Diversity of True Bugs (Heteroptera) in Various Habitats of the Lama Forest Reserve in Southern Benin

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Abstract

The effect of forest use on the diversity and community structure of Heteroptera was investigated in the Lama forest reserve in southern Benin. Bugs were collected using funnel pitfall traps, ground photo-eclectors, Malaise traps, flight traps and sweep-nets. In each of the following nine habitats, four replicate sites were monitored over a 12-month period: semi-deciduous forest, lowland forest, dry forest, abandoned settlements, *Chromolaena odorata* thicket, young teak plantations, old teak plantations, firewood plantations and isolated forest fragments. The 893 specimens of Heteroptera collected represented 104 species which belong to 16 families. 80.4% of all these specimens were from Alydidae, Lygaeidae, Reduviidae and Pentatomidae while, 74.0 % of all species collected belong to Reduviidae, Lygaeidae, Pentatomidae and Coreidae. The total number of specimens collected from different habitats ranged from 48 in young teak plantations to 290 in lowland forest, and the total of number of species from 21 species in semi-deciduous forest to 48 in isolated forest fragments. Overall no significant differences in species richness among habitats were documented. Shannon-Wiener diversity indices were highly variable among forest types, ranging from 0.90 in lowland forest to 3.41 in isolated forest fragments. Evenness ranged from 0.27 in lowland forest to 0.94 in young teak plantations. We found a significant positive correlation between the age of forest and the Heteroptera abundance as well as Berger-Parker dominance, but evenness was negatively correlated with the age of forest. Although we found no significant differences in species richness among forest individual habitats, species richness, Shannon index and Berger-Parker dominance differed significantly among disturbed and undisturbed forest within the *Noyau Central*. Finally two indicator species were documented for two of the disturbed habitats.

Key words: natural forest; degraded forest; forest plantation; Heteroptera; diversity; indicator species, Shannon-Wiener indice, Berger-Parker indice.

Diversité des pucerons vrais (Hétéroptères) dans des habitats variés de la Forêt Classée de lae Lama au Sud Bénin

Résumé

L'effet de l'utilisation de la forêt sur la diversité et la structure des communautés d'hétéroptère a été étudié dans la forêt classée de la Lama au sud du Bénin. Les pucerons ont été collectés à l'aide de pièges d'interception, de photo-éclecteurs de sol, de pièges malaise, de pièges aériens d'interception et de filet de fauchage. Quatre sites (répétitions) ont été échantillonnés pendant 12 mois dans chacun des habitats suivants à savoir : la forêt dense semi décidue, la forêt dense humide, la forêt dense sèche, les anciens ménages, les jachères à *Chromolaena odorata*, les jeunes plantations de teck, les vieilles plantations de teck, les plantations de bois de feu et les reliques de forêts sacrées isolées. Les 893 hétéroptères collectés représentent 103 espèces appartenant à 16 familles. 80.4% de tous les spécimens collectés appartiennent aux familles Alydidae, Lygaeidae, Reduviidae et Pentatomidae tandis que 74.0 % des espèces collectées appartiennent aux Reduviidae, Lygaeidae, Pentatomidae et Coreidae. Le nombre total de spécimens collectés dans les différents habitats varie de 48 dans les jeunes plantation de teck à 290 dans la forêt dense humide et le nombre total d'espèces collectées de 21 dans la forêt dense semi décidue à 48 dans les reliques de forêts sacrées. Aucune différence significative en terme de richesse spécifique n'est notée entre les différents habitats. L'indice de

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Shannon-Wiener était hautement variable entre les différents types de forêts de 0,90 dans la forêt dense humide à 3,41 dans les reliques de forêts sacrées. L'équitabilité varie de 0,27 dans la forêt dense humide à 0,94 dans les jeunes plantations de teck. Une corrélation positive significative a été notée entre l'âge des forêts, l'abondance des hétéroptères et l'indice de Berger-Parker mais l'équitabilité était négativement corrélée avec l'age des forêts. Bien qu'il n'y a pas de différence significative entre les différents habitats pris de façon individuelle, la richesse spécifique, l'indice de Shannon et de l'indice de Berger-Parker diffèrent significativement entre les zone perturbée par les activités humaines et les zones non perturbée du noyau centrale de la forêt. Enfin, 2 espèces indicatrices ont été enregistrées pour deux des habitats perturbés étudiés.

