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Seasonal and microhabitat differences alter ant predation of a globally disruptive coffee pest

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ABSTRACT

Agroecosystems benefit from biological control services, yet predatory activity by natural enemies, like ants, can be highly spatio-temporally variable. Heterogeneity in perennial coffee agroecosystems is not driven by the crop itself, but rather climate at the regional scale and managed shade trees and herbaceous plant layers at the local scale. We examined the effects of both inter-annual seasonal and microhabitat variation on the predatory function of ground-foraging ants on a globally disruptive coffee pest, the coffee berry borer (*Hypothenemus hampei*). During the dry and rainy seasons, we measured prey removal rates of the borer by ants across three distinct litter treatments. We found significantly higher rates of prey removal during the dry season and, to a lesser extent, in plots with greater leaf litter and lower soil temperatures. Our results indicate that both large scale processes like inter-annual seasonal variation in climate and small-scale differences in microhabitat refugia can influence pest predation activity by natural pest control agents in coffee agroecosystems.

1. Introduction

Pest suppression and biological control services provided by natural enemies enhance ecological and economic benefits by improving yields and crop marketability while reducing use of pesticides (Naylor and Ehrlich, 1997). Biological control is the result of predation and parasitism by a wide variety of species including birds, spiders, ladybird beetles, mantisflies, wasps, fungi and ants. In many temperate agroecosystems growing annual crops, however, natural enemy populations and their effects on pests can be unpredictable and or erratic, which may in part be attributed to the frequency and/or intensity of disturbance regimes due to crop turnover and seasonal climate shifts (Morris et al., 1996; Landis et al., 2000). Tropical agroforestry systems, on the other hand, experience relatively low disturbance as they generally produce perennial tree crops and experience minimal variation in seasonal temperature, both of which may benefit natural enemy populations. As a result, biological control may be especially efficacious in tropical, perennial agroforestry systems like coffee.

1.1. Spatio-temporal variation in biological control

Biological control is highly variable across time and space, and an improved understanding of that variability is necessary to identify management practices that promote biological control services and maximize pest suppression in agroecosystems (Bommarco et al., 2013). Ecosystem variability can affect biological control at multiple spatial and temporal scales (Bengtsson et al., 2002; Tscharntke et al., 2007). For example, landscape level heterogeneity supports natural enemy diversity, abundance, and often enhanced pest control (Thies et al., 1999; Östman et al., 2001). Yet, smaller scale variation can also strongly affect biological control services. Microclimate changes associated with cover crops (Morris et al., 1996), leaf debris, or other ground covers (Landis et al., 2000) moderate temperature and humidity that may constrain the activity or behavior of predators (Orr et al., 1997). Managing microhabitats for natural enemies provides additional resources (*e.g.* pollen, nectar, alternative prey) (Altieri and Whitcomb, 1979) or may provide refugia from unfavorable management (*e.g.* pesticide application, tilling), which can increase predator abundance (Symondson et al., 2002).

Although climate and seasonal variability are recognized as important to natural enemy abundance and biological control, (Barbosa, 1998; Tscharntke et al., 2007), studies of temporal variation in biological control are less common than studies of spatial scale variability and generally focus on the endogenous changes to the agroecosystems (*e.g.* phenology of crops) rather than exogenous temporal variability (*e.g.* seasonality and climate) (Rusch et al., 2013). Seasonal variability of climate in perennial agroforestry systems is important for a few reasons. First, seasonal variations in temperature set physiological

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limits on growth and reproduction of many arthropod predators and pests (Bale and Hayward, 2010). Second, predator populations are likely adapted to pest phenologies that are themselves tied to climate (Barbosa, 1998). Third, predators may utilize alternative food resources or other nutrients depending on the season (Chen et al., 2004; Rico-Gray et al., 2006).

1.2. Ants as predators in tropical agroforests

In perennial tropical coffee agroforests, ants aid in the suppression of many coffee pests (De la Mora et al., 2015; Gonthier et al., 2013; Larsen and Philpott, 2010; Philpott et al., 2012). The coffee berry borer, *Hypothenemus hampei*, (hereafter, borer) is globally one of the most damaging coffee pests because it directly impacts coffee yields. This small beetle (˜2 mm) bores into the fruit and lays eggs, employing the fruit as both shelter and a food resource for the larvae throughout the growing season. The lifecycle of the borer is tightly linked with the phenology of the coffee plant. Gravid females emerge from old berries at the onset of the rainy season to colonize new berries (Damon, 2000). However, the absence of berries during the dry season requires that borers try to survive the dry season in the refuge of the old berries until the new coffee berries form (Gutierrez et al., 1998).

