AGROFORESTRY MANAGEMENT, SEASONAL CHANGES, BIODIVERSITY AND MULTITROPHIC INTERACTIONS OF COFFEE ARTHROPODS

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CHAPTER 1

AGROFORESTRY MANAGEMENT, SEASONAL CHANGES, BIODIVERSITY AND MULTITROPHIC INTERACTIONS OF COFFEE ARTHROPODS

GENERAL INTRODUCTION

Introduction

Anthropogenic alteration of landscapes has lead to a world-wide decline in biodiversity, theateaning ecosystem functioning (Dirzo & Raven, 2003). Conversion of pristine forests into agricultural land-use areas is the leading cause of biodiversity loss. More recently, human-altered landscapes have increasingly gained attention for their potential to conserve biodiversity of a variety of taxa (Bawa *et al.*, 2004). In the tropics, which make up the most part of global biodiversity hotspots (Myers *et al.*, 2000), traditional land-use systems such as coffee agroforestry in Latin America have been emphasized as important habitats for conservation of biodiversity (Moguel & Toledo, 1999; Perfecto *et al.*, 2003; Gordon *et al.*, 2007). Such forest-like agroecosystems are characterized by high tree diversity and complex vegetational structure resembling natural forests (Lozada *et al.*, 2007).

In addition to biodiversity conservation, traditional coffee agroforests may also contribute to reduction of pest problems due to its vegetational structural characteristics. Management of agroforests largely varies between farmers and influences biotic habitat factors such as vegetational diversity and density, which in turn determine abiotic factors like temperature and relative humidity (Rao *et al.*, 2000; Klein *et al.*, 2002). Microclimatic conditions operating at habitat scale often play an important role in structuring arthropod populations and community patterns in the field (Yarnes & Boecklen, 2005; Luoto *et al.*, 2006). Seasonality may also affect natural populations through changes in environmental conditions and resources variation (Wolda, 1988; Nestel *et al.*, 1994). Moreover, current theory predicts lower densities of herbivores in more vegetationally diverse habitats (Root, 1973; Landis *et al.*, 2000). In this context, lower herbivore densities in more diversified habitats are expected as a consequence of larger natural enemy populations and lower concentration of host plants (Root, 1973). As a result, herbivores are expected to attain larger populations in simple, intensively managed agroecosystems than in diverse, extensively managed ones.

Studies predicting and explaining arthropod population patterns have been usually conducted under laboratory conditions and extrapolated to a field scale (Enserink, 2002). Such studies have often yielded contrasting results because only few population-driving factors like biotic interactions can be studied in the laboratory. In the field, many mechanisms driving arthropod populations such as management of agroecosystems and associated changes in microclimatic conditions as well as natural enemies may interact. The real world field situation is often difficult to predict, however, only results from the field scale can be used to give arthropod management recommendations.

In this study, we used replicated field experiments to assess how agroforestry management and season affect the community of coffee-inhabiting mites. Additionally, we investigated whether agroforestry management can affect population dynamics and population stage structure of three important coffee pests. We also studied the role of single abiotic and biotic habitat parameters, which defined agroforestry types, in influencing coffee pest densities. Finally, we combined laboratory and field studies to determine the relative importance of small-scale biotic interactions versus large-scale agroforestry management and natural enemies for influencing coffee pests in the field.

The following questions were addressed:

1. How agroforestry management and season affect species richness and densities of the community of coffee-inhabiting mites? (Chapter 2)
2. Does agroforestry management affect population dynamics and population stage structure of coffee pests? (Chapter 3)
3. Which environmental habitat variables are the most important predictors of coffee pests? How great are the contribution of single environmental variables in explaining pest densities? (Chapter 4)
4. Do pests prefer uninfested coffee plants in order to increase their reproductive success? Does agroforestry type, which differed in management intensity, influence arthropod populations in the field in a way which can not be predicted by laboratory experiments? (Chapter 5)

Study region and agroforestry types

The research was carried out on private farms spread across the coffee-growing region of Jipijapa, province of Manabi, Ecuador (Fig. 1.1). The region is highly dominated by agriculture land-use systems and lies at an altitude ranging from 108 to 466 m a.s.l. The mean monthly temperature is 25.6 ºC and the average monthly rainfall is 115.9 mm. The region is characterized by marked dry and rainy seasons, with the rainy season lasting from December to May. The original vegetation is a semi-deciduous forest, which has been converted to agriculture, mainly traditional coffee agroforests. Coffee is grown by small-scale farmers in forest-like traditional agroforests, which are established by replacing the forest understorey with coffee plants and characterized by high shade tree diversity and complex-vegetational structure.

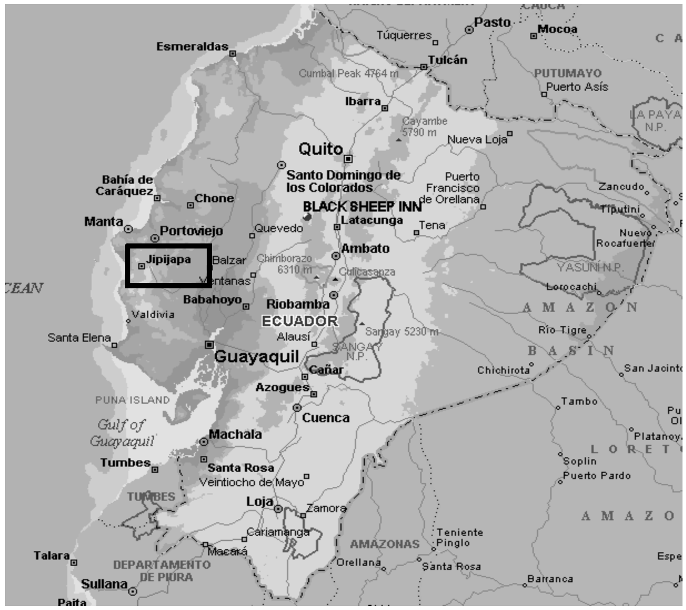

Fig. 1.1. Map showing the study region around the town of Jipijapa (1°19´60″ S, 80°34´60″ W), province of Manabi, Ecuador.

We selected three agroforestry types according to local management (Fig. 1.2):

a. Simple-shade agroforests (SS): managed agroforests with low shade tree diversity (4-9 tree species), simple vertical structure, tree density regulated to reduce shading and understorey relatively open; 8 study sites.

b. Complex-shade agroforests (CS): managed agroforests with intermediate shade tree diversity (9-12 tree species) and complex vertical structure with a multi-layered canopy; 8 study sites.

c. Abandoned coffee agroforests (AC): abandoned agroforests for 10-15 years due low revenues and currently resembling secondary forests, high shade tree diversity (14-20 tree species) and forest regeneration; 6 study sites.

The three agroforestry types differed in environmental variables measured in all study sites. Simple-shade and complex-shade agroforests had higher temperature and coffee density compared to abandoned coffee agroforests. In contrast, higher values of relative humidity were found in abandoned agroforests compared to simple-shade and complex-shade agroforests. Abandoned agroforests had highest values of canopy cover and tree diversity, whilst complex-shade and simple-shade had intermediate and lowest, respectively. Study sites (0.7 to 2 hectares) were located at least 2 km apart and did not receive agrochemical inputs.

Fig. 1.2. The three agroforestry types selected: (a) simple-shade agroforests, (b) complex-shade agroforests, and (c) abandoned-coffee agroforests.

Study organisms

Highland coffee *Coffea arabica* L. is an important cash crop in tropical America, in which it is cultivated in traditional agroforests by small-scale producers from Mexico to northern South America (Moguel & Toledo, 1999). Coffee suffers from many phytosanitary problems, including pest arthropods such as the spider mite *Oligonychus ilicis* (Acari: Tetranychidae), the coffee leaf miner *Leucoptera coffeella* (Lepidoptera: Lyonetiidae), and the coffee berry borer *Hypothenemus hampei* (Coleoptera: Curculionidae: Scolytinae) (Le Pelley, 1973; Reis & Souza, 1986) (Fig. 1.3). Either spider mite or leaf miner attacks may reduce the photosynthetic area and cause premature defoliation, particularly in the dry season. Berry borer is a beetle considered the most important coffee pest (Murphy & Moore, 1990). Berry borer larvae and adult stages feed inside coffee berries, affecting the quality and drastically reducing yields. The main natural enemies associated with spider mites and leaf miners in the study region are predatory mites of the family Phytoseiidae and a eulophid parasitoid, respectively. There is not any important natural enemy associated with berry borers in the region where the study took place.

Fig. 1.3. The three major coffee pests in tropical America: (a) spider mites, (b) leaf miners, and (c) berry borers.

Chapter outline

Chapter 2 addresses the seasonal changes in the diversity of coffee-inhabiting mites in relation to agroforestry management. It demonstrates that management intensification, from abandoned, complex-shade to simple-shade agroforests, negatively affected species richness of coffee mites. In general, more species and higher densities of mites were found in the dry season compared to the rainy season. Phytophagous mite species attained higher densities in simple-shade agroforests, while densities of entomophagous species were not affected by management practices. Overall, a pest spider mite and its predatory mite attained higher densities in more intensively managed agroforests during the dry season. Additionally, predator-prey ratios were higher in complex-shade agroforests, indicating that the predatory mite contributed to spider mite suppression in low-intensity agroforests. Vegetationally diverse agroecosystems such as complex-shade and abandoned agroforests have the potential to conserve mite diversity, and therefore should be incorporated into landscape conservation programs.

Chapter 3 investigates how agroforestry management affects the population dynamics of coffee pests (i.e. spider mites, leaf miners, and berry borers). Furthermore, it examines how specific developmental stages of coffee pests respond to management practices. This chapter shows that agroforestry management affects seasonal patterns of coffee pests with higher peaks being reached in more intensively managed agroforests. Further, there was an interacting effect of vegetational diversity and developmental stages of coffee pests, in which specific pest developmental stages built up higher densities in more intensively managed agroforests. Seasonal and population structure responses need to be taken into account in arthropod population dynamic studies across different habitat types, because responses change with season and developmental stages.

Chapter 4 focuses on the relative importance of single environmental habitat variables on densities of coffee pests (i.e. spider mites, leaf miners, and berry borers). This chapter uses hierarchical partitioning methods and demonstrates that the environmental habitat variables temperature, humidity, and tree diversity explained most of the variation of coffee pest densities. Spider mite density was positively related to temperature, while leaf miner and berry borer densities were negatively correlated to humidity and tree diversity, respectively. Environmental habitat variables determining a given habitat may play a key role for understanding the effects of land use on pest densities. Understanding such species-environmental relationships provide insights on how to predict and manage pests in the field.

Chapter 5 combines laboratory and field experiments to study the relative importance of biotic interactions and agroforestry management on densities of coffee pests in the field. This chapter shows that preference matched fitness under laboratory conditions, leading to the prediction that coffee pests would avoid conspecific and heterospecific competitors in the field. However, coffee pest densities were positively correlated in the field, thereby contrasting with predictions from the laboratory. Management intensity, which was defined by abiotic and biotic habitat variables, proved to be more important than preference and fitness for influencing densities of coffee pests in the field. Laboratory and field studies need to be combined in order to determine the relative importance of small-scale versus large spatial scale experiments influencing populations in the field.

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CHAPTER 2

TEMPORALLY-MEDIATED RESPONSES OF THE DIVERSITY OF ENTOMOPHAGOUS AND PHYTOPHAGOUS COFFEE MITES TO AGROFORESTRY MANAGEMENT

Adenir Teodoro, Alexandra-Maria Klein and Teja Tscharntke

Abstract

Managed agroecosystems have been emphasized for its biodiversity conservation value, however it remains unclear how biodiversity is affected by management practices over time. We assessed the seasonal response of the community of coffee-inhabiting mites to agroforestry management (simple-shade agroforests, complex-shade agroforests, and abandoned coffee agroforests) in Ecuador. Species richness of coffee mites was negatively affected by management intensification, with more species in less-disturbed abandoned agroforests in either dry or rainy season. Overall, the community of coffee-inhabiting mites varied seasonally, with more species and higher densities in the dry season than in the rainy season. Higher densites of phytophagous mites were found in simple-shade agroforests, while entomophagous species did not respond to management practices. The predatory mite *A. herbicolus* and the pest spider mite *O. ilicis* responded to management and season, both species generally attained higher densities in simple-shade agroforests during the dry season. In addition, predator–prey ratios were higher in complex-shade than in simple shade agroforests, proving that the predatory mite in low-intensity agroforests contributed to spider mite suppression in the field. In conclusion, our results show that the coffee mite community responded both to seasonal changes and to management of agroforests, and that vegetationally diverse habitats such as complex-shade and, in particular, abandoned coffee agroforests contribute to conservation of mite diversity.

Key words: season, management practices, biodiversity conservation, Ecuador

Introduction

Anthropogenic habitat modification has led to a global decline in biodiversity, which has recently turned the conservation focus from natural to managed habitats (Bawa *et al.*, 2004). However, the contribution of such managed habitats to year-round conservation is less clear as studies analyzing diversity patterns over time are rarely conducted (but see Tylianakis *et al.*, 2005). Traditional coffee (*Coffea arabica* L.) agroforests have been highlighted as important areas for biodiversity conservation of a variety of taxa within agricultural landscapes (Moguel and Toledo, 1999; Perfecto *et al.*, 1997, 2003; Pineda *et al.*, 2005; Gordon *et al.*, 2007). In addition to conservation of biological diversity, agroforests may also contribute to pest reduction due to its low concentration of host plants and improvement of the natural biological control provided by natural enemies (Root 1973; Landis *et al.*, 2000).

In Ecuador, such forest-like agroecosystems are established by replacing the forest understorey with coffee shrubs and are characterized by high tree diversity and complex vegetational structure (Lozada *et al.*, 2007). Farmers may also replace some forest trees by fruit and timber species. Shade tree pruning and weeding as well as other agroforestry management practices determine environmental variables such as temperature and relative humidity, which in turn may affect biodiversity and densities of arthropods in the field (Perfecto and Vandermeer, 1996; Rao *et al.*, 2000; Klein *et al.*, 2002; Philpott, 2005). Season is a further important factor potentially influencing arthropod populations in the field, especially in regions with marked dry and rainy seasons (Nestel *et al.*, 1993; Philpott *et al.*, 2006) due to temporal variation in temperature, rainfall and resource availability (Wolda, 1988; Guedes *et al.*, 2000). However, little is known on the temporally-mediated effects of different habitats to diversity patterns.

In this study, we focus on the community of coffee-inhabiting mites and assess how mites are affected by management of agroforests and season in Ecuador. Mites (Arachnida: Acari) are one of the most diverse of all invertebrate taxa, including phytophagous, entomophagous and fungivorous species (Walter and Proctor, 1998). Since mite communities comprise species of different trophic levels, the study of its fauna can provide insights on how habitat modification affect biodiversity and ecosystem function.

We asked the following questions:

1. How agroforestry management and season affect species richness and density of mites on coffee?

2. Do agroforestry management and season affect phytophagous and entomophagous mite species equally?
3. How a predatory mite species and a pest spider mite species respond to agroforestry management and season?

Materials and methods

Study region and site selection

The study was carried out on private farms located within the coffee-growing region of Jipijapa (1°19′60″ S, 80°34′60″ W), province of Manabi, Ecuador. The study region is dominated by agriculture and lies at an altitude between 108 and 466 m a.s.l. The mean monthly temperature (± SE) is 25.66 ± 0.06 °C and the average monthly rainfall is 115.99 ± 35.09 mm. The rainy season lasts from December to May (www.inamhi.gov.ec). The natural vegetation is a semi-deciduous forest and coffee is traditionally cultivated under a diverse canopy of shade trees on small-holder farms in the region. The original vegetation has been converted to agriculture, predominantly coffee agroforests, which often have sharp borders with other land-use types such as cattle pasture, annual crops (mainly maize and rice), and patches of fragmented forest.

Three agroforestry management types were selected: simple-shade agroforests (managed with 4-9 tree species, simple vertical structure, tree density regulated to reduce excessive shading and understorey relatively open, 8 study sites), complex-shade agroforests (managed with 9-12 tree species, complex vertical structure, 8 study sites) and abandoned coffee agroforests (abandoned for 10-15 years due to low economic returns and currently resembling secondary forests, 14-20 shade tree species, forest regeneration and only few old coffee plants remaining, 6 study sites) totaling 22 study sites. The three agroforestry types were characterized based on environmental variables measured in all study sites. Simple-shade and complex-shade agroforests had higher temperature ($P < 0.01$) and coffee density ($P < 0.0001$) than abandoned coffee agroforests. In contrast, higher values of relative humidity ($P < 0.001$) were found in abandoned agroforests compared to simple-shade and complex-shade agroforests. Abandoned agroforests had highest values of canopy cover ($P < 0.0001$) and tree diversity ($P < 0.0001$), whilst complex-shade and simple-shade had intermediate and lowest values, respectively. Farmers do not use any agrochemicals or fertilizers and all study sites were located at least 2 km apart. The size of coffee farms ranged from 0.7 to 2 hectares.

Mite surveys

We sampled coffee-inhabiting mites in the three types of agroforests (in all 22 study sites) twice during the rainy season (February and March 2005) and twice during the dry season (October and November 2005). We randomly chose 4 coffee plants located in the centre of each study site to avoid edge effects and collected 6 leaves per plant (two leaves from each part, i.e., top, medium, and bottom), totaling 24 leaves per study site per evaluation. The leaves were placed into paper bags and morphoespecies were separated and counted using a binocular microscope (Stemi SV 11, Zeiss, Germany) in the laboratory.

Statistical analyses

We calculated the abundance-based coverage estimator (ACE) and Chao 1 estimates of mite species richness to determine whether our samples were close to species saturation using Estimates 7.5 (Colwell, 2004). Afterwards, we tested correlation between observed and estimated species richness per site for each season (dry and rainy season).

Repeated measures Anovas with type I sequential sums of squares were performed to determine the effect of agroforestry management on species richness, density, and predator-prey ratio over seasons using Statistica 7.0 (StatSoft Inc 1984-2004). Whenever differences in season were found, further one-way Anovas followed by post hoc Fisher LSD tests were carried out to test differences between agroforestry types within each season.

Results

A total of 23 mite species from 12 families, one species from the order Acaridida and two additional species belonging to the order Mesostigmata were found across all study sites during both seasons (Appendix 1). Predatory mites of the family Phytoseiidae and fungivorous mites of the family Tydeiidae were the most diverse families with four species each, while the pest spider mite *Oligonychus ilicis* of the family Tetranychidae followed by the phytoseiid mite *Amblyseius herbicolus* were the most abundant species (Appendix 1). The number of observed and estimated mite species were highly correlated according to Pearson correlations ($r > 0.90$, $P < 0.001$, n= 22; for both dry and rainy seasons). Therefore, we decided to use original mite species richness data.

