Agricultural and Forest Entomology (2009), **11**, 295–300 DOI: 10.1111/j.1461-9563.2008.00417.x

Agroforestry management affects coffee pests contingent on season and developmental stage

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

*Agroecology, Department of Crop Science, University of Göttingen, Waldweg 26, D-37073, Göttingen, Germany, *Environmental Sciences, Policy and Management, 137 Mulford Hall, University of California, Berkeley, CA 94720-3114, U.S.A. and †EPAMIG-CTSM/EcoCentro, PO Box 176, 37200-000, Lavras, MG, Brazil*

Abstract

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

2 We investigated the population dynamics of red spider mites, coffee leaf miners, and coffee berry borers in three management types of coffee agroforests: increasing plant diversity from a 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 red spider mites were observed from August to December, coffee leaf miners from December to February, and coffee berry borers from May to July. Moreover, specific developmental stages of red spider mites, coffee leaf miners, and coffee berry borers differed in their responses to agroforestry management. During all stages, red spider mite reached higher densities in simple-shade agroforests compared with complex-shade and abandoned agroforests. Meanwhile, coffee leaf miner densities decreased from simple-shade to complex-shade and abandoned agroforests, but only for larvae, not pupae. Similarly, only coffee berry borer adults (but not eggs, larvae and pupae) demonstrated a response to agroforestry management. Environmental variables characterizing each agroforestry type proved to be important drivers of pest population densities in the field.

4 We emphasize the importance of considering seasonal differences and population structure while investigating arthropod responses to different habitat types because responses change with time and developmental stages.

Keywords Coffee berry borers, coffee leaf miners, developmental stages, red spider mites.

Introduction

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

Coffee agroforestry systems differ in amount of shade, which is dependent on shade tree diversity and density (Moguel & Toledo, 1999; Klein *et al.*, 2002a; Lozada *et al.*, 2007). Management of vegetational diversity affects abiotic variables such as temperature and relative humidity which in turn affect arthropod population dynamics in agroecosystems (Risch, 1980; Prischmann *et al.*, 2005; Barbar *et al.*, 2006; Teodoro *et al.*, 2008).

Correspondence: A. Teodoro. Tel: +49 551 392257; fax: +49 551 398806; e-mail: ad.teodoro@yahoo.com

Although several studies have investigated the effects of plant management in agroecosystems on arthropod population dynamics, very few studies have addressed how specific arthropod developmental stages respond to vegetational management (but see Harmon *et al.*, 2003). Arthropod developmental stages may differ in their responses to agroecosystem management (Harmon *et al.*, 2003). In this study, we investigated how agroforestry management affects the population dynamics of three major arthropod coffee pests, namely, red spider mites, coffee leaf miners, and coffee berry borers over time 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 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.

Materials and methods

Study system

The 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 in tropical America (Le Pelley, 1973; Reis & Souza, 1986). Colonies of red spider mites are found on the upper leaf surface, which may drop prematurely during heavy infestations (Reis & Souza, 1986). Red spider mites build up larger population densities during the dry season resulting in a reduction in photosynthesis rate (Fahl *et al.*, 2007) whereas densities are drastically reduced in the rainy season as a consequence of rainfall washing off mite colonies on leaves (Reis & Souza, 1986). Coffee 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 coffee leaf miner is the major coffee pest in Brazil and is widely distributed throughout tropical America (Vega *et al.*, 2006). The coffee 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). The coffee berry borer is native to Africa and is now present in almost all coffee-producing regions of the world, threatening millions of smallholder farmers whose subsistence depends on coffee (Vega *et al.*, 2006).

