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Predator–prey ratios on cocoa along a land-use gradient in Indonesia

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Abstract. Tropical landscapes are dominated by agroecosystems, but the potential value of agroecosystems for the survival of species is often overlooked. In agroecosystems, species conservation is especially important when functional groups such as predators are affected. In Central Sulawesi, we sampled arthropods on cocoa in a gradient of land-use intensity from extensively used forest gardens to intensively used agroforestry systems. The abundance and diversity of all arthropods did not correlate with land-use intensity, so human impact was not followed by high species losses. However, the number of species and abundance of the phytophagous arthropods increased and that of the entomophagous arthropods decreased with land-use intensity. The reduced predator–prey ratio in intensified systems can be related to their reduced species richness of shade trees and the changed microclimate (increased temperature, decreased humidity and canopy cover). In conclusion, transformation of traditional into intensified agroforestry systems had a great impact on arthropod community structure on cocoa. Since predator–prey ratios decreased with increasing land-use intensity, local farmers should have least pest problems in the traditionally diversified agroforestry systems.

Key words: agroforestry, arthropods, biological control, conservation, Sulawesi, *Theobroma cacao*

Introduction

Managed ecosystems, especially agroecosystems, dominate tropical landscapes, and remnant primary forest is often only patchily embedded in the agricultural landscape (Power 1996; Schelhas and Greenberg 1996; Laurance and Bierregaard 1997). Natural ecosystems make up only about 5% of the terrestrial environment in contrast to approximately 50% of land that is currently under agricultural production and 20% in commercial forestry (Western and Pearl 1989). Efforts to preserve biodiversity have focused on these natural ecosystems and the potential value of agroecosystems for conservation has been often ignored (but see Pimentel et al. 1992; Perfecto et al. 1996, 1997; Watt et al. 1997; Moguel and Toledo 1999; Power and Flecker 2000).

Traditionally, coffee *Coffea canephora* Pierre ex Froehner (Syn.: *C. robusta* Lind.) and cocoa *Theobroma cacao* L. are grown under a canopy of shade trees that may be remnants of the original forest or have been deliberately planted. The structural and floristic complexity of shade trees may support relatively high biodiversity, and appear to serve as surrogates of natural forest for many species (Perfecto et al. 1996, 1997; Greenberg et al. 2000; Rice and Greenberg 2000). Microclimatic conditions also change with the structure and complexity of shade trees (Perfecto and Vandermeer 1996). The major change in species composition of land-use systems comes with the modernization of traditional agroforestry into unshaded plantations (Lawton et al. 1998).

Arthropods account for more than half of global species richness, with most arthropod species being herbivorous insects and their parasitoids (Stork 1991). Therefore, the response of community structure and plant–insect interactions to land-use changes is of major interest. When richness of functional groups like predators and parasitoids is affected by land use, essential ecosystem functions may also suffer (Didham et al. 1996; Daily et al. 1997). In agroecosystems, structural complexity, species richness, and biological control are often correlated, as seen for example in the mortality of tropical maize pests (Perfecto 1990; Altieri 1995) or in the parasitism of rape pollen beetle (Thies and Tscharntke 1999; Tscharntke 2000). Diversification of land-use systems is known to often enhance the impact of natural enemies on herbivores (Russell 1989; Corbett and Rosenheim 1996; Thies and Tscharntke 1999).

According to the ‘natural enemies hypothesis’ (Root 1973; Russell 1989) agroecosystems with high floristic and structural diversity have low abundance of phytophagous species. Alternative food resources in such systems may support higher populations of entomophagous arthropods, and a shade canopy may enhance predator populations that would not survive in unshaded plantations (Greenberg et al. 2000).

