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Climate consequences for ecosystem functions, production and producer responses in coffee agroecosystems

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CLIMATE CONSEQUENCES FOR ECOSYSTEM FUNCTIONS, PRODUCTION AND PRODUCER RESPONSES IN COFFEE AGROECOSYSTEMS

A dissertation submitted in partial satisfaction
of the requirements for the degree of

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in

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with an emphasis in ECOLOGY AND EVOLUTIONARY BIOLOGY

By

Katherine K. Ennis

December 2019

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ABSTRACT

CONSEQUENCES OF CLIMATE FOR ECOSYSTEM FUNCTIONS, PRODUCTION AND PRODUCER RESPONSES IN COFFEE AGROECOSYSTEMS

Katherine K. Ennis

Coffee is an important commodity crop, providing livelihoods for hundreds of millions worldwide. Like most plants and agricultural crops, coffee is anticipated to be strongly impacted by climate change forecasts. Grown at high altitudes and often accompanied by shade trees that provide additional ecosystem and conservation value, coffee is particularly climate sensitive requiring specific rainfall regimes for flower and fruit development. In this research I used ecological and interdisciplinary approaches to examine different effects of seasonality and climate change on coffee systems.

In the first two chapters I examine the role of seasonality in predator-pest interactions of a tropical coffee agroforestry system in the highest coffee producing municipality of Chiapas, Mexico. Specifically, I use experiments and field manipulations to assess the impact of seasonal rainfall as a driver of changes to insect communities and predator-prey consumption patterns between natural biocontrol agents (ants) and coffee insect pests. I find that ant predation is affected by microclimate and seasonal rainfall and that reduced rainfall alters ecological communities and ecosystem functions.

In the third chapter, I use environmental and socio-economic approaches to examine the impact of climate and price fluctuations on coffee production and

producers in Mexico. Combining spatially-explicit historical climate, production and price data from all coffee-growing municipalities in Mexico, I examined trends of climate and coffee production and then further characterized and quantified coffee producer's responses to changing conditions of climate and price. I found that coffee-specific climate variables contributed to a 60% decline in Mexican coffee production since its peak in the 1990s, and that farmers' management responses to soaring temperatures, limited rainfall and price volatility are generally limited to reducing the proportion of planted area they harvest each year.

In sum, my research examines seasonal climate impacts on coffee agroecosystem communities, functions and production. Specifically, I find (1) an unexplored potential effect of shifting seasonal climate on the natural biological control provided by ant predators; and that (2) climate change has already affected coffee production in Mexico, but producers have limited capacity to respond to changes. The findings of this research highlight the potential consequences of unmitigated global climate change for coffee agroecosystems and farmworker livelihoods.

DEDICATION

To Grandmère,

A true pioneer and scholar.

Et tu puer dei.

Jabberwocky

'Twas brillig, and the slithy toves
Did gyre and gimble in the wabe:
All mimsy were the borogoves,
And the mome raths outgrabe.

"Beware the Jabberwock, my son!
The jaws that bite, the claws that catch!
Beware the Jubjub bird, and shun
The frumious Bandersnatch!"

He took his vorpal sword in hand;
Long time the manxome foe he sought—
So rested he by the Tumtum tree
And stood awhile in thought.

And, as in uffish thought he stood,
The Jabberwock, with eyes of flame,
Came whiffling through the tulgey wood,
And burbled as it came!

One, two! One, two! And through and through
The vorpal blade went snicker-snack!
He left it dead, and with its head
He went galumphing back.

"And hast thou slain the Jabberwock?
Come to my arms, my beamish boy!
O frabjous day! Callooh! Callay!"
He chortled in his joy.

'Twas brillig, and the slithy toves
Did gyre and gimble in the wabe:
All mimsy were the borogoves,
And the mome raths outgrabe.

-Lewis Carroll

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INTRODUCTION

The tropics are a highly biodiverse region home to some of the highest levels of species richness and endemism globally, yet this biodiversity is threatened by two major forces, climate change and agricultural intensification. Tropical regions are expected to experience much higher average annual temperatures and more extreme and variable precipitation (Bony et al. 2013). At the same time, agricultural intensification is expanding in the tropics, contributing to declines in forest cover, homogenizing tropical landscapes, increasing pressure on ecosystems and constraining rural livelihoods (Shaver et al. 2015). The coupled interactions of climate change and agricultural intensification are likely to exacerbate impacts to ecosystems, agricultural production and livelihoods.

Forecasts of climate change for tropical regions indicate temperature increases of about 4.2ºC and shifts in total precipitation that vary regionally by the end of the century (Bony et al. 2013). The tropics provide a relatively constant thermal environment in which many organisms are not acclimated to extreme seasonal fluctuations in temperature. This may explain the high sensitivity of tropical regions to temperature variability (Seddon et al. 2016). Moreover, reduced growth and productivity associated with high temperatures provide evidence for tropical thermal limits and suggest that rising temperatures may impact future tropical forests (Doughty and Goulden 2008).

Climate change is also likely to manifest through changes in precipitation. Precipitation is the strongest driver of ecological patterns in the tropics (Comita and

Englebrecht 2009), especially for tropical regions that exhibit strong seasonality. Understanding both the effects of precipitation and seasonality is, therefore important to understanding future climate effects on communities and ecosystem functions (Condit 1998, Feng et al. 2013). For example, many tropical regions are sensitive to lower precipitation and longer dry seasons, which is expected to cause increased tree mortality rates (Lenton et al. 2008) and which may have consequences for nutrient cycling and species interactions.

Tropical regions are home to millions of people who are dependent on agriculture for their livelihood. Coffee, specifically, provides livelihoods to an estimated 125 million people around the tropics (Osorio 2002). Over the past two decades, coffee prices have declined considerably, frequently dropping below the cost of production – making coffee growing financially precarious for producers (Henderson 2019). The price declines are related to several factors including global over-supply (Ponte 2002), institutional and policy changes (Eakin et al. 2006), and extreme weather (Ubilava 2012).

Coffee is a very climate-sensitive crop due to both direct physiological responses of the coffee plant to microclimate conditions and to indirect effects of climate on coffee production through impacts of key associated species and processes in coffee systems. Traditionally grown beneath a canopy of shade trees, it is grown best at mid-to high altitudes (800-1400 m) that minimize exposure to extreme temperatures (Läderach et al. 2011). Coffee phenology closely follows regional rainfall patterns and is therefore very sensitive to precipitation shifts (DaMatta 2004).

The sensitivity of coffee to both temperature and precipitation fluctuations makes it especially vulnerable to the effects of climate change. This is made evident in future climate suitability studies that predict substantial losses in suitable coffee habitat in nearly all growing regions. Worldwide estimates suggest a loss of 50% in suitable coffee-growing land by 2050 (Bunn et al. 2015).

Coffee production is also affected by ecological plant-insect or other multitrophic interactions that are themselves subject to the effects of climate change. For instance, increasing pest abundances and changing pollinator communities due to climate change is likely to affect future coffee habitat suitability (Ghini et al. 2008, Jaramillo et al. 2011, Kutywayo et al. 2013, Imbach et al. 2017). However, we continue to lack a clear understanding of how climate, and especially precipitation, affects interactions between pollinators and the coffee plant, and between pests and predators.

Furthermore, it is increasingly clear that ecological aspects of future coffee production are inextricably linked with complex socio-economic dynamics. Indeed, coffee disease epidemics have been linked to interacting effects of climate, low coffee prices, and farm management. Low profitability can cause producers to reduce their management effort, which in turn increases vulnerability to climate-associated disease outbreaks (Avelino et al. 2015). Quantifying the extent to which climate and markets affect coffee management decisions, however, will be important for prioritizing and assessing adaptation management options.

The following studies build on years of prior research in coffee agroecosystems at UC Santa Cruz and elsewhere. The studies use data collected from field work completed in the Soconusco region of Chiapas, Mexico as well as data collected and compiled data on coffee agroecosystems found throughout Mexico. In this research I aim to contribute to a greater understanding of climate effects on species interactions in coffee agroecosystems and to advance the integration of ecological and socio-economic research in human-modified systems.

Coffee is a compelling research study system as it has significant implications for conservation and people. First, global coffee production frequently overlaps with identified biodiversity hotspots. The very location of coffee production makes it important for the protection of many species. Second, coffee is a shade tolerant, understory shrub traditionally grown under a canopy of trees. While not all coffee management is produced under shade trees, Mexico has an estimated 90% of coffee grown with some level of shade trees (Moguel and Toledo 1999). Coffee growing systems with high shade tree diversity often resemble natural tropical forests and may be relevant to some tropical restoration or secondary tropical forests. Third, the shade trees confer numerous ecosystem and management benefits. At a larger scale these include greater societal benefits like supporting high levels of biodiversity, watershed protection and carbon sequestration. At intermediate and local scales, trees provide soil enrichment and erosion control, crop protection, weed suppression, resistance to drought, extreme temperature fluctuations (Da Matta 2004) as well as food and fiber for people that work in these agroecosystems. Finally, coffee systems support many people's livelihoods in the tropics. Thus, these systems provide a unique way to simultaneously examine issues of conservation, production and the consequences of intensification on human-dominated landscapes on ecosystems and people.

The first two chapters emphasize the role of climate and seasonality on insect communities, pest control services, and on other important ecological functions and communities in coffee agroecosystems. This research emphasizes impacts outside of "bottom-up effects" like soil nutrient available and abiotic effects on coffee physiology. Instead, these first ecological chapters focus on above ground interactions, like pest predation, that also impact coffee and coffee production. I work specifically with the coffee berry borer (*Hypothenemus hampei*) and their primary predators, ants. The coffee berry borer (hereafter, borer) is the most widespread and destructive coffee pest (Jaramillo et al. 2011) now found in every major coffee-growing region (Chapman et al. 2015). The gravid female adults drill into the green coffee berry and lays eggs. The larvae then consume the interior of the bean, rendering the fruit unmarketable. Conservative damage estimates from the borer exceed $500 million annually (Vega et al. 2003). At the farm level, borer infestations can result in 75% harvest loss (Vega 2004). Understanding temporal variation in predatory activity of ants on the borer may help elucidate the extent of the role of ants in providing natural pest control to coffee.

In the first chapter, I identify a seasonal and climate component to natural pest control functions. To do so, I compared predation removal rates by litter quantity, management and season. Differences between the rainy and dry season were used as a surrogate for the potential roll of climate change and precipitation effects on important trophic interactions like pest predation. Here, I found that ant predation of the borer is higher in the dry season, but also varies with leaf litter presence. In the second chapter I apply an experimental approach to elucidate potential mechanism behind climate associated changes in found pest control. I used rainout shelters to reduce rainfall in established plots and then recorded the effects on important community and ecosystem responses including herbaceous biomass, coffee growth, arthropod abundances, decomposition, and ant predation of the borer. I found that reduced precipitation and soil moisture caused declines in plant biomass and arthropod community abundance as well as decomposition and borer removals.

Taken together, these results support the idea that ant foraging is affected by microclimate and that ant diets vary with seasonal precipitation. I further uncover an important role of ground-foraging ants in pest control of the coffee berry borer. The life history of the borer follows the phenology of the coffee plant. The borer population is limited during the dry season when there are no coffee berries to colonize (Gutierrez et al. 1998). Through this research I find that the limited population growth of the borer coincides with the higher predation of the borer and therefore may provide important pest control of the borer population. However, the relationship of borer populations and ant predation may be decoupled should climate change make borers less susceptible than ants to rising temperatures. Or, should rainfall become more intermittent throughout the year with climate change, the region may become more aseasonal and with a less pronounced rainy-dry season. If more aseasonal rainfall results in higher prey abundance year round, then ants may not preferentially choose to feed on borers during the critical period of the dry season when borers populations are growth-limited.

This research further indicates that lower seasonal precipitation can slow decomposition rates. This, in turn, could affect nutrient cycling and the acquisition of nutrients by aboveground producer-based and belowground decomposition-based food webs. Slower nutrient turnover due to increased dryness may reduce micro and macro nutrients available for coffee plants. Coffee maintenance cannot be mechanized easily and labor represents the highest cost of production (Gay 2006). As a result, producers will also incorporate integrated practices such as the use of legume (nitrogen-fixing) shade trees to increase available nitrogen to surrounding coffee plants.

My results also demonstrate that reduced precipitation can reduce herbaceous biomass and over a longer period of time may impede coffee growth. Greater herbaceous biomass could compete for nutrients with coffee, but it may also provide increased habitat complexity that generally supports higher natural enemy populations in agroecosystems (Chaplin-Kramer et al. 2011). Greater herbaceous biomass also could provide a more stable microclimate and buffer soil organism from more extreme temperature fluctuations.

These results also support the idea that precipitation effects on plant distributions can scale-up through ecosystems from plants to herbivores, omnivores and predators. In this case, my research shows that arthropod abundances, overall, follow plant biomass and decline in response to reduced precipitation. Differential effects of altered seasonal rainfall on trophic groups, like predators and herbivores, can change the community composition of arthropods such that predatory arthropods increase. Even small changes in relative proportions could increase oscillations in predator-prey dynamics. For example, drier conditions may reduce the diversity of arthropods and/or increase the likelihood of boom-bust cycles between predators and prey found in many simplified agroecosystems (Vandermeer and Goldberg 2013).