Study region and site description

The study was carried out on private farms located in the coffee-growing region of Jipijapa (1°19′60″S, 80°34′60″W), province of Manabi, Ecuador. The study region is dominated by coffee, pasture, and annual crops (Segarra, 2004) and has an altitudinal range from 108 to 466 m above sea level, a mean monthly temperature (±SE) of 25.66 ± 0.06°C and an average monthly rainfall of 115.99 ± 35.09 mm. The rainy season begins in December and finishes in May (Tylianakis *et al.*, 2005). 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, eight study sites), complex-shade agroforests (managed with 9–12 shade tree species, complex vertical structure, eight study sites), and abandoned coffee agroforests (abandoned for 10–15 years owing to low economic returns and currently resembling secondary forests, 14–20 shade tree species, forest regeneration and only few old coffee plants remaining, six study sites) totaling 22 study sites (Teodoro *et al.*, 2008). 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. 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. The three agroforestry types were characterized based on correlations between abiotic (temperature and relative humidity) and biotic (canopy cover, tree diversity and coffee density) environmental variables recorded in all study sites. During an entire year, temperature and relative humidity were recorded monthly under standardized conditions (on sunny days between 10.00–15.00) after placing a digital thermohygrometer on the ground for 10 min. 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. In all study sites, tree species were recorded in a series of nine quadrats (10 × 10 m) (Lozada *et al.*, 2007), and the Shannon-Wiener index was calculated as a measurement for tree diversity. 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) compared with abandoned coffee agroforests. In contrast, higher values of relative humidity ($F_{2,19}$=10.36, P < 0.001) were found in abandoned agroforests compared with simple-shade and complex-shade agroforests. Abandoned agroforests had the highest values of 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 had intermediate and lowest, respectively (data not shown).

Red spider mite and coffee leaf miner surveys

In all study sites, we sampled red spider mites and coffee leaf miners over time to assess seasonal population dynamics and stage structure changes in relation to agroforestry management.

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

Coffee berry borer survey

Coffee berry borers were surveyed in the three management types of agroforests during the 6-month coffee production period in 2005 (from February to July). In each evaluation, 10 coffee plants per study site located at least 5 m away from habitat boundaries were randomly chosen and 60 fruits per plant were collected (20 from each part, i.e. top, medium, and bottom). Care was taken to collect only well-developed unripe and ripe coffee fruits as small berries are not a suitable substrate for the development of coffee berry borers. Overripe berries were not sampled in our study. The fruits were opened and the number of all developmental stages of coffee berry borers (i.e. eggs, larvae, pupae, and adults) was counted using a binocular microscope. We averaged the number of coffee berry borers at each site.

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 were used to test differences between agroforestry management types on the number of pests within each month.

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 were used to test the effect of agroforestry management on densities of each pest developmental stage.

Additionally, we tested the effects of measured environmental variables on densities of red spider mites, coffee leaf miners, and coffee berry borers using general linear models (GLMs) on a per study site level, with agroforestry type as a random factor and each environmental variable as a continuous variable.

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

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

Coffee berry borer densities increased significantly 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 coffee berry borers per study site varied over the season (Fig. 1c; $F_{5,95} = 4.51$, $P = 0.0009$).

Population stage structure in respect to agroforestry management

Red spider mite population stage structure was affected by agroforestry management. Densities of all developmental stages of red spider mites per study site were higher in simple-shade agroforests compared with 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 coffee leaf miner larvae per study site were affected by agroforestry management, with higher densities in simple-shade agroforests compared with 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 coffee 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 coffee 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.

Coffee berry borer adults responded differently to agroforestry management. The number of adult coffee berry borers per study site was higher in simple-shade and complex-shade agroforests compared with abandoned coffee agroforests