Mots clés : forêt naturelle; forêt dégradée; plantation de teck; hétéroptère; diversité; espèce indicatrice, indice de Shannon-Wiener, indice de Berger-Parker.

Introduction

The true bugs (Heteroptera) are an ecologically very diverse group, including phytophagous, saprophagous and predatory species (Dolling, 1991). Both larval stages and adults live in similar habitats and respond sensitively to environmental changes (Otto, 1996). Some species are generalists while others are specialists. Studies in agricultural landscapes have shown that bug diversity correlates strongly with total insect diversity. Therefore, bugs have been used as highly representative indicators in previous biodiversity assessments (Duelli and Obrist, 1998; Duelli et al., 1999; Giulio et al., 2001). However, no studies have investigated the diversity of Heteroptera in tropical forest ecosystems.

There is plentiful ecological information about true bugs, yet its relevance is highly variable. Many papers deal with individual species of economic importance (pests or beneficials), and only few studies provide a wider overview of global bug assemblages (Fauvel, 1999). Many studies show that insect communities are most species-rich in closed forest (Morse et al., 1988; Barlow and Woiwod, 1989), but it is not sure whether this also holds for true bugs assemblages.

In this paper we study the diversity of Heteroptera in natural forest, degraded forest, teak plantations, firewood plantations (*Senna siamea*) and isolated forest fragments of the Lama forest reserve, and identify species that can be used as indicators of specific forest habitats. We also study the relationship between true bug diversity and habitat characteristics (environmental variables).

Materials and Methods

Study area

The study was conducted in the Lama forest reserve (southern Benin), one of the last remaining forests located in the so-called "Dahomey Gap". Lama forest lies between 6° 55.8' to 6° 58.8' N and 2° 4.2' to 2° 10.8' E (Fig. 1). The soils are mainly vertisols, but towards the borders of the reserve (old teak plantations and forest fragments) the vertisols are gradually replaced by sandy ferralsols (Specht, 2002). The climate is relatively dry, with an annual precipitation of 1,100 mm. Two rainy seasons and two dry seasons can be distinguished. The natural vegetation is a semi-deciduous forest belonging to the drier peripheral semi-evergreen Guineo-Congolian rain forest system (White, 1983; Adjanohoun, 1989).

Nine habitats, representing all major vegetation formations within the reserve boundary, and a few forest remnants outside the reserve were included for this study. Each was replicated four times, giving a total of 36 study sites. Five of these forest types were located in the Noyau central (NC) and four outside.

1. Semi-deciduous forest (SF, 1,937 ha) with *Afzelia africana, Ceiba pentandra, Dialium guineense, Diospyros mespiliformis, Drypetes floribunda, Celtis brownii* and

Mimusops andongensis as dominant tree species.

2. *Cynometra megalophylla* lowland forest (LF, part of SF), area flooded in the rainy season.
3. *Anogeissus leiocarpus* dry forest (DF, 1,222 ha), a secondary forest with trees reaching 20 m in height.
4. Abandoned settlements (AS, 166 ha) of the Holli population, characterized by the presence of oil palm (*Elaeis guineensis*), guajava (*Psidium guajava*) and secondary regrowth.
5. Perennial *Chromolaena odorata* thicket (CT, 1452 ha), growing on former farmland. *C. odorata* is an invasive species encroaching open canopy patches, forest clearings as well as fallow land.
6. Young teak plantations (YT, 7,200 ha), planted between 1985 and 1995 on vertisol around the NC.
7. Teak plantations (OT, 2,200 ha), planted between 1955 and 1965 on ferralsol.
8. Firewood plantations (FP, 2,400 ha), planted between 1990 and 1992. These forests are composed of fast growing firewood species such as *Senna siamea* and *Acacia auriculiformis* to satisfy the firewood demand and to avoid deforestation.
9. Isolated forest fragments (IF) are isolated patches of forest (< 1 ha) situated outside the Lama forest reserve. They are surrounded by farmland or degraded savannah and are considered as sacred groves by people practicing the voodoo cult.