In conclusion, responses of herbivore and natural enemy communities may be used to characterize different types of land use. Here we characterized a land-use gradient with abiotic parameters and entomophagous and phytophagous arthropods, sampled by sweep-netting on cocoa. We tested the following two hypotheses:

1. The gradient in land-use intensity, from traditional to modernized agroforestry systems, can be characterized by a change in biotic and abiotic parameters.
2. Land-use intensity does not affect all arthropod species equally. The entomophagous species should be negatively affected, and the phytophagous species positively influenced.

Material and methods

Study area and experimental sites

The study was carried out from October 1998 to March 1999, in a site located in Central Sulawesi, at the margin of the Lore-Lindu National Park near Palu. We chose a land-use gradient of agroforestry systems dominated by coffee and cocoa. We selected natural forest and five agroforestry types, differing in land-use intensity: (1) intensively used, 2-year old agroforestry systems, (2) extensively used, 4- to 5-year old agroforestry systems, (3) 8-year old homegardens, (4) intensively used forest gardens in the forest margin, (5) extensively used forest gardens in the forest margin, and (6) natural forest as reference inside the near-natural forest. For these five land-use and one natural forest types we selected two replicates each. These 12 study sites had a minimum size of 0.5 ha and a minimum distance to the nearest neighbour of 500 m.

Characterization of land-use intensity

We characterized land-use intensity with abiotic and biotic habitat parameters. We measured the diurnal temperature (°C), relative humidity (%) and day-light intensity (Lux) under standardized conditions (sunny days, 8–10 a.m.) at 3 days. For measuring the temperature and relative humidity, we used a combined hygro-thermometer, placed at 1.5 m height in the coffee and cocoa trees. For the relative light intensity we used a luxmeter (range: 0.1–20000 Lux) on the ground, which was always slightly shadowed by a paper sheet to reduce light intensity.

The biotic parameters included the number of plant species within a 10 m^2 plot, mapped two times per study system, according to Braun-Blanquet (1964). The plots were randomly selected. For each plot we estimated the percent cover of vegetation, the mean height of vegetation, separately for trees, shrubs and herbs, and the percentage cover of dead organic materials, such as dead branches and leaves.

Arthropod sampling

From November 1998 to January 1999 we sampled the arthropods on three cocoa trees per study site. For one sample we caught the arthropods by sweep-netting (40 cm diameter) with three sweeps on each of three cocoa trees. Per study system we sampled three times for every 2 weeks. We calculated total abundance and the number of species for each of the 10 systems. Due to this sampling method, we caught more leaf-attacking than fruit-attacking species. The samples were carried out only in the agroforestry systems, because the two natural-forest systems did not include cultivated plants like cocoa. We chose the forest plots only as reference to the agroforestry plots to characterize the changes of abiotic condition with land-use intensity. For the identification of the arthropods we used Donald et al. (1981). We identified the arthropods in the field, so most species could only be identified to families and morphospecies (see Oliver and Beattie 1996). Foraging guilds were determined according to Kalshoven (1981). We only included species, with known feeding preferences from phytophagous and entomophagous species.

Statistical analysis

Statistical analysis of the data was performed using the software Statgraphics Plus 3.0 (Manugistics 1996). If necessary, logarithmic or square root-transformed variables were used to achieve normal distribution. Pearson correlations were used for the analysis of normally distributed data, while Spearman rank correlations were used for ordinal data (Sokal and Rohlf 1995). The habitat parameters were closely intercorrelated, so we used a factor analysis to express covariation of the parameters.

Results

Characterization of land-use intensity

We chose the following sequence of agroforestry systems for our gradient in land-use intensity: (1) near-natural forest, (2) extensively managed forest garden, (3) intensively managed forest garden, (4) homegarden, (5) extensively managed agroforestry system, and (6) intensively managed agroforestry system. The three abiotic habitat parameters, relative humidity, day-light intensity and temperature, and the three biotic habitat parameters, percent canopy cover, average height of the trees and percentage of dead organic materials, were highly intercorrelated, thus we used a factor analysis to connect all these parameters (Figure 1). The resulting factor was closely correlated with the above-mentioned sequence of the land-use gradient ($y = 6.43 - 0.37x$, $F = 113.72$, $r^2 = 0.92$, $n = 12$, $P < 0.001$). The near-natural forest, as well as the extensively and intensively managed forest gardens were situated in the forest. In contrast, the homegardens, extensively and intensively agroforestry sites were situated outside the forest and established after a complete clearing of the natural forest with subsequent planting of shade trees and crops.