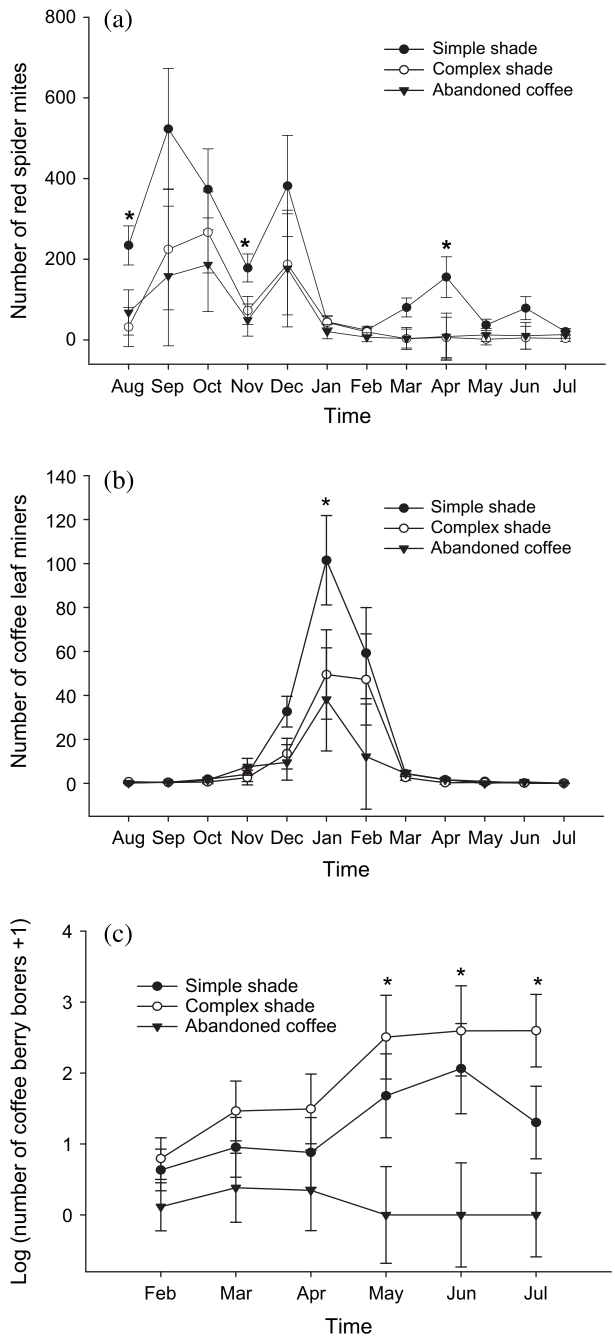

Figure 1 Seasonal changes in the number of: (a) red spider mites, (b) coffee leaf miners, and (c) coffee berry borers per study site in relation to agroforestry management, i.e. simple-shade agroforests, complex-shade agroforests, and abandoned coffee agroforests. Means ± SE are given and all developmental 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 ($P < 0.05$).

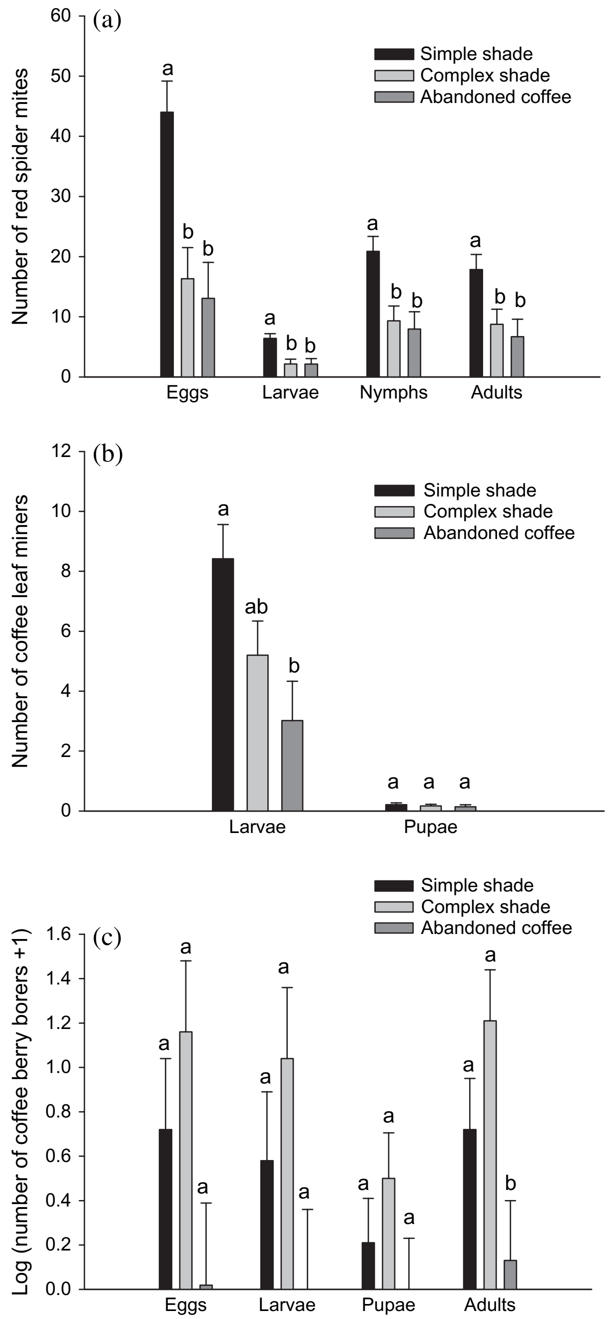

Figure 2 Population structure of: (a) red spider mites (eggs, larvae, nymphs, and adults), (b) coffee leaf miners (larvae and pupae), and (c) coffee berry borers (eggs, larvae, pupae, and adults) per study site in relation to agroforestry management, i.e. simple-shade agroforests, complex-shade agroforests,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

(Fig. 2c; $F_{2,19} = 4.45$, $P = 0.024$). The remaining developmental stages of coffee 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: $F_{2,19} = 1.35$, $P = 0.282$).