Despite finding several seasonal precipitation effects in coffee agroecosystems, there were few effects of management or agricultural intensification. I found no effect of management type (organic vs. conventional), nor shade cover on seasonal ant borer removal. And, I found no effects of shade cover on the plants or decomposition. The effect of shade did, however, interact with reduced rainfall for arthropod abundances, but only for herbivores and predators. Shade also changed borer removal rates with ants removing more borers from lower shade coffee. Effects of shade management on arthropods may be due to a high sensitivity to microclimate conditions or simply an ability to move to preferred conditions. In general, the lack of an effect of shade management suggests that shaded coffee systems are fairly robust to changes in climate and differences in management. This is surprising given that many other studies find strong effects of shade on a variety of ecological communities and ecosystem functions (De Beenhouwer et al. 2013). This discrepancy with my findings may be attributed to a relatively narrow range of shade cover used in my study, or to the small sample size at the scale of whole farms.

In the final chapter, I use novel climate and response variables to quantify how coffee producers across Mexico responded to variable economic and climate conditions over the course of the last two decades. I use spatially-explicit approach to examine producer responses over 15 years to changes in price and climate. I find that coffee producers are subject to a changing climate and volatile prices and that their management responses do not always work in their favor. Choosing to harvest less of your coffee crop in a year with lower prices, for example, means that producers leave berries on the plant. These berries provide critical resources for borers and increase their overwintering populations which will reduce marketable coffee beans in the following year. Climate and prices are both stressors to which producers respond with changes in management approaches. Perhaps a result of the rapid fluctuation of global prices, producers are better able to respond to climate impacts than to prices. I also identify that the primary means of response to changing conditions from a producer is to alter the proportion of harvested area relative to the other responses I examined (*i.e.*, changing planted area and management effort). I found that producers do not respond to changing conditions by altering planted area. And, while they do respond by increasing management effort, the benefits of the increased management efforts do not coincide with the timing of the change in price. These time lags in production make it difficult to respond to the short-term impacts of global prices. Overall, this study highlights how time scales and time lags in responses may impact the ability of coffee producers to adapt to increasingly difficult climate and economic conditions.

In sum, I demonstrate the potential consequences of climate on multiple aspects of coffee production and coffee agroecosystems. I identify a seasonal component to ant predation of the most critical coffee pest, the coffee berry borer. I further show that multiple ecosystem functions are sensitive to even minor changes in precipitation and decline with reduced precipitation. Finally, I demonstrate and quantify how producers respond to multiple production stressors of price and climate. This research illuminates some of complexity behind climate change and the consequences for ecosystems and human livelihoods.

CHAPTER 1: Seasonal and microhabitat differences alter ant predation of a globally disruptive coffee pest

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. 2012). 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, Ostman 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. 1990).

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 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. 1998).

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 (Baker and Barrera 1993, Damon 2000, 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 (Wilkinsen 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 (15º 11' N, 90º 20' W) near the border 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 ~40ºC for 10 minutes. 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 2014 (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 Team 2015).

3. Results

Leaf litter manipulation resulted in a range of litter depths from 0-15cm. 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* (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 predatory functioning 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.

Authors' contributions

KKE conceived of the study. KKE and SMP designed this study, KKE conducted the field and laboratory work. KKE conducted data analysis and wrote the first draft and SMP provided editorial content.

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Table 1.1. 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

Figure 1.1. 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 points and line represent experiments conducted during the rainy season and the orange represents experiments conducted during the dry season.

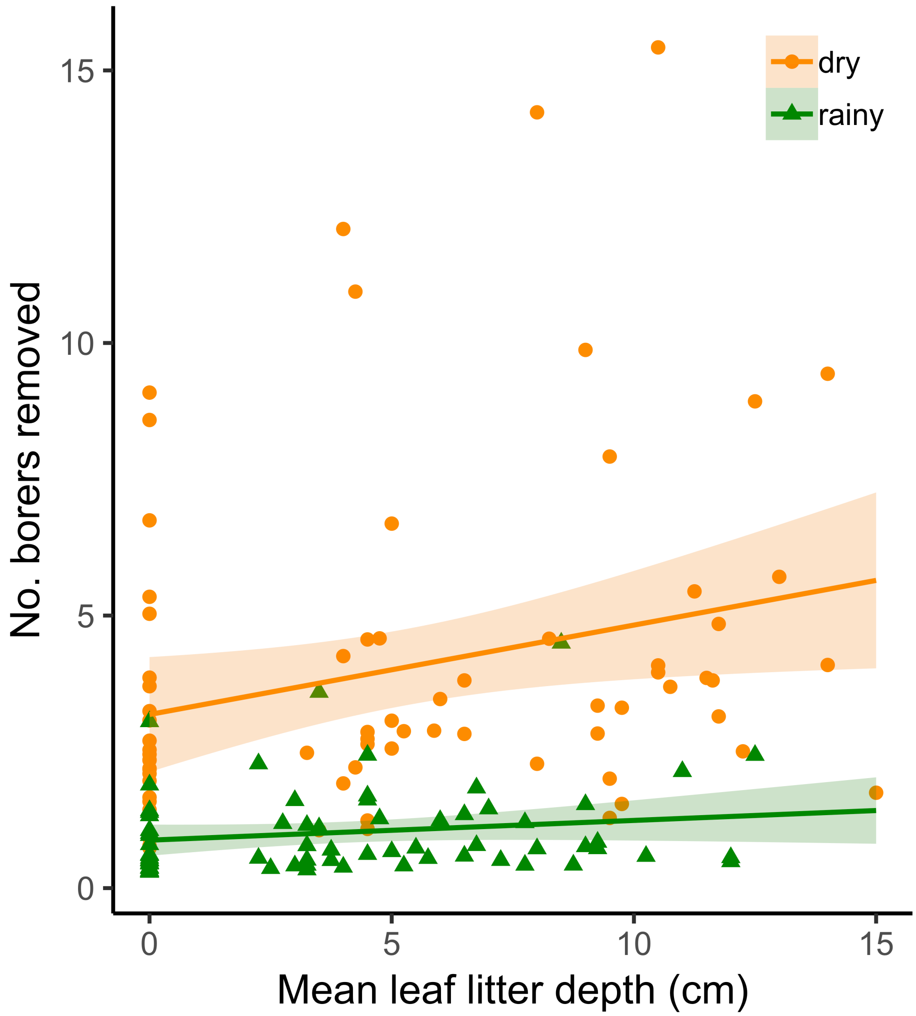


Figure 1.2. Season and leaf litter treatment effects on cumulative hazard experienced by a borer over the 25 min. experiment. The cumulative hazard describes the probability that a borer at time (t) is removed (a) during the dry season and (b) during the rainy season. Light blue line and shading represent no litter ("none") with 95% CI; blue represents "ambient" and dark blue represents the "added" leaf litter treatment.

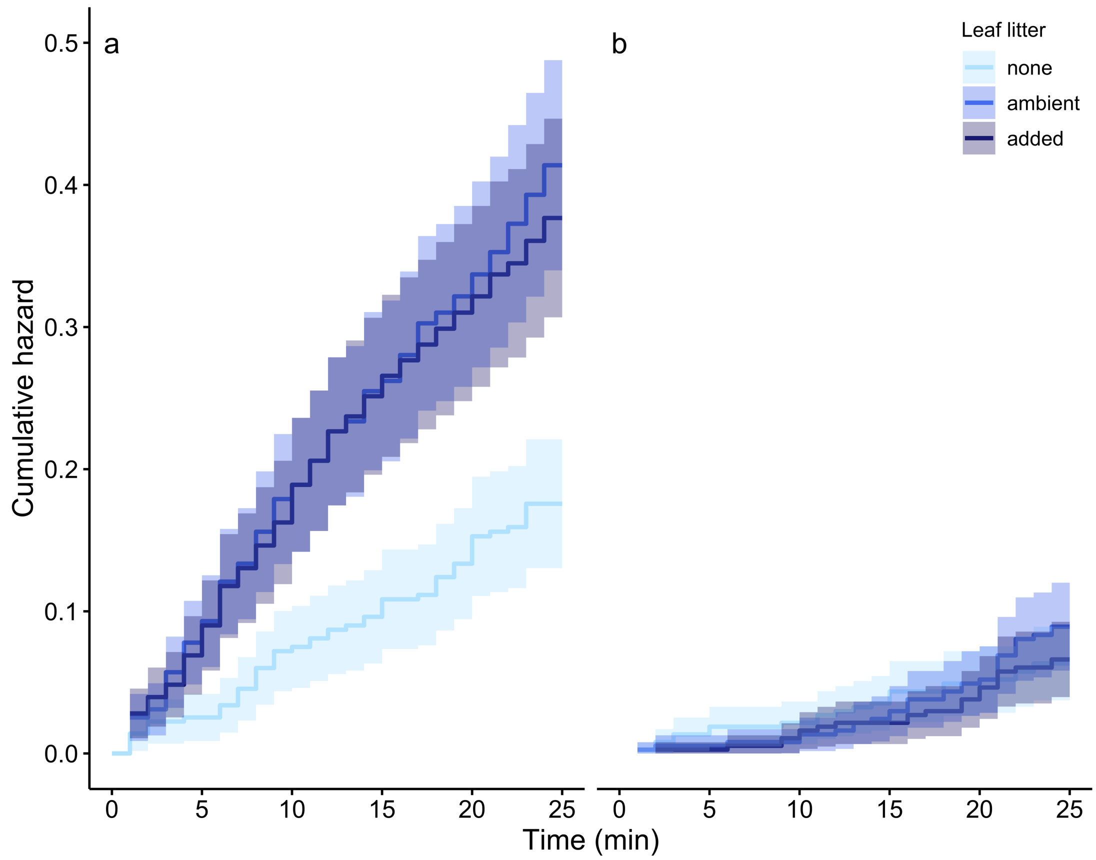
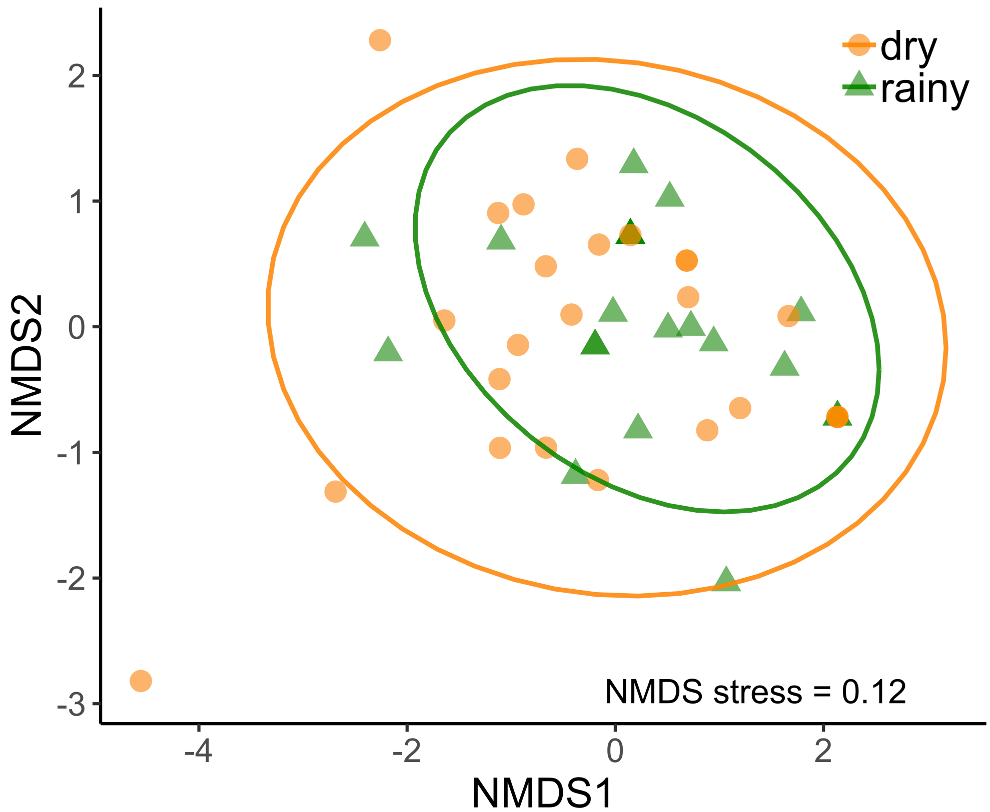


Figure 1.3. Non-metric multidimensional scaling plots comparing species composition of ant visitors recorded at each site by season. Orange circles represent species composition of visitors at sites during the dry season and green triangles represent species composition of visitors at sites during the rainy season with 95% ellipses.



CHAPTER 2: Rainfall reduction alters ecological communities and limits ecosystem function in coffee agroecosystems

Abstract

Climate change is predicted to cause precipitation declines across many tropical regions. Although wet tropical regions experience abundant annual rainfall, precipitation is consistently identified as central to species distributions in the tropics. Tropical agricultural systems are also expected to be affected by declines in precipitation, with more pronounced effects associated with greater agricultural intensity. Coffee is a grown throughout the tropics, but is highly sensitive to seasonal precipitation and is expected to be strongly affected by climate change. Coffee is also commonly grown alongside shade trees which are an indicator of management intensity. We used rainfall exclusion plots set in a high and low-shade coffee farm to test the responses of ecological communities and ecosystem functions to reduced rainfall in low- and high shade coffee. Overall, we found significant effects of reduced rainfall on plant and insect communities as well as decomposition and ant predation, but few relationships with farm shade level. Rainfall reductions negatively affected herbaceous biomass, most arthropod trophic groups, litter decomposition rates and ant predation, but positively affected arthropod predators. Low and high-shade farm differences, on the other hand, impacted only herbivore and predator abundances and ant predation. These findings suggest that for tropical regions short-term seasonal declines in rainfall may have long-term consequences that scale through ecosystems.