Seasonal species richness and density in relation to management

Season had a strong effect on mite species richness, so that more species were found in the dry season compared with the rainy season ($F_{1,41}$ = 36.42, P < 0.0001). Agroforestry management also influenced mite species richness, with the mean number of species per study site being higher in abandoned agroforests compared to simple-shade agroforests in the dry season ($F_{2,41}$ = 5.25, P < 0.01), and more species being found in abandoned agroforests, intermediate in complex-shade and lowest in simple-shade agroforests during the rainy season ($F_{2,41}$ = 8.09, P < 0.01; Fig. 1a).

Mite densities varied seasonally, with higher densities being reached in the dry compared to the rainy season ($F_{1,41}$ = 21.92, P < 0.0001), whereas no effect of agroforestry management on mite densities was found ($F_{2,41}$ = 1.39, P = 0.25).

Seasonal responses of entomophagous and phytophagous species to management

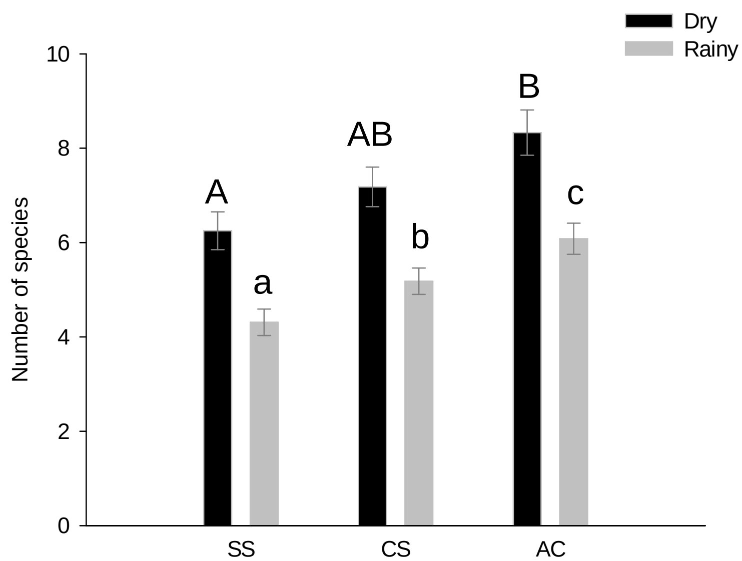
We evaluated the responses of entomophagous and phytophagous mite species to management and season. As entomophagous we included species of the families Phytoseiidae, Camerobidae, Cheyletidae, Cunaxidae, Ascidae, Stigmaeidae, and to the order Mesostigmata; and as phytophagous we considered species belonging to the families Tetranychidae, Tenuipalpidae and Tarsonemidae (Appendix 1). Species from other families and order Acaridida were not included in the analyses as they were either fungivorous species or had their feeding guild not identified.

There was a significant effect of season on entomophagous mite species, so that more species were found in the dry season than in the rainy season ($F_{1,41}$ = 25.79, P < 0.0001). Management practices influenced species richness of entomophagous mites, higher number of species in abandoned coffee agroforests compared to simple-shade and complex shade agroforests either in the dry ($F_{2,41}$ = 5.03, P = 0.01) or rainy season ($F_{2,41}$ = 19.02, P < 0.0001) (Fig. 1b). Conversely, species richness of phytophagous mites were affected neither by season ($F_{1,41}$ = 1.11, P = 0.29) nor by management of agroforests ($F_{2,41}$ = 0.45, P = 0.63) (Fig. 1c).

Higher densities of entomophagous mites were found in the dry season compared to the rainy season (Log + 1 transformed data: $F_{1,41}$ = 41.84, P < 0.0001), while no effect of management was found (Log + 1 transformed data: $F_{2,41}$ = 0.51, P = 0.6). Higher densities of phytophagous mites were also found during the dry season than in the rainy season (Log + 1 transformed data: $F_{1,41}$ = 20.43, P < 0.0001). Furthermore, phytophagous mites attained higher densities in simple-shade agroforests than in complex-shade and abandoned agrofrests during the dry

(Log + 1 transformed data: $F_{2,41} = 6.13$, $P < 0.01$) and the rainy season (Log +1 transformed data: $F_{2,41} = 3.54$, $P = 0.03$).

a.



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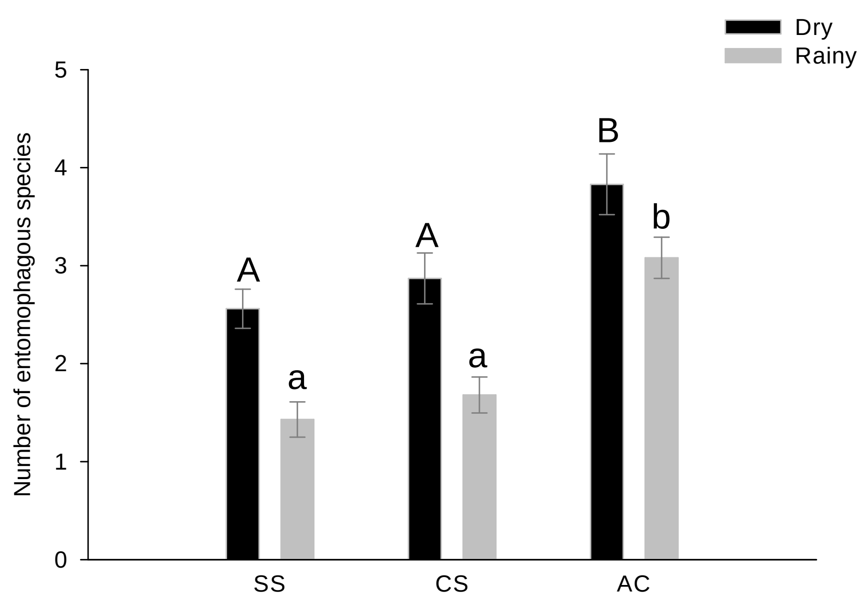

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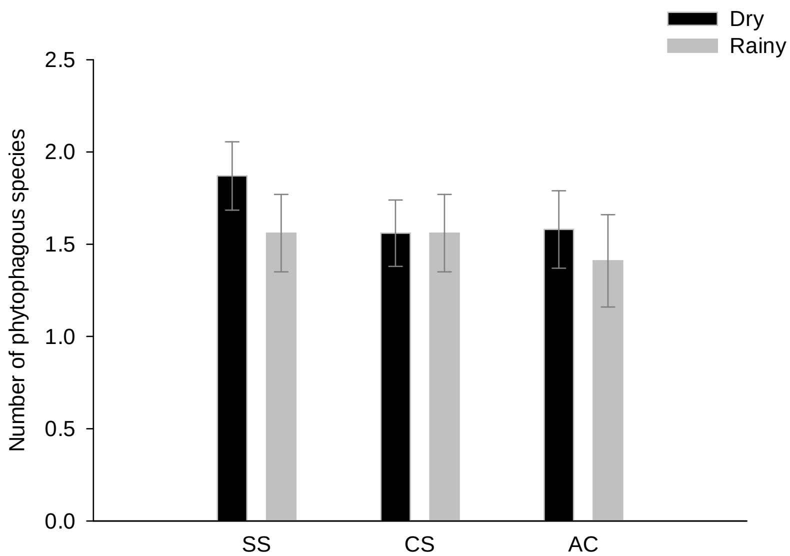


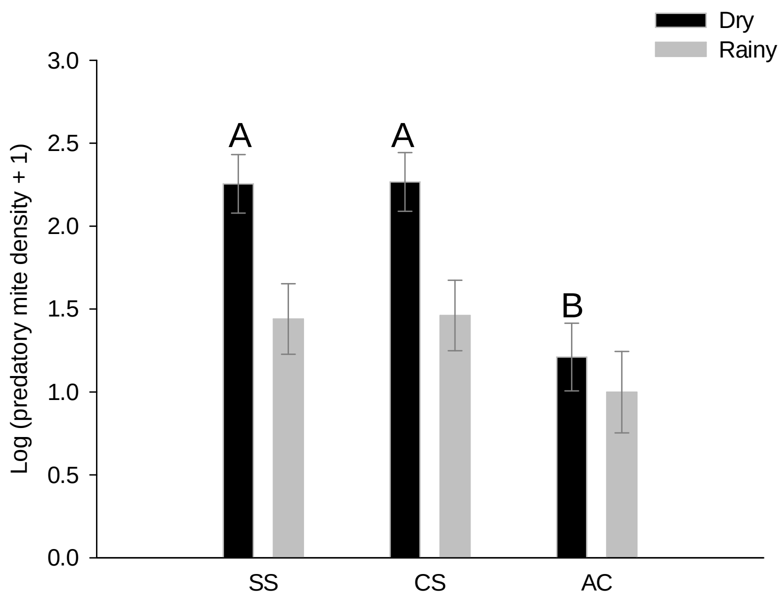
Fig. 1- Species richness of coffee-inhabiting mites: (a) all species, (b) entomophagous, and (c) phytophagous species in the dry and rainy season in relation to agroforestry management (SS= simple-shade agroforests, CS= complex-shade agroforests, and AC= abandoned coffee agroforests). Means ± SE per study site are presented and different letters indicate significant differences between agroforestry types within season based on one-way Anovas.

Responses of some species to management and season

We investigated the seasonal response of the two most abundant species found across study sites and seasons, the predatory mite *A. herbicolus*, and the pest spider mite *O. ilicis*, to management of agroforests. There was a significant time effect for the predatory mite *A. herbicolus*, with higher peaks being reached in the dry season compared to the rainy season ($F_{1,41}$ = 19.04, P < 0.0001). The number of predatory mites per study site was higher in simple-shade and complex-shade agroforests compared to abandoned coffee agroforests in the dry season ($F_{2,41}$= 9.63, P < 0.001), while there was no effect of agroforestry management on densities of the predatory mite in the rainy season ($F_{2,41}$ = 1.23, P = 0.30; Fig. 2a).

The number of the spider mite *O. ilicis* per study site varied significantly between seasons, with greater densities in the dry season compared to the rainy season ($F_{1,41}$ = 61.08, P < 0.0001). In both seasons, the number of spider mites per study site was higher in simple-shade agroforests than in complex-shade and abandoned coffee agroforests (dry: $F_{2,41}$ = 6.07, P < 0.01; rainy: $F_{2,41}$ = 6.27 , P < 0.01; Fig. 2b).

a.



b.

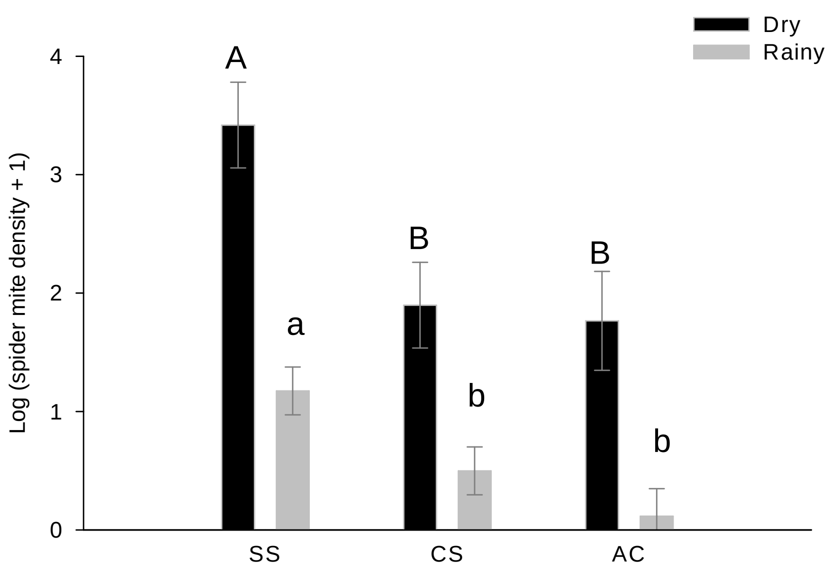


Fig. 2- Densities of (a) the predatory mite *A. herbicolus,* and (b) the pest spider mite *O. ilicis* in the dry and rainy season in relation to agroforestry management (SS= simple-shade agroforests, CS= complex-shade agroforests, and AC= abandoned coffee agroforests). Means ± SE per study site are shown and different letters represent significant differences between agroforestry types within season based on one-way Anovas.

Seasonal predator-prey ratios according to management

Higher predator–prey ratios (abundance of the predatory mite *A. herbicolus* to abundance of the spider mite *O. ilicis*) were found in the rainy season than in the dry season ($F_{1,41}$ = 4.05, P = 0.05). Predator–prey ratios were higher in complex-shade compared to simple-shade and abandoned coffee agroforests during the dry season ($F_{2,41}$ = 5.55, $P < 0.01$), while management practices did not affect predator–prey ratios in the rainy season ($F_{2,41}$ = 1.68, P = 0.19; Fig. 3).

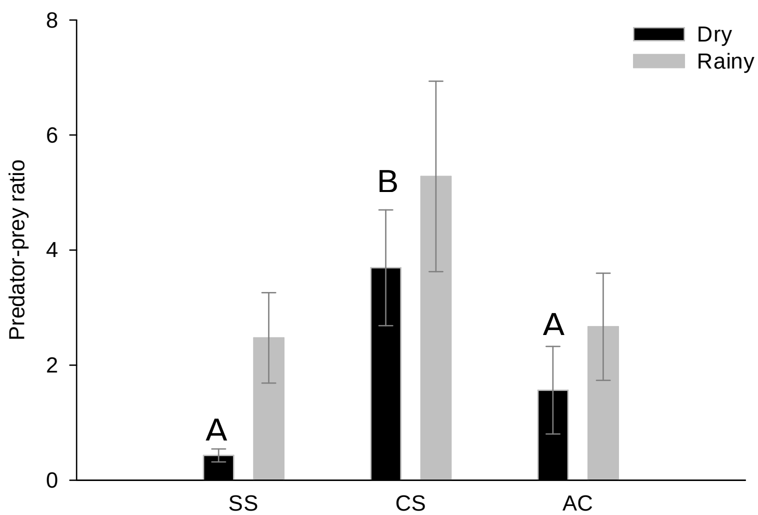


Fig. 3- Predator–prey ratios (abundance of the predatory mite *A. herbicolus* to abundance of the pest spider mite *O. ilicis*) during the dry and rainy season in relation to agroforestry management (SS= simple-shade agroforests, CS= complex-shade agroforests, and AC= abandoned coffee agroforests). Means ± SE per study site are given and different letters indicate significant differences between agroforestry types within season based on one-way Anovas.

Discussion

Our results showed that species richness and density of coffee-inhabiting mites changed contingent on agroforestry management and season. Overall, management intensification, from abandoned, complex-shade to simple-shade agroforests, negatively affected coffee mites, and this response was strongly influenced by seasonality.

Mite species richness declined with agroforestry intensification, so that more species were found in vegetationally diverse abandoned coffee agroforests. Similar patterns of diversity loss related to habitat alteration has also been shown for other taxa (Nestel *et al.,* 1993; Perfecto *et al.,* 2003; Shahabuddin *et al.,* 2005), emphasizing the importance of less disturbed habitats to biodiversity conservation.

Mite species richness and density varied seasonally, with more species and higher densities in the dry season compared with the rainy season. Similar seasonal patterns were found for species richness and densities of entomophagous and for densities of phytophagous mites. Seasonal changes in diversity and densities of arthropods in tropical regions have been reported in many studies and have been attributed to differences in environmental conditions such as temperature and precipitation over time (Guedes *et al.,* 2000; Philpott *et al.,* 2006). The region where our study took place is characterized by heavy rainfalls during the rainy season, which might have negatively influenced the mite community.

Although density of coffee mites was not affected by management practices, phytophagous mites built up higher populations in simple-shade than in complex-shade and abandoned coffee agroforests. Likewise, the pest spider mite *O. ilicis* attained highest densities in simple-shade agroforests compared to complex-shade and abandoned coffee agroforests in either dry or rainy season. The predatory mite *A. herbicolus* was also more abundant in less vegetational diverse simple-shade and complex-shade agroforests compared to abandoned coffee agroforests but only in the dry season. These patterns of higher densities in more intensively managed agroforests might have been driven by differences in abiotic habitat variables such as temperature and humidity characterizing each agroforestry type, as microclimatic habitat variables often influence animal populations in the field (Perfecto and Vandermeer, 1996; Klein *et al.,* 2002). Moreover, these results are in accordance with theory predicting higher pest densities in less vegetationally diverse agroecosystems but contrast with predictions of higher densities of predators in more vegetational diverse agroecosystems (Root, 1973; Landis *et al.,* 2000).

The spider mite *O. ilicis* is an important coffee pest and its most important natural enemies are predatory mites of the family Phytoseiidae such as *A. herbicolus* (McMurtry and Croft, 1997). Predator-prey ratios were higher in complex-shade than in simple-shade and abandoned agroforests during the dry season, revealing that the predatory mite contributed to suppression of the spider mite in low-intensity agroforests.

Our results acknowledge the role of agroforestry management and season in influencing the community of coffee mites. Furthermore, complex-shade and abandoned coffee agroforests as well as the predatory mite *A. herbicolus* contributed to suppression of populations of the spider mite *O. ilicis* in the field. We conclude that vegetationally diverse agroforests, especially abandoned agroforests, have the potential to conserve mite diversity, and therefore should be considered into landscape conservation programs.

Acknowledgements

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Appendix 1- Coffee-inhabiting mites in relation to agroforestry management (SS= simple-shade agroforests, CS= complex-shade agroforests, AC= abandoned coffee agroforests) during the dry and rainy season. Pooled numbers per agroforestry type and season are given.