Relationships between environmental variables and pest densities

Densities of coffee pests were affected by environmental habitat variables. Red spider mite density increased with temperature ($F_{1,260} = 13.13$, $P = 0.005$, $R^2 = 0.09$), decreased with relative humidity ($F_{1,260} = 30.67$, $P < 0.0001$, $R^2 = 0.15$), tree diversity ($F_{1,18} = 5.41$, $P = 0.03$, $R^2 = 0.32$), and canopy cover ($F_{1,18} = 5.22$, $P = 0.03$, $R^2 = 0.32$), and was not correlated with coffee density ($F_{1,18} = 2.88$, $P = 0.06$, $R^2 = 0.32$). Densities of coffee leaf miners were negatively related to relative humidity ($F_{1,260} = 10.79$, $P = 0.001$, $R^2 = 0.04$) and canopy cover ($F_{1,18} = 10.33$, $P = 0.04$, $R^2 = 0.23$), positively related to temperature ($F_{1,260} = 16.11$, $P < 0.001$, $R^2 = 0.05$), and not related to tree diversity ($F_{1,18} = 1.39$, $P = 0.40$, $R^2 = 0.23$) and coffee density ($F_{1,18} = 1.72$, $P = 0.197$, $R^2 = 0.22$). Densities of coffee berry borers (log + 1 transformed data) were positively correlated with temperature ($F_{1,128} = 4.09$, $P = 0.04$, $R^2 = 0.19$), negatively correlated with tree diversity ($F_{1,18} = 8.36$, $P = 0.009$, $R^2 = 0.39$), and not related to relative humidity ($F_{1,128} = 3.46$, $P = 0.06$, $R^2 = 0.19$), canopy cover ($F_{1,18} = 2.44$, $P = 0.13$, $R^2 = 0.34$), and coffee density ($F_{1,18} = 1.07$, $P = 0.382$, $R^2 = 0.15$).

Discussion

Over time, agroforestry management affected population dynamics of coffee pests. 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. Red spider mites reached higher peaks throughout time in intensively managed, lower vegetational diverse simple-shade agroforests compared with 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 red spider mites in simple-shade agroforests compared with the other two agroforestry types (Fig. 2a). The effects of vegetational management on dynamics of red spider mites are in agreement with results of Prischmann *et al.* (2005), who found that low- and high-input grapevine agroecosystems had the greatest densities of the three tetranychid mites than non-managed ones.

Coffee leaf miners showed a significant interaction between time and agroforestry type, in that more coffee leaf miners were found in January during the rainy season in simple-shade agroforests than in complex-shade and abandoned agroforests (Fig. 1b). During the rainy season in the region, coffee leaf miners increased from December to February and showed a unimodal population fluctuation with a peak in January. Similar results were found by Nestel *et al.* (1994), who investigated the role of shaded and unshaded coffee agroforests on population dynamics of coffee leaf miners in Mexico. They did not find any effects of agroforestry management on coffee leaf miner densities, but reported a significant time effect, with higher population densities between March and May. Additionally, coffee 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 coffee 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 coffee berry borers responded to agroforestry management, with more individuals in simple and complex shade than in abandoned agroforests (Fig. 2c). Berry ripeness is known to influence coffee berry borer densities in the field, but in this study we collected only well-developed unripe and ripe coffee berries, avoiding small under-developed fruits which are a poor substrate for berry borers. Moreover, as our surveys lasted until the harvest we did not collect overripe berries, in which berry borers are reported to survive from 1 year to another in the field.

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 a local level. Similarly, management effects could be only shown in distinct months.