We used simple linear regressions of the single habitat parameters with land-use intensity to show relations between the six habitat parameters and the land-use gradient (Figure 1(A)–(F)). Day-light intensity and temperature increased with increasing land-use intensity, while relative humidity, percent canopy cover, tree height and percentage of dead organic materials decreased.

The number of shade tree species declined with increasing land-use intensity ($y = 15.89 - 0.96x$, $F = 54.54$, $r^2 = 0.84$, $n = 12$, $P < 0.001$) and of the herb layer. Species richness of all plants (including herbs) was not related to land-use intensity. The number of fruit and crop species showed a correlation in a polynomial regression ($y = -1.85 + 2.09x - 0.12x^2$, $F = 7.29$, $r^2 = 0.61$, $n = 12$, $P = 0.01$) with the greatest diversity in the homegardens, i.e. at intermediate land-use intensity.

Predator–prey ratios in the land-use gradient

Altogether we sampled 1409 arthropod individuals of nine orders and 37 families by sweep-netting on cocoa. The most abundant order was the Diptera with 751 individuals, followed by the Coleoptera with 212 individuals, the Hymenoptera with 106 individuals (including the Formicoidea with 71 individuals), the Araneida with 88

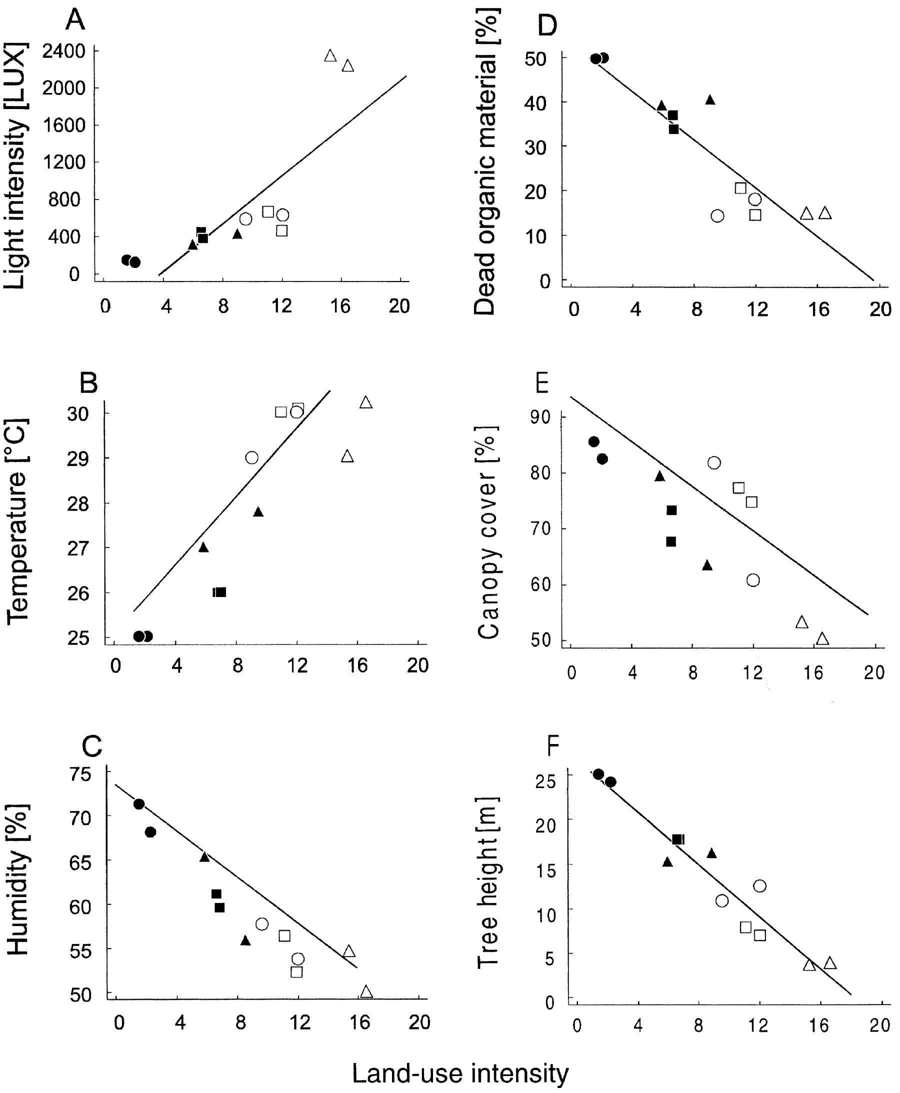

Figure 1. Correlation between the land-use intensity and habitat parameters. Land-use intensity was calculated by factor analysis of six habitat parameters. Abiotic habitat parameters: (A) relative light intensity [LUX] ($y = -294.78 + 128.45x$, $F = 19.77$, $r^2 = 0.66$, $n = 12$, $P = 0.001$); (B) temperature [°C] ($y = 24.84 + 0.38x$, $F = 38.24$, $r^2 = 0.79$, $n = 12$, $P < 0.001$); (C) relative humidity [%] ($y = 78.87 - 1.93x$, $F = 87.55$, $r^2 = 0.89$, $n = 12$, $P < 0.001$). Biotic habitat parameters: (D) dead organic material [%] ($y = 48.47 - 3.37x$, $F = 43.00$, $r^2 = 0.81$, $n = 12$, $P < 0.001$); (E) canopy cover [%] ($y = 99.05 - 2.55x$, $F = 16.37$, $r^2 = 0.62$, $n = 12$, $P = 0.002$); (F) tree height [m] ($y = 25.08 - 1.47x$, $F = 117.68$, $r^2 = 0.92$, $n = 12$, $P < 0.001$). (●) = Near-natural forest; (■) = extensively managed forest garden; (▲) = intensively managed forest garden; (○) = homegarden, (□) = extensively managed agroforestry system; (△) = intensively managed agroforestry system.

Table 1. The phytophagous and entomophagous arthropods sampled on cocoa.

Group of arthropods	Number of individuals	r_S
Entomophagous arthropods		
Araneidae	60	−0.09 NS
Asilidae	12	−0.74**
Cantharidae	18	−0.80**
Coccinellidae	16	0.77**
Ichneumonidae	12	0.09 NS
Reduviidae	11	−0.58*
Tettigoniidae	16	−0.33 NS
Thomisidae	28	0.06 NS
Phytophagous arthropods		
Chrysomelidae	90	0.63**
Coleoptera (other than Chrysomelidae)	88	0.54*
Geometridae	16	−0.75**
Miridae	20	−0.21 NS
Lycaenidae	19	0.32 NS
Psychidae	11	0.79**
Trypetidae	15	0.09 NS

For groups with at least 10 individuals and with an occurrence in more than three land-use types, we show the rank correlation with the land-use intensity, r_S = correlation coefficient according to Spearman, P = significance level *<0.1, **<0.05, *** <0.01, $n = 10$.