		Dry season			**Rainy season**			
Family	**Species**	**SS**	**CS**	**AC**	**SS**	**CS**	**AC**	**Total**
Tetranychidae	*Oligonychus ilicis*	862	330	152	70	22	2	**1438**
Phytoseiidae	*Amblyseius herbicolus*	177	166	45	62	96	32	**578**
	Amblyseius aeralis	0	0	3	0	0	4	**7**
	Metaseiulus sp	0	1	0	0	0	0	**1**
	Proprioseiopsis neotropicus	2	1	0	0	0	0	**3**
Tenuipalpidae	*Brevipalpus phoenicis*	55	14	8	26	10	2	**115**
Meyerrellidae	*Triophtydeus* sp	123	125	109	32	48	18	**455**
Camerobidae	*Neophyllobius* sp	0	0	1	2	0	6	**9**
Tydeiidae	*Metallorrya* sp	3	59	44	0	0	22	**128**
	Pretydeus sp	0	0	1	2	6	0	**9**
	Tydeus sp	28	20	23	6	12	4	**93**
	Tydeiidae sp	1	0	0	0	0	0	**1**
Tarsonemidae	*Tarsonemidae* sp1	6	15	14	46	42	112	**235**
	Tarsonemidae sp2	0	2	0	0	0	0	**2**
Cheyletidae	*Cheyletidae* sp	3	1	9	0	0	0	**13**
Cunaxidae	*Cunaxidae* sp1	10	3	5	0	0	6	**24**
	Cunaxidae sp2	5	13	1	2	6	10	**37**
Oribatidae	*Oribatidae* sp1	0	0	2	4	0	0	**6**
	Oribatidae sp2	1	3	1	4	2	2	**13**
	Oribatidae sp3	0	2	0	0	0	0	**2**
Ascidae	*Ascidae* sp	3	7	14	0	4	4	**32**
Stigmaeidae	*Stigmaeidae* sp1	1	0	0	0	0	0	**1**
	Stigmaeidae sp2	40	56	64	2	4	16	**182**
Acaridida[a]	*Acaridida* sp	11	12	2	0	50	0	**75**
Mesostigmata[a]	*Mesostigmata* sp1	2	5	0	0	0	8	**15**
	Mesostigmata sp2	2	3	7	0	0	0	**12**
Total		**1335**	**838**	**505**	**258**	**302**	**248**	

[a]order

CHAPTER 3

AGROFORESTRY MANAGEMENT AFFECTS COFFEE PESTS CONTINGENT ON SEASON AND DEVELOPMENTAL STAGE

A. Teodoro, A.M. Klein, P.R. Reis and T. Tscharntke

Abstract

1 Management of vegetational diversity in agroecosystems is a potentially regulating factor of pest population dynamics in the field and may affect developmental stages in different ways.

2 We investigated the population dynamics of spider mites, leaf miners and berry borers in three management types of coffee agroforests, increasing plant diversity from few shade tree species (simple-shade agroforests), intermediate shade tree species (complex-shade agroforests) to high shade tree species (abandoned coffee agroforests) in Ecuador. Furthermore, we studied how changes in agroforestry management affect population stage structure of each coffee pest.

3 Our results show that agroforestry management affected seasonal patterns of coffee pests in that higher densities of spider mites were observed from August to December, leaf miners from December to February, and berry borers from May to July. Moreover, specific developmental stages of spider mites, leaf miners and berry borers differed in their responses to agroforestry management, proving an interacting effect of vegetational diversity and developmental stages of coffee pests. Spider mite of all stages reached higher densities in simple-shade agroforests compared to complex-shade and abandoned agroforests, leaf miner densities decreased from simple-shade to complex-shade and abandoned agroforests, but only for larvae, not pupae. Similarly, only berry borer adults (but not eggs, larvae and pupae) showed response to agroforestry management.

4 We emphasize the importance to consider the seasonal differences of specific arthropod developmental stages to vegetational management while investigating arthropod population dynamics across different habitat types.

Keywords spider mites, leaf miners, berry borers, developmental stages.

Introduction

Highland coffee *Coffea arabica* L. is an important cash crop in tropical America traditionally grown in shaded agroforests from Mexico to northern South America (Perfecto *et al.*, 1996; Moguel & Toledo, 1999). These coffee agroecosystems have been recognized as important areas for biological diversity conservation due to its complex vegetation structure and high plant diversity (Perfecto *et al.*, 2003; Pineda *et al.*, 2005; Tylianakis *et al.*, 2005; Lozada *et al.*, 2007; Gordon *et al.*, 2007).

Several coffee agroforestry management types have been recognized differing in shade regulation, shade tree diversity and tree density (Moguel & Toledo, 1999; Klein *et al.*, 2002; Lozada *et al.*, 2007). Management of vegetational diversity controls biotic variables such as temperature and relative humidity which in turn affect arthropod parameters like population dynamics in agroecosystems (Risch, 1980; Prischmann *et al.*, 2005; Barbar *et al.*, 2006).

Although several studies have investigated the effects of plant management in agroecosystems on arthropod population dynamics, only few published studies have addressed how specific arthropod developmental stages respond to vegetational management (see Harmon *et al.*, 2003). Arthropod developmental stages may differ in their responses to agroecosystem management. In this study, we investigated how agroforestry management affects the population dynamics of three major arthropod coffee pests, namely, spider mites, leaf miners and berry borers over an entire year in a coffee-growing region in Ecuador. Moreover, we tested how different pest developmental stages respond to agroforestry management.

We asked the following questions:

1- Does agroforestry management type (i.e., simple-shade, complex-shade, and abandoned coffee agroforests) affect population dynamics of coffee pests over time? We predicted that coffee pests would reach higher peaks and therefore attain higher population densities in more intensively managed agroforests.
2- Does agroforestry management affect the population stage structure of coffee pests? We hypothesized that some developmental stages might be more sensitive than others to vegetational management.

Study system

The coffee red spider mite *Oligonychus ilicis* McGregor (Acari: Tetranychidae), the coffee leaf miner *Leucoptera coffeella* Guérin-Méneville (Lepidoptera: Lyonetiidae), and the coffee berry borer *Hypothenemus hampei* Ferrari (Coleoptera: Curculionidae: Scolytinae) are the main coffee pests reported in tropical America (Le Pelley, 1973; Reis & Souza, 1986). Colonies of spider mites are found on the upper leaf surface, which may drop prematurely during heavy infestations (Reis & Souza, 1986). Leaf miners are monophagous on *Coffea* spp. feeding in the parenchyma of the leaves (Le Pelley, 1973) and cause a reduction in their photosynthetic area and premature defoliation (Reis & Souza, 1986). The berry borer is a beetle considered as the most serious coffee pest worldwide (Murphy & Moore, 1990). Both adult and larval stages feed inside coffee berries, affecting the quality and reducing yields (Le Pelley, 1973).

Materials and methods

Study region and site description

The study was carried out on private farms located in the coffee-growing region of Jipijapa (1º19'60" S, 80º34'60" W), province of Manabi, Ecuador. The study region is dominated by agriculture (agroforestry, predominantly coffee: 54.8%, pasture: 16.2%, and annual crops: 1.9%; Segarra, 2004) and situated with an altitude range between 108 and 466 m a.s.l. The study region has a mean monthly temperature (± SE) of 25.66 ± 0.06 ^{o}C and an average monthly rainfall of 115.99 ± 35.09 mm. The rainy season begins in December and finishes in May (www.inamhi.gov.ec). The natural vegetation is a semi-deciduous forest and coffee is traditionally cultivated by small-scale producers under a diverse canopy of shade trees. The original vegetation has been converted to agriculture, predominantly coffee agroforests, which often have sharp borders with other land-use types such as cattle pasture, annual crops, and forest remnants.

We selected three agroforestry types according to local management: simple-shade agroforests (managed with 4-9 shade tree species, simple vertical structure, tree diversity regulated to reduce excessive shading and understorey relatively open, 8 study sites), complex-shade agroforests (managed with 9-12 shade tree species, complex vertical structure, 8 study sites), and abandoned coffee agroforests (abandoned for 10-15 years due to low economic returns and currently resembling secondary forests, 14-20 shade tree species, forest regeneration and only few old coffee plants remaining, 6 study sites) totaling 22 study sites. The management of simple-shade and complex-shade agroforests depends on individual farmer experience and includes hand-weeding once or twice per year and coffee harvest. The three agroforestry types were characterized based on correlations between abiotic and biotic habitat variables recorded in all study sites. Simple-shade and complex-shade agroforests had higher temperature (*P* < 0.01) and coffee density (*P* < 0.0001) compared to abandoned coffee agroforests. In contrast, higher values of relative humidity (*P* < 0.001) were found in abandoned agroforests compared to simple-shade and complex-shade agroforests. Abandoned agroforests had highest values of canopy cover (*P* < 0.0001) and tree diversity (*P* < 0.0001), whilst complex-shade and simple-shade have intermediate and lowest, respectively (data not shown). No agrochemicals were used in any study sites, which were located at least 2 km apart. The size of coffee farms ranged from 0.7 to 2 hectares.

Spider mite and leaf miner surveys

We sampled spider mites and leaf miners in all study sites over time to assess seasonal population dynamics and stage structure changes of coffee pests in relation to agroforestry management.

In each study site, we randomly chose 20 coffee plants located at least 5 meters away from habitat boundaries to avoid edge effects and evaluated 120 leaves (six per plant) at monthly intervals during a whole year (from August 2004 to July 2005). In each survey, all developmental stages of spider mites (i.e., eggs, larvae, nymphs, and adults) and two developmental stages of leaf miners (i.e., larvae and pupae) were recorded using a binocular microscope (Stemi SV 11, Zeiss, Germany). We averaged densities of spider mites and leaf miners on a per-site basis.

Berry borer survey

Berry borers were surveyed in the three management types of coffee agroforests during the 6-month coffee production period of 2005 (from February to July). In each evaluation, ten coffee plants per study site located at least 5 meters away from habitat boundaries were randomly chosen and 60 fruits per plant were collected (20 from each part, i.e., top, medium and bottom). The fruits were opened and the number of all developmental stages of berry borers (i.e., eggs, larvae, pupae, and adults) was counted using a binocular microscope. We averaged the number of berry borers on a per-site level.

Data analyses

Repeated measures ANOVAs were used to examine the population change of coffee pests in the three agroforestry management types over time. One-way ANOVAs followed by post hoc Fisher LSD tests (*P* < 0.05) were used to test differences between agroforestry management types on the number of pests within each month. Additionally, we tested the effects of coffee shrub density on densities of spider mites, leaf miners and berry borers using general linear models (GLMs). Because there was only one value of coffee density per study site, its effects were tested on a per study site level with agroforestry type as a random factor and coffee density as a continuous variable.

Using repeated measures ANOVAs to remove variance explained by seasonal effects, we analyzed the influence of agroforestry management on population stage structure of each coffee pest. Post hoc Fisher LSD tests ($P < 0.05$) were used to test the effect of agroforestry management on densities of each pest developmental stage.

Densities of berry borers were log+1 transformed to achieve assumptions of a normal distribution. All analyses were performed using Statistica 7.0 (StatSoft Inc. 1984-2004).

Results

Seasonal population dynamics in relation to agroforestry management

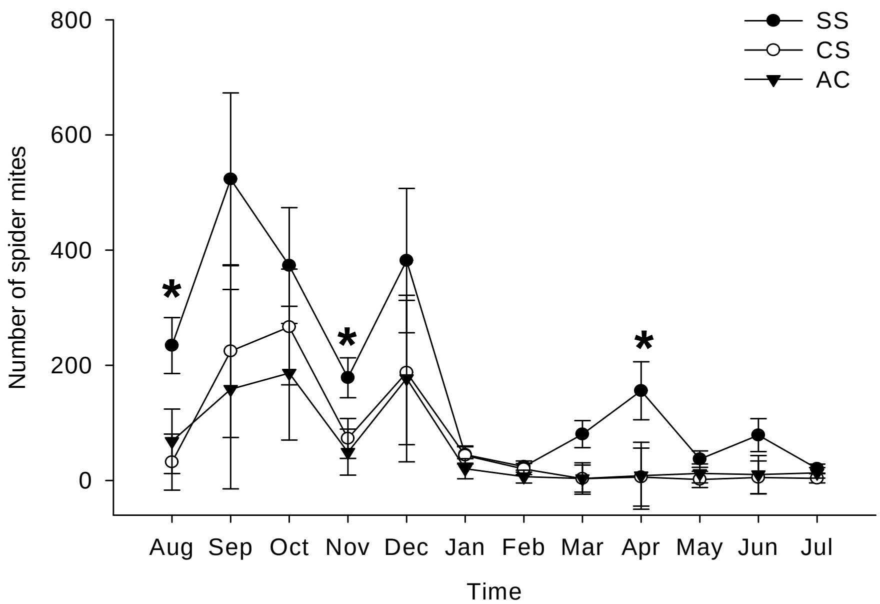
The number of spider mites per study site significantly varied throughout the season, leading to a statistically significant time effect (Fig. 1a; $F_{11,209} = 8.39$; $P < 0.0001$). Overall, high densities of spider mites were observed from August to December (dry season) but decreased rapidly in January probably due to heavy rains, remaining lower until July. More pronounced peaks of spider mites in simple-shade agroforests throughout the year (Fig. 1a) led to higher densities in this agroforestry type compared to complex-shade and abandoned agroforests ($F_{2,19} = 4.45$; $P = 0.025$).

Higher densities of leaf miners were found between December and February with a sharp peak in January (Fig. 1b), leading to a significant time effect ($F_{11,209} = 17.26$, $P < 0.0001$). Furthermore, there was a significant interaction between time and agroforestry type ($F_{22,209} = 1.77$, $P = 0.021$) driven by a higher leaf miner density in January in simple-shade agroforests (Fig. 1b). The number of leaf miners per study site did not differ between simple-shade, complex-shade and abandoned coffee agroforests ($F_{2,19} = 2.47$, $P = 0.111$).

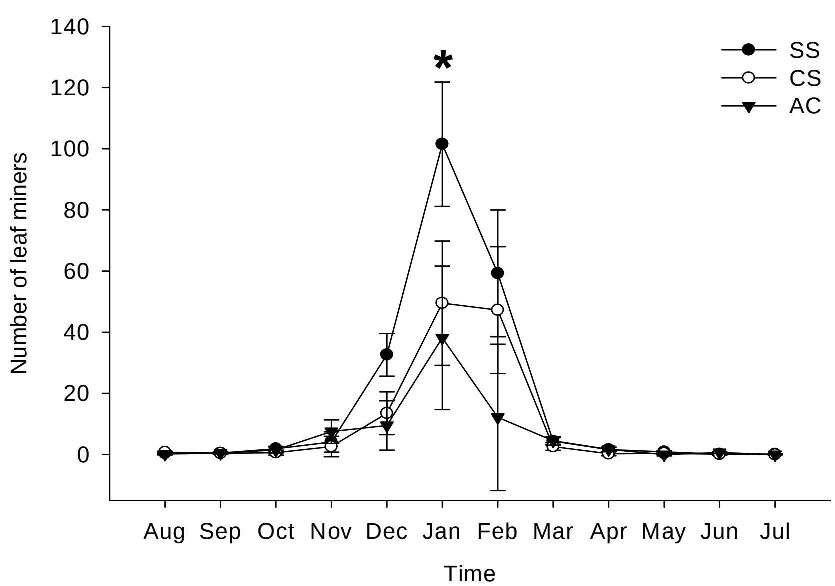
Berry borer densities significantly increased in simple-shade and complex-shade agroforests throughout the coffee-growing season (Fig. 1c), leading to higher densities in these agroforestry types than in abandoned coffee agroforests ($F_{2,19} = 4.21$, $P = 0.030$). Also, the number of berry borers per study site varied over the season, leading to a significant time effect (Fig. 1c; $F_{5,95} = 4.51$, $P = 0.0009$).

Coffee shrub density did not significantly affect any coffee pest density on a per site basis (spider mites: $F_{1,18} = 2.88$, $P = 0.064$, $R^2 = 0.32$; leaf miners: $F_{1,18} = 1.72$, $P = 0.197$, $R^2 = 0.22$; berry borers: $F_{1,18} = 1.07$, $P = 0.382$, $R^2 = 0.15$).

a.



b.



c.

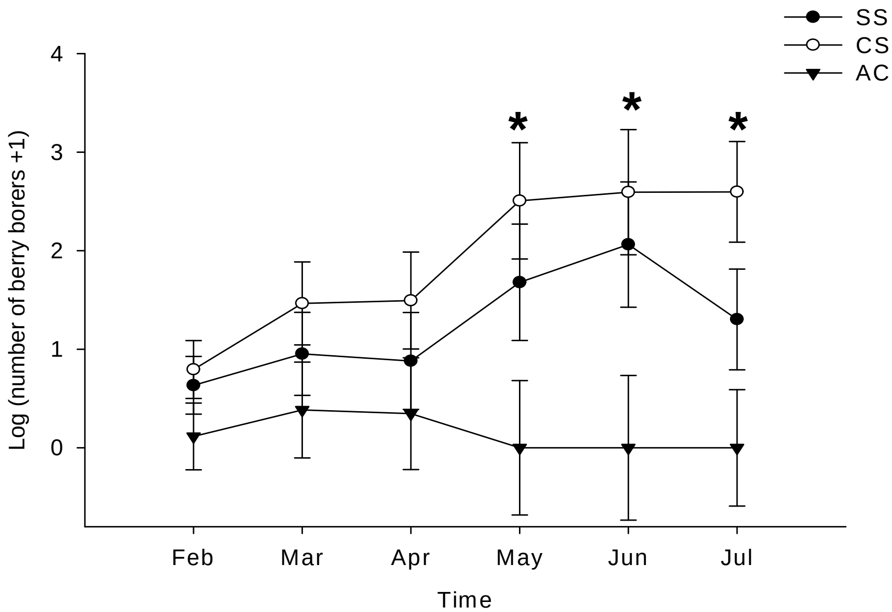


Fig. 1- Seasonal changes in the number of: (a) spider mites, (b) leaf miners, and (c) berry borers per study site in relation to agroforestry management, i.e., SS= simple shade, CS= complex shade, and AC= abandoned coffee agroforests. Means ± SE are given and all developmental stages are pooled. Asterisks represent significant differences between agroforestry management types based on one-way anovas with post-hoc Fisher LSD tests within each month.