1. Introduction

Climate change in the tropics is expected to increase average annual temperatures and result in more extreme and variable precipitation (Dai 2013). Precipitation is a key driver of ecological patterns in the tropics (Comita and Englebrecht 2009), especially for tropical regions that exhibit strong seasonality. The effects of both precipitation and seasonality are, therefore important to understanding future climate effects on communities and ecosystem functions (Condit 1998, Feng et al. 2013). Indeed, wet tropical ecosystems may be more sensitive to rainfall declines relative to other more xeric habitats (Hawkes and Keitt 2015, Homyak et al. 2017).

In tropical agricultural systems, farm management intensification is coupled with climatic stressors and may compound issues for ecosystems, production and livelihoods (Lin et al. 2008, Lawrence and Vandercar 2014, Shaver et al. 2015). Indeed, ecosystem functions, like pest control, confer specific benefits to humans (Kremen 2005) and are critical in agroecosystems where plant productivity is a primary economic concern. Despite understanding importance of ecosystem services, there remains little understanding of plant-insect or multitrophic responses to climate change in any system (Jamieson et al. 2012), much less in managed, tropical systems (Wu et al. 2011, Homyak et al. 2017).

Coffee is traditionally an understory crop grown throughout the tropics beneath a canopy of shade trees (Moguel and Toledo 1999). The coffee plant is a long-lived perennial crop, but it is sensitive to temperature, precipitation and microclimate conditions. This climate sensitivity makes coffee especially vulnerable to the effects of climate change and is likely to cause shifts in habitats suitable for growing coffee. In Mexico and throughout Central America, coffee-growing regions are projected to experience less rainfall and an increasing number of droughts (IPCC 2014).

In this study, we manipulated rainfall across two farms (a low and high-shade farm) to assess a number of ecological responses to reductions in rainfall and farm shade management in coffee agroecosystems of southern Mexico. We examine community-level responses of plants and insects, as well as functional responses of decomposition and pest control, to determine how interactive effects of reduced rainfall and changes in management can scale through ecosystems.

1.1. Rainfall and seasonality effects on soil decomposition

Decomposition of litterfall is a vital component of nutrient cycling in tropical systems (Tiessen et al. 1994) where high rainfall over long periods can leach soil nutrients and limit primary productivity (Malhi et al. 2004, Vitousek et al. 2010). Declines in rainfall are generally expected to reduced decomposition rates. However, the relationship between rainfall, microbes and soil decomposition is not always clear. Rainfall manipulations in Mediterranean and tropical biomes found no effect of reduced soil moisture on litter decomposition rates (Nepstad et al. 2002, Yuste et al. 2010, Homyak et al. 2017). Rainfall can alter organic matter decomposition via changes to soil moisture that affect soil microarthropods and other decomposers (Lensing et al. 2005, Williams 2007, Landesman et al. 2011).

1.2. Rainfall and seasonality effects on plants and insects

Primary productivity, species distributions and diversity of plant communities are correlated with rainfall gradients. Even in tropical forests where rainfall is abundant, plant distributions and diversity are associated with annual rainfall (Gentry 1982, Wright 1992) and seasonality (Condit et al. 2013). Thus, we expect changes in rainfall patterns to affect plant growth and population dynamics (Gorton et al. 2019).

Generally, arthropod populations follow plant populations (Gentry 1982, Richards and Coley 2006, Hilt et al. 2007). Indeed, tropical insect abundance is linked with seasonal changes in rainfall and humidity, where abundance increases during the rainy season (Wheeler and Levings 1988, Wolda 1988). However, some specific taxonomic groups do not consistently correlate with tropical rainfall patterns. In some studies, tropical dung beetles, gall wasps, moths and ants have shown no relationship with rainfall and/or seasonality (Blanche 2000, Escobar and Chancón de Ulloa 2000, Intachat et al. 2000). These discrepancies in association with rainfall in the tropics may be related to differences in seasonality (*i.e.*, more distinct rainy-dry seasons) (Janzen 1973, Hilt et al. 2007) or related to the different feeding guild and or trophic level of the arthropod (Richards and Coley 2006).

1.3. Rainfall and seasonality effects on ants and ant predation

Ants in particular display inconsistent responses to tropical seasonality and rainfall. In some cases, soil moisture and seasonality are associated with greater ground ant foraging activity and abundance (Levings 1983, Kaspari 1993, Hahn and Wheeler 2002, Grimbacher et al. 2018), while other studies find limited or no effect of season on ground ant activity (De la Mora et al. 2015) and still others find negative associations of seasonal rainfall on ant nesting densities or ant abundance (Kaspari et al. 2000, Ennis and Philpott 2019). While it is not clear what may cause these differences, evidence suggests apparent differences in ant abundances may be attributed to differences in sampling scale (Kaspari et al. 2000) or ant guild (*e.g.,* subterranean, litter, wood-nesting) (Hahn and Wheeler 2002, Delsinne et al. 2013).

Tropical ants are important predators (Floren et al. 2002, Sam et al. 2015, Seifert et al. 2016). Ant nutritional requirements are thought to vary seasonally (Davidson et al. 2003), thus affecting predation activity. Indeed, various studies link tropical seasonality with differences in prey activity (Molleman et al. 2016, Tiede et al. 2017, Ennis and Philpott 2019), but there is no direct mechanism linking ant predation to rainfall or soil moisture differences. In tropical agricultural systems, ants act as natural pest control agents in tropical agricultural systems (Philpott and Armbrecht 2006, Van Mele 2008). In coffee agroecosystems ants are the primary predator of the coffee berry borer, *Hypothenemus hampei* (Coleoptera: Scolytidae) (Morris et al. 2018) -- a devastating pest that results in a direct loss of yield (Damon 2000).

1.4. Shade management and microclimate effects

Coffee is a shade tolerant crop and is often grown beneath a canopy of trees. Shaded coffee systems are common in Central America, and particularly in and Mexico, but the degree of shade maintained by growers varies considerably, ranging from very diverse high shaded systems to sparse shaded monocultures (Moguel and Toledo 1999, Jha et al. 2014). Depending on the level of shade and the management of the coffee, these agroforestry systems may mirroring the ecological conditions of natural forest systems. For example shaded farms mitigate daily air and soil temperature extremes, maintaining more constant air humidity and soil moisture (DaMatta et al. 2007, Lin 2007, Lin 2010). Changes to these microclimatic conditions (like temperature, humidity, soil moisture) can affect ecosystem functions, like decomposition rates and pest control (Ennis and Philpott 2019). Shaded coffee farms may also, however limit solar radiation to the soil and therefore can limit herbaceous cover.

1.5. Coffee production

Coffee production throughout much of the world and especially in Central America is rainfed, and therefore production is dependent on ambient rainfall (Lin et al. 2008, Jha et al. 2014). Coffee requires an abundance of rainfall growing best with ~1500 mm annual rainfall that follows a specific water regime during the annual flower and fruit development (Cannell 1985, Carr 2001, DaMatta 2004). The effect of climate change on rainfall patterns is difficult to predict and variable by region, but generally lower overall precipitation and more intense rainfall is anticipated for many regions including Central America (IPCC 2014).

1.6. Relevance of present study

Changes in rainfall patterns are predicted for Central America. Yet, relative to temperate areas, few studies have simultaneously assessed multiple ecosystem and community responses to manipulated rainfall in the tropics. We used a field experiment to examine the effects of reduced rainfall and farm shade management on herbaceous biomass, coffee growth, and arthropod community composition as well as the ecosystem functions of decomposition and borer predation. Specifically, we asked how reduced rainfall affects (1) aboveground herbaceous biomass, (2) coffee growth, (3) total arthropod abundance, (4) individual arthropod trophic levels (*e.g.,* herbivores, omnivores, parasitoids and predators), (5) decomposition rates of leaf litter and (6) ant predation rates of a coffee pest, the coffee berry borer.

Based on plant and arthropod responses to seasonality and rainfall gradients, we expect that aboveground herbaceous biomass, coffee growth, and total arthropod abundance (driven by changes in herbivores) will be lower in reduced rainfall conditions. We expect slower decomposition rates, but higher ant predation in reduced rainfall conditions due to findings from previous ant predation studies in this region (Ennis and Philpott 2019). We further expect that the high-shade farm might partially compensate or even negate effects of reduced rainfall and losses in soil moisture.

2. Materials and Methods

2.1. Study site

We chose two very large (>250 ha) adjacent organic coffee farms in the Soconusco region of Chiapas, Mexico: (1) Finca Irlanda (15º10′24″N, 92º20′10″W) at about 900 m and (2) Finca Santa Anita (15º10′06″N, 92º21′00″W) at about 800 m in elevation. We selected these farms based on perceived differences in canopy cover and to represent the range of shade management practices in the region: Finca Irlanda, the low-shade farm, had more intensive shade management (72.5% on average) and Finca Santa Anita, the high-shade farm, had less intensive shade management (86.9% on average, Table1). Otherwise, management practices are similar across the two farms. The farms border each other, are organic, very large, at high altitude and have very similar vegetation complexity.

Total annual rainfall in the region over the past 70 years averages about 6500 mm, with most of that falling between May-September. Average rainfall in July, for example, varies between 25-42 mm per day.

2.2. Rainfall exclusions

To examine the effects of reduced rainfall on multiple agroecosystem function, we attempted to limit rainfall to the extent expected in future climate forecasts. We established 20 pairs of plots, with each pair consisting of one reduced rainfall plot and one ambient rainfall plot. Ten pairs were placed in each farm, and each pair of plots (called a site) were a minimum of 30 m apart from one another. Each plot measured 4 m × 2 m, with a 0.5 m buffer on all sides creating an interior sampling area of 3 m × 1 m. Each plot was covered at 1 m height by either transparent plastic tarp (reduced rainfall) or deer mesh (ambient rainfall). Canals were dug around the outside of the upslope side of each plot to limit rainfall runoff into the plot (Fig. 1). To ensure that the exclusions effectively excluded rain, but did not change light or temperature conditions, we monitored each plot regularly for light, soil temperature, and air humidity and temperature. To determine the magnitude of the effect of limited rainfall we took soil samples and calculated the percent weight by water in plots. Plots were checked weekly or biweekly throughout the duration of the experiment to ensure the integrity of the structures, to replace or repair mesh and or transparent plastic and to remove leaf litter and other debris from the top of the shelters.

2.3. Sampling methods

2.3.1. Light, air temperature and humidity measurements

We measured light levels with a quantum light meter (Apogee Instruments Quantum Integral Sensor and Meter BQM-S, Logan UT) of photosynthetic photon flux (μmol m-2s-1) at eight points within each sampling plot – four measurements around 0.8 m above the soil surface and 0.2 m above the surface. We measured air temperature and humidity with data loggers (iButton Hygrochron, Maxim Integrated San Jose, CA) at about 0.5 m height in the center of each plot for 24 h at the time the plots were established and then again three and six months after establishment. We placed a rain guard over data loggers to prevent moisture from hitting the sensors. We measured soil surface temperature with a soil thermometer at 3 cm below the surface at the time of establishment, and three and six months after establishment.

2.3.2. Site characteristics

At each site, consisting of one pair of plots, we measured vegetation characteristics including tree density, tree species, tree height, percent canopy cover, and the number of coffee bushes within a 10 m radius of center of the site, identified as the mid-point between the two plots. We calculated average percent canopy cover at each site by averaging the canopy density measured with a concave spherical densiometer (Forestry Suppliers, Concave Model C, Jackson, MS) at the center of the site and at 10 m in each cardinal direction. For each farm there may be differences in farms that we did not capture, including use of chemical inputs,

2.3.3. Soil moisture

We randomly selected two areas to extract soil samples from each treatment and control plot at three and six months after plot establishment using a stainless steel tubular soil auger to extract surface 0-10 cm soil. After collecting the soil, we weighed and dried the soil in a drying oven and continued to dry and weigh the samples until each sample no longer lost additional weight.

2.3.4. Aboveground herbaceous biomass

To compare herbaceous biomass between the reduced rainfall and ambient conditions we randomly selected two 0.25 m × 0.25 m areas in each reduced rainfall and ambient plot and collected all above ground plant biomass during the third and sixth month of the experiment. The plant material was then identified to morphospecies, dried and weighed.

2.3.5. Coffee growth

For coffee growth comparisons we planted a coffee seedling in the center of each plot in month three of the experiment and measured its growth over the remainder of the study. Seedlings all came from the Finca Irlanda nursery and were the same variety, root stock and were grown in the same conditions prior to planting in the field. To compare effects on coffee growth, we measured the height of the coffee plant at four and six months.

2.3.6. Arthropod collection and identification

We used standard pitfall and sweep net collection methods to sample insects to test the effects of limited rainfall on arthropod communities. Nine pitfalls traps consisting of 50 mL centrifuge tubes filled with salt water were placed within each plot in a grid for 24-hr in the fourth and sixth month of the experiment. We sampled the vegetation for insects in each plot using a sweep net for 30 s intervals in the fourth and last month. For all arthropod samples, we classified individuals as adults or immatures to account for differences in feeding guild by life stage. We then identified each individual to the family level. Family level taxonomic resolution provides sufficient ecologically resolution in the study of community composition and functional diversity (Cardoso et al. 2011, Timms et al. 2013, Lamarre et al. 2016). Two other families required identification to subfamily due to the diversity of life history strategies (*e.g.*, Carabidae, Staphylinidae). Then we assigned each arthropod family to a trophic group based on its most common food source as found in the literature (Gauld and Bolton 1988, Hodkinson and Casson 1991, Lawrence et al. 1999, Marshall 2006, Lamarre et al. 2016).