Ants are biological control agents of the borer both in the coffee plant itself (Gonthier et al., 2013; Larsen and Philpott, 2010; Philpott et al., 2012) and on the ground (Armbrecht and Gallego, 2007; Trible and Carroll, 2014) where ground-foraging ants prey up on borers in and outside of the fallen, infested coffee fruits (Damon, 2000; Baker and Barrera, 1993; Aristizábal et al., 2018; Morris et al., 2018). Despite this, little is known about seasonal and microhabitat variation in ant predation on the borer.

1.3. Micro-habitat and micro-climate effects on ant foraging and behavior

Habitat structure, including aspects of arboreal and herbaceous vegetation as well as ground cover, can influence ant foraging behavior and may enhance or impede foraging success. Ant body size, relative to gap size within the leaf litter structure, is an important predictor of ant foraging success (Farji-Brener et al., 2004; Kaspari, 1993; Sarty et al., 2006). For example, larger ants are less successful in habitats with smaller interstitial gaps (Gibb, 2005). In contrast, smaller ants may be less successful in simple habitats, relative to larger ants, due to harsher abiotic conditions and greater risk of parasitism or predation (Wilkinson and Feener, 2007).

Habitat complexity may also influence interspecific competition among foraging ants. Interspecific competition plays a key role in the structure of ant communities (Ennis and Philpott, 2017; Parr, 2008; Savolainen and Vepsalainen, 1988), so a disruption of competitive hierarchies via habitat complexity may affect ant behaviors and functions. Certain habitats (simple or complex) may provide an advantage to ant species that are less effective competitors allowing them to escape or avoid more aggressive species (Gibb and Parr, 2010).

Changes in habitat complexity may also alter microclimate, thereby influencing ant activity (Perfecto and Vandermeer, 1996). For example, increased canopy cover in agroforests can limit evapotranspiration and maintain higher relative humidity (Lin et al., 2007). Likewise, leaf litter cover may reduce soil moisture losses during longer seasonal dryness or higher temperatures (Vandermeer et al., 1998; Lin and Richards, 2007).

1.4. Questions and hypotheses

We examined how seasonality and microhabitat complexity influence pest suppression services provided by ground-foraging ants in a working coffee agroecosystem. We used a sentinel pest removal experiment, coupled with measures of local and landscape habitat features, and a ground cover manipulation to test: (1) Does predation on a coffee pest by ants vary by season? And, (2) Do other local or landscape factors, such as management (*i.e.* organic vs. conventional growing practices), vegetation, canopy cover or microhabitat effects of leaf litter and soil temperature affect prey removal rates of a coffee pest?

2. Methods

2.1. Site description

We conducted this study in the Soconusco region of Chiapas, Mexico (15° 11′ N, 90° 20′ W) near the boarder of Guatemala. We selected 25 sites, across six different farms, between 600–1203 m in elevation that represented both organic and conventional coffee farm production. All farms were shaded polyculture coffee systems where low shade farms had about 40% shade and high shade farms had about 85% shade. We selected each site to be at least 100 m from all other sites. At each site we measured elevation using a GPS (Garmin GPSMAP 76) unit and canopy cover using a convex spherical densiometer based on an average of four measurements.

2.2. Experimental design

Within each site we established three adjacent 1 m^2 plots within which we randomly assigned to one of three leaf litter treatments: no litter, ambient litter, and added litter. We initially cleared all litter from each plot. Then we replaced ambient litter to its plot. The litter from the no litter treatment was added to the added litter treatment. We returned 24 h after litter manipulation to conduct the predation experiment. Within each of the 3, 1 m^2 plots we measured leaf litter depth, soil temperature at four different points and estimated the percentage of herbaceous ground cover using a quadrat as a visual guide for approximate coverage.