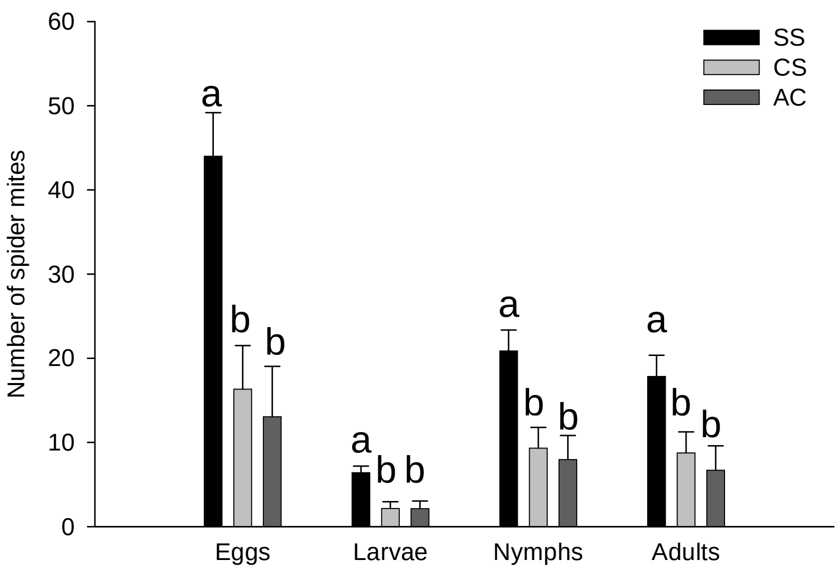
Population stage structure according to agroforestry management

Spider mite population stage structure was affected by agroforestry management. Densities of all developmental stages of spider mites per study site were higher in simple-shade agroforests compared to complex-shade and abandoned coffee agroforests (Fig. 2a; eggs: $F_{2,41} = 10.12$, $P < 0.001$; larvae: $F_{2,41} = 8.92$, $P < 0.001$; nymphs: $F_{2,41} = 7.64$, $P = 0.001$; adults: $F_{2,41} = 5.14$, $P = 0.01$).

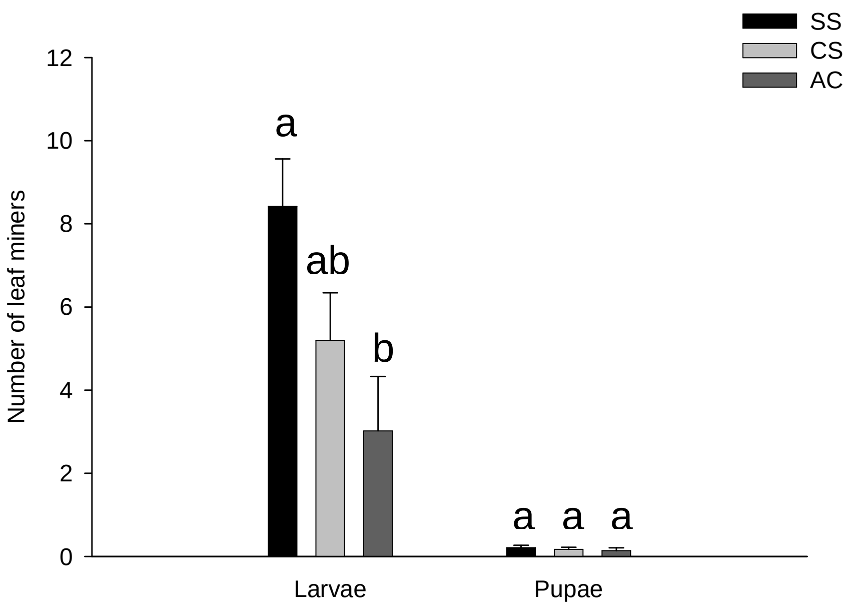
Densities of leaf miner larvae per study site were affected by agroforestry management, with higher densities in simple-shade agroforests compared to abandoned coffee-agroforests, although there were no significant differences in the number of larvae between simple-shade and complex-shade agroforests (Fig. 2b; $F_{2,41} = 4.98$, $P = 0.011$). However, densities of leaf miner pupae per study site did not differ between agroforestry types (Fig. 2b; $F_{2,41} = 0.29$; $P = 0.748$). The number of leaf miner larvae that transformed into pupae was reduced in all agroforestry types, emphasizing the great mortality inflicted mainly by natural enemies and environmental variables during this developmental stage.

Adults of berry borer were sensitive to agroforestry management. The number of adult berry borers per study site were higher in simple-shade and complex-shade agroforests compared to abandoned coffee agroforests (Fig. 2c; $F_{2,19} = 4.45$, $P = 0.024$). The remaining developmental stages of berry borers did not respond to agroforestry management (Fig. 2c; eggs: $F_{2,19} = 2.64$, $P = 0.096$; larvae: $F_{2,19} = 2.30$, $P = 0.127$; pupae: $F_{2,19} = 1.35$, $P = 0.282$).

a.



b.



c.

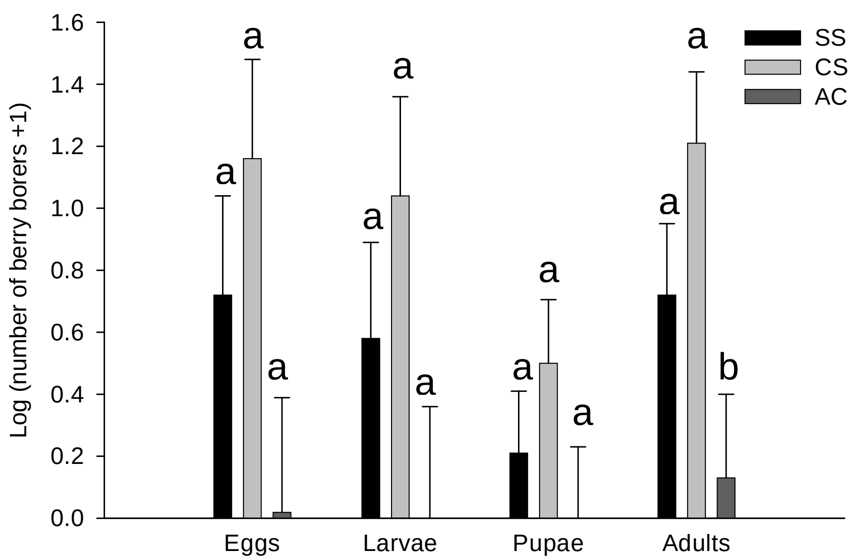


Fig. 2- Population structure of: (a) spider mites (eggs, larvae, nymphs, and adults), (b) leaf miners (larvae and pupae), and (c) berry borers (eggs, larvae, pupae, and adults) per study site in relation to agroforestry management, i.e., SS= simple shade, CS= complex shade, and AC= abandoned coffee agroforests. Means + SE are shown. Different letters indicate significant differences of each pest developmental stage between agroforestry management types based on post hoc Fisher LSD test ($P < 0.05$).

Discussion

Agroforestry management affected population changes of coffee pests over time. Furthermore, specific developmental stages of coffee pests responded differently to agroforestry management.

The three coffee pests showed different patterns of seasonal population dynamics according to agroforestry management. Spider mites reached higher peaks throughout time in intensively managed, lower vegetational diverse simple-shade agroforests compared to complex-shade and abandoned coffee agroforests resulting in higher population densities in this agroforestry type. This pattern was consistent with higher densities of all developmental stages of spider mites in simple-shade agroforests compared to the other two agroforestry types (Fig. 2a). The importance of vegetational management on dynamics of tetranychid mites related here supports results of Prischmann *et al.*, (2005), who found that low and high input grapevine agroecosystems had greater densities of three spider mite species (Acari: Tetranychidae) than nonmanaged ones in Southcentral Washington in the U.S.A.

Leaf miners showed a significant interaction between time and agroforestry type, in that more leaf miners were found in January during the rainy season in simple-shade agroforests than in complex-shade and abandoned agroforests (Fig. 1b). Leaf miners increased from December to February during the rainy season in the region and showed a unimodal population fluctuation with a peak in January, leading to a significant time effect in repeated measures ANOVA. Similar results were found by Nestel *et al.*, (1994), who investigated the role of shaded and unshaded coffee agroforests on population dynamics of leaf miners in Mexico. They did not find effects of agroforestry management on leaf miner densities, however a significant time effect, with higher population densities between March and May. Additionally, leaf miner larvae, but not pupae, responded to agroforestry management, with more larvae in simple-shade than in abandoned coffee agroforests (Fig. 2b).

The number of berry borers increased over the coffee growing season in simple-shade and complex-shade agroforests until the harvest in mid-July, but remained constant in abandoned coffee agroforests. Moreover, only adults of berry borers were sensitive to agroforestry management, with more individuals in simple and complex shade than in abandoned agroforests. The remaining developmental stages of berry borers did not respond to agroforestry management (Fig. 2c).

The three agroforestry types studied here differed in temperature, relative humidity, canopy cover, tree diversity, and coffee density. Environmental variables have been referred to influence several arthropod population parameters (Roininen *et al.*, 1996; Yarnes & Boecklen, 2005; Hofmann & Mason, 2006). Hence, environmental variables characterizing each agroforestry type might have played a key role in influencing the population dynamics and stage structure patterns found here. Therefore, the lower pest densities in more diverse, extensively managed agroforests might be related to high vegetational diversity and complexity in these agroforestry management types according to current theory (Root, 1973; Landis *et al.*, 2000).

Interestingly, the stage structure of coffee pests was affected by agroforestry management, highlighting that each pest developmental stage experiences and responds differently to the vegetational diversity and further related environmental habitat variables acting at local level. Similarly, management effects could be only shown in distinct months.

In conclusion, our results emphasize the importance of vegetational management in influencing coffee pest seasonal population trends, with higher peaks being reached in more intensively managed agroforests. In addition, specific developmental stages of each coffee pest responded to local vegetational management, so that intensive managed agroforests supported higher densities of coffee pests. However, effects were contingent on season and developmental stages. Understanding the outcome of agroforestry management needs to consider the season and pest developmental stage to avoid partially misleading conclusions on pest control.

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CHAPTER 4

ENVIRONMENTALLY-MEDIATED COFFEE PEST DENSITIES IN RELATION TO AGROFORESTRY MANAGEMENT, USING HIERARCHICAL PARTITIONING ANALYSES

Adenir Teodoro, Alexandra-Maria Klein, Teja Tscharntke

Abstract

Understanding pest density patterns in the field is important to account for distinct environmental variables potentially influencing populations across different habitat types. Here, we assessed the relative importance of single environmental abiotic and biotic variables on densities of three major coffee pests, i.e., spider mites, leaf miners and berry borers, in simple, complex and abandoned agroforests of coastal Ecuador, using hierarchical partitioning methods. Most of the independent variation in spider mite and leaf miner densities was accounted for by the abiotic variables temperature and relative humidity, while agroforestry type, relative humidity and tree diversity were more important in explaining densities of berry borers. Furthermore, densities of spider mites and berry borers, but not leaf miners, were affected by agroforestry type, with lower densities in structurally complex agroforests. In conclusion, very different environmental variables influence coffee pest population density. Understanding such species density-environmental relationships provide insights on how to predict and manage populations in the field.

Keywords: spider mites; leaf miners; berry borers; abiotic and biotic habitat variables

1. Introduction

Agroforestry has been emphasized for its biodiversity conservation potential due its forest-like structure (Perfecto et al., 1996; Perfecto et al., 2003; Pineda et al., 2005; Tylianakis et al., 2005; Mcneely and Schroth, 2006) and may also contribute to pest reduction due its complex vegetational structure (Root, 1973; Landis et al., 2000).

Management of agroecosystems controls biotic factors such as tree diversity and density, which in turn influence abiotic parameters such as temperature and relative humidity (Rao et al., 2000; Klein et al., 2002). Such environmental variables often play a key role in structuring natural populations and community structure (Roininen et al., 1996; Yarnes and Boecklen, 2005; Hofmann and Mason, 2006; Luoto et al., 2006, 2007). Studies on species-environment relationships may provide important insights into the proximate fine-scale environmental variables influencing patterns in the field (Miller et al., 2004; Cushman and McGarigal, 2004).

For instance, Heikkinen et al. (2005) calculated the relative contribution of habitat quantity, food resources and microclimatic variables on the abundance of the clouded apollo butterfly (Parnassius mnemosyne L.) in Southwestern Finland. They found that quantifying habitat features (area of semi-natural grassland and deciduous-mixed forest), the amount of resources (host plant and nectar-plant abundance) and microclimate (radiation and windiness) explained highest fractions of the variance for the abundance of the apollo butterfly. Here, we elucidate the relationships between single environmental variables at local scale to densities of three coffee pests, namely spider mites, leaf miners and berry borers in coastal Ecuador. We measured abiotic and biotic habitat variables in 22 agroforestry sites to quantify environmental changes and classified agroforestry types according to local management, so that we could determine the relative contribution of each single habitat variable and agroforestry type to densities of each coffee pest, using hierarchical partitioning methods.

We asked specifically, (1) Which environmental variables are the most important predictors of each coffee pest? (2) How great are the independent and joint contribution of the environmental variables in explaining pest densities? Furthermore, we examined how coffee pest densities change between agroforestry types, i.e. simple, complex and abandoned agroforests.

1.1. Study system

Highland coffee Coffea arabica L. is an important cash crop in tropical America, where it is grown traditionally in agroforests under a diverse canopy of shade trees from Mexico to northern South America (Perfecto et al., 1996; Moguel and Toledo, 1999). Spider mites Oligonychus ilicis McGregor (Acari: Tetranychidae), leaf miners Leucoptera coffeella Guérin-Méneville (Lepidoptera: Lyonetiidae) and berry borers Hypothenemus hampei Ferrari (Coleoptera: Curculionidae: Scolytinae) are known to be the main coffee pests in tropical America (Le Pelley, 1973; Reis and Souza, 1986). Spider mites form colonies on the upper surface of the leaves, which may drop prematurely during heavy infestations (Reis and Souza, 1986). Leaf miners are monophagous on Coffea spp. and their larvae feed in the parenchyma of the leaves (Le Pelley, 1973) causing a reduction in their photosynthetic area and premature defoliation (Reis and Souza, 1986). The berry borer is a beetle considered as the most serious coffee pest worldwide (Murphy and Moore, 1990). Both adult and larval stages feed inside coffee berries, affecting the quality and reducing yields (Le Pelley, 1973).

2. Material and methods

2.1. Study region and site selection

The study was conducted on private farms located within the coffee-growing region of Jipijapa (1°19´60″ S, 80°34´60″ W). The region is located in the province of Manabi, Ecuador and all farms are situated at an altitude ranging from 108 to 466 m a.s.l. The study region has a mean monthly temperature (± SE) of 25.6 ± 0.1 °C and an average monthly rainfall of 115.9 ± 35.1 mm. The rainy season starts in December and ends in May (www.inamhi.gov.ec). The natural vegetation corresponds to semi-deciduous forest, and coffee is traditionally cultivated under a diverse canopy of shade trees on small-holder farms in the region. The original vegetation has been converted to agriculture, predominantly coffee agroforests, which can have sharp borders with other land-use types such as pasture, annual crops, and patches of fragmented forest.

The three habitat types selected were simple-shade agroforests (managed agroforests with 4-9 shade tree species, simple vertical structure, tree density regulated to reduce excessive shading and understorey relatively open, 8 sites), complex-shade agroforests (managed with 9-12 shade tree species, complex vertical structure with a multi-layered canopy, 8 sites) and abandoned coffee agroforests (abandoned for 10-15 years due to low revenues and currently resembling secondary forests, 14-20 shade tree species, forest regeneration and only few old coffee plants remaining, 6 sites) totaling 22 study sites (see table 1 and also Lozada et al., 2007). The management of simple-shade and complex-shade agroforests dependes on individual farmer experience and includes hand-weeding once or twice per year and harvest.

No agrochemicals were used in any site and the minimum distance between sites was around 2 km. The size of coffee farms ranged from 0.7 to 2 hectares.

2.2. Environmental habitat variables

We measured abiotic (temperature and relative humidity) and biotic (canopy cover, tree diversity and coffee density) habitat variables in all 22 study sites to quantify environmental characteristics associated with agroforestry type. Temperature and relative humidity were measured monthly during an entire year under standardized conditions (on sunny days between 10:00-15:00 and in the center of each plantation to avoid edge effects) after placing a digital thermohygrometer (Robert E. White Instruments, Boston, USA) on the ground for 10 minutes. In each month, at least one measurement of temperature and relative humidity in all 22 study sites during coffee pest surveys was conducted and mean values for the period are given. It was not possible to record temperature and relative humidity in all 22 study sites in the same day because of the distance between them and logistic issues, but an effort was made to do measurements within a 3-day period in all sites in each month. Canopy cover (%) was estimated by eye twice (in September 2004 during the dry season and in January 2005 during the rainy season) by the same observer in the center of the nine quadrats described below during coffee pest surveys. Coffee shrub density was assessed once by counting the number of coffee shrubs/ ha in all study sites. Tree species were counted once in a series of nine quadrats (10 x 10 m) laid out in a 3 x 3 grid distanced between the centers of the quadrats of 25 m along both axes in all study sites. The number of all canopy trees with stems greater than 10 cm diameter at breast height (DBH) were recorded (Lozada et al., 2007), and we calculated the Shannon-Wiener index as a measurement for tree diversity.

2.3. Spider mite and leaf miner surveys

We carried out field surveys of spider mites (adults, nymphs, larvae and eggs) and leaf miners (pupae and larvae) in the three types of coffee agroforests at monthly intervals over a whole year (from August 2004 to July 2005). In each study site, we randomly selected 20 coffee plants located at least 5 meters away from habitat boundaries and conducted monthly surveys of spider mites and leaf miners. We evaluated 120 coffee leaves per study site (six per plant) in each survey, and averaged the number of spider mites and leaf miners (all developmental stages pooled) on a per-site basis.

2.4. Berry borer survey

Berry borers were evaluated in the three agroforestry types during the 6-month coffee production period of 2005 (from February to July). We randomly chose 10 coffee plants (located at least 5 meters away from habitat boundaries) per study site and collected 60 fruits per plant (20 fruits from each part, i.e., top, medium and bottom). The fruits were opened and the number of adults, pupae, larvae and eggs of berry borers were counted using a binocular microscope (Stemi SV 11, Zeiss, Germany). All developmental stages were pooled and the number of berry borers was averaged per study site.

2.5. Statistical analyses

We carried out Pearson correlations with all measured environmental habitat variables. The majority (9 out of 10) of the correlations were significant ($p < 0.05$; results not shown), indicating collinearity between variables. The highest correlations were observed between temperature and relative humidity ($r_p = -0.96$, $p < 0.0001$) and between canopy cover and tree diversity ($r_p = 0.79$, $p < 0.0001$). Since abiotic and biotic habitat variables were highly intercorrelated we could not use traditional regression methods to separate effects of single environmental predictors on the response variable. We addressed this problem using hierarchical partitioning, which is a technique dealing with collinearity (Mac Nally, 1996; Heikkinen et al., 2004, 2005). This method estimates the percentage of explained variance of each predictor variable into independent and joint contribution with all other variables, considering all possible models in a multivariate regression (Mc Nally, 1996, 2000; Heikkinen et al., 2004, 2005). Specifically, we used hierarchical partitioning analyses to assess the relative contribution of single abiotic and biotic habitat variables (temperature, relative humidity, canopy cover, tree diversity and coffee density) and agroforestry type to densities of each pest species. Partitioning analyses were conducted with the R statistical package (Mc Nally and Walsh, 2004), using the "hier.part package" (R 2.3.1 R development core team 2004). One-way anovas were performed to determine differences in environmental variables between agroforestry types. Linear regressions between coffee pest densities and environmental variables were performed using Statgraphics plus for Windows version 5.1 (Anonymous, 2001). Repeated measures anovas with type I sequential sums of squares were used to test the effect of the three differently managed agroforestry types on densities of each pest species, removing variance explained by seasonality, using Statistica 7.0 (StatSoft Inc.