The three agroforestry types studied here differed in temperature, relative humidity, canopy cover, tree diversity, and coffee density. Such environmental habitat variables are known to influence arthropod population parameters (Roininen *et al.*, 1996; Yarnes & Boecklen, 2005; Hofmann & Mason, 2006). In this study, environmental variables characterizing each agroforestry type proved to play a key role in influencing density patterns of coffee pests in the field. For instance, densities of red spider mites, coffee leaf miners, and coffee berry borers were generally positively influenced by temperature and negatively affected by relative humidity. Overall, pests built up higher populations in intensively managed agroforests, which were characterized by higher temperature and lower relative humidity values. Similarly, specific developmental stages of coffee pests generally attained higher densities in more intensively managed agroforests. Therefore, the lower pest densities in more diverse, extensively managed agroforests are related to high vegetational diversity and complexity in these agroforestry management types, which affect local environmental variables that in turn influence pest densities. This is in line with predictions of lower pest densities in more diverse, vegetationally complex agroecosystems (Root, 1973; Landis *et al.*, 2000).

Top-down control carried out by natural enemies are important factors regulating pest population densities in the field (Klein *et al.*, 2002b), but in another study carried out in the same study sites we found that natural enemies did not seem to play an important role in influencing coffee pest densities in the three agroforestry types. Densities of the two major natural enemies associated with red spider mites and coffee leaf miners in the region of study, the predatory mite *Amblyseius herbicolus* Chant (Acari: Phytoseiidae) and a eulophid parasitoid (Hymenoptera: Eulophidae), respectively, did not differ between the three agroforestry types. Additionally, there was no important natural enemy such as parasitoids associated with coffee berry borers in the study region (A. Teodoro, A.M. Klein & T. Tscharntke, unpublished data).

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. Environmental variables characterizing habitat types were important drivers of pest population densities in the field. In order to understand the outcome of agroforestry management on arthropod population parameters, you need to consider the season and population stage structure to avoid partially misleading conclusions, because responses change with season and developmental stage.

Acknowledgements

We thank Free de Koning, Betty Pico, and Roland Olschewski of the project BioSys (Evaluation of biological diversity of land-use systems in a mega-diverse region of Ecuador) for their support and help. We also thank Renato Merchán, Cesar Calderón, and Angel Chóez for assistence with fieldwork, all smallholders for their permission to conduct experiments on their farms, five reviewers and the editor for helpful comments on the manuscript. A.T. was supported by CAPES/Brasília – Brazil and further financial support came from the German Ministry of Education and Research (BMBF, Bioteam program).

References

Barbar, Z., Tixier, M.S., Cheval, B. & Kreiter, S. (2006) Effects of agroforestry on phytoseiid mite communities (Acari: Phytoseiidae) in vineyards in the South of France. *Experimental and Applied Acarology*, **40**, 175–188.

Fahl, J.L., Queiroz-Voltan, R.B., Carelli, M.L.C., Schiavinato, M.A., Prado, A.K.S. & Souza, J.C. (2007) Alterations in leaf anatomy and physiology caused by the red mite (*Oligonychus ilicis*) in plants of *Coffea arabica*. *Brazilian Journal of Plant Physiology*, **19**, 61–68.

Gordon, C., Manson, R., Sundberg, J. & Cruz-Angón, A. (2007) Biodiversity, profitability, and vegetation structure in a Mexican coffee agroecosystem. *Agriculture, Ecosystems and Environment*, **118**, 256–266.

Harmon, J.P., Hladilek, E.E., Hinton, J.L., Stodola, T.J. & Andow, D.A. (2003) Herbivore response to vegetational diversity: spatial interaction of resources and natural enemies. *Population Ecology*, **45**, 75–81.

Hofmann, T.A. & Mason, C.F. (2006) Importance of management on the distribution and abundance of Staphylinidae (Insecta: Coleoptera) on coastal grazing marshes. *Agriculture, Ecosystems and Environment*, **114**, 397–406.

Klein, A.M., Steffan-Dewenter, I., Buchori, D. & Tscharntke, T. (2002a) Effects of land-use intensity in tropical agroforestry systems on coffee flower-visiting and trap-nesting bees and wasps. *Conservation Biology*, **16**, 1003–1014.

Klein, A.M., Steffan-Dewenter, I. & Tscharntke, T. (2002b) Predator-prey ratios on cocoa along a land-use gradient in Indonesia. *Biodiversity and Conservation*, **11**, 683–693.

Landis, D.A., Wratten, S.D. & Gurr, G.M. (2000) Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annual Review of Entomology*, **45**, 175–201.

Le Pelley, R.H. (1973) Coffee insects. *Annual Review of Entomology*, **18**, 121–142.