In each 1 m^2 plot, we placed three card baits with five borers on each card, for a total of 15 borers per plot and 45 borers per site. Borer baits were prepared the evening before the experiment with borers collected live from the field and then killed in a drying oven at ˜40 °C for 10 min. We stored the prepared baits in the refrigerator overnight to prevent decay of the beetles. Preliminary trials revealed no significant difference in ground foraging ant preference between live or recently killed borers. Borers are slow moving and clumsy beetles that are easily grabbed by ants. Even so, using live borers would have required the use of glue to keep them from leaving the bait card and therefore affected our ability to study ant removal rates. Specifically, the use of glue would likely impede the removal by ants increasing handling time, reducing ant nest mate recruitment and making it difficult to differentiate between an attempted removal by an ant or the lack of removal altogether. Furthermore, if the baits were prepared with live borers, the borers would be attached to the card for extended periods of time prior to exposure to the predatory ants resulting in the likelihood of a portion of the borers dying. For these reasons, we used dead borers to facilitate the aims of the study as is commonly done with studies of the coffee berry borer (De la Mora et al., 2015). Prior to placing the cards in the plot, we first cleared small areas (~ 10 cm in diameter) of leaf litter and then dampened the cards with water so they were flush with soil and easily accessible to small and large ground-foraging ants. Then, every minute for 25 min. following the placement of the first bait card we recorded the number of remaining borers on each card and identified the ants removing the borers. We also recorded all visitors during the trial including the species identity, when the visit occurred during the 25 min. trial, on which litter treatment the visitor was found and if the visitor was seen removing the borer. We did not collect unidentified visitor ant species during the trial period for identification in the lab unless the visitor was found on the bait at the end of the trial period. Collection of visitors during the trial would have likely disrupted the potential removal of a borer or limited potential ant recruitment. All predation trials took place between 7am-11am on only sunny or partly sunny days. We conducted the trials at all site in both February (rainy season) and June 2012 (dry season).

2.3. Statistical analyses

We analyzed the effect of season (dry or rainy), elevation, management (*i.e.* organic or conventional), leaf litter treatment, canopy cover, soil temperature, and herbaceous cover in a generalized linear mixed effects model with a Poisson distribution for count data and site included (N = 25) as a random effect. We selected the best model by comparing corrected AIC values across all possible models. We then averaged those models with less than a two point difference in AIC values to determine the overall effect of the most important factors.

For censused, minute-by-minute data from each trial, we used a Cox proportional hazard regression analysis to simultaneously evaluate leaf litter and seasonality on a borer's likelihood of 'surviving' the experimental trial. This analysis provides direct comparisons of the influence of multiple factors with hazard ratios corresponding to effect sizes. We used leaf litter treatment (categorical) for the purposes of visualizing the data, but performed the analysis separately for both mean leaf litter depth and leaf litter treatment. We then used a survival analysis with logrank test to compare the seasonal differences in borer 'survival' over the experimental period. The logrank tests the null-hypothesis that there is no difference between groups at any time point.

We compared species composition of ant visitors in the dry and rainy seasons for all ant visitors to the baits during the removal trials. Non-ant visitors were excluded from community composition analyses. We used non-metric multidimensional scaling (NMDS) to visualize differences in ant communities and assessed statistical differences in community composition by season with a permutational multivariate analysis of variance (PERMANOVA) comparison of the Bray-Curtis distance matrix. We performed all analyses and made all graphics in R (R Core Development Team 2015).

3. Results

Leaf litter manipulation resulted in a range of litter depths from 0 to 15 cm. Average depth after manipulation was 0.0 cm ± 0.0 for no leaf litter, 4.56 cm ± 0.24 for the ambient litter, and 9.51 cm ± 0.37 for the added litter treatment across sites. The number of borers removed per plot was significantly higher with higher leaf litter depth ($p < 0.0001$), in the dry season ($p < 0.0001$) and in sites with lower mean soil temperature ($p = 0.041$) (Fig. 1). Mean vegetation cover was included in the best fit model, but did not have a significant effect on borer removal ($p = 0.08$), There was no significant effect of elevation, management, or canopy cover on borer removal rates by ants.

The hazard probability of borer removal by ants was significant for both season (Cox proportional hazard, $p < 0.0001$, Fig. 2) and leaf litter ($p < 0.0001$). During the rainy season trials borers experienced 76% reduction in the likelihood of removal by an ant while leaf litter (across seasons) increased the likelihood of removal by 6%. Finally, a direct comparison of the borer seasonal survival curves revealed a significant difference between seasons (logrank test, $p < 0.0001$).

We recorded a total of 241 visitors with a mean of 9.6 ± 1.0 (SE) per site in the dry season and 116 with a mean of 4.6 ± 0.5 (SE) per site in the rainy season to the borer bait cards. All recorded visitors were ants aside from two Staphylinidae larvae that were not observed removing the borers and were not included in the community analyses. Not surprisingly, we witnessed a lower proportion of the total borer removals (number of ant visits resulting in removal divided by the total number of borers removed during the trial) when the ants were more active during the dry season (30.2%) relative to the less active rainy season (69.9%). However, among all ant visits, the proportion seen removing borers was relatively consistent across seasons with 50.9% and 48.2% of visits resulting in removal in the dry and rainy season, respectively.