We excluded the families in the order Diptera due to the lack of available resources for both identification and classification. We excluded subclasses in Acari and Collembola because although their families can span many trophic levels (Chaires-Grijalva et al. 2016, Potapov et al. 2016), their contribution to the producer arthropod food web is primarily as prey items. For example, some Acari and Collembola are important predators of other microarthropods in the decomposer food web. However, assigning them as equivalent predators to hemipteran or spider predators would not fit the purposes of our study to examine the composition of arthropod trophic levels in producer food webs.

2.3.7. Decomposition rates

To measure decomposition rates, we prepared decomposition bags using nylon mesh with 1.5-mm^2 holes and filled each one with a 5 cm × 5 cm square of dried and weighed leaf material. We collected all leaves of approximately the same maturity from branches of a single individual *Inga micheliana* shade tree – a common species used in region in coffee production. In each plot, two mesh nylon (1.5-mm^2 holes) decomposition bags were secured to the ground with nails and left for a period of four months. After collecting the bags, we gently removed attached soil, then dried and weighed the remaining leaf material to get the total proportion weight loss.

2.3.8. Borer removal experiment

To assess predation rates on the coffee berry borer, we conducted prey removal experiments each month for the duration of the experiment. On mornings between 0900h and 1100h prior to the afternoon rains, we placed borer bait cards in each plot's sampling area and recorded the number of borers remaining after 25 min as in Ennis and Philpott (2019). Each bait card consisted of five dead borers on roughly 3 cm × 3 cm piece of a dampened index card which served to both keep the borers lightly affixed to the card without using glue (and easily removed by ants) and made the card flush with the soil surface. For each plot we used nine bait cards for a total of 45 borers in each plot.

2.4. Statistical analyses

We used generalized linear mixed model and linear mixed effect models to test the effects of reduced rainfall and the low- and high-shade farms on each of the seven community and two functional responses (e.g., aboveground herbaceous biomass, coffee growth, arthropod abundance overall and within each trophic level, decomposition rate, and borer predation rate).

For herbaceous biomass and decomposition rates we used linear mixed effect models with a random effect of sample by site. For coffee growth and decomposition rates we also used a linear mixed effect model, but with only a random effect of site. Although we took multiple coffee growth measurements over the course of the experiment, the response variable is a single value that takes the difference between the end and initial height. For decomposition rates, the samples were collected at the same time so we used the average of the two samples. For overall arthropod abundance, arthropod abundance of each trophic level, and borer removal, we used generalized linear mixed models with a random effect of sample by site. Data for overall arthropod abundance and abundance within each trophic level were fit with a Poisson distribution; borer removal data was fit with a binomial distribution and logit link. We performed all analyses and made all graphics in R (R Core Team 2016).

3. Results

3.1. Farm and plot level differences

Total rainfall in this area for 2015 was approximately 3500mm, which is substantially lower than the historical average of 6500 mm for these farms. We found differences in canopy cover and tree abundance between the two farms, but tree height, tree species richness and number of coffee plants did not differ (Table 1). In comparing the plots for differences in abiotic characteristics, we found no differences in relative humidity, air temperature, light levels or soil temperature by rainfall treatment or by farm (Table 2, 3). However, we did find that the rainfall exclusion treatment did limit soil moisture by an average of 6.9% relative to the ambient rainfall plots, ranging from an 2.9% to 16.4% in average individual plot differences (averaged across samples). We also found significant differences in soil moisture by farm, with an average difference of 4.4%. In two instances, prior to collecting the second round of soil samples, the plastic covering on the rainfall exclusion treatments went missing. In those cases, we took soil samples the same day as the other plots and replaced the plastic the following day; thus, we expect these measurements are a conservative estimate of differences in soil moisture.

3.3. Plant and arthropod effects

3.3.1. Aboveground herbaceous biomass

Aboveground herbaceous biomass was significantly lower in reduced rainfall conditions ($p = 0.0003$ Fig. 2A), but differences in farm shade management did not significantly affect biomass ($p = 0.60$) and there was no significant interaction between rainfall treatment and farm shade management ($p = 0.12$).

3.3.2. Coffee growth

Coffee seedling growth did not differ with rainfall treatment ($p = 0.35$), or farm shade management ($p = 0.16$) and there was no significant interaction between rainfall treatment and farm shade management ($p = 0.71$, Fig. 2B).

3.6. Arthropod abundance and community effects

Arthropod abundance differed with rainfall treatment ($p < 0.0001$), but was not different between farm shade management ($p = 0.20$). However, there was a rainfall by farm shade management interaction ($p < 0.0001$) indicating that arthropod abundance was lower in reduced rainfall but only in the low-shade farm (Fig. 2C)

Abundance of each trophic level (*i.e.*, herbivores, omnivores, parasitoids and predators), was lower in the reduced rainfall compared with ambient plots (Fig. 2D). We found significantly fewer omnivores ($p = 0.037$) and parasitoids ($p = 0.039$) in reduced rainfall treatments and significant interactions of reduced rainfall and farm shade with herbivores ($p < 0.0001$) and predators ($p < 0.0001$). For herbivores, there was an interaction between rainfall treatment and farm shade management such that the decline in herbivorous arthropods occurred only in reduced rainfall in the low-shade farm. There was also a significant interaction between the factors for predator abundance, however in this case, the predators increased in reduced rainfall, but only in the low-shade farm.

3.4. Ecosystem function effects

3.4.1. Decomposition rates

Reduced rainfall significantly slowed decomposition rates ($p = 0.0001$, Fig. 2E). But decomposition rates did not differ with farm shade management ($p = 0.34$) and there was no significant interaction between farm shade management and rainfall reduction ($p = 0.43$).

3.4.2. Borer removal experiment

Reduced rainfall treatments had significantly lower borer removal rates ($p < 0.0001$) and removal in the high-shade farm was lower than in the low-shade farm ($p = 0.01$), but there was no significant interaction between rainfall treatment and farm shade management ($p = 0.82$, Fig. 2F)

4. Discussion

In this study, we tested the effects of reducing rainfall in a tropical coffee agroforest on plant growth, insect abundance and community composition, and two ecosystem functions as a proxy for understanding the predicted changes in annual rainfall expected in the study region with climate change impacts. We found significant effects of rainfall reduction, despite relatively high total rainfall in both reduced rainfall and ambient conditions, with important implications for conservation, soil fertility and pest control. Although our exclusions only reduced rainfall across a very small area, several characteristics of the plant and insect community, as well as decomposition and predation were all significantly affected, indicating that patchy changes in rainfall expected with climate change may scale to affect the coffee agroecosystem.

4.1. Effects on plant and arthropod communities

4.1.1. Plant responses

We found less herbaceous biomass in response to rainfall limitation. Declines in primary productivity from lower soil moisture content are not particularly surprising, as water is a physiological requirement for plant production. On the other hand, to find differences in biomass when total rainfall in this region is equivalent to that of a tropical rainforest ecosystem is surprising. That is, our rainfall exclusion treatment of, on average, only 7% moisture limitation was sufficient to cause changes in plant production in a region where water may not generally be considered a limiting factor for plant growth. In contrast to aboveground herbaceous biomass, coffee seedlings were not affected by differences in soil moisture. This is somewhat surprising as vegetative coffee growth tends to follow seasonal rainfall distributions (Maestri and Barros 1977), with water availability as the key component to stimulate growth following reduced growth in the dry season (DaMatta et al. 2007). The lack of a significant effect on coffee growth may be attributed to the timing of planting and the differences in growth rates between annual and perennial plants. The coffee plants were not planted when the plots were first established, leaving only four months of experimental measurements. Also, herbaceous plants grow more quickly than perennial coffee plants and are therefore likely to respond in short time scale relative to perennial plants (Garnier 1992). Similarly, perennial plants like coffee may be less susceptible to water limitation than short-lived annual herbaceous plants.

4.1.2. Arthropod community responses

Overall, rainfall limitation negatively affected arthropod abundance. Specifically, total arthropod abundance was lower in the reduced rainfall treatment. Arthropod food webs are corollaries of many food webs that are generally dominated by herbivorous primary consumers (Polis 1991). Given the decline in herbaceous material under rainfall limited conditions and dominance by herbivores, we might expect a decline in arthropods.

Although we found that total arthropod abundance (all trophic levels combined) declined in reduced rainfall treatments, this was not true for each individual trophic level. We found that herbivores, omnivore and parasitoid arthropods declined in reduced rainfall conditions, but arthropod predator populations, like spiders and assassin bugs, increased. Arthropod predators can be less responsive to changes in tropical seasonality relative to herbivore populations and lag in response to changes in herbivore populations (Richards and Coley 2006). While differences in mobility are sometimes cited as drivers of population differences between taxonomic groups (Gonthier et al. 2014), differences in mobility are unlikely to be a factor in these results. Both herbivore and predator in this study were made up of more or less equivalently mobile species. Most herbivorous species were hemipteran hoppers and orthopterans (*e.g.*, katydids, crickets, grasshoppers) with very few lepidopteran larvae (*e.g.,* caterpillars). Likewise, most of the predator arthropods were spiders and hemipteran assassin bugs – all mobile species. That herbivore populations followed the availability of local plant production also suggests that herbivores were not limited by mobility.

4.2. Ecosystem function responses

4.2.1. Decomposition

We found a ~10% decline in decomposition rates under rainfall limitation conditions. Decomposition is, in part, dependent on humidity (Krishna and Mohan 2017), so to find lower rates of decomposition under rainfall limitation is not surprising. Lower soil moisture can limit microbial biomass which is a strong predictor for organic matter decomposition (Jiang et al. 2013). Also, moisture reduction may reduce contact of soil substrate with soil microbes and their extra-cellular enzymes (Jassal et al. 2008).

Changes in decomposition rates affect primary productivity and can scale-up through the ecosystem. Indeed, nutrients accumulated in herbaceous plant material – which are important for primary consumers – reflect local soil nutrient availability (Furch and Junk 1997) that is in turn limited by local decomposition rates. On longer time scales, arthropods and other consumers may respond to differences in herbaceous nutritional content as a result of soil nutrients and decomposition differences. However, it is unlikely that the changes in arthropod abundances we found reflect this process given the short time scale of this project.

4.2.2. Borer removal and pest control implications

We expected dryer soil conditions to result in higher borer removal rates as seasonal dryness during the winter is associated with higher prey removal (Ennis and Philpott 2019), but instead, ants removed fewer borers in reduced rainfall conditions.

While studies of ant predatory activity demonstrate variability by seasonality in the tropics, the studies are almost exclusively of ants foraging in understory foliage or trees (but see De la Mora et al. 2015) and the findings are inconsistent. Several studies have found higher predatory activity of ants in understory foliage in the rainy season (Armbrecht and Gallego 2007, Molleman et al. 2016) and in some cases, irrespective of ant abundance (Tiede et al. 2017). Other studies have found no differences in ant predatory activity in understory plants by season (Richards and Coley 2006, De la Mora et al. 2015).

Our results could support findings of higher ant predatory activity in wetter conditions, but this contradicts previous findings of greater predation in the dry season found using identical methods and the same ground-foraging ant community (Ennis and Philpott 2019). We found that omnivores (made up nearly exclusively by ants) were less abundant in the dryer plots, so this reduction in predation activity may be a result of shifting foraging patterns or nest site preference for higher soil moisture conditions. Ants are very mobile and adapt easily to changing conditions. A typical ant foraging range is about 2 m^2 (Jacquemin et al. 2012, Ennis and Philpott 2017), yet ants can also respond to variable conditions by moving their colonies' nests to more favorable conditions (Perfecto and Vandermeer 1996). Ants may have moved their nests and/or altered foraging patterns to those areas outside the boundaries of the reduced rainfall plots in response to either soil moisture loss or lack of available herbaceous plant/insect resources. Therefore, these results are likely less indicative of seasonal shift in foraging but rather a result of ants shifting their nest sites to preferred microclimate conditions (Perfecto and Vandermeer 1996, Philpott et al. 2010) or following the populations of herbaceous plants and herbivorous insects found in ambient rainfall conditions.

4.3. Shade management

Shaded coffee systems generally moderate microclimates by mitigating moisture loss in the air and soil (Lin 2008). Therefore, we anticipated a potential interactive effect between the high shade farm and rainfall conditions such that the effects of reduced rainfall conditions in the low-shade farm would be rescued in the high shade farm, essentially resulting in similar effects as higher rainfall. Put another way, we expected there a smaller effect, or lack of an effect, in reduced in the high-shade relative to the low-shade farm. However, we found very few significant associations with differences in farm shade level. There was no effect of farm shade management in herbaceous plant biomass, coffee growth, or decomposition. The lack of a relationship with farm shade level suggests that (1) rainfall is more limiting in these areas relative to tree cover and/or (2) the average difference between high and low shade canopy cover (about 14.4%) is not large enough to detect an effect.

An exception to the lack of an effect with farm shade level was found in arthropod abundances and ant pest predation. Interestingly, these findings are consistent with other studies in similar systems that have found associations of arthropod abundance and ant predation with shade (Philpott et al. 2008). For arthropods, herbivore and predator communities were associated with differences in farm shade level. We found that in the high-shade farm, the reduced rainfall did not have an effect on total herbivore abundance. However, reduced rainfall had a strong negative effect on herbivores in the low-shade farm. Similarly, predator abundance did not vary with rainfall in the high-shade farm, but was higher in reduced rainfall plots in low-shade farm. Arthropod abundances associations are found in other studies in similar systems (Philpott et al. 2008).

We also found that higher ant predation of borers in low shade coffee. Differences in coffee shade can affect ground ant community composition, ground ant activity (Nestel and Dickschen 1990, Armbrecht et al. 2005, Armbrecht and Gallego 2007). However, studies of ant predation either find no effects of shade (De la Mora et al. 2015) or find lower predation of the borer in low shade coffee (Armbrecht and Gallego 2007). This discrepancy then in shade effects on ant predation may be due to lack of abundant insect prey found in lower shade coffee (Philpott et al. 2008), or may be due to differences in the lack of differences between high and low shade treatment classifications.