1984-2004). Densities of berry borers were log+1 transformed to achieve assumptions of a normal distribution.

3. Results

3.1. Environmental habitat variables

Agroforestry types differed significantly for each environmental variable (Table 1). Simple-shade and complex-shade agroforests were characterized by higher temperature and coffee density compared to abandoned agroforests. In contrast, higher values of relative humidity were found in abandoned agroforests than in simple-shade and complex-shade agroforests. Abandoned agroforests had highest values of canopy cover and tree diversity, whilst complex-shade and simple-shade had intermediate and lowest values, respectively.

Table 1- Environmental variables measured in all 22 study sites for the three agroforestry types (SS= simple-shade agroforests, CS= complex-shade agroforests, and AC= abandoned coffee agroforests). Means ± SE are given and different letters show significant differences between agroforestry types based on post hoc Tukey LSD tests.

Agroforestry type	Temperature (ºC)	Relative humidity (%)	Canopy cover (%)	Tree diversity [a]	Coffee density (shrubs/ ha)
SS	30.3 ± 0.5 a	59.9 ± 1.2 a	49.8 ± 2.7 a	0.4 ± 0.1 a	2891.7 ± 139.1 a
CS	29.0 ± 0.5 a	62.9 ± 1.5 a	59.8 ± 2.9 b	1.0 ± 0.1 b	2370.4 ± 290.7 a
AC	26.9 ± 0.4 b	69.0 ± 0.9 b	72.9 ± 1.4 c	2.1 ± 0.1 c	924.1 ± 139.0 b
P	< 0.01	< 0.001	< 0.0001	< 0.0001	< 0.0001

[a] Shannon-Wiener diversity index was calculated

3.2. Hierarchical partitioning analyses

The relative contributions of the environmental variables differed markedly among the pest species analyzed.

3.2.1. Spider mites

The majority (59.8%) of the explained variation was related to the joint effects of the variables for spider mite densities (Fig. 1a). Temperature had the highest total (independent + joint) value, and also the highest independent contribution (15.9%), followed by relative humidity (8.9%) and agroforestry type (5.8%). The biotic habitat variables canopy cover, tree diversity and coffee density had lower independent values for spider mites. Agroforestry type (12.8%), temperature (12.2%), tree diversity (12.1%) and relative humidity (10.8%) were characterized by high joint contributor values, while canopy cover and coffee density by lower values.

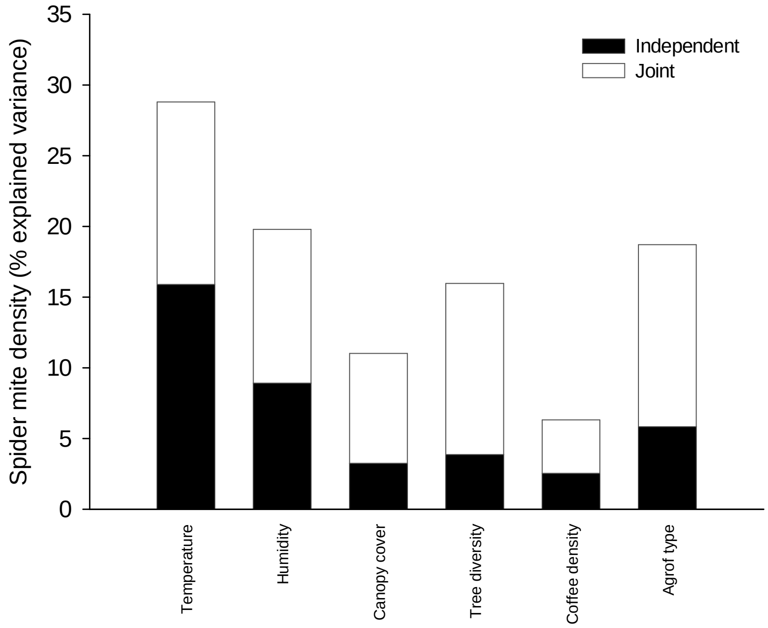
3.2.2. Leaf miners

Joint effects of the variables accounted for 59.5% of the explained variance for leaf miner densities (Fig. 1b). Relative humidity showed the highest total (27.6%) and independent (14.3%) values, whereas agroforestry type (14.8%) followed by relative humidity (13.3%), canopy cover (12.0%) and temperature (11.1%) had higher joint effects compared to tree diversity (6.1%) and coffee density (1.9%).

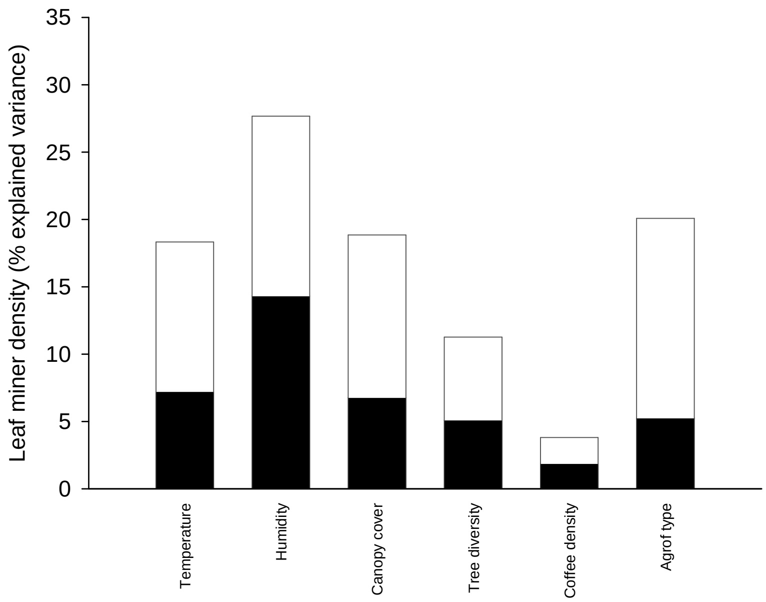
3.2.3. Berry borers

In contrast to spider mites and leaf miners, independent effects of the variables explained over half of the variation (51.0%) for densities of berry borers (Fig. 1c). Agroforestry type alone explained 30.2% of the total value, and was also characterized by the highest independent value (15.1%), followed by relative humidity (9.8%) and tree diversity (9.3%). Joint contribution explained 48.9% of the variation, with agroforestry type exhibiting the highest contribution (15.0%), followed by relative humidity (9.5%) and tree diversity (8.5%). Temperature, canopy cover and coffee density explained lower portions of variation.

a.


Spider mite density (% explained variance)
35
30
25
20
15
10
5
0
Independent
Joint
Temperature
Humidity
Canopy cover
Tree diversity
Coffee density
Agrof type

b.


Leaf miner density (% explained variance)
35
30
25
20
15
10
5
0
Temperature
Humidity
Canopy cover
Tree diversity
Coffee density
Agrof type

c.

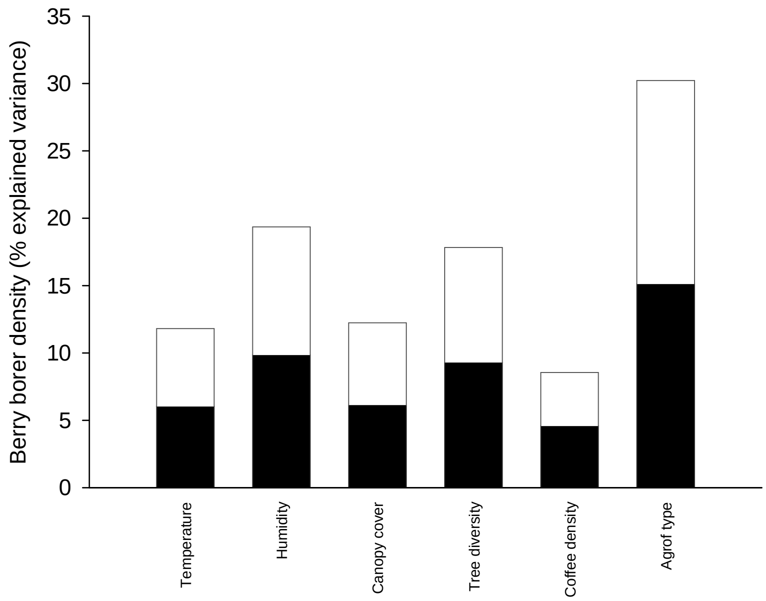
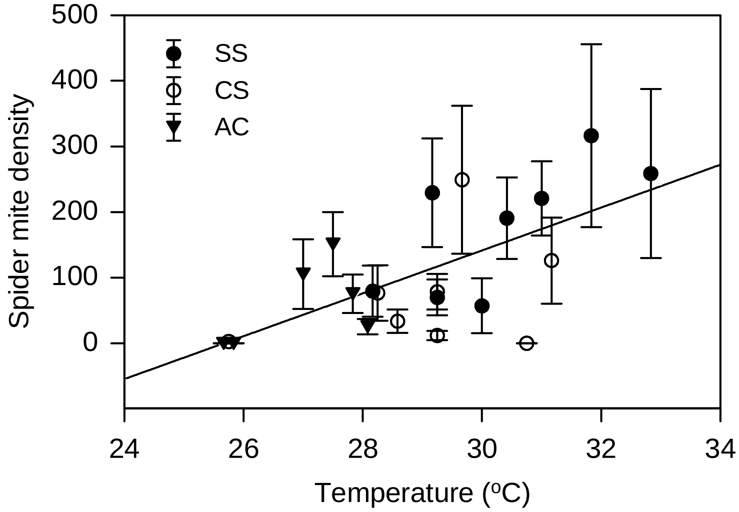


Fig. 1- Hierarchical partitioning analyses showing the independent and joint effects (shown as percentage of the total explained variance) of the five habitat variables and agroforestry type (i.e., simple-shade agroforests, complex-shade agroforests, and abandoned coffee agroforests) for densities of: (a) spider mites (b) leaf miners, and (c) berry borers.

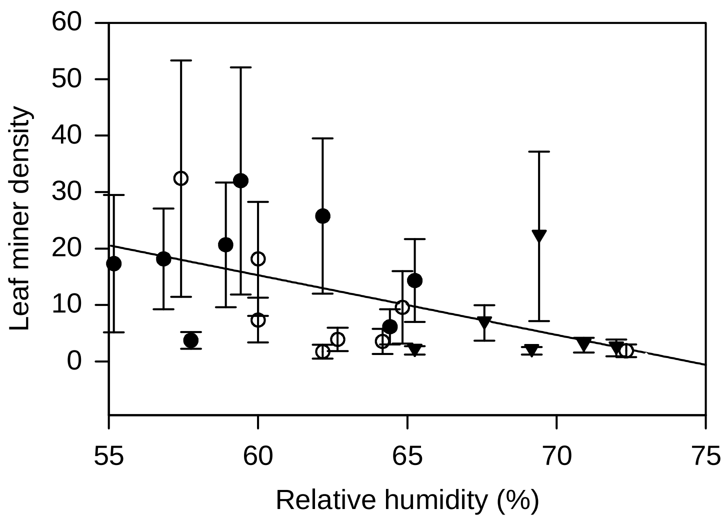
3.3. Relationships between coffee pests and environmental variables

Linear regressions revealed that measured environmental variables have significant effects on coffee pest densities ($p < 0.05$), confirming results from hierarchical partitioning. Density of spider mites was positively correlated with temperature (Fig. 2a) and coffee density, and negatively correlated with relative humidity, canopy cover and tree diversity. Leaf miner density linearly decreased with increasing relative humidity (Fig. 2b) and canopy cover, and increased with temperature. In addition, leaf miner density was not related to tree diversity and coffee density. Berry borer density was negatively related to tree diversity (log+1 transformed data; Fig. 2c), relative humidity and canopy cover, and positively correlated to temperature and coffee density.

a.


500
400
300
200
100
0
Spider mite density
SS
CS
AC
24
26
28
30
32
34
Temperature (ºC)

b.


60
50
40
30
20
10
0
Leaf miner density
55
60
65
70
75
Relative humidity (%)

c.

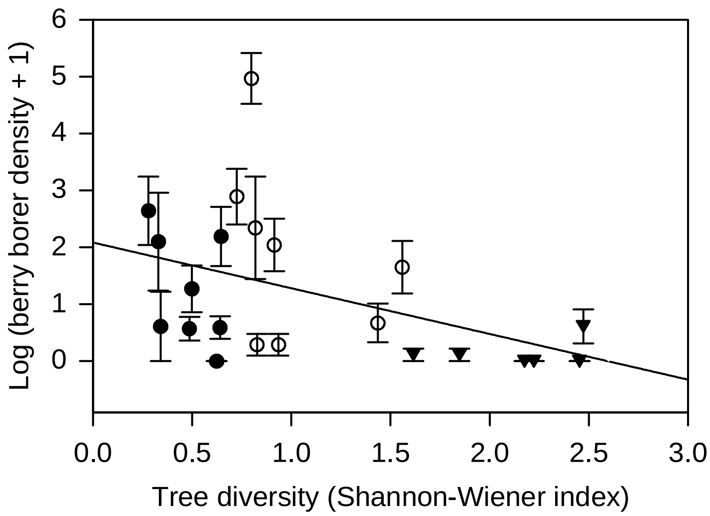


Fig. 2- Some relationships between coffee pests and environmental variables in different agroforestry management types (Filled circles = simple-shade agroforests, open circles = complex-shade agroforests, filled triangles = abandoned coffee agroforests). (a) spider mites and temperature (y = - 425 + 18.3x, $F_{1,262}$ = 19.66, p < 0.0001, R^2= 6.98), (b) leaf miners and relative humidity (y = 45.7 – 0.5x, $F_{1,262}$ = 10.92, p < 0.01, R^2= 4.00), (c) log (berry borers + 1) and tree diversity (y = 2.1 - 0.8x, $F_{1,130}$ = 20.12, p < 0.0001, R^2= 13.40). Mean number ± SE per study site are shown.

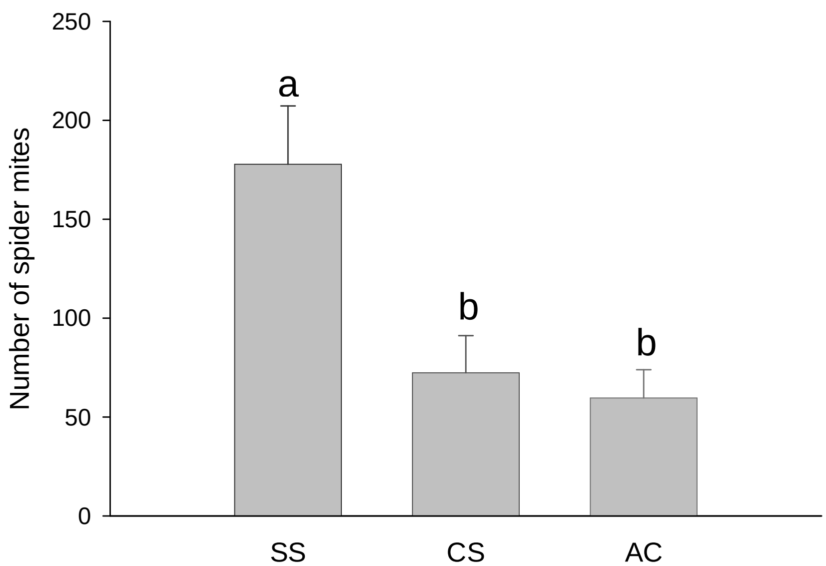
<u>3.4. Pest densities in the three agroforestry types</u>

Agroforestry type influenced densities of spider mites and berry borers, but not leaf miners (seasonality analyses results not shown). The mean number of spider mites per study site did not differ between complex-shade and abandoned coffee agroforests, but was significantly higher at simple-shade agroforests ($F_{2,19}$ = 4.45, p = 0.025; Fig. 3a). The mean number of spider mites at simple-shade agroforests (177.7 + 29.4) was more than twice as large than in complex-shade (72.3 + 18.8) and abandoned coffee agroforests (59.5 + 14.3).

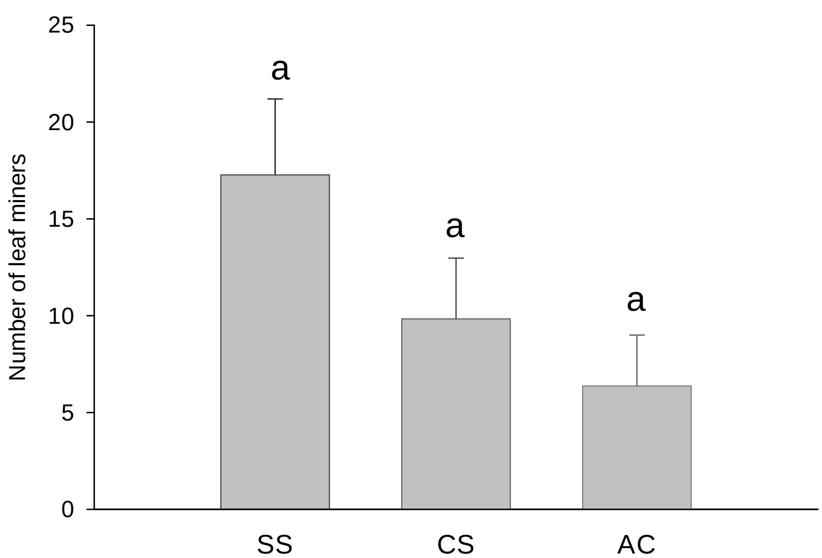
Densities of leaf miners were not affected by agroforestry types (Fig. 3b). The mean number of leaf miners per study site was (17.2 + 3.9) in simple-shade agroforests, (9.8 + 3.1) in complex-shade, and (6.3 + 2.6) in abandoned coffee agroforests ($F_{2,19}$ = 2.46, p = 0.11).

Moreover, simple-shade (1.2 + 0.2) and complex-shade (1.9 + 0.2) agroforests had higher number of berry borers per study site than abandoned coffee agroforests (0.1 + 0.06) (log+1 transformed data; $F_{2,19} = 4.21$, $p = 0.030$; Fig. 3c).

a.



b.



c.