The most common ant species observed were *Pheidole protensa*

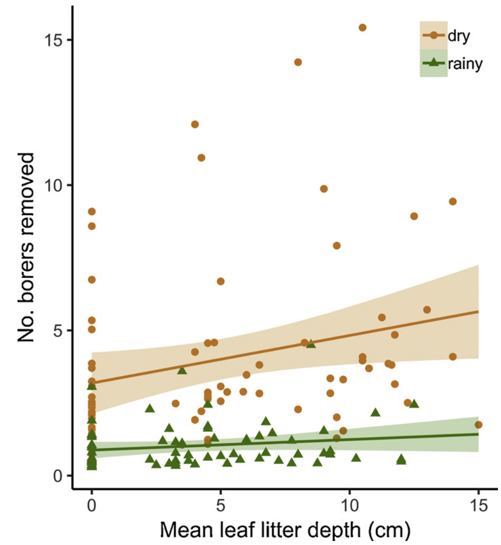

Fig. 1. Impacts of leaf litter removal and season on coffee berry borer removal by ants. Graph shows results from the best-fit generalized linear model based on AIC values. The number of borers removed from the bait during the 25 min. experiment by season by mean leaf litter depth of experimental plots. Both season and litter are significant factors in borer removal rates. The green triangles represent experiments conducted during the rainy season and the orange circles represent experiments conducted during the dry season.

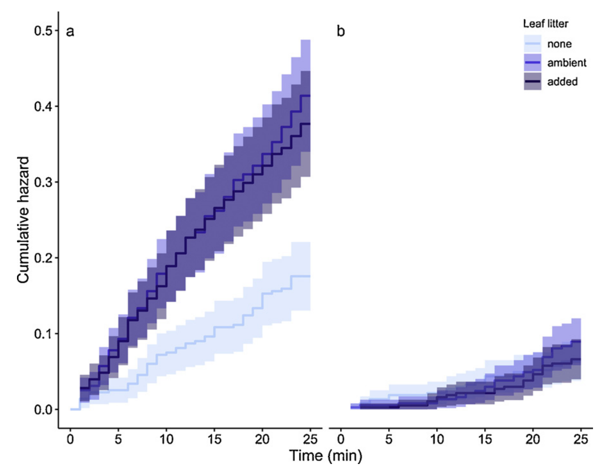

Fig. 2. Season and leaf litter treatment effects on cumulative hazard experienced by a borer over the 25 min. experiment. The cumulative hazard describes the probability that a borer at time (*t*) is removed (a) during the dry season and (b) during the rainy season. Light blue line and shading represent no litter ("none") with 95% CI; blue represents "ambient" and dark blue represents the "added" leaf litter treatment.

Table 1
Percent of total ant visits and recorded ant removals by season for the most common seven ant species.

Ant species	Visits		Removals	
	dry	rainy	dry	rainy
Pheidole protensa	38.9	43.0	44.0	40.0
Pheidole synanthropica	14.1	14.0	16.5	23.6
Solenopsis geminata	9.5	10.5	15.6	18.2
Wasmannia auropunctata	5.8	7.0	7.3	0
Unidentified	3.7	1.7	0.9	0
Gnamptogenys wheeleri	3.3	6.1	2.8	3.6
Nylanderia sp. 1	3.3	4.4	0	1.8

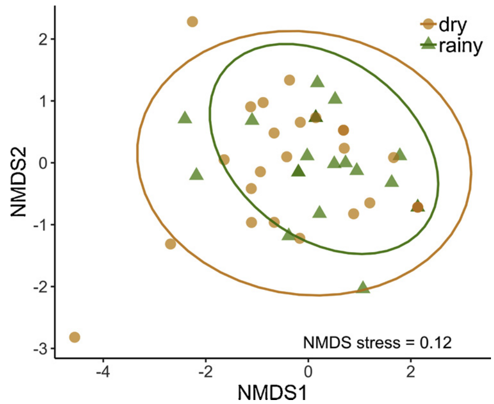

Fig. 3. Non-metric multidimensional scaling plots comparing species composition of ant visitors recorded at each site by season. Orange circles represent species composition of visitors at sites during the dry season and green triangles represent species composition of visitors at sites during the rainy season with 95% ellipses.

(37.5% of all visitors), *Pheidole synanthropica* (14.1%), *Solenopsis geminata* (9.9%) and *Wasmannia auropunctata* (8.5%). The species visitation rank did not vary much by season (Table 1), nor did the composition of ant visitors by site between seasons (Fig.3, PERMANOVA, $F_{1,48} = 1.55$, $p = 0.12$).