While we are confident that the primary distinction between farms is caused by differences in shade management, it is possible that these interactions effects between shade management and rainfall could be related to differences in farm management characteristics that we did not measure. For example, certain group of organisms may more susceptible to (organic) pesticides, or herbivores may be affected by fertilizers applied via changes to microbial composition or nutrient composition in plants.

5. Conclusions

Our study finds that small changes in rainfall can have significant effects on tropical agricultural ecosystems and ecological communities. Here, we provide evidence that tropical systems, and especially tropical agricultural systems, are very sensitive to differences in precipitation (Wright 1992, Jiang et al. 2013, Seddon et al. 2016). Through our test of reduced rainfall effects on predator-pest interactions and general arthropod abundances, this study further has very narrow and broad-reaching implications for ecosystems. For example, we found very specific effects of reduced rainfall on predator-pest interactions between an ant guild and one pest species – an interaction that is particularly relevant to coffee production. And, we also found sweeping effects of reduced rainfall across trophic levels from herbaceous plants to arthropod predators. Surprisingly, we did not find strong associations of these ecosystem and community responses to differences in the low and high-shade farms, which may be due to the relatively high (72%) canopy cover of the "low-shade" farm. Despite this, and with the exception of ant predation rates, the high-shade farm sites had consistently greater functioning and arthropod abundances relative to the low-shade farm, even though few of these associations were significant. Also, the differences in magnitude of the difference between rainfall treatments in the high- and low-shade also appear relatively consistent, providing further evidence of sensitivity to rainfall despite the higher shade and greater soil moisture found in the high-shade farm. The sensitivity of these systems to differences in rainfall suggest that the predicted precipitation declines for many tropical regions may have notable consequences for wet tropical ecosystems generally, and tropical agroecosystems, specifically.

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Table 2.1. Average vegetation measurements from each site by farm and statistics from comparative *t*-tests. Measurements were taken within a 20-m diameter circle from a center point located equidistant from each paired plot. Each site included one ambient and exclusion plot.

	low shade farm	**SE**	**high shade farm**	**SE**	***t***	***p*-value**
Canopy cover (%)	72.45	5.3	86.89	2.5	**-2.47**	**0.03**
No. of shade trees	5.90	0.4	9.20	1.1	**-2.85**	**0.01**
Mean tree height (m)	9.95	0.8	11.69	0.9	-1.50	0.15
Mean tree richness	4.30	0.4	5.50	0.7	-1.46	0.17
No. of coffee plants	86.50	13.8	79.50	6.8	0.45	0.66

Table 2.2. Average abiotic plot measurements by rainfall treatment across both farms and statistics from comparative *t*-tests. Measurements were taken within the sampling area of each plot.

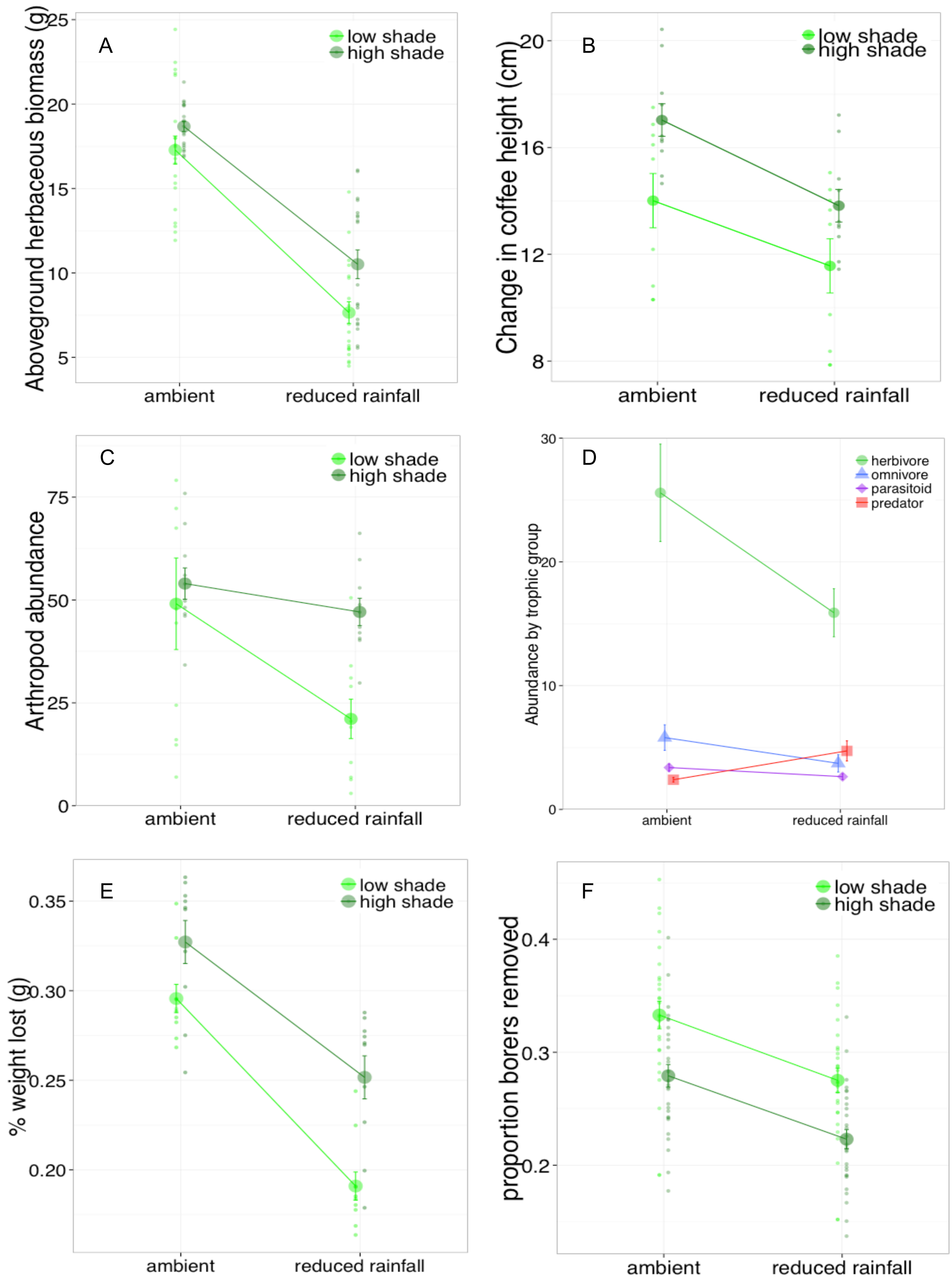
	ambient	**SE**	**rainfall excluded**	**SE**	***t***	***p*-value**
Relative humidity (%)	95.05	0.32	95.10	0.91	-0.05	0.96
Temperature (ºC)	21.05	0.13	21.36	0.22	-1.24	0.30
Light (PAR)	99.61	12.41	108.83	14.68	-0.48	0.63
Soil temperature (ºC)	22.24	0.13	22.20	0.10	0.24	0.81
Soil water (%)	37.65	0.70	30.06	0.76	**7.33**	**<0.0001**

Table 2.3. Average abiotic plot measurements by high and low shade farm across both rainfall treatment and statistics from comparative *t*-tests. Measurements were taken within the sampling area of each plot.

	low shade farm	**SE**	**high shade farm**	**SE**	***t***	***p*-value**
Relative humidity (%)	95.08	0.43	95.57	0.58	-0.68	0.51
Temperature (ºC)	21.20	0.67	21.39	0.07	-1.27	0.24
Light (PAR)	116.47	10.20	91.98	15.86	1.30	0.21
Soil temperature (ºC)	22.17	0.15	22.28	0.06	-0.63	0.54
Soil water (%)	31.67	0.98	36.04	0.78	**-3.48**	**0.0008**

Figure 2.1. Photos of rainfall exclusion and ambient controls. (A) Rainfall exclusion treatment with plastic, (B) small canal dug outside of plots to divert water from running into plots, (C) mesh covering for ambient control plots, (D) and (E) show two sites (each with a pair of plots) with both exclusion treatment and ambient control plots.

Figure 2.2. Responses to ambient and rainfall exclusion treatments ('reduced rainfall') for (A) aboveground biomass, (B) coffee growth, (C) arthropod abundance, (D) and arthropod feed group abundance, (E) decomposition and (F) borer removal rates. In panels A-D and F light green represents the low shade farm (higher management intensity) and dark green represents the high shade (lower management intensity). For (D), green circles are herbivores, blue triangles are omnivores, purple diamonds are parasitoids and red squares are predators.


A
low shade
high shade
Aboveground herbaceous biomass (g)
25
20
15
10
5
ambient
reduced rainfall
B
low shade
high shade
Change in coffee height (cm)
20
16
12
8
ambient
reduced rainfall
C
low shade
high shade
Arthropod abundance
75
50
25
0
ambient
reduced rainfall
D
herbivore
omnivore
parasitoid
predator
Abundance by trophic group
30
20
10
0
ambient
reduced rainfall
E
low shade
high shade
% weight lost (g)
0.35
0.30
0.25
0.20
ambient
reduced rainfall
F
low shade
high shade
proportion borers removed
0.4
0.3
0.2
ambient
reduced rainfall

CHAPTER 3: A changing climate for coffee: Yield declines and producer responses in Mexico

Abstract

Coffee's climate sensitivity contributes to extreme production and price fluctuations. However, as coffee is a perennial crop, producers have difficulty responding to short-term market shifts. Combining historical climate, production and price data from all coffee-growing municipalities in Mexico, we examined trends of climate and coffee production and then characterized and quantified coffee producer's responses to changing conditions of climate and price. we collected and collated production, price, climate and topographic data from Mexican and U.S. governmental agencies and non-governmental organizations. Using a spatially-explicit approach we found that coffee-specific climate variables contributed to a 60% decline in Mexican coffee production since its peak in the 1989, and that farmers' management responses to soaring temperatures, variable rainfall and price volatility are generally limited to improving yields via management efforts and altering the amount of crop they harvest.

1. Introduction

Coffee is an economically important global commodity, with more than 10 million metric tons grown annually (ICO 2019) across more than tropical 80 countries (Vega 2006). Traditionally grown as an understory crop, coffee provides livelihoods to more than 125 million people (Osorio 2002) most of whom are smallholder farmers dependent on the export of coffee.

Climate change is expected to have widespread impacts on the global coffee supply and coffee producers (Bunn et al. 2015). The coffee plant itself is a long-lived perennial crop, but it is sensitive to temperature, precipitation and microclimate conditions. This climate sensitivity makes coffee especially vulnerable to the effects of climate change and is likely to cause shifts in habitats suitable for growing coffee. Shifts to productive regions will affect all aspects of the coffee supply-chain, but may have strongest impacts on farmers who generally have no alternative to growing coffee and few resources, constraining their adaptive capacity. Given widespread production across many tropical landscapes and dependence of so many farmers and farmworkers on coffee production, farmers' responses to production changes are likely to have massive implications for food and health security, migration and land use change.

Many studies of climate change or weather effects (*e.g.*, El Niño, hurricanes) on coffee employ one of two broad approaches. The first uses forecast models to predict the loss of coffee based on bioclimatic variables at relatively low spatial resolution. These have been helpful to identify those regions most vulnerable to climate change and the scale of threat to coffee production. However, these studies are limited in scope, addressing one or two regional coffee growing areas. These forecast models often lack the precision in spatial resolution that is now more readily available and use models with standardized climate variables rather than climate variables specifically tailored for the study system. For example, WorldClim bioclimatic variables (*e.g.* mean temperature of wettest quarter, mean diurnal range) were developed to be broadly applied to many organismal or ecological systems and are widely used in coffee studies, but may or may not be relevant to coffee production.

Another set of studies has mostly examined producer responses by using interviews and surveys to study farmer responses to dramatic price declines (*e.g.,* Eakin et al. 2006), climate change (*e.g.,* Frank et al. 2011, Harvey et al. 2018) or extreme weather (*e.g.,* Tucker et al. 2010). These studies provided in-depth insight into the complex effects of cultural identities, economics and climate/weather conditions that affect farmers and their responses to stressors. And yet, qualitative studies are often limited in breadth due to time and cost constraints, and may complement a more quantitative approach to examining farmer responses.

Coffee farmers have already observed and experienced issues related to rising temperatures and increasingly variable rainfall (Harvey et al. 2018). And there is now enough available quantitative data to examine initial impacts of climate change and other critical economic variables on coffee production. In this study we couple long-term, spatially referenced coffee production and management data with high resolution climate data to provide a clearer understanding of the various impacts of climate and price on production and how farmers respond. This study provides two unique contributions: (1) organism-specific climate variables and (2) quantified producer responses based on management data.

1.1. Climate change effects on global production of coffee

Globally traded coffee consists of two distinct species each with its own characteristics and growing requirements. Robusta coffee (*Coffea canephora*) is produced more commonly in countries of South East Asia (ICO 2019). Robusta coffee can tolerate slightly higher temperatures, but does not produce high quality beans. Higher quality Arabica coffee (*Coffea arabica*) is more commonly grown in Central and South America and East Africa and makes up more than 70% of total commercial production (Ubilava 2012). Although of higher quality, Arabica coffee is more susceptible to temperature variability and is generally grown at higher elevations to avoid extreme high temperatures (Davis et al. 2012).