Lozada, T., de Koning, G.H.J., Marché, R., Klein, A.M. & Tscharntke, T. (2007) Tree recovery and seed dispersal by birds, comparing forest, agroforestry and abandoned agroforestry in coastal Ecuador. *Perspectives in Plant Ecology, Evolution and Systematics*, **8**, 131–140.

Moguel, P. & Toledo, W.M. (1999) Biodiversity conservation in traditional coffee systems of Mexico. *Conservation Biology*, **13**, 11–21.

Murphy, S.T. & Moore, D. (1990) Biological control of the coffee berry borer, *Hypothenemus hampei* (Ferrari) (Coleoptera: Scolytidae): previous programmes and possibilities for the future. *Biocontrol News and Information*, **11**, 107–117.

Nestel, D., Dickschen, F. & Altieri, M.A. (1994) Seasonal and spatial population loads of a tropical insect: the case of the coffee leaf-miner in Mexico. *Ecological Entomology*, **19**, 159–167.

Perfecto, I., Mas, A., Dietsch, T. & Vandermeer, J. (2003) Conservation of biodiversity in coffee agroecosystems: a tri-taxa comparison in southern Mexico. *Biodiversity and Conservation*, **12**, 1239–1252.

Perfecto, I., Rice, R.A., Greenberg, R. & Van der Voort, M.E. (1996) Shade coffee: a disappearing refuge for biodiversity. Shade coffee plantations can contain as much biodiversity as forest habitats. *BioScience*, **46**, 598–608.

Pineda, E., Moreno, C., Escobar, F. & Halffter, G. (2005) Frog, bat, and dung beetle diversity in the cloud forest and coffee agroecosystems of Veracruz, Mexico. *Conservation Biology*, **19**, 400–410.

Prischmann, D.A., James, D.G. & Snyder, W.E. (2005) Impact of management intensity on mites (Acari: Tetranychidae, Phytoseiidae) in Southcentral Washington wine grapes. *International Journal of Acarology*, **31**, 277–288.

Reis, P.R. & Souza, J.C. (1986) Pragas do cafeeiro. *Cultura do cafeeiro: fatores que afetam a produtividade* (ed. by A. B. Rena, E. Malavolta, M. Rocha and T. Yamada), pp. 338–378. Piracicaba, Brasil.

Risch, S. (1980) The population dynamics of several herbivorous beetles in a tropical agroecosystem: the effect of intercropping corn, beans and squash in Costa Rica. *Journal of Applied Ecology*, **17**, 593–612.

Roininen, H., Price, P.W. & Tahvanainen, J. (1996) Bottom-up and top-down influences in the trophic system of a willow, a galling sawfly and inquilines. *Oikos*, **77**, 44–50.

Root, R.B. (1973) Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecological Monographs*, **43**, 95–124.

Segarra, P. (2004) *Informe técnico del mapa de uso del suelo y cobertura vegetal 1:50000 de la zona comprendida entre Jipijapa, Noboa y Paján provincia de Manabí*. Proyecto Bio-Sys, Universidad de Göttingen, Alemania y Corporación Ecopar, Quito, Ecuador.

StatSoft Inc., (1984–2004) *Statistica for Windows (Software-System for Data-Analyses), Version 7.0*. StatSoft Inc., Tulsa, Oklahoma.

Teodoro, A., Klein, A.M. & Tscharntke, T. (2008) Environmentally mediated coffee pest densities in relation to agroforestry management, using hierarchical partitioning analyses. *Agriculture, Ecosystems and Environment*, **125**, 120–126.

Tylianakis, J.M., Klein, A.M. & Tscharntke, T. (2005) Spatiotemporal variation in the diversity of hymenoptera across a tropical habitat gradient. *Ecology*, **12**, 3296–3302.

Vega, F.E., Posada, F. & Infante, F. (2006) Coffee insects: ecology and control. *Encyclopedia of Pest Management* (ed. by D. Pimentel) [WWW document]. URL http://www.dekker.com/sdek/issues~content=t713172972 [accessed on 12 March 2008].

Yarnes, C.T. & Boecklen, W.J. (2005) Abiotic factors promote plant heterogeneity and influence herbivore performance and mortality in Gambel´s oak (*Quercus gambelii*). *Entomologia Experimentalis et Applicata*, **114**, 87–95.

Accepted 26 August 2008
First published online 11 March 2009