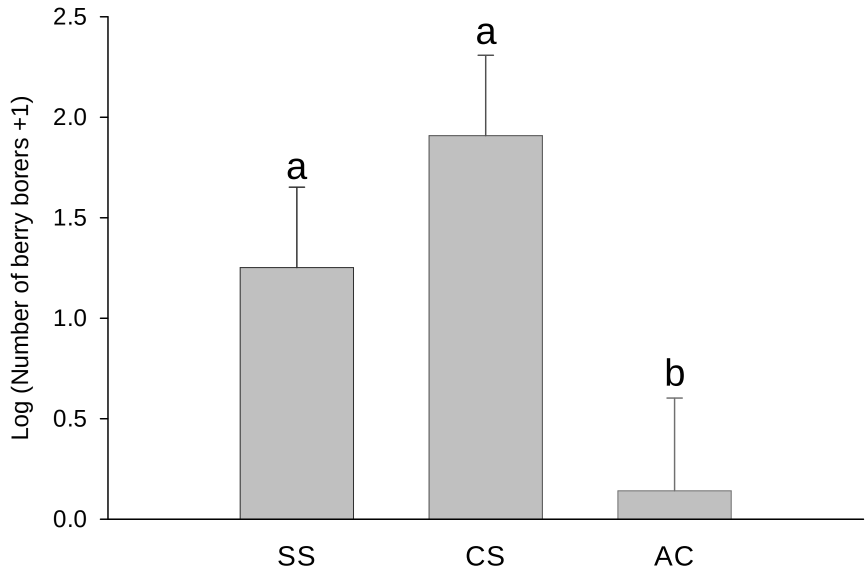


Fig. 3- Mean (+SE) number per study site of: (a) spider mites, (b) leaf miners, and (c) berry borers in the three agroforestry types (SS= simple-shade agroforests, CS= complex-shade agroforests, and AC= abandoned coffee agroforests). Letters indicate significant differences between agroforestry types in a post hoc Fisher LSD test ($p < 0.05$).

4. Discussion

We show that the influence of single environmental habitat variables, changing with local management, on coffee pest densities varied considerably. Moreover, two of the three coffee pests exhibited lower densities in less intensively managed agroforests.

Local management of agroforests determines environmental abiotic and biotic variables (Klein et al., 2002; Shahabuddin et al., 2005; Table 1 this study), which in turn may explain the density patterns found here for the pests in the three differently managed coffee agroforests (Figs. 3a-c). The mean number of spider mites was highest in simple-shade agroforests, which had a less diverse vegetation and consequently higher temperature and lower relative humidity values. The role of temperature and relative humidity on mites has been emphasized by many studies (Gotoh et al., 2004a; Gotoh et al., 2004b; Broufas and Koveos, 2001; De Vis et al., 2006; Figs. 1a and 2a). For instance, Gotoh et al. (2004a) showed that the intrinsic rate of natural increase (r_m) of the spider mite Tetranychus puerariicola (Acari: Tetranychidae) on kidney bean (Phaseolus vulgaris) increases with increasing temperature. Additionally, Bonato et al. (1995) studied the effects of relative humidity on two spider mite species, the cassava green mite Mononychellus progresivus and the cotton red mite Oligonychus gossypii on cassava. They found that low (30%) and high (90%) relative humidity negatively affected development, fecundity, and survival of both spider mite species compared to intermediate (60%) relative humidity. Moreover, neither M. progresivus nor O. gossypii completed their life cycle under a relative humidity of 90%.

Leaf miner densities were unaffected by agroforestry type, although the numbers tended to be higher in simple-shade agroforests. The results of hierarchical partitioning in this study (see also Fig. 2b), support findings of Yarnes and Boecklen (2005) that temperature and relative humidity affect the performance and mortality of two leaf miner species, Phyllonorycter sp. and Cameraria sp. (Lepidoptera: Gracillariidae: Nepticulidae) in Gambel´s oak Quercus gambelii in USA. Also, Nestel et al. (1994) showed that temperature influenced positively densities of the coffee leaf miner L. coffeella along an elevation gradient in Mexico, whereas no effect of plant structural diversity was found between shaded and unshaded coffee plantations.

Densities of berry borers were drastically reduced in abandoned coffee agroforests compared to the other two agroforestry types. We found in hierarchical partitioning that agroforestry type had the highest independent contribution for berry borer densities, while other local environmental variables also contributed significantly to explain densities of this pest (Fig. 1c). In contrast, a study by Soto-Pinto et al. (2002) in rustic coffee plantations in Mexico using pearson correlations found that berry borer incidence was not related to similar environmental variables such as shade species richness and diversity, canopy cover, and coffee density, which explained high portions of variance for densities of berry borers in our study. These contrasting results might have been driven by many factors including differences in methodological and statistical approachs between studies. For instance, while Soto-Pinto et al., 2002 tested the relationship between vegetation attributes and incidence of berry borers with correlation analyses, we used hierarchical partitioning methods which enabled us to calculate the contribution of single environmental variables to densities of berry borers. Additionally, linear regressions between environmental variables and densities of berry borers confirmed results from hierarchical partitioning. The importance of relative humidity and tree diversity for explaining significant portions of the independent variance for densities of berry borers is also emphasized by hierarchical partitioning (see also Fig. 2c). The reduced resource availability in abandoned coffee agroforests (low coffee shrub and, consequently low berry density) might have influenced the low attack rates of the coffee berry borer, although, coffee density explained only a little of the variance for densities of berry borers in hierarchical partitioning.

Furthermore, we found in a parallel study conducted in the same study sites that top-down control exerted by natural enemies did not appear to play a major role in influencing coffee pest population densities across the different agroforestry types. The population densities of the two main natural enemies associated with spider mites and leaf miners in the study region, the predatory mite Amblyseius herbicolus Chant (Acari: Phytoseiidae) and a eulophid parasitoid (Hymenoptera: Eulophidae), respectively, did not differ between simple, complex and abandoned agroforests. In addition, we did not find any parasitoid species or important natural enemy attacking berry borers in the region of study (A. Teodoro, unpublished data). Therefore, their potential influence on the coffee pests studied here might be disregarded.

5. Conclusions

The results found here for spider mite and berry borer densities, but not leaf miners, are in line with hypotheses predicting lower pest densities in more complex agroecosystems (Root, 1973; Landis et al., 2000). Moreover, we depicted the single contribution of environmental variables for coffee pest densities, emphasizing that abiotic and biotic habitat variables determining a given habitat type may play a key role for understanding the effects of land use on pest densities. In conclusion, our results suggest that while studying arthropod density patterns in the field, it is important to take into account the proximate effects of environmental explanatory variables operating at local scales. Understanding such species-environment relationships provide insights on how to predict and manage populations in the field.

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CHAPTER 5

FROM THE LAB TO THE FIELD: CONTRASTING EFFECTS OF MULTITROPHIC INTERACTIONS AND AGROFORESTRY MANAGEMENT ON COFFEE PEST DENSITIES

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Abstract. 1. Only few factors influencing pest populations can be studied in the laboratory. However, many population-driving factors interact in the field, therefore, complementary laboratory and field approaches are required for reliable predictions of real world patterns and processes.

2. Laboratory and field experiments with red spider mites *Oligonychus ilicis* McGregor (Acari: Tetranychidae) and leaf miners *Leucoptera coffeella* Guérin-Méneville (Lepidoptera: Lyonetiidae) on coffee plants *Coffea arabica* L. were combined to study the relative importance of biotic interactions, including resource preferences and natural-enemy impact, and habitat factors such as agroforestry type and management intensity.

3. In the laboratory, leaf discs cut from undamaged coffee plants were significantly preferred by spider mites over those from plants infested with conspecific mites, leaf rust pathogens *Hemileia vastatrix* Berkeley & Broome or leaf miners, resulting in higher reproductive success. Similarly, undamaged plants were preferred by leaf miners over spider mite-infested plants. However, in the field, spider mite densities were positively correlated with leaf miner and leaf rust densities, thereby contrasting with laboratory predictions. Hence, the importance of biotic interactions expected from lab experiments was suppressed by environmental conditions in the field. Furthermore, intensified agroforestry was characterized by higher spider mite densities, while predatory mite *Amblyseius herbicolus* Chant (Acari: Phytoseiidae), leaf miner and parasitoid (Hymenoptera: Eulophidae) densities were not related to agroforestry management.

4. In conclusion, patterns found in the laboratory did not hold for the field, emphasizing the difficulties of extrapolating small-scale experiments to larger spatial scales and the need to combine both approaches.

Key words. competition, land-use management, leaf miners, rust pathogens, spider mites.

Introduction

Patterns and processes found at small spatial scales are often little related to those on larger scales, as shown for invasive plants, locally negatively related to native plant diversity, but regionally positively (Jarnevich *et al.*, 2006). Further examples include, the plant diversity-productivity relationship, which is positive in experimental plants, but negative in real communities (Lepš, 2004), and the response of pollinators to flower resource density (positive at small and negative at large scales, Veddeler *et al.*, 2006). Laboratory experiments are often used to explain and predict patterns found in the field (Enserink, 2002; Hofsvang *et al.*, 2005; Stastny *et al.*, 2006). Standardized lab experiments allow to evaluate the influence of clearly defined parameters, but the number of testable interactions is limited. Biotic interactions such as competition can be studied in the lab, but many real world determinants of species distributions and patterns cannot be addressed in this way. In the field, a wealth of additional and possibly confounding factors are involved, which may result in patterns contrasting with the lab. The complex environment in the field is often difficult or impossible to predict, but only results on the field scale can be used to give practically important management recommendations. Therefore, integrating laboratory and field studies is often a sucessful approach. For example, Thaler *et al.* (2001) showed that flea beetles preferred non-defended tomato plants in the lab, and this preference led to lower densities of beetles on defended plants in the field.

Such preference-performance expectations are in line with the optimal foraging theory, which predicts that animals choose their resources (e.g., host plants or prey) to increase fitness (Jaenike, 1986; Stephens & Krebs, 1986) and avoid conspecific or heterospecific competitors. In addition to competition, which may be evaluated with lab experiments, other factors such as agroforestry management and vegetation diversity are known to affect populations of arthropods in agroecosystems (Klein *et al.*, 2002a; Bianchi *et al.*, 2006; Tylianakis *et al.*, 2006). Moreover, natural enemies may regulate pest densities in the field (Settle *et al.*, 1996; Klein *et al.*, 2002b). Root (1973) postulated two hypotheses to explain herbivore densities in simple and diversified habitats. The enemy hypothesis predicts larger natural enemy densities in diversified habitats due to availability of alternative food and suitable microhabitats, and consequently lower pest densities. The resource concentration hypothesis predicts that herbivores are more likely to attain larger populations in monocultures due to the concentration of their host plants. In addition, the structure and complexity of shade trees in agroforests determine microclimatic conditions, which in turn affect arthropod population densities (Perfecto & Vandermeer, 1996). Therefore, pests might attain larger populations in simple, intensively managed habitat types compared with diverse, extensively managed ones (Tscharntke *et al.*, 2005).

One of the most diverse agroecosystems in the Americas are coffee agroforests. Highland coffee *C. arabica* is an important cash crop and grown traditionally under a diverse canopy of shade trees from Mexico to northern South America (Moguel & Toledo, 1999). Many pests and diseases have been reported on coffee, such as the coffee red spider mite *O. ilicis*, the coffee leaf miner *L. coffeella* and the leaf rust *H. vastatrix* (Le Pelley, 1973; Reis & Souza, 1986). Colonies of spider mites are found on the upper leaf surface, which may drop prematurely as a consequence of higher infestation (Reis & Souza, 1986). Leaf miners are monophagous on *Coffea* spp. and their larvae feed in the parenchyma of the leaves (Le Pelley, 1973) causing a reduction in their photosynthetic area (Reis & Souza, 1986). Leaf rust is a widespread coffee disease in the tropics, and its damage is mainly caused by a combination of reduction in the photosynthetic capacity and premature defoliation at high infection levels (Kushalappa & Eskes, 1989). The predatory mite *A. herbicolus* and a eulophid parasitoid are the principal natural enemies found in the study region associated with spider mites and leaf miners, respectively (A. Teodoro, unpublished data).

To our knowledge, no published studies have addressed the relative importance of small-scale biotic interactions versus large-scale land-use management and presence of natural enemies for pest densities in agroforests. The outcome of laboratory bio assays with manipulated field experiments and field surveys were combined to identify the factors influencing populations of spider mites and leaf miners in the field.

The following specific predictions were tested:

1. Spider mites prefer undamaged coffee plants over those infested by con- and heterospecific organisms, because undamaged plants should be of better quality, and therefore benefit the mites. Similarly, leaf miners are predicted to prefer undamaged coffee plants over spider mite-infested plants.

2. Agroforestry type, differing in management intensity, influences the density of spider mites, leaf miners and their natural enemies in the field in a complex way, which cannot be simply predicted by the results of lab experiments.

Materials and methods

Mite rearing and plants

Spider mites were collected from coffee agroforests (see details on the study region below) and reared on six-month old potted coffee plants (*Coffea arabica* L., var. Caturra), which supported roughly 22 leaves each. Coffee plants containing spider mite colonies were placed inside a cage consisting of a wooden frame (100 x 50 x 92 cm) covered with a 1 mm mesh size.

Six-month old potted coffee plants were infested with around 100 adult spider mites two weeks before experiments and showed visible damage but were not overexploited. Mined plants were obtained by placing coffee plants for one week in a coffee agroforest heavily infested with leaf miners. Leaf rust-infected plants were obtained by gently rubbing leaves of undamaged plants with wet cotton-wool saturated with rust spores. Plants were kept inside cages (see above) and sprayed daily with water in order to favour rust infection. Typical yellow circular spots on the upper surface and yellow spores on the underside of leaves were usually visible within 25-35 days, indicating rust infection.

Preference of spider mites

Individual two-choice arenas were used to investigate the preference of spider mites. Leaf discs (2.5 cm diameter) were taken from coffee plants, cut in half, and two halves (each from a different treatment) were glued together using the instant adhesive Super Bonder (Henkel Loctite, Connecticut, U.S.A.). The discs were put underside down in a Petri dish covered with wet cotton wool. An entomological pin was put in the centre of each disc. A single unmated spider mite female (15-17 days old), which was at the beginning of her reproductive period (Reis & Alves, 1997), was placed on the pin and its position was recorded after one hour and 24 hours. The following two-choice experiments were carried out: (1) undamaged (without pests or rust pathogens) disc halves vs. disc halves previously infested by conspecific mites, (2) undamaged disc halves vs. mined disc halves, and (3) undamaged disc halves vs. disc halves infected by rust pathogens. All disc halves were cleaned with wet cotton-wool to remove mites and their products such as faeces, webs, eggs and moult skins from conspecific-infested treatments. Undamaged, mined and rust-infected disc halves were also cleaned in the same way. Each mined disc had only one mine covering ca. 30 % of the mined half. Similarly, care was taken to ensure only one rust pustule per disc that covered ca. 30 % of the rust-infected half. Each experiment was replicated 47 – 63 times. To avoid pseudoreplication

(Hurlbert, 1984), different animals and leaf discs were used in each replicate, and each disc half was taken from a different plant.

Reproductive success of spider mites

For each treatment, a single unmated spider mite female (15-17 days old) was placed on a coffee leaf disc. Discs were placed individually underside down in a small Petri dish covered with wet cotton-wool. Progeny and mortality assessments were made daily for seven days. The following treatments were tested: (1) undamaged discs (without pests or rust pathogens), (2) previously conspecific-infested discs, (3) mined discs, and (4) leaf rust-infected discs, with 20 replicates each. In each replicate, animals were tested only once and each leaf disc taken from a different plant. Using data from reproduction and mortality, we calculated the instantaneous rate of increase (r_i) of spider mites as a fitness measure. This index is calculated using the equation $r_i= [\ln (N_f/N_o)]/\Delta t$, where N_f is the final number of living mites (including eggs and immatures), N_o is the initial number of mites, and Δt is the interval (days) elapsed between the start and the end of the bioassay (Walthall & Stark, 1997). The instantaneous rate of increase is closely correlated with the intrinsic growth rate (r_m) and positive r_i-values indicate population increase, whereas negative r_i-values indicate decrease and $r_i= 0$ a stable population (Walthall & Stark, 1997).

Preference of leaf miners (field manipulation)

The preference of the coffee leaf miner was studied on undamaged or spider mite-infested plants, following a method modified after Pallini *et al.* (1997). Six potted coffee plants were arranged in a circle (80 cm diameter) in a coffee agroforest that was infested naturally with leaf miners. Half of the plants were undamaged and half infested with spider mites (as described above). In each experiment, plants with and without spider mites were alternated, so that each spider mite infested plant had two neighbouring undamaged plants and vice versa. Sticky glue was applied at the base of each plant to deter crawling insects such as ants. Wild leaf miners were allowed to oviposit on undamaged or spider mite infested plants for a period of 26 days in the coffee agroforest. Afterwards, the number of living larvae of leaf miners per leaf in each plant was recorded and referred to as preference. The experiment was replicated four times, each time with different undamaged and infested plants, but in the same coffee agroforest, so we used a repeated block design, with four blocks in time, each containing six plants.

Field sampling

The study region is located around the town of Jipijapa (17N 546800 m, E 9849274 m) in the province of Manabi, Ecuador, and is situated at an altitude between 108 and 466 m a.s.l. Field studies were conducted in three different types of coffee agroforests to determine whether population densities of spider mites were correlated with population densities of leaf miners and leaf rust. Furthermore, the effect of agroforestry type and management intensity (see below) on the density of spider mites, leaf miners, and their respective natural enemies, predatory mites and parasitoids was investigated. The three habitats selected were simple-shade agroforests (intensively managed with 4-9 shade tree species and understorey often cleared, 8 sites), complex-shade agroforests (extensively managed with 9-12 shade tree species, 8 sites) and abandoned coffee agroforests (abandoned for 10-15 years, 14-20 shade tree species, forest regeneration and only few old coffee plants left, 6 sites) totaling 22 study sites. No agrochemicals were used in the study sites. The minimum distance between agroforestry sites was ca. 2 km. In each study site, 20 coffee plants were randomly selected and a monthly survey of spider mites, leaf miners, leaf rust, predatory mites and parasitoids was conducted during an entire year. 120 coffee leaves per study site (six per plant) were evaluated in each survey. Abiotic (temperature and relative humidity) and biotic (canopy cover, tree diversity and coffee density) habitat variables were measured in all agroforestry sites to quantify environmental changes associated with agroforestry type and with increasing management intensity. Temperature and relative humidity were measured monthly (10:00-15:00) with a digital thermohygrometer (Robert E. White Instruments, Boston, U.S.A.). Canopy cover (%) was estimated by eye twice (in September 2004 during the dry season and in January 2005 during the wet season) and coffee shrub density/ ha was counted once in all study sites. Tree species were recorded in a series of nine quadrats (10 x 10 m) in all study sites (Lozada *et al*., 2007), and the Shannon-Wiener index was calculated as a measurement for tree diversity.