Several coffee studies have focused on habitat suitability for future coffee production. Indigenous Arabica coffee – the coffee that provides the genetic diversity of Arabica – is facing a nearly 100% loss of bioclimatically suitable habitat in the Ethiopian highlands by 2080 (Davis et al. 2012). Forecasts of commercial coffee in Central America suggest reductions of 30-70% in suitable coffee growing land by 2050 (Laderach et al. 2011). Worldwide estimates suggest a loss of 50% in suitable coffee-growing land by 2050 across all climate emission scenarios (Bunn et al. 2015). Additionally concerning is that most cultivated varieties of coffee comprise a very narrow range of genetic variation (Anthony et al. 2001) relative to indigenous coffee. This reduced diversity of commercial coffee combined with the predominantly self-fertilizing and a long-lived nature of coffee, makes it likely to adapt slowly to climate shifts.

These forecasts are not overly conservative because coffee is particularly sensitive to weather conditions and thus vulnerable to the threats of climate change. This sensitivity is derived from direct impacts on the plant's physiology as well as indirect impacts limiting suitable farming land, and/or increasing pest populations. Coffee (especially Arabica coffee) has specific water requirements to induce flowers and produce fruits. Floral bud initiation begins during a period of water stress, but flowers open only after initial seasonal rains. As a result, continuous rainfall without at least a short respite of water stress can lead to scattered harvests and low yields (Cannell 1985). At the same time, however, freely available water is required during the period of rapid fruit expansion to ensure the quality of the beans (Lin et al. 2008). And, at any point during the growing season, prolonged droughts and water stress will cause coffee plants to shed their leaves, making them unable to produce flowers or fruits.

Temperature also plays an important role in coffee growth. Arabica coffee is more susceptible than Robusta coffee to extreme temperatures. Specifically, *C. arabica* photosynthesis and growth rates are impeded at daily temperatures below 12˚C and above 24˚C, leaving only a narrow 12˚C window of optimal growth (Nunes et al. 1968). Exposure to temperatures higher than 30˚C for extended periods results in accelerated leaf loss and declines in plant health (Drinnan and Menzel 1995) and at temperatures above 34˚C photosynthetic production stops altogether (Nunes et al. 1968). Likewise, exposure to low temperatures and frost are extremely damaging to coffee. Indeed, cold surges in Brazil during 1994 and 1995 caused 50% declines in production and resulted in dramatic increases in world coffee prices (Marengo et al. 1997, Maizels et al. 1997).

Problems resulting from direct, physiological effects on coffee from climate change will be exacerbated by indirect effects of climate impacts on coffee pests. Several coffee pests are predicted to experience population growth or expansion in response to projected climate scenarios in some coffee growing regions. At least two studies thus far have examined how large-scale changes to temperature and precipitation pattern may impact the distribution and abundance of coffee pests (Ghini et al. 2008). The coffee nematode (*Meloidogyne incognita*) and the coffee leaf miner (*Leucoptera coffeella*) are expected to benefit from to climate change impacts in Brazil. Coffee nematode damage leads to increased root disease characterized by necrosis of coffee tissue and reduced absorption of water and nutrients leading to yield loss and in some cases, plant death (Ghini et al. 2008). The coffee leaf miner causes severe leaf tissue damage that can result in yield loss. Both coffee nematodes and the coffee leaf miner are predicted to increase in infestation and increase the number of generations per year (Ghini et al. 2008). Likewise, climate projections indicate expanded population of the coffee berry borer (*Hypothenemus hampei*). The coffee berry borer is considered to be the most widely distributed and economically damaging coffee pest because the females bore directly into the coffee fruits, rendering them unmarketable (Damon et al. 2000). The climate models of the borer revealed similar results to that of the nematode and leaf miner, but in this case, the authors projected an annual doubling of borer generations as well as upslope migration (Jaramillo et al. 2011). Studies of coffee diseases highlight the importance of temperature and rainfall as factors in predicting incidence and severity of disease (Yáñez-López et al. 2012). More recent studies have emphasized the potential impact of climate change on the coffee leaf rust fungus (*Hemileia vastatrix*) (Avelino et al. 2015, McCook and Vandermeer 2015, Bebber et al. 2016, Liebig et al. 2019).

The sensitivity of coffee to even small changes in climate combined with the indirect effects of pests and disease indicate why coffee is not expected to fare well in under future climatic scenarios where both temperatures are expected to rise and rainfall is expected to decrease and/or become more variable. Yet, future production of coffee is not singularly dependent on climate and weather conditions, because effects from larger global markets, policies and producer behaviors are important consideration in future coffee production.

1.2. Producer responses to changing conditions

Farmers are accustomed to variability, but smallholder farmers (≤10ha) are especially vulnerable to production and market volatility as their production is often dependent on rainfed production systems and they have fewer resources and/or lack access to resources (O'Brien and Leichenko 2000; Leichenko and O'Brien 2002). Farmers responses are varied and can include changes in crop management, planting area, crop variety or species and labor costs; but it can also include migration (Eakin et al. 2006, Tucker et al. 2010). Crop management responses encompass changes that focus on increased intensification in one extreme or conservation and agroecological practices on the other. For example, increases in agrochemical and fertilizer use, crop density, shade tree plantings or the maintenance/pruning of crops may be responses to volatile market, climate and production. The type of response from the farmer will depend on their perceptions of risk as well as the type of crop (*e.g.*, perennial, annual), feasibility and financial restrictions farmers face.

Coffee producers are, on average, smallholder farmers and consistently face production losses due to extreme weather or seasonal abnormalities in temperature and precipitation. Surveys and interviews of coffee producers suggest that farmers have observed climate change and its impacts on production but their management responses are mixed and range from adopting no new strategies to expensive long-term changes such as planting alternative crops, increasing/decreasing planted area and tree planting (Harvey et al. 2018). In Mexico, coffee producers report noticing climate change impacts on coffee production – specifically from increased moisture – but also expressed unwillingness to adjust new practices intended to mitigate production impacts from climate (Frank et al. 2011). In contrast, coffee producers in Guatemala, Honduras and Costa Rica said they had adjusted management practices (most commonly planting trees and increasing chemical use) due to experiencing climate impacts (Harvey et al. 2018).

Coffee prices are yet another challenge faced by coffee producers. Volatility of coffee prices is likely to be compounded by climate change as coffee price volatility is often a result of weather-related shocks (Mehta and Chavas 2008). And, prior to the most recent studies, unpredictability in coffee price was identified as the primary concern of small coffee producers over effects of weather, pests and disease, illness and unemployment (Tucker et al. 2010). Producer response to price volatility is difficult to isolate from their response to overall price declines or increases of coffee yields – in other words the difference between long-term variation in price versus short-term price shocks. However, the perennial nature of coffee farming suggests that even though a producer may make changes to their management (*e.g.* increased fertilization, pruning or planting), planting or harvesting area plan after a particular change in price or set of events, decisions are most likely informed by the past volatility of the market. Most research on coffee producer responses to prices studied the impact of low coffee prices of producer decisions in the aftermath of the precipitous decline in global prices from 1999-2003 known as the coffee crisis. These studies found low and variable coffee prices can drive producers to change the total planted area, plant alternative crops, switch to higher value organic production or migrate to the US (Lewis 2005, Eakin et al. 2006, Tucker et al. 2010).

1.3. Relevance of present study

Our study seeks to understand the impacts of climate and price on production and producer responses using recent historical data that provide insight into how these impacts have already manifested in coffee production in Mexico. To do so, we first quantify climate effects on coffee production by state over a 27-year period. Then, we characterize producer responses to variations in price and climate (using variables known to be important for coffee development and production) over the course 15-year period by municipality. This lengthy time scale over nearly three decades of data makes this study unique in the area of climate and coffee research and provides substantial data to address our research foci.

Mexico provides an important case study for the changes to coffee production as it is the ninth largest producer of coffee world-wide and the second largest producer in Central America (ICO 2019). Mexico produces high-quality coffee as the second largest producer of organic coffee (Potts et al. 2014) where more than 95% of production is Arabica coffee (Flores 2017) and nearly 90% is shade grown (Moguel and Toledo 1999). Furthermore, coffee-growing regions of Mexico are projected to face increasing droughts and variability in rainfall in addition to rising temperatures (IPCC 2014).

This study is among the first to study and quantify producer responses to prices and climate changes across a large scale of a significant coffee producing country over a relatively long time period of production. Identifying these responses is important to creating policy that aids in addressing specific adaptation needs (Harvey et al. 2018). Ultimately, the results of these realized impacts might better address production and livelihood concerns.

2. Materials and methods

2.1. Overview

We performed two separate analyses: (1) an examination of how yields have changed across Mexico, aggregated by state, from 1980-2017 and (2) an evaluation of coffee producer responses to changing climate using biologically relevant coffee climate metrics and economic (*i.e.* price and quality) conditions across Mexico, by municipality, from 2003-2017.

2.2. Analysis of change in yields and climate, 1980-2017

To examine the change in yields by state over time, we use annual coffee yields by state for the years 1980-2017 (SIAP 2017) and fit a linear mixed effect model with a random effect of state to examine the change in yields over time by state. We used state aggregated data because data by smaller production units (i.e. municipalities) were not available prior to 2003. The use of state aggregated production data enables us to describe trends in coffee production over a longer, 27-year period. We used linear mixed effects models to evaluate the relationship between yields over time and temperature over time with year as the fixed effect and state as the random effect.

2.3. Production and climate metrics and extraction to areas of production

We used annual coffee production, yield and price data by municipality for the years 2003-2017 and joined this dataset with a spatially referenced municipality map of Mexico (INEGI 2012). We used digital elevation models (NASA/METI/AIST/Japan Spacesystems, and U.S./Japan ASTER Science Team 2009) to isolate the regions within each coffee-producing municipality that fall between 400-1600m in elevation. This range is considered the most suitable for coffee production in Mexico under current climate conditions (Laderach et al. 2011). We then separated each 400-1600m elevation range within each municipality into three elevation groups (400-800m, 800-1200 and 1200-1600m) in order to extract more precise climate data for each municipality. Disaggregating in this way is important because climate variability and its impacts on coffee production are likely to exhibit substantial differences across the elevation range, where baseline mean annual temperatures vary from 16º to 26ºC across the 400-1600m change in elevation found in Mexican coffee-growing regions.

We obtained historical temperature and precipitation data at 1×1 km resolution from Daymet gridded monthly averages data (Thornton et al. 2016). Next, we calculated climate metrics especially important to coffee physiology, including the number of months where the average daily maximum temperature was greater than 30ºC, total annual rainfall, and the coefficient of variation in rainfall as a measure of rainfall variability (DaMatta et al. 2007) and extracted these variables for each year and elevation level within each municipality. We specifically chose these temperature variables because they are critical to coffee growth; daily temperatures that exceed 30ºC strongly impede coffee growth (DaMatta et al. 2007). Rainfall variability and total annual rainfall are used in standardized climate metrics (*e.g.,* WorldClim Bioclimatic variables) and are also likely important for coffee given it specific rainfall requirements during flower bud formation and throughout berry expansion. We then calculated a single area-weighted mean across elevation levels within each municipality for each climate variable in each year.

2.4. Calculation of economic variables

We chose to use global over local coffee prices to examine price impacts on producer responses. While the local data is available (*e.g.,* farmgate prices used in coffee quality), local data is affected by coffee quality which, in turn is affected by local weather. Therefore, we used the global coffee price from International Coffee Organization's data on monthly historical coffee prices (ICO 2019) as these data are likely to be more independent of Mexican prices. Specifically, we used the 'Colombian milds' price for our global price comparison as it is most similar in coffee taste to that of Mexican coffee's 'other milds' classification, but is likely to be more independent of Mexican prices (Calo 2005). We used the current year's global price as well as one and two year lagged global prices to examine producer responses at various time scales. We did this because management changes in response to price changes may take time to implement and therefore may not be reflected in the same year as the price fluctuation.

To estimate coffee quality, we averaged farmgate prices per metric ton by municipality and year (SIAP 2017), converted it to USD per pound and then adjusted the inflation rate to reflect that of the global price data. We used price per pound of coffee as it is a standard used in international coffee trading markets. We then took the difference between the annual global and local price as an estimate of coffee quality.

2.5. Producer response analyses

We examined three different plausible producer responses to external pressures of climate and price, including, (1) change in planted area; (2) proportion of harvested area; and (3) yield, as a proxy for management effort. Change in planted area is the proportional change in area planted in the following year. Producers may choose to plant more or less area in coffee as a direct or indirect result of changes in climate, prices or other factors affecting production. The proportion of harvested area is the total area of harvested coffee divided by the total area in coffee production. Producers may vary the proportion of harvested area due to labor costs or shortages, price fluctuations, quality or climate. Finally, we considered yield (metric tons/ha) as a producer response and proxy for management effort. Producers, for example, may increase management intensity to reduce weeds and pests, prune coffee plants, limit shade trees and/or add amendments to soil – all of which are intended to directly impact yields. We then examined how the climate and price variables affected the three identified producer responses using linear mixed effect models with a random effect of year and state by municipality to account for differences by year and within each location. We performed all analyses and made all graphics in R (R Core Team 2019).

3. Results

3.1. Coffee production, 1980-2017

Overall average annual coffee production (in metric tons) by state has significantly declined since 1980 (Fig. 1, linear mixed model, $p<0.0001$). Since its peak in 1989, total Mexican coffee production has declined by 60.7% and average yields declined by 53.2%. In contrast, total planted area of coffee has remained relatively steady; declining by only 0.2%. Chiapas, Veracruz, Puebla and Oaxaca were by far the largest coffee producing states representing 33.9, 24.7, 15.6 and

14.6% of total production from 1980-2017, respectively while the remaining states each comprised 3.7% or less of total production (Fig. 2a). Trends were similar for planted area (Fig. 2b).