individuals and the Lepidoptera with 67 individuals. For the remaining orders (Heteroptera, Saltatoria, Neuroptera, Thysanoptera) we recorded less than 50 individuals per order. We separated entomophagous from phytophagous species in case the feeding mode was clear (Table 1). We computed correlations between the land-use intensity and the taxonomic groups represented by more than 10 individuals in more than three different land-use types. The entomophagous Asilidae, Cantharidae and Reduviidae showed a negative, the Coccinellidae a positive correlation with the land-use intensity. The phytophagous Chrysomelidae, Coleoptera (other than Chrysomelidae) and Psychidae (caterpillars) were positively, the Geometridae (caterpillars) negatively correlated with land-use intensity. Arthropods that could not be related to the entomophage–phytophage dichotomy included residual Diptera (303 individuals < 4 mm, 377 individuals > 4 mm). The Formicoidea increased with land-use intensity ($y = -7.65 + 1.23x$, $F = 6.01$, $r^2 = 0.43$, $n = 10$, $P = 0.04$). We excluded the Formicoidea from this analysis, because of the many feeding types involved. Some species caused damage on cultivated plants, some enhanced sap-sucking herbivores and some were predators (pers. observ.; Kalshoven 1981).

The abundance and species number of all arthropods was not significantly correlated with the land-use intensity ($y = 26.43 + 0.90x$, $F = 1.88$, $r^2 = 0.19$, $n = 10$, $P = 0.21$). In addition to Table 1, we included the Braconidae, Chalcididae, Chrysopidae, Sphecidae and Tachinidae in the statistical analysis of the entomophagous group. The Noctuidae and Arctiidae (caterpillars), the Buprestidae, Bruchidae, Curculionidae, Membracidae, Notodontidae and few further other Heteroptera represented the herbivores. The chrysomelid beetles caused obvious leaf damage,