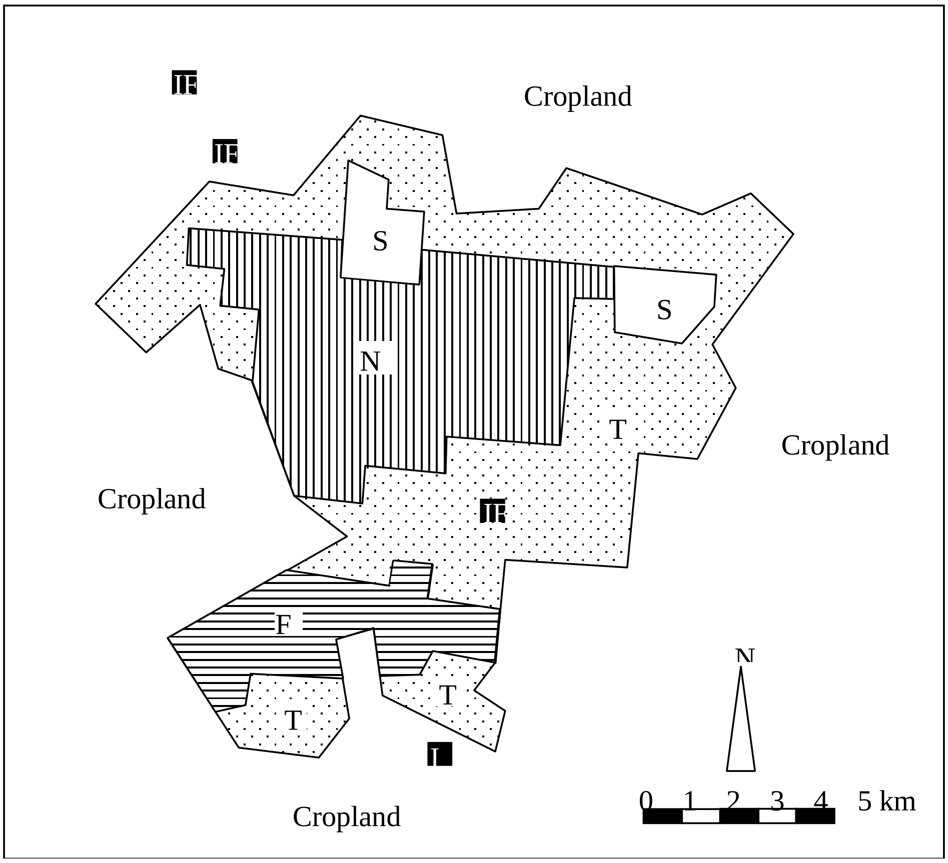

Figure 1. Map of the Lama forest reserve. NC = *Noyau central*, T = teak plantation, FP = firewood plantation, S = settlement, IF = (not to scale) isolated forest fragment