3.2. Changes in temperature, 1980-2017

Average annual daily maximum and daily minimum temperatures have increased in coffee-producing municipalities of Mexico since 1980, with a precipitous increase occurring around 2010 (linear mixed model, average minimum temperature: $p<0.0001$; average maximum temperature: $p<0.0001$; Fig. 3).

3.3. Producer response: change in planted area, 2003-2017

Neither climate nor economic factors affected a producer's response to increase or decrease planted area over the 15-year period (Fig. 4a, linear mixed model, all factors: $p>0.10$). Indeed, planted area has seen very little change over the past decades relative to other responses (Fig. 5).

3.4. Producer responses: climate factors, 2003-2017

Producers did respond to climate factors by altering harvested area and to a greater extent managing yields. The number of months with daily average maximum temperature greater than 30ºC resulted in fewer hectares harvested and lower yields, which may be a biological response to the temperature, but could also be a response of producers to limit harvest if high temperatures result in scattered yields or low quality beans (Fig. 4b, 4c, linear mixed model, harvested area: $p<0.0001$; yield: $p<0.0001$). Similarly, greater variability in rainfall throughout the year (measured by monthly averages) resulted in less area harvested and lower yields (Fig. 4, linear mixed model, harvested area: $p=0.007$; yield: $p=0.01$). Higher total annual rainfall, however, resulted in increased harvested area ($p<0.0001$) and higher yields ($p<0.0001$). There was no effect of the proportion of the coffee habitat at lower elevations within a municipality on area harvested ($p=0.73$) nor yield ($p=0.23$).

3.5. Producer responses: economic factors, 2003-2017

Producer's decisions to change harvested area and management of yields varied in response to economic factors. Higher coffee quality resulted in significant increases in harvested area (Fig 4, linear mixed model, $p=0.0002$) and marginally significant increases in yield management ($p=0.05$). Responses to global prices were mixed. For harvested area, the current year's global price had no effect, while the prior year had a significant negative effect ($p<0.0001$) and the global price two years prior had a significant positive effect ($p<0.0001$). For management effort (*i.e.*, yield), the current year's and prior year's global price had no effect (current year: $p=0.44$; prior year: $p=0.18$), while the global price two years prior had a significant negative effect ($p=0.0002$). In other words, global prices in current and one year ago have no effect on management effort/yields but, global prices from two years prior are associated with lower management efforts/yields.

4. Discussion

4.1. Climate impacts on coffee production

This study reveals staggering declines in coffee production throughout Mexico during the study period and starting as early as 1989. The decline in production is mirrored by declines in yield but not by total planted area of coffee; suggesting that the documented production declines are related to declines in yield and not as a result of land taken out of coffee production.

Prior research attributes much of the early onset of yield declines to political, economic, and institutional changes (Ponte 2002, Ponte 2004, Eakin et al. 2006). Our research does not contradict these findings, but rather highlights another, likely strong, contributing factor of climate to coffee declines. Indeed, our results indicate that the climate effects on coffee are no longer a future problem, but a current problem as the climate has already negatively affected coffee yields in Mexico. While we expected a negative effect of climate on coffee, the dramatic losses in yield highlight that the sensitivity of coffee to even subtle climatic shifts may be more significant than anticipated. Optimal annual temperatures for *C. arabica* occur between a relatively narrow window of 18-21ºC (DaMatta & Ramalho 2006). But, while average annual temperatures do not appear to have changed much prior to 2000, it is possible that other climatic changes to evening temperatures, humidity, or rainfall variability contributed to these declines which can impact coffee germination, fruit set, fruit load and fruit weight among other productivity characteristics (DaMatta & Ramalho 2006).

Climate suitability mapping has consistently demonstrated the problematic future for coffee given the changing climate. However, many studies rely on standardized climate variables with results that lack strong predictive power across growing regions. The importance of different variables tends to vary considerably by locality and region (Schroth et al. 2009, Laderach et al. 2011, Bunn et al. 2015a, Bunn et al. 2015b, Chemura et al. 2015). For example, 'precipitation of the wettest month' provides the most explanatory power for reduced climate suitability in Nicaragua, but 'mean temperature of driest quarter' has the most explanatory power in Veracruz, Mexico (Laderach et al. 2011). Likewise, in global evaluations of coffee suitability, responses to standardized climate variables varied drastically depending on specified agroecological climatic zones (Bunn et al. 2015b). While these approaches are valuable, especially for large scale assessments at global scales, it would be useful for future studies to consider the use of coffee physiology-specific climate variables as these results are likely to be more consistent across climatic growing localities and regions and thus may provide predictive power in future modelling scenarios. One recent exception, are models that incorporate the effects of rising of CO_2 from climate change on coffee production that employ coffee-specific responses to elevated CO_2. Using temperature and coffee-specific responses to CO_2, DaMatta et al. (2019) find that declines in climate suitability for some regions may be lower than previously estimated.

4.2. Producer response: change in planted area

We found strong overall responses of producers in the form of the proportion of harvested area and management investment, but no response in planted area. Only a small fraction of all municipalities recorded any change in planted area over the entire study period (Fig. 5). The low response reveals that changing the amount of land in coffee may not be an easy, economically viable or even feasible response to changing climatic and economic conditions. Several things may explain why changing total planted area appears uncommon. First, from a production perspective coffee are long-lived plants (20-50 years) that are expensive to buy and plant and require 2-5 years after planting before bearing fruit – all of which make it more difficult to increase planted area in response short term changing conditions like price and weather. Second, in much of Mexico, coffee is often grown along steep montane slopes and in otherwise difficult growing conditions, making producing alternative commodity or local crops less appealing. Third, multiple government policies play a role in productive landscapes and land tenure of Mexico. Indeed, until the early 1990's the Federal Government incentivized and encouraged the intensification of farmlands to focus exclusively on coffee production. And, land redistribution efforts from the Mexican government in 1990s also limited the land area held by one family or individuals impeding the ability to acquire additional land. Finally, in several coffee producing areas there may not be additional viable land to cultivate.

4.3 Producer responses to climate variables

In harvested area and management effort, producers responded consistently to climate variables. We found that producer responses followed the expected physiological response of the coffee plants. That is, producers harvested more coffee area and increased yields/intensified management effort for higher yields in years with higher total rainfall, but harvested less and reduced management effort and lower yields in years with higher rainfall variability and with more days with high temperatures above 30ºC. Coffee requires an abundance of rainfall, usually at least

1500mm/year, yet the variability in distribution of that rainfall can also affect flower and fruit production. More than any other variable measured, we found that high maximum temperatures had the strongest negative effect on harvested area and yield. High maximum temperatures, especially those above 30ºC, reduce coffee growth, quality and yields (DaMatta & Ramalho 2006).

4.4. Producer responses to economic conditions

4.4.1. Responses to coffee quality

Producer responses (*i.e.* planted area, harvested area ratio, yield/management effort) to economic conditions of coffee production are less consistent than their responses to climate impacts – with the exception of coffee quality. In years with higher coffee quality, producers harvest more of their crop area and have higher yields. This result suggests that producers are aware of the value of their crop relative to the global market and are able to capitalize on the added value by increasing yields and harvesting more of their crop.

4.4.2. Global prices and harvested area

Responses to global coffee prices are not as straightforward as they are to coffee quality and climate. We find that producers do not change the proportion of area harvested during years with higher prices but in the year following a high price year, producers harvest less of the planted coffee area. This discrepancy in response may be because the additional cost of harvesting more area does not translate into increased profits for the producer. Global prices are not always reflected in local markets (as is indicated by our 'coffee quality' metric) and do not necessarily translate into higher prices for producers. Mexican producers may also be wary of the volatile coffee market that can leave them vulnerable to exploitative local intermediaries even during high price years (Henderson 2019). Indeed, when prices decline below the cost of production, many producers in Mexico, for example will opt to take wage labor positions rather than harvest their crop (Henderson 2019).

Yet another explanation is that the amount of harvest may be more dependent on the productivity of the coffee itself and may reflect the differences in productivity that arise from biennial bearing. Biennial bearing (*aka*. alternate bearing) is common in many fruiting trees and occurs when trees tend to produce more than average in one year and less than average in the following year. In coffee fruit production this oscillation is not well understood, but it has been attributed to a tradeoff between branch and fruit development (Bote & Jan 2016). In high production years more energy is put into developing fruits at the cost of developing new branches and in low production years more energy is put into branch growth that will support more fruit production in the subsequent year (Bernardes et al. 2012). Some evidence suggests that this cycle can be manipulated to improve quality or increase yields to take advantage of higher prices in a particular year (Bote & Jan 2016). This fruit load management could allow producers to increase fruit loads in one year but may then result reduced fruit loads in the following year.

4.4.3. Global price, management and yields

Our findings indicate that management manipulations for contemporaneous and second year yield improvements, if done, are not effective response to global price. In part, this is because the metric of yield that we use as a partial proxy for management effort, is also subject to physiological responses to climate and other environmental stressors. And, while producers may response quickly in an effort to increase yields, the effect of increased yields may occur over several successive years. That is, management efforts may be implemented immediately and in response to increased prices (*e.g.,* pruning shade trees, planting new coffee plants) but the desired effect of increased yields may not be realized for 2-15 years after the management change. By contrast, the producer response to harvest more or less of their planted coffee area is a response that producers can implement immediately and will have an effect in the same year. This may be why the variation in responses is so much lower in harvested area relative to yield changes.

Yields appear to be singularly negatively affected by higher global prices from two years ago, or lower prices now, following high prices. This suggests that increased management effort in response to higher prices in the current and previous year may result in lower years two years later. Likely this is an effect of the delay in management improvements to yields coupled with the physiological biennial bearing of coffee.

4.4. Data limitations

While our consistent results provide a level of robustness to some findings, there are several limitations to the dataset that restrict our ability to identify potential mechanisms behind the relationships. First, because data are aggregated by municipality, we were not able to include average farm size as a factor in our analysis, despite the fact that previous studies find that decision making may be influenced by farm size (Haggar et al. 2013). This data is important because the behavior and response of producers may change depending on how much land they have in production or how much funding they have to pay laborers to harvest. We also lacked data on production type (*e.g.* organic vs. conventional) or shade management. Shade trees in coffee production can maintain cooler surface air temperatures, humidity, soil water retention and may improve natural pest control services or pollination (Jha et al. 2014). The effect of shade trees on coffee production at this scale may provide some insight into the future of coffee production in mitigated long-term climate effects on production. Finally, this data set does not distinguish between Arabica (*C. arabica*) and Robusta (*C. canephora*) coffee plants. Robusta coffee produces beans that are much lower in quality than that of Arabica, however the plant is less sensitive to climate, pests and diseases and produces higher yields. About 95% of coffee produced in Mexico is Arabica (Gay et al. 2006), yet Robusta is expected to grow in popularity and may provide another way for producers to adapt to the changing climate conditions. Should Robusta begin to replace Arabica throughout Central America this may result in increased yields, but lower prices to farmers as it produces lower quality beans.

5. Conclusions

Climate change has already impacted coffee production and producer decisions in Mexico, currently the tenth largest producer of coffee in the world. In high elevation coffee-growing regions maximum temperatures are now about 30ºC – which is document here and in other studies as having a strong negative impact on the coffee plant and coffee production. At the same time, coffee prices continue to be very volatile, exacerbating the ability of producers to respond. Generally speaking, higher consumer coffee prices do not translate into higher prices for producers. However, should climate severely reduce global coffee supply, prices to coffee producers may increase. This study indicates that coffee producers cannot generally capitalize on high market prices, but still have some capacity to adapt to changing conditions that is limited to harvesting capacity and management efforts to improve yields. Yet, under more extreme weather conditions producers may not be able to increase yields or may not gain additional benefit from harvesting more land, thus limiting their capacity to adapt.

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Figure 3.1. Average annual coffee yield by state, 1980-2017.

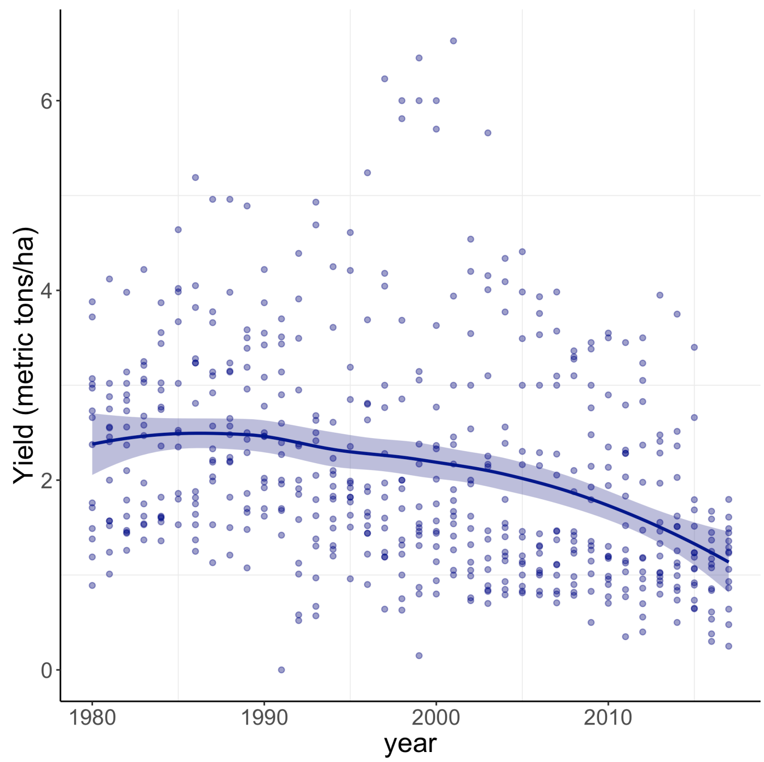


Figure 3.2. Map of (A) average annual production by municipality averaged from 2003-2017 and (B) total average area planted (ha) in coffee.

