that perhaps the ants reduce the abundance of a vector of the rust.

There was a clear scale dependency of the top-down effect at the site level, as a significant difference in pest levels between ant colony and reference trees was not detectable at 10 m distance from the trees. Given the rather low density of colonies (often <1 colony per ha) this implies that the low levels of herbivory and rust near trees with ant colonies are exceptions rather than the rule across a larger area. Other studies in different ecosystems have also found strong small-scale spatial patterning in ant effects with declines of these effects at tens of meters from their colonies (Wimp and Whitham 2001, Atlegrim 2005), even where ant foraging distances are much longer. Such small-scale mosaics of top-down control are probably very common in nature. It seems logical to assume that predators with a fixed colony would be more likely to create such mosaics than free-ranging predators (Brodmann et al. 1997). Many studies

on the effect of predators on herbivory use exclusion experiments on random branches across a site (Gras et al. 2016). Perhaps an even deeper understanding of the dynamics of top-down control could be attained by taking into account small-scale variability in predator abundances, driven for example by colony distributions.

Top-down control could potentially vary across larger spatial scales if the predator varies in abundance along some management or environmental gradient. In our study system, the density of ant colonies did vary systematically, with higher densities in less-managed coffee systems and at lower altitudes. Ants showed a weak preference for certain tree species over others, even if the ants seemed to be generalists and mostly avoided small trees (and thus tree species that never become large). Variability in top-down control across landscapes has often been attributed to differences in the abundance of predators (Gras et al. 2016, Aristizábal and Metzger 2018). In contrast to this expectation, we did not find any effect of ant colony density on the variability in top-down effect between sites. Yet, we suggest that top-down control could still vary between farms even with a similar abundance of the predator, for example due to environmentally mediated differences in herbivore density or changes in the interactions between herbivores and ants (e.g., due to the environment changing foraging behavior). We observed such cross-landscape variability of top-down control by ants on free-feeding herbivory, which was larger in systems with low management intensity. Yet, this did not result in lower levels of free-feeding herbivory in these systems because the general level of free-feeding herbivory was higher at reference trees in sites with little management. A different pattern was found for the suppression of the skeletonizer. In this case, the incidence of this species was suppressed more in sites with a high proportion of surrounding tree cover. The suppression was higher in parts of the landscape with lower densities of the skeletonizer implying that the top-down control mechanism amplified an already present spatial variability in herbivory from the skeletonizer. One promising area of future research may be to identify how the environment affects herbivore density, and how herbivore density and the environment jointly affect the interaction between ants and herbivores, e.g., due to density and behavioral changes (cf. Abdala-Roberts et al. 2010, Boesing et al. 2018).

Management implications

While the main focus of the study was on ecological theory, it is still interesting to view the results from the perspective of the farmer, and express the effect sizes into potential economic benefits and applications. Intensifying coffee management primarily threatens forest specialists, including trees, birds, and ants (see, e.g., Perfecto and Vandermeer 1996, Aerts et al. 2011). It seems that the *Crematogaster* ants in our system also are negatively affected by intensification. It remains unknown, whether

this is due to adverse conditions for the ants in these sites or due to the active removal of nests by the managers. However, it seems not related to change in species composition of trees between little and more intensively managed coffee sites, since preferred tree species for ant colonies occur in all systems (Aerts et al. 2011). It is interesting to note that in a nearby landscape farmers place their beehives in trees with *Crematogaster* spp. colonies to protect the honey from driver ants (Adgaba et al. 2014). This together with the possibility of top-down control suggests that an artificial increase of number of colonies might be beneficial. However, to the equation should also be added that farmers in our study area generally see *Crematogaster* ants as pests due to the nuisance they cause during coffee harvesting (personal communication). Since most smallholder farmers rely on natural pest control, a better understanding of how top-down control varies across space and time can be valuable for developing better farming practices (Médiène et al. 2011). Moreover, agroforestry systems are often associated with richer biodiversity, which might allow for better natural pest control, although our understanding of the mechanisms is still limited (Staver et al. 2001). In this study, we found that ants could be beneficial. However, to what extent the levels of top-down suppression that we recorded at the closest shrubs are significant in terms of enhancing yields on these shrubs is difficult to know without careful monitoring of the yield over longer time scales. However, at a stand scale the effect on the overall yield is likely minimal. If we multiply the largest reduction of herbivory (50%) with the largest extent we found an effect (5 m radius around an ant colony) with the largest density per hectare (three colonies) we still end up with an estimated reduction of herbivory with only 1.2% at the stand scale. This suggests that the net benefit for the farmers in terms of yield gain from the *Crematogaster* ants likely is small when seen in isolation. However, we may speculate that the total level of top-down control by natural enemies on coffee pests and diseases might still stabilize the yields and reduce outbreaks of different kinds of pests, and probably the *Crematogaster* ants play a role in this together with other ants, birds, and bats (see, e.g., Gras et al. 2016).

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.3376/suppinfo

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Data (Hylander et al. 2021) are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.rfj6q579c