4. Discussion

In this study we demonstrate microhabitat differences at very small spatial scales and intra-annual seasonal variation have a strong impact on how ants behave as natural pest control agents in the biological control of globally important pest, the coffee berry borer. We found higher rates of pest removal during the dry season, with increased microhabitat refugia (*i.e.* litter) and lower soil temperatures.

4.1. The role of microhabitats and seasonality on biological control of the borer

Microhabitats are important for maintaining ant biodiversity in coffee-forest agricultural matrices (Armbrecht and Perfecto, 2003). However, greater microhabitat complexity can impede ant movement, especially for smaller ants (Gibb and Parr, 2010). Despite this, we found that the addition of litter resulted in higher prey removal rates, particularly during the dry season. This suggests that microhabitat complexity may provide important refugia for ants, but especially when the climate is hotter and drier. This is further supported by the negative effect of soil temperature on prey removal rates.

The role of climate and seasonality and their effects on ant populations and predation rates are less well studied. Seasonality in temperate ecosystems is a determining factor of cyclical insect populations, but it is unclear how insect populations respond in less environmentally stressful regions like the tropics where seasonality is driven by changes in precipitation regimes and not temperature. Although the differences we found between seasons in prey removal rates could be attributed to other random fluctuations throughout the year, our study suggests that inter-annual seasonal variation may play a role in ground-foraging ant behavior and biological control. And, in contrast to a previous study of ant removal on fly pupae (De la Mora et al., 2015), ours aligns with other studies that find higher predation rates among spiders during droughts (McCluney and Sabo, 2009). Differences in prey removal rates between seasons may be due to seasonal changes in prey availability, nutritional deficiencies as a result of larger seasonal resource limitation (Chen et al., 2004) or seasonal changes to ant colony growth and production of younger life stages that alter the nutrient requirements of the colony.

4.2. Ground-foraging ants and control of the borer

Although less well studied in their contribution to borer control relative to arboreal foraging ants, ground-foraging ants play a diverse and unique role in the suppression of the borer (Armbrecht and Gallego, 2007). Ground-foraging ant diversity is very high and frequently higher than arboreal foraging species (Ennis and Philpott, 2017; Longino and Nadkarni, 1990). Similarly, ground ants have high levels of functional diversity in physiological characteristics, like body size, as well as behavioral traits, like foraging and competitive strategies, that can influence borer removal rates and may be facultative or antagonistic to the overall control of the borer. For example, smaller ants can extract borers from the berries and competitively dominant ant species are faster at removing borers found outside the berries, but are also territorial and thus potentially limit other species access to borer (Trible and Carroll, 2014).

Ground-foraging ants are also uniquely important in the control of the borer because they predate on borers year-round from fallen, old or dried berries; even after harvest when there are no remaining new berries for the borer to colonize in the coffee plants (Damon, 2000; Baker and Barrera, 1993; Aristizábal et al., 2018). Our study further emphasizes the importance of the ground ants because it is during the dry season when new coffee berries are not available (post-harvest) that we find the ants are most actively foraging and removing borers. Thus, if the population of the borers are growth limited during the dry season – as indicated by it's coupled lifecycle with the coffee plant (Gutierrez et al., 1998) – and the ant activity we recorded is reflective of natural consumption rates of the borer, then the role of ground ant predators during the dry season could be critical to the control of the larger borer population.

5. Conclusions and management implications

The high variability in natural pest control services creates a barrier to adoption and implementation of biological control practices. A greater understanding of drivers of the variability can enhance the efficacy of pest control agents, like ants in coffee agroecosystems.

Specifically, leaf litter is important for maintaining ant biodiversity (Armbrecht et al., 2005), ant density and nest size (McGlynn et al., 2009). This study affirms the importance of litter because it promotes ant activity, ant predatory function and provides a refuge from dry soils and hot temperatures, especially in the dry season. The benefits of leaf litter, however, extend beyond promoting ant biodiversity and function. Leaf litter is most commonly cited to enhance soil fertility. Indeed, leaf litter inputs maintain soil organic matter, which is associated with increased nutrient availability and reduced leaching of nutrients from soil (Beer, 1988). Leaf litter also contributes to increased water filtration, storage and availability (Lin and Richards, 2007). The role of leaf litter cover in coffee production is therefore directly and indirectly beneficial to coffee production. A consistent schedule of pruning in a moderately shaded coffee agroforestry system will likely increase litter inputs and improve micro-habitats for ground-foraging predators like ants, while simultaneously increasing nutrient availability for the coffee plants.

The role of seasonal differences in predator function and activity highlights the importance of climate in biological control, and specifically how the lack of rainfall in the tropics may be important to natural biological services provided by ants.

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