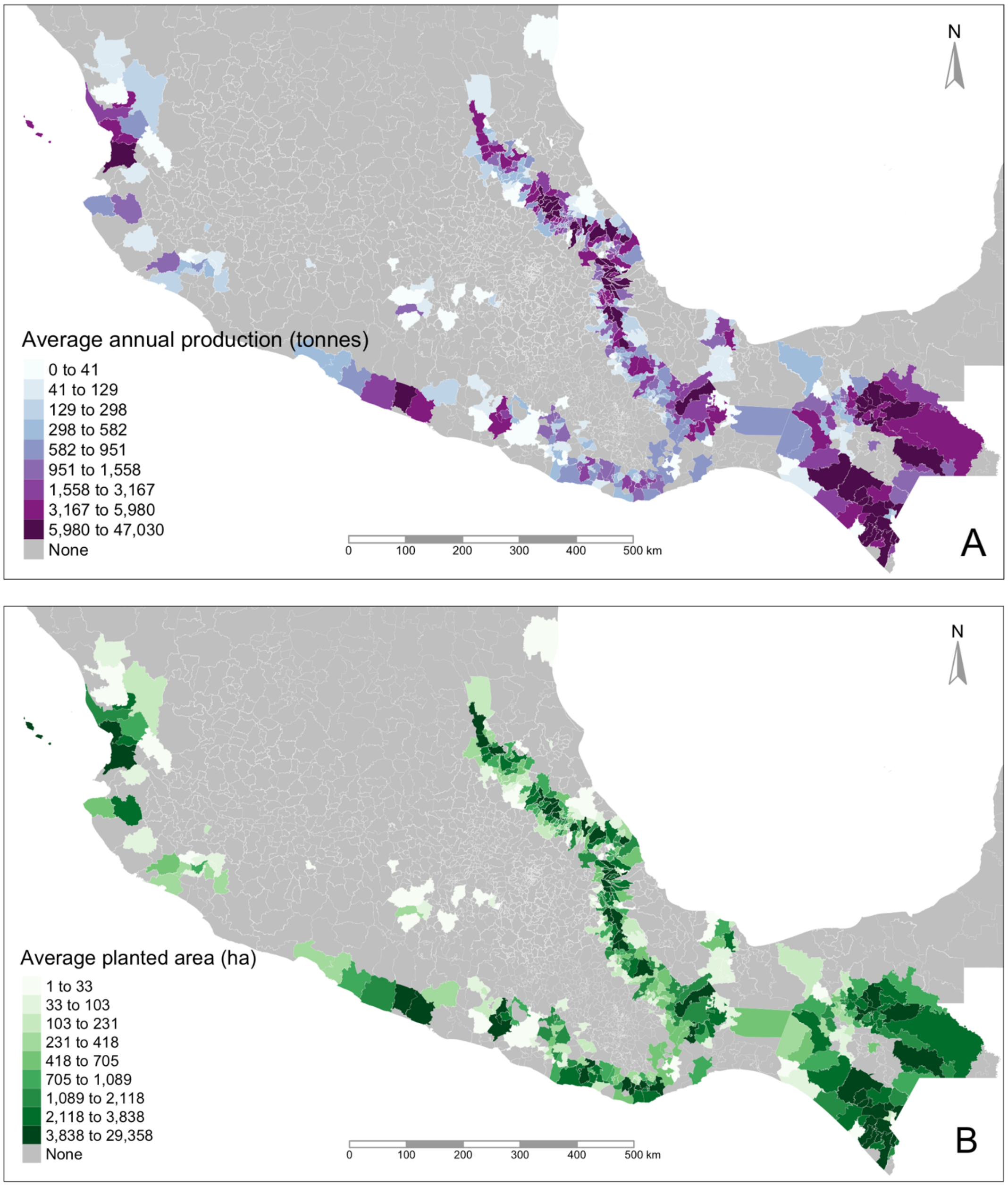


Figure 3.3. Average monthly (A) maximum and (B) minimum temperature for elevations between 400-1600m within coffee growing municipalities (weighted proportionally by elevation area within each municipality), 1980-2017. Data fit with locally-weighted scatterplot smoothing (LOESS).

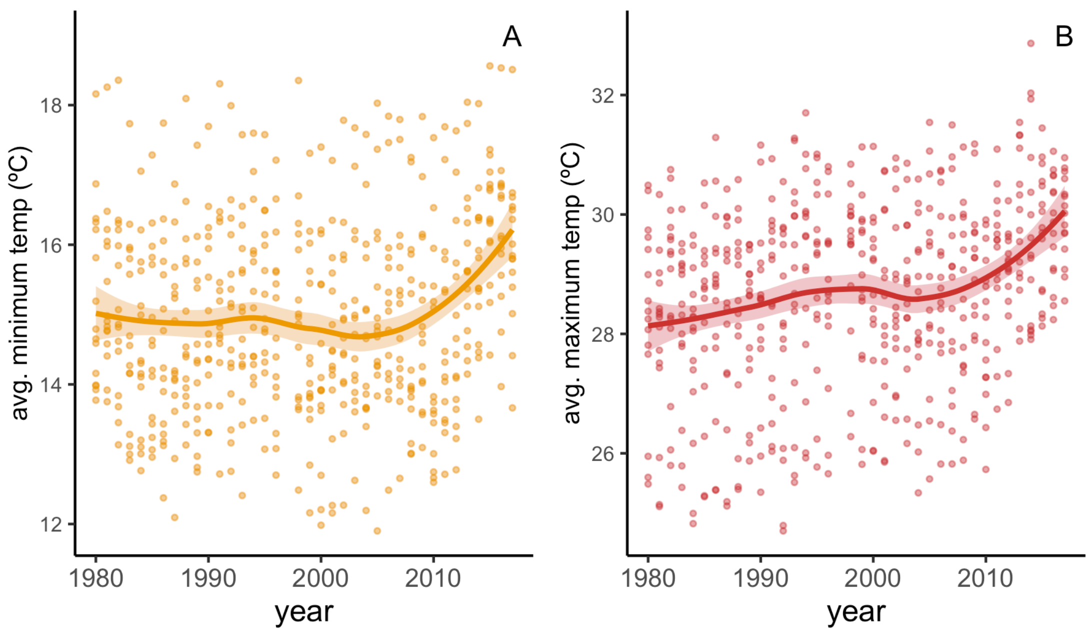


Figure 3.4. Standardized regression coefficients of coffee producer responses of (A) change in planted area (B) proportion of harvested area and (C) yield to changes in climate and price.

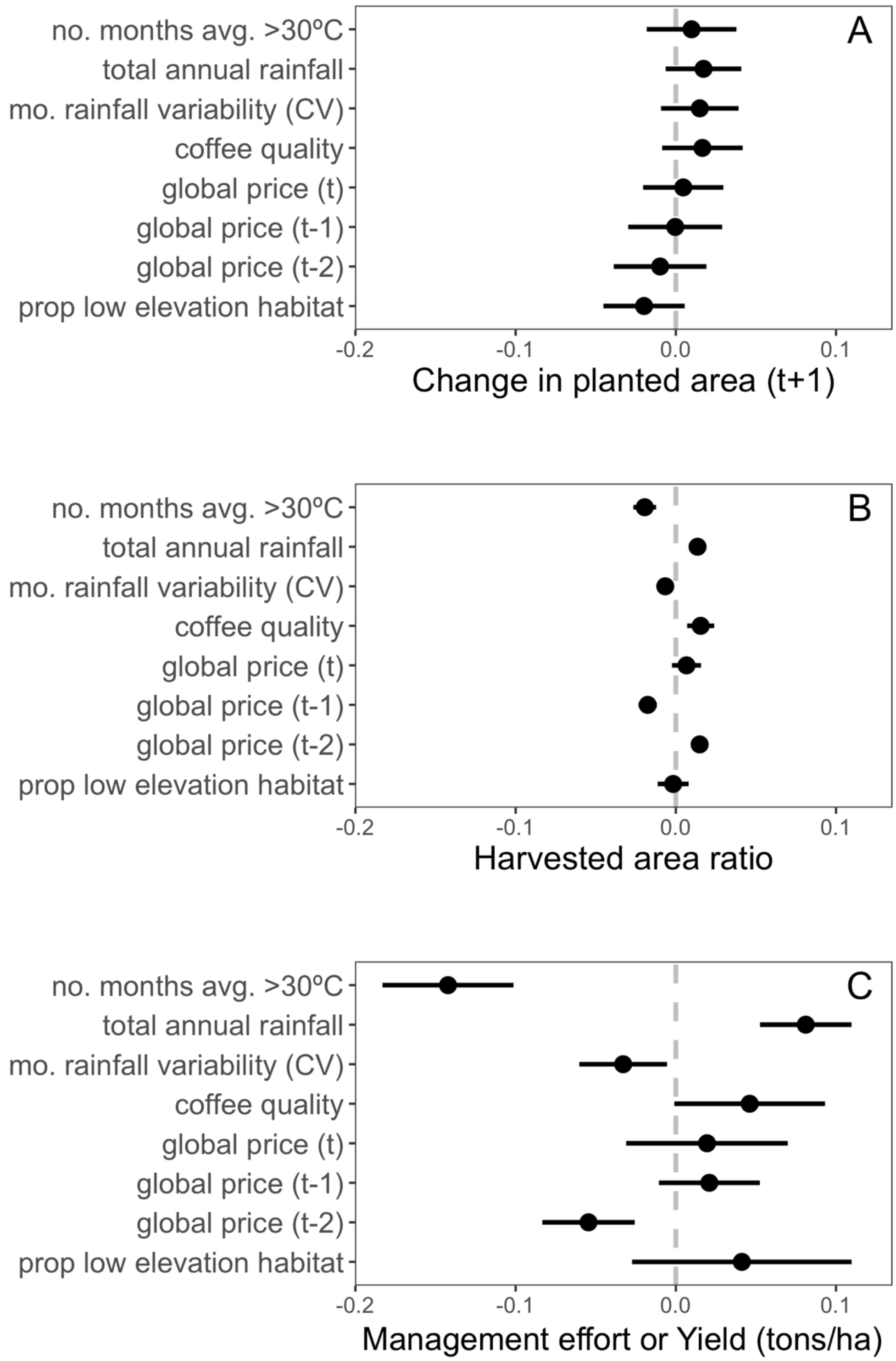
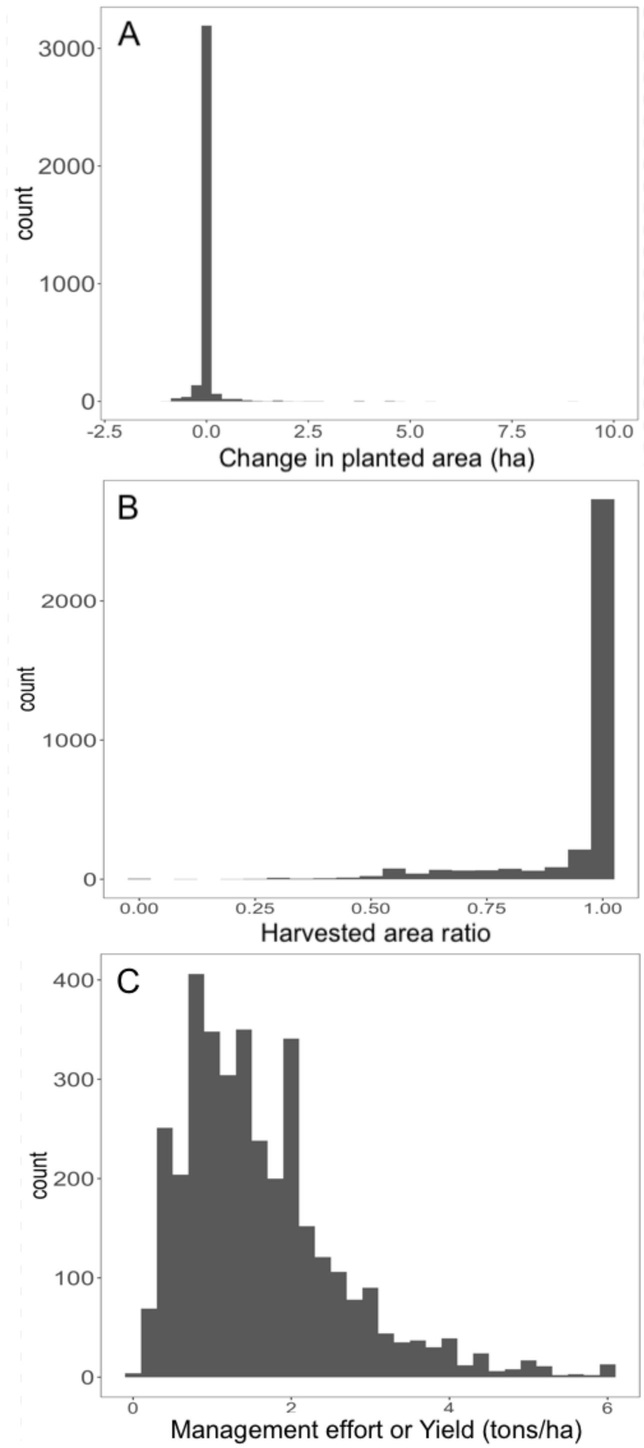


Figure 3.5. Frequency distributions of producer responses for (A) change in planted area, (B) harvested area ratio and (C) management effort.



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Chapter 1

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