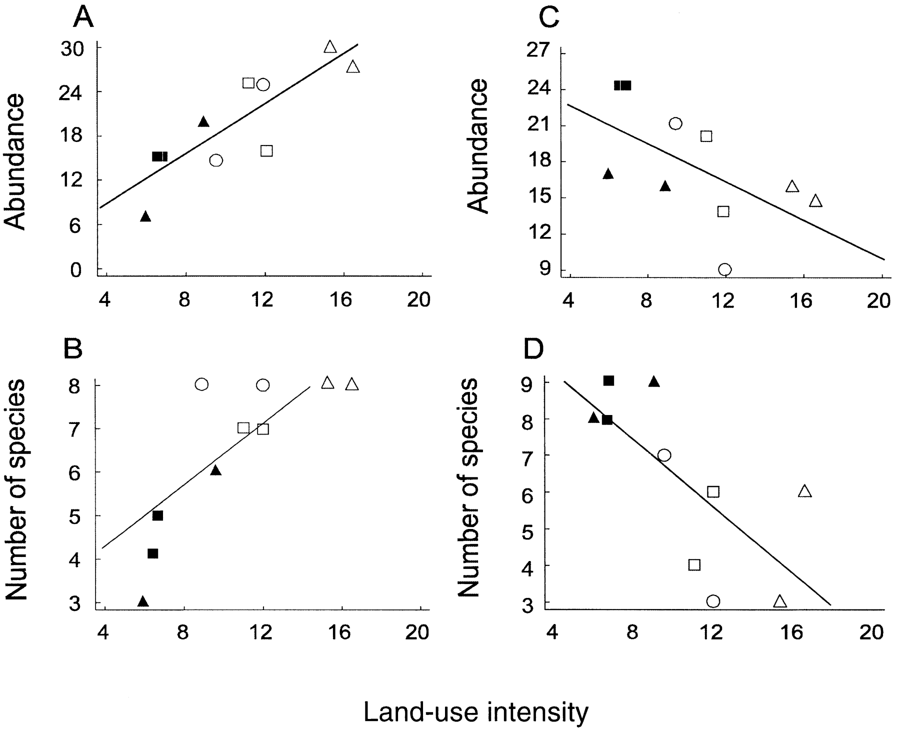

Figure 2. Effects of land-use intensity on abundance and number of species. (A) Abundance of phytophagous arthropods ($y = 3.54 + 1.68x$, $F = 20.85$, $r^2 = 0.72$, $n = 10$, $P = 0.002$); (B) number of phytophagous arthropod species ($y = 3.26 + 0.35x$, $F = 17.98$, $r^2 = 0.69$, $n = 10$, $P = 0.009$); (C) abundance of entomophagous arthropods ($y = 22.63 - 0.78x$, $F = 4.03$, $r^2 = 0.33$, $n = 10$, $P = 0.071$); (D) number of entomophagous arthropod species ($y = 9.62 - 0.46x$, $F = 8.21$, $r^2 = 0.50$, $n = 10$, $P = 0.021$). (■) = Extensively managed forest garden; (▲) = intensively managed forest garden; (○) = homegarden; (□) = extensively managed agroforestry system; (△) = intensively managed agroforestry system.

while the mealy bugs and most of the true bugs (Miridae), e.g. *Helopeltis* sp., were fruit-sucking herbivores. We also observed some true bugs feeding on leaf tissue. The abundance of phytophagous species increased with increasing land-use intensity (Figure 2A), whereas abundance of entomophagous species decreased (Figure 2C). Equally, the number of phytophagous species increased with increasing land-use intensity (Figure 2B), whereas the number of entomophagous species decreased (Figure 2D). In consequence, the predator–prey ratios was negatively correlated with land-use intensity (Figure 3).

Discussion

The results showed that the arthropod community on cocoa changed greatly with land-use intensity of agroforestry systems. The abundance of phytophagous arthropods increased with land-use intensity, while the abundance of entomophagous

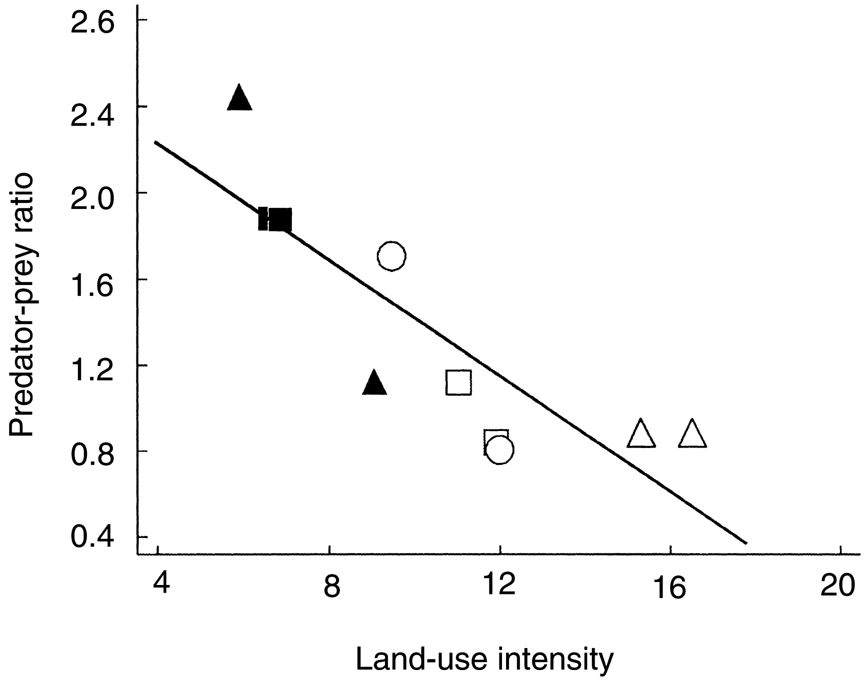

Figure 3. Effects of land-use intensity on the predator–prey ratio (abundance of predators to abundance of herbivores) ($y = 2.24 - 0.14x$, $F = 20.89$, $r^2 = 0.72$, $n = 10$, $P = 0.002$). (■) = Extensively managed forest garden; (▲) = intensively managed forest garden; (○) = homegarden; (□) = extensively managed agroforestry system; (△) = intensively managed agroforestry system.