Statistical analyses

For the preference studies of spider mites, two-sided binomial tests (Pallini *et al.*, 1997) were used in order to analyse differences in the fractions of mites choosing either of the two disc halves. Preference of leaf miners for undamaged versus spider mite-infested plants in the field manipulation study was analysed with linear mixed effects models, using block entering first as a random factor and treatment (control vs. spider mite infested) as a fixed factor. One-way ANOVAs were used to characterize agroforestry types with habitat variables, to analyse spider mite reproduction, and to determine the differences in management intensity between agroforestry types. Spearman rank correlations were used to analyse relationships between all measured habitat variables (Sokal & Rohlf, 1995). Because abiotic and biotic habitat variables were intercorrelated, a factor analysis was used for data reduction (Klein *et al.*, 2002a). The resulting factor (hereafter "management intensity") was significantly positive related to temperature and density of coffee plants, negatively related to canopy tree cover and tree diversity and humidity (Table 1), and had an eigenvalue of 3.69 that explained 73.86 % of the variance in the five habitat variables. General linear models (GLMs) with type I sequential sums of squares were used to test the influence of leaf miners and leaf rust on the density of spider mites. Agroforestry type and time entered the model as random factors to remove variance explained by the coarse environmental differences associated with the different management types and by seasonal repeated measures, followed by leaf miner or leaf rust densities as a fixed factor. Subsequently, the influence of "management intensity" and agroforestry type (i.e. simple-shade agroforests, complex-shade agroforests or abandoned coffee agroforests) on population densities of spider mites and leaf miners was tested, using GLMs. Agroforestry type entered the model first as a fixed factor, followed by management intensity as a covariable, and interactions between the two predictors. GLMs were also used to test the effects of management intensity on densities of predatory mites and parasitoids. Whenever necessary, data were log+1 transformed to meet assumptions of a normal distribution. Analyses were performed using Statistica 7.0 (StatSoft Inc., 1984-2004).

Table 1- Spearman´s rank correlations for abiotic and biotic habitat variables measured in all 22 study sites. (Correlations with "management intensity", calculated by a factor analysis combining five habitat parameters – see methods).

	Management intensity	Temperature (ºC)	Relative humidity (%)	Canopy cover (%)	Tree diversity
Temperature (ºC)	0.88*	_	_	_	_
Relative humidity (%)	-0.89*	-0.96*	_	_	_
Canopy cover (%)	-0.88*	-0.67*	0.69*	_	_
Tree diversity [a]	-0.89*	-0.71*	0.69*	0.80*	_
Coffee density	0.69*	0.44*	-0.39 n.s.	-0.65*	-0.76*

[a]Shannon index was calculated for tree diversity. Significance level, $P < 0.05$.

Results

Preference of spider mites

(1) Spider mite infested leaves

Spider mites preferred undamaged disc halves over previously conspecific-infested disc halves after one and 24 hours. Of 47 mites tested, 72.34 % preferred undamaged and only 27.66 % preferred previously conspecific-infested disc halves (Fig. 1a, top bar; $P < 0.05$) after one hour. After 24 hours, 76.60 % chose undamaged disc halves (Fig. 1a, bottom bar; $P < 0.001$).

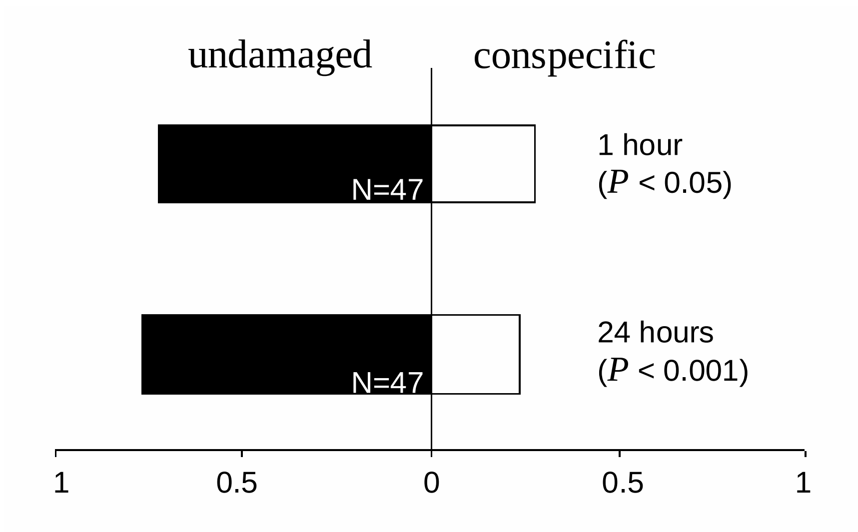
(2) Rust-infected leaves

Spider mites also showed preference for undamaged disc halves over rust-infected disc halves. Of 63 mites tested, 65.08 % chose undamaged disc halves and 34.92 % chose rust-infected disc halves after one hour (Fig. 1b, top bar; $P < 0.05$). After 24 hours, 73.02 % of the mites were found on undamaged disc halves (Fig. 1b, bottom bar; $P < 0.001$).

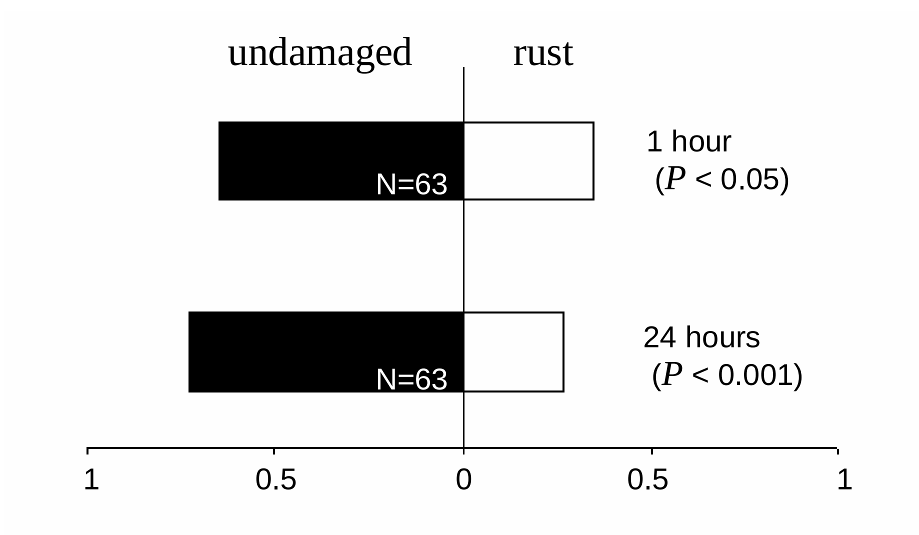
(3) Mined leaves

Spider mites preferred undamaged disc halves over mined disc halves. Of 49 mites tested, 69.40 % preferred undamaged half discs and 30.60 % preferred mined half discs after one hour (Fig. 1c, top bar; $P < 0.05$). After 24 hours, even 87.76 % of spider mites preferred undamaged half discs (Fig. 1c, bottom bar; $P < 0.0001$).

a.



b.



c.

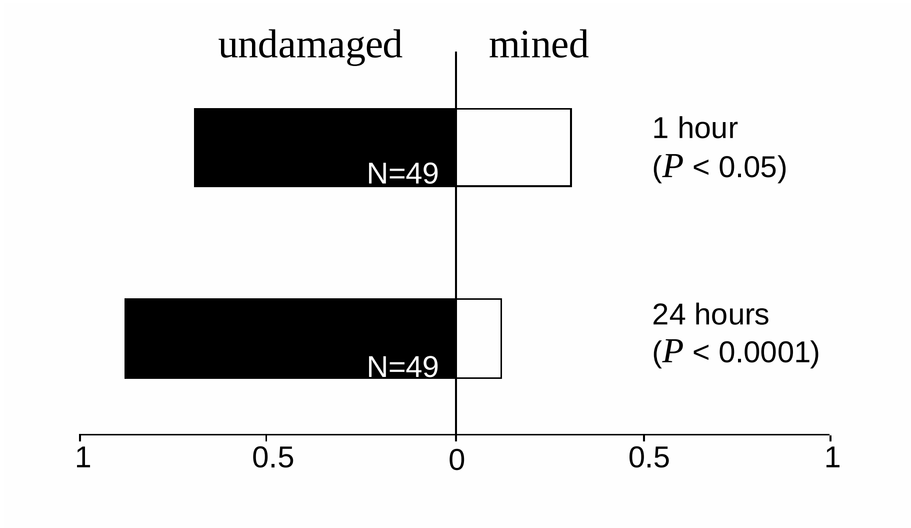


Figure 1- Fractions of spider mites in a two-choice arena when offered the choice between: undamaged disc halves (left) and (a) conspecific-infested disc halves, (b) rust-infected disc halves, and (c) mined disc halves (right) after one (top bar) and 24 hours (bottom bar). Numbers inside bars represent the number of replicates. Significance level is given (two-sided binomial test).

Reproductive success of spider mites

The progeny production (eggs and immatures) of spider mites was highest on undamaged discs, intermediate on rust-infected discs, and lowest on conspecific infested and mined discs ($F_{3,76}$= 66.02, P < 0.0001). The total number of offspring produced per female (in 7 days) on mined discs was reduced by up to 41.74% compared with those produced on undamaged discs (data not shown). Consequently, the instantaneous rate of increase was highest on undamaged discs, followed by rust, and lowest on conspecific and mined discs ($F_{3,76}$= 45.49, P < 0.0001; Fig. 2). Hence, spider mites reared on undamaged discs for seven days had a higher growth rate compared with those reared on infested discs.

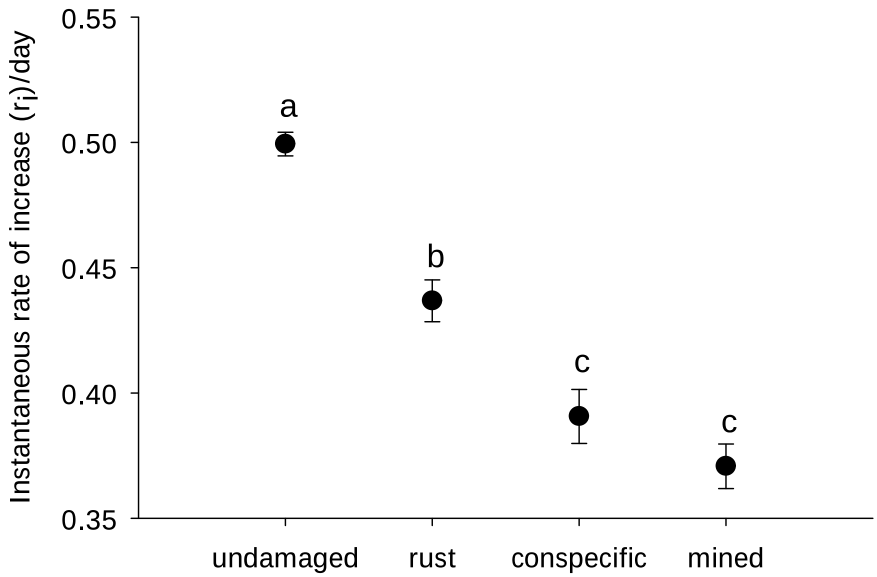


Figure 2- Instantaneous rate of increase (r_i/ day) per female of spider mites feeding on undamaged, rust infected, previously conspecific or mined leaf leaf discs for 7 days. Means ± SE are given. Letters indicate significant differences between treatments in a post hoc Tukey HSD test ($P < 0.05$).

Preference of leaf miners

The number of leaf miner larvae found per leaf after 26 days was significantly (nearly fourfold) higher on undamaged plants compared with spider mite-infested plants ($F_{1,19}$= 23.82, $P < 0.001$; Fig. 3).

Field sampling

During field surveys over an entire year, spider mite densities were positively correlated with leaf miner densities ($F_{1,230}$= 8.14, $P < 0.01$, R^2= 0.70) and with leaf rust densities ($F_{1,230}$= 13.04, $P < 0.001$, R^2= 0.71; Fig. 4).

Simple-shade and complex-shade agroforests had higher temperature ($F_{2,19}$= 8.91, $P < 0.01$), and coffee density ($F_{2,19}$= 20.49, $P < 0.0001$) than abandoned coffee agroforests. Conversely, highest values of relative humidity ($F_{2,19}$= 10.36, $P < 0.001$) were found in abandoned coffee agroforests and lowest values in simple-shade and complex-shade agroforests. Abandoned coffee agroforests were also characterized by highest canopy cover ($F_{2,19}$= 17.89, $P < 0.0001$) and tree diversity ($F_{2,19}$= 63.42, $P < 0.0001$), while complex-shade and simple-shade agroforests had intermediate and lowest values, respectively. The management intensity factor was significantly affected by agroforestry types ($F_{2,21}$= 55.55, $P < 0.0001$), such that simple-shade agroforests had higher management intensity values, whilst complex-shade agroforests and abandoned coffee agroforests had intermediate and lower management intensity values respectively.

Management intensity was significantly positive related to spider mite densities ($F_{1,20}$= 5.52, $P < 0.05$; Fig. 5a). Agroforestry type influenced the density of spider mites significantly ($F_{2,19}$= 5.35, $P < 0.05$), with highest densities in simple-shade agroforests and lowest in complex-shade and abandoned coffee agroforests. In contrast, leaf miner densities were not affected by agroforestry type ($F_{2,19}$= 2.38, $P = 0.124$, data not shown) or by management intensity within each type ($F_{1,20}$= 1.14, $P = 0.300$; Fig. 5b). Furthermore, management intensity was neither related to densities of predatory mites ($F_{1,20}$= 0.16, $P = 0.686$; Fig. 5c) nor to densities of parasitoids ($F_{1,20}$= 0.73, $P = 0.403$; Fig. 5d).

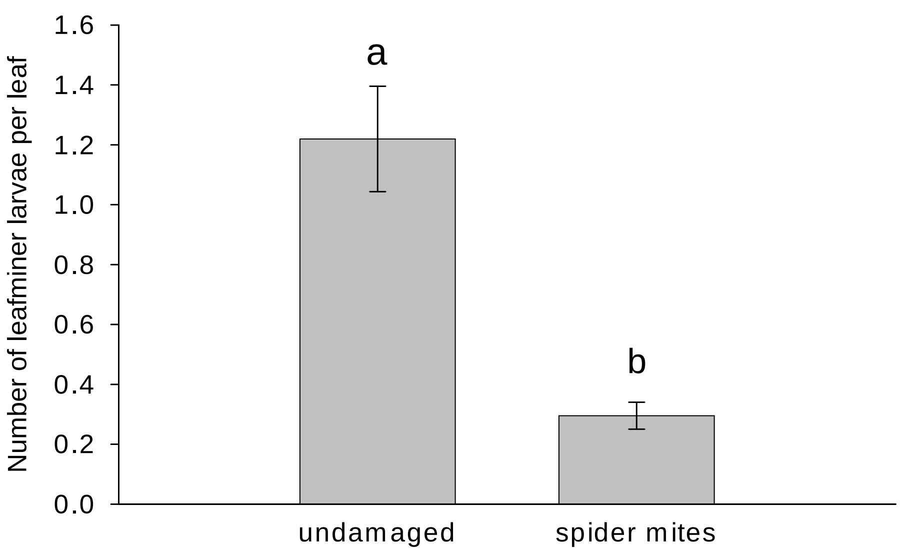


Figure 3- Mean number of leaf miner larvae per leaf on undamaged or spider mite infested plants. Six potted coffee plants, three undamaged plants and three spider mite infested plants, were placed in a circle in a naturally leaf miner infested coffee agroforest. Arithmetic means ± SE and data from four replicate experiments are shown. Different letters indicate significant differences between treatments in a post hoc Tukey HSD test ($P < 0.05$).