arthropods decreased. As a result, the predator–prey ratio on cocoa decreased significantly with increasing land-use intensity. This pattern is in support of the 'natural enemies hypothesis' (Root 1973). This hypothesis predicts that plant species-rich land-use systems support many insect predators, which enhance the control of herbivore populations. Species richness of the shade trees was in fact reduced in the intensive land-use systems. A diverse canopy may provide a diverse resource base for insect predators, including a diverse layer of decaying organic material, providing shelter and alternative resources for entomophagous species (Power 1996). In addition to the diversity gradient in the shade trees, the land-use gradient differed significantly in relative humidity, day-light intensity, temperature, percentage canopy cover, average height of the trees and percentage of dead organic materials. The shadow due to the canopy appears to be a major factor influencing the arthropod community (Perfecto and Vandermeer 1996; Perfecto et al. 1996, 1997; Power 1996; Power and Flecker 1996; Greenberg et al. 2000). The canopy cover affects the microclimate of the understory (Perfecto and Vandermeer 1996; Perfecto et al. 1996), and can be used as an indirect estimation of moisture, temperature and leaf litter (Beer 1987). Perfecto et al. (1997) found a dramatic loss of arthropods concomitant with the transformation of traditional coffee plantations to coffee monocultures. Stress from insect attack is most obvious on plantation cocoa trees having minimal or no shade (Young 1994). Changes of abiotic conditons may also change leaf chemistry, but we could not address this hypothesis in our study.

The increasing predator–prey ratio with land use could be an important factor in pest control. It suggests that local farmers should have least pest problems in the traditionally diversified agroforestry systems, including many shade trees with dense canopy. Commonly, agrochemicals are used to control pests and weeds in cocoa systems (Soule et al. 1990). Using insecticides and the removal of shade are two major factors in the development of pest species on cocoa (Leston 1970). Due to environmental problems, human health and the often-induced resistance of target species through agrochemicals, we have to find other possibilities to reduce pests (Rice and Greenberg 2000). The commonest pests on cocoa are mealybugs and true bugs (Leston 1970; Kalshoven 1981). Both are fruit-sucking species, but also attack leaves. Some true bugs are vectors of viral disease (Rice and Greenberg 2000). Butterflies, moths and beetles are also well-known pests on cocoa (Leston 1970; Young 1994). Similarly, in our study some lepidoptera larvae and the chrysomelid beetles were commonly found foraging the young cocoa leaves. They also are known as important cocoa pests. In our samples the spiders were the most common entomophagous arthropods. We observed Miridae caught by spider webs, so some Araneidae may be impact natural enemies of the true bugs. Ants can be important predators, but they also defend homopteras, e.g. mealybugs (Leston 1970; Kalshoven 1981; Young 1994) or lycanid caterpillars (Fiedler 1996). These pests were most common in the intensively managed and slightly shaded cocoa cultivation in our study. Thus abundance of ants increasing with land-use intensity may have been related to changed host densities. We need more research to address the role of an increasingly diverse predatory community, because of the complexity of trophic relationships (Rice and Greenberg 2000).

Our results did not show changes in total abundance and total species number of the arthropods with reduced shade, but the community structure with respect to the foraging guilds changed. These findings support observations that some taxa are surprisingly little sensitive even to extreme habitat modification (Lawton et al. 1998), and some populations seem to be even enhanced by land use. In a parallel study, species richness of solitary bees and trap-nesting wasps increased with land-use intensity, whereas social bees declined (Klein et al. 2001).

In conclusion, land-use intensity did not affect total species richness of cocoa arthropods, but phytophagous and entomophagous arthropods responded differentially. These results show that management practices had a great impact on arthropod community structure. Since predator–prey ratios greatly decreased with increasing land-use intensity, local farmers should have least pest problems in traditionally diversified agroforestry systems, while land-use intensification should release insect pests from possible control by their natural enemies. Future research will experimentally establish the role of natural enemies for the biological control of the most impact pest population.

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