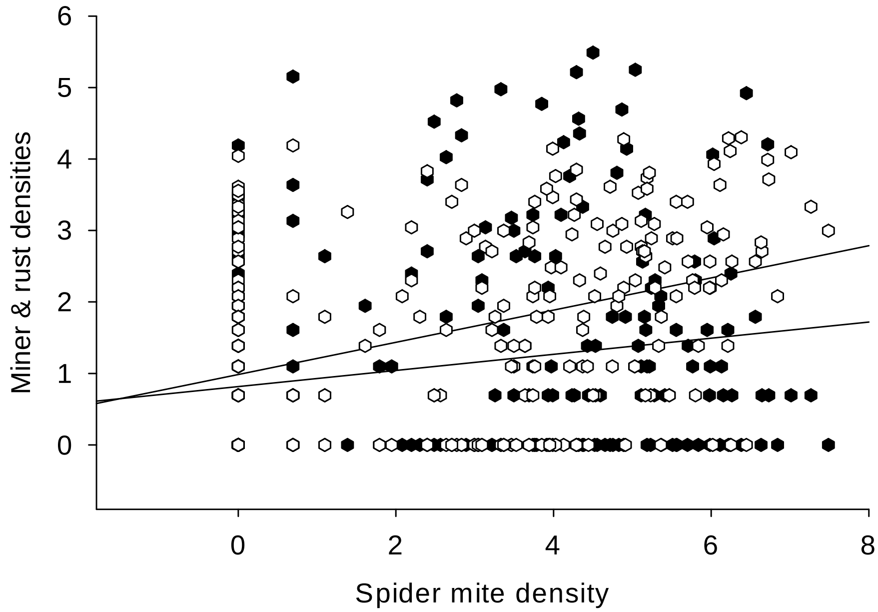
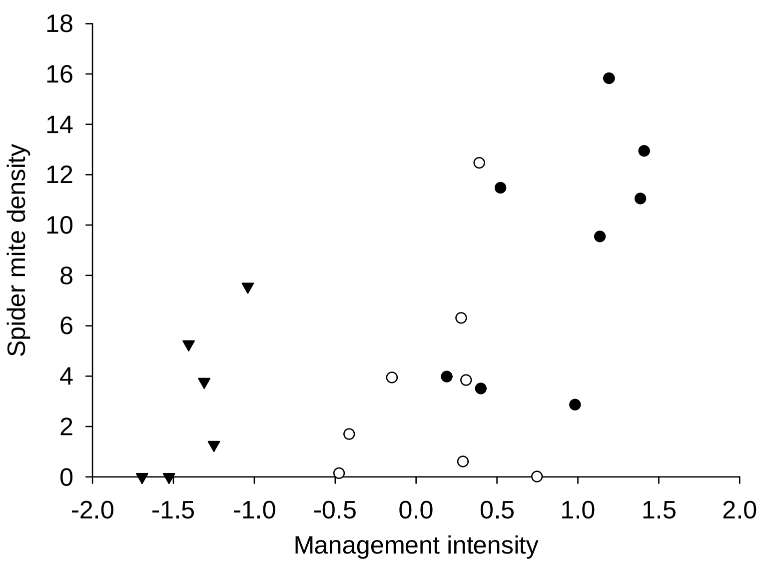
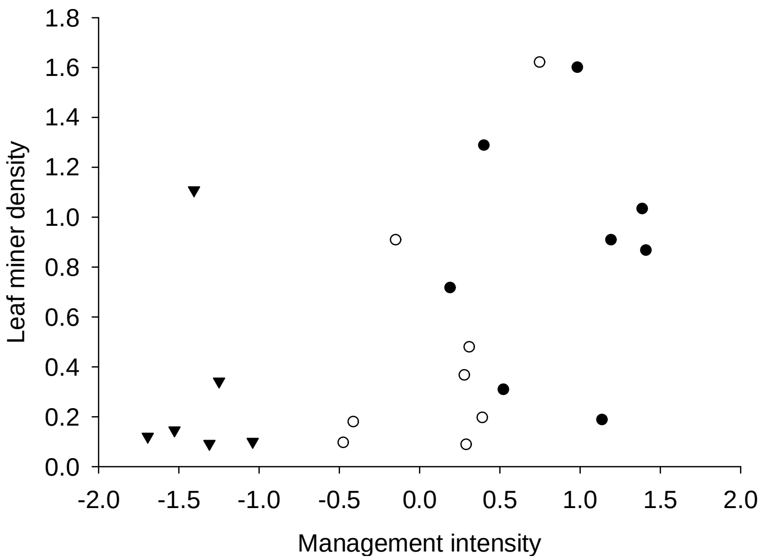


Figure 4- Correlations between densities of: spider mites and leaf miners (filled hexagons; lower regression line), and spider mites and leaf rust (open hexagons; upper regression line) in the field. Log + 1 transformed data and monthly values per study site over a whole year are given.

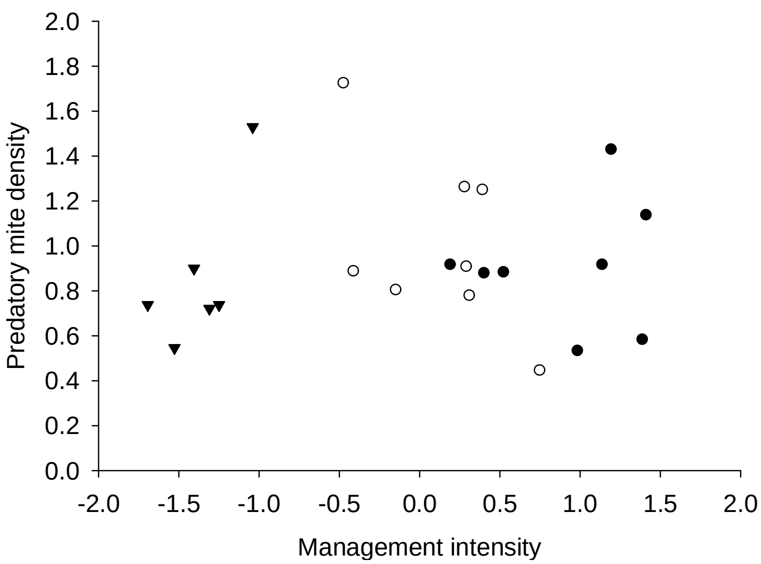
a.



b.


Leaf miner density
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
-2.0
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
2.0
Management intensity

c.


Predatory mite density
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
-2.0
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
2.0
Management intensity

d.

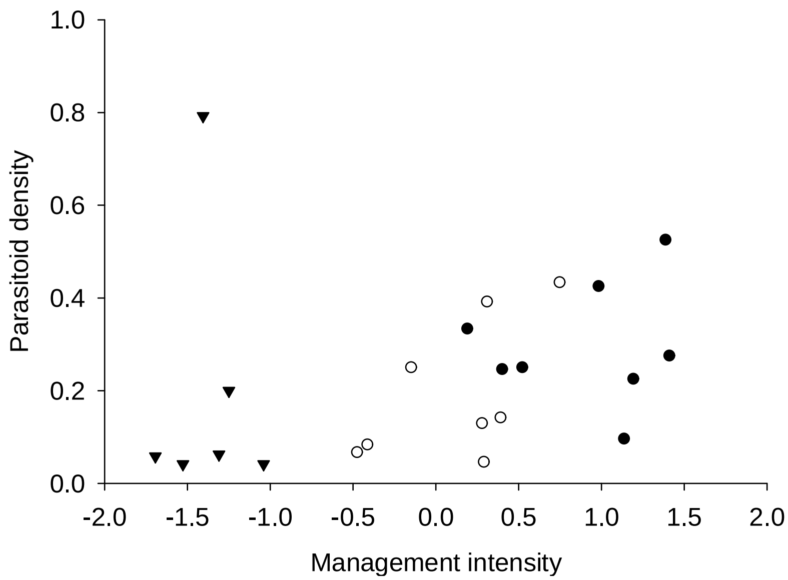


Figure 5- Management intensity in relation to densities of (a) spider mites, (b) leaf miners, (c) predatory mites, and (d) parasitoids. Means per plant for each study site are shown. Management intensity was calculated by combining 5 abiotic and biotic habitat variables using a factor analysis (see methods, Table 1). High management intensity values indicate intensified agroforests (as for simple-shade agroforests). Filled circles = simple-shade agroforests, open circles = complex-shade agroforests, filled triangles = abandoned coffee agroforests.

Discussion

Preference-performance results from the laboratory led to the prediction that coffee pests avoid interspecific competitors. However, this prediction was not supported by field observations. Rather, agroforestry type and management intensity proved to be more important than preference and fitness on a leaf scale for influencing densities of spider mites under field conditions.

In the laboratory, spider mites showed strong preferences for undamaged over pest or pathogen infested disc halves. In all experiments, the preference for undamaged disc halves was more pronounced after 24 hours, indicating that some mites needed time to evaluate leaf quality. Spider mites feeding on conspecific, leaf miner infested or rust infected leaf discs had lower fecundity and reduced growth rates compared with those spider mites that had fed on undamaged discs.

Induced resistence might have played an important mediating role in the avoidance of infested leaves by spider mites in our experiments (Bernays & Chapman, 1994). For example, Stout *et al.* (1998) found that previous feeding by the noctuid larvae *Helicoverpa zea* increased resistence of tomato to an aphid species *Macrosiphum euphorbiae*, a spider mite species *Tetranychus urticae*, a noctuid species *Spodoptera exigua* and to the phytopathogen *Pseudomonas syringae*. Similarly, former herbivory by spider mites on cotton cotyledons caused newly produced, uninjured leaves to be more resistent to the two-spotted spider mite *Tetranychus urticae* than undamaged plants (Karban & Carey, 1984).

As spider mite preference matched fitness under laboratory conditions, in accordance with predictions from optimal foraging theory, the same trend could be expected in the field. However, population densities of spider mites were positively correlated with population densities of leaf miners and leaf rust (even after removing variance explained by agroforestry types and seasonality) in the field, thereby contrasting with lower preference and reduced fitness on infested plants predicted by lab studies.

Spider mites produced larger populations in simple-shade agroforests than in complex-shade and abandoned coffee agroforests. The higher pest density in intensified agroecosystems is often related to changes in abiotic and biotic habitat variables (Perfecto & Vandermeer, 1996; Klein *et al.*, 2002a). In this study, increasing management intensity, from high to low structural agroforest complexity was associated with increasing temperature and coffee density as well as decreasing humidity, canopy cover, and tree diversity and was related to density of spider mites in the field. The higher pest density in intensified systems support findings from cocoa agroforests in Indonesia, where higher densities of phytophagous species in intensively- compared with extensively-managed cocoa agroforests, was related to similar changes in abiotic habitat variables (Klein et al., 2002b). Hence, microclimatic variables in the field appeared to be major mechanisms behind spider mite density patterns found here.

Naturally colonising leaf miners strongly preferred undamaged coffee plants over spider mite-infested coffee plants in a manipulative field choice experiment. Similarly, Digweed (2006) found that the leaf-mining sawfly *Profenusa thomsoni* (Hymenoptera: Tenthredinidae) avoided ovipositing on birch leaves, damaged artificially or by previous infestations with the leaf-mining *Fenusa pumila* (Hymenoptera: Tenthredinidae). In this study and in contrast to spider mites, population densities of leaf miners were not influenced by agroforestry type or by management intensity, supporting findings of Nestel *et al*. (1994) who also did not find differences in leaf miner density between shaded and unshaded coffee agroecosystems.

Reduced predator-prey ratios in intensified systems may also contribute to pest problems (Settle *et al.*, 1996; Klein *et al.*, 2002b), but in this study, there were no differences in the densities of the main predatory mite and parasitoid found in the three agroforestry types of the region, so we might disregard their potential influence on spider mite and leaf miner densities (Figs. 5c and 5d, respectively).

In conclusion, the results reported here show the difficulty in predicting field patterns from laboratory results and vice versa, making questionable any management guidelines from a laboratory approach in isolation. Avoidance of intraspecific and interspecific competition, and corresponding resource preference in the lab studies, contrasted with field performance where spider mite, leaf miner and rust densities were positively correlated. Agroforestry intensification enhanced pest densities in the field, so that diversified complex and abandoned agroforests, which had a lower level of management intensity, benefited from reduced pest problems. Those population density patterns were driven by environmental variables acting at the field scale. Therefore, lab and field studies should be combined in order to determine the relative importance of local management driving mechanisms influencing arthropod densities in the field.

Acknowledgements

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SUMMARY

Ongoing landscape anthropogenic modification in the tropics has caused biodiversity losses of many taxa, threatening key ecosystem processes. Traditional coffee agroforests, which are the only forest-like vegetation remaining in some regions of the tropics, have been emphasized as important refuges for biodiversity and may also contribute to pest supression due its complex vegetational structure. Agroforestry management largely varies among coffee farmers and may influence arthropod population patterns through changes in environmental conditions. Ecological interaction experiments between organisms are often used to predict and explain field patterns and processes. However, many population-driving factors such as environmental variables are determined by land-use management, making real world field patterns difficult to predict from small-scale experiments.

The study was conducted on private farms located in the coffee growing region of Jipijapa, province of Manabi, Ecuador. The region is considered a hotspot for biodiversity conservation and its original vegetation has been converted to agriculture. We selected three coffee agroforestry types according to local management: simple-shade agroforests with low shade tree diversity, complex-shade agroforests with intermediate shade tree diversity, and abandoned coffee agroforests with high shade tree diversity.

We assessed the role of agroforestry management and season on influencing the community of coffee-inhabiting mites (Chapter 2). We show that management intensification, from abandoned, complex-shade to simple-shade agroforests negatively affected species richness of mites on coffee. Further, more species and higher densities of mites were found in the dry season compared to the rainy season. Overall, a pest spider mite and its predatory mite attained higher densities in more intensively managed agroforests during the dry season. Additionally, higher predator-prey ratios were found in complex-shade agroforests, indicating that the predatory mite contributed to spider mite reduction in low-intensity agroforests.

We investigated the population dynamics of coffee pests (i.e. spider mites, leaf miners, and berry borers) in relation to agroforestry management. Furthermore, we assessed how specific developmental stages of coffee pests respond to agroforestry management (Chapter 3). We show that agroforestry management affects seasonal patterns of coffee pests with higher peaks being reached in more intensively managed agroforests. Further, there was an interacting effect of vegetational diversity and developmental stages of coffee pests. Overall, specific pest developmental stages built up higher densities in more intensively managed agroforests.

We determined the relative importance of single environmental habitat variables on densities of coffee pests using hierarchical partitioning analyses (Chapter 4). We found that the environmental habitat variables temperature, humidity, and tree diversity explained most of the variation of coffee pest densities. Spider mite density was positively related to temperature, while leaf miner and berry borer densities were negatively correlated to humidity and tree diversity, respectively.

Finally, we combined laboratory and field experiments to study the relative importance of biotic interactions and agroforestry management on densities of coffee pests in the field (Chapter 5). We show that preference matched fitness under laboratory conditions, leading to the prediction that coffee pests would avoid conspecific and heterospecific competitors in the field. However, coffee pest densites were positively correlated in the field, thereby contrasting with predictions made from the laboratory. Moreover, management intensity, which was defined by abiotic (temperature, humidity) and biotic (canopy cover, tree diversity, coffee density) habitat variables, proved to be more important than preference and fitness for influencing densities of coffee pests in the field.

In conclusion, vegetationally diverse agroecosystems such as complex-shade and abandoned agroforests have the potential to conserve mite diversity, and therefore should be incorporated into landscape conservation programs. Seasonal and population structure need to be taken into account in arthropod population dynamic studies across different habitat types, because responses depended on season and developmental stages. Abiotic and biotic habitat variables determining a given habitat may play a key role for understanding the effects of land use on pest densities. Understanding such species density-environmental relationships provide insights on how to predict and manage pests in the field. Laboratory and field studies need to be combined in order to determine the relative importance of small and large spatial scale experiments influecing population densities in the field.

RESUMO

A modificação antropogênica da paisagem nos trópicos tem causado perdas da biodiversidade de diferentes grupos taxonômicos, ameaçando importantes processos ecológicos.

Agroflorestas de café manejadas de forma tradicional são os únicos remanescentes de vegetação com considerável sombra em algumas regiões tropicais, e têm sido enfatizadas como importantes áreas de refúgio para a biodiversidade e pela sua contribuição na supressão de pragas devido a sua complexa estrutura vegetacional. O manejo de agroflorestas varia grandemente entre cafeicultores e pode influenciar padrões populacionais através de mudanças nas condições ambientais. Experimentos sobre interações ecológicas entre organismos são geralmente usados para predizer e explicar padrões e processos encontrados no campo. Não obstante, muitos fatores que influenciam populações, como variáveis ambientais, são determinados pelo uso da terra, tornando padrões reais no campo difíceis de prever a partir de experimentos conduzidos em escalas menores.

O estudo foi conduzido em pequenas propriedades rurais localizadas na região cafeicultora de Jipijapa, na província de Manabi, Equador. Essa região é considerada importante para a conservação da biodiversidade (hotspot) e sua vegetação original foi convertida em agricultura.

Foram selecionadas três agroflorestas de café, de acordo com o manejo local praticado pelos cafeicultores: agroflorestas com baixa diversidade arbórea, agroflorestas com diversidade arbórea intermediária, e agroflorestas abandonadas com uma alta diversidade arbórea.

No capítulo 2, estudou-se o papel do manejo de agroflorestas e da sazonalidade na comunidade de ácaros na cultura do café. A intensificação do manejo de agroflorestas afetou negativamente a riqueza de espécies de ácaros na cultura do café. Ademais, foram encontradas mais espécies e maiores densidades de ácaros na época seca comparada com a época chuvosa. Em geral, um ácaro-praga e seu ácaro predador atingiram maiores densidades populacionais durante a época seca e em agroflorestas manejadas de forma mais intensiva. Adicionalmente, maiores razões predador-presa foram encontradas em agroflorestas com diversidade arbórea intermediária.

No capítulo 3, investigou-se a dinâmica populacional de pragas de café (ácaro-vermelho-do-cafeeiro, bicho-mineiro-do-cafeeiro, e broca-do-cafeeiro) em relação ao manejo de agroflorestas. Adicionalmente, foi acessado o efeito do manejo de agroflorestas sobre as diversas fases de desenvolvimento de cada praga. O manejo de agroflorestas influenciou padrões populacionais de pragas do café, sendo que maiores picos populacionais ocorreram em agroflorestas manejadas de forma mais intensiva. Além disso, houve uma interação entre a diversidade vegetacional e a estrutura populacional, na qual as diferentes fases de desenvolvimento das pragas atingiram maiores densidades em agroflorestas manejadas de forma mais intensiva.

No capítulo 4, foi determinada a importância relativa de variáveis ambientais sobre densidades de pragas de café usando análises de partição hierárquica. As variáveis ambientais temperatura, umidade relativa, e diversidade arbórea explicaram a maior parte da variância da densidade das pragas de café. A temperatura influenciou positivamente densidades do ácaro-vermelho-do-cafeeiro, enquanto a umidade relativa e a diversidade arbórea influenciaram negativamente densidades do bicho-mineiro-do-cafeeiro e da broca-do-cafeeiro, respectivamente.

No capítulo 5, experimentos de laboratório e de campo foram combinados, para se estudar a importância relativa de interações bióticas e do manejo de agroflorestas sobre a densidade de pragas de café no campo. Preferência e sucesso reprodutivo equipararam-se em condições de laboratório, levando-se a predição de que as pragas iriam evitar competidores coespecíficos e heteroespecíficos no campo. No entanto, densidades das pragas de café foram positivamente correlacionadas no campo, portanto, contrastando com predições baseadas em experimentos de laboratório. Ademais, a intensidade de manejo, definida por variáveis bióticas e abióticas, foi mais importante do que a preferência e o sucesso reprodutivo sobre densidades de pragas de café no campo.

Concluindo, agroecossistemas com intermediária e alta diversidade arbórea têm o potencial de conservar a diversidade de ácaros, e portanto, deveriam ser incorporados em programas de conservação de paisagens. Sazonalidade e estrutura populacional devem ser consideradas em estudos de dinâmica populacional de artrópodes em diferentes hábitats, pois as respostas mudam com a época do ano e com as diferentes fases de desenvolvimento. Variáveis abióticas e bióticas determinando um dado hábitat podem ter um importante papel no entendimento dos efeitos do uso da terra sobre densidades populacionais de pragas. O entendimento da relação entre a densidade populacional de espécies e variáveis ambientais ajuda na predição e manejo de pragas no campo. Estudos de laboratório e de campo devem ser combinados para se determinar a importância relativa de experimentos conduzidos em pequenas e grandes escalas espaciais sobre densidades populacionais de artrópodes no campo.

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