Sampling methods

A similar combination of collecting methods was used in each site to sample Heteroptera. The sampling devices included one Malaise traps, about three quarters the size of Townes' model (Townes, 1972), three funnel pitfall traps (collecting jar in plastic sleeves, funnel 11 cm (top) and 3 cm (exit tube) in diameter), roofed with a transparent plastic sheet 20 cm in diameter (Southwood, 1978), one 0.75 m^2 rectangular ground photo-elector equipped with one pitfall trap (Mühlenberg, 1993), one flight trap intercepting insects between 1.0 and 1.5 meter above the ground (top and bottom funnels 50 cm in diameter, black netting as intercepting surfaces) (Wilkening et al., 1981). The traps were placed on transects oriented north-south, using the same design at all sites. Distances between sites of the same forest type ranged from 0.3 km to 19.0 km. A minimum distance of 20 m (small patches) or 50 m (large patches) was maintained between sampling sites and patch borders. The sampling started in May 2001 and finished in April 2002. The collection vials were filled with 0.5% formaldehyde as preservative, with a few droplets of detergent to lower the surface tension. Heteroptera were collected once monthly for one week. An exception was the sampling period in May 2001 which lasted two weeks. In addition to traps we also used sweep nets to collect Heteroptera. Samples were taken twice at a height of 0-3 m from the vegetation adjacent to the stationary traps (≈ 3 m), once during the dry season (October to December 2002) and once during the rainy season (April to June 2003). Around each trap, 20 sweeps were made, totalling 120 sweeps per site. The net was emptied after a series of 10 sweeps. All adult Heteroptera were sorted to morphospecies, using general keys for preliminary identification to the family level. They were later identified to species at the International Institute of Tropical Agriculture (IITA) in Benin. Voucher specimens were deposited at the IITA Biodiversity Center. The analysis was done on morphospecies level if species identification was difficult (e.g., some Lygaeidae).

The vegetation composition and cover was analyzed between July and September 2001 and again between December and January 2002, using the Braun-Blanquet method (unpublished data). Moreover data were collected on the canopy cover, and the undergrowth vegetation cover. Canopy cover was estimated using a spherical densitometer (Forest Densiometer Model-C, Lemmon), a hand-held, concave mirror with gridlines, held at 1 m from the ground. Openings in the canopy were manually counted within the grid, and a conversion factor yielded the canopy cover value. Four measurements were made to the North, South, West and East of each site, and the mean was calculated (Lemmon, 1957).

The age of each forest type was assessed according to its known history. Semi-deciduous forest, lowland forest and isolated forest fragments were considered to be more than 100 years old. The age of the plantations were exactly known and the age of degraded forest habitats was assessed according to resettlement of people from the forest.

Data analysis

Arthropod assemblages are often compared using similarity and/or diversity indices. Many different diversity and richness indices exist, each with its own strengths and weaknesses. No single index encompasses all characteristics of an ideal index, i.e., high discriminant ability, low sensitivity to sample size, and ease in calculation (Marguran, 1988). This is why we decided to combine different indices reflecting species richness, dominance and diversity heterogeneity. These indices provide a basis to interpret differences in Heteroptera diversity among forest types. We chose some of the most commonly used and most often recommended indices (e.g., Samways, 1983; Southwood, 1987; Margurran, 1988; Krebs, 1989; Roth et al., 1994): species richness (S), Shannon index (H), Berger-Parker index (D), and evenness (E). A brief explanation of each index follows:

S: Species richness is simply the total number of species in a community. It provides a great deal of information about the community and represents an instantly comprehensible expression of diversity (Margurran, 1988). As an index, S is easily conceptualized and comparable across habitats.

H: Shannon's index of diversity (Price, 1997) reflects both evenness and richness (Colwell and Huston, 1991) and is commonly used in diversity studies (Krebs, 1989). It is calculated according to:

$$\mathbf{H = -\sum P_{\mathit{i}} \ln P_{\mathit{i}};\ \mathit{i} = 1 - n}$$

where n is the number of species and P_i is the proportion of the *i*th species in the total. Samples having high species richness and similar abundance between species will generate high H values.

D: The Berger-Parker dominance measure expresses the proportional importance of the most abundant species (Margurran, 1988). The Berger-Parker index or $P_{i(\max)}$ is the proportion of the most abundant species.

E: Evenness indicates the degree of homogeneity in abundance between species and is based on the Shannon index of diversity. Both the Berger-Parker dominance index and Evenness index are important measures of heterogeneity. Shannon evenness is calculated according to:

$$\mathbf{E = H / H_{max} = H/\ln S,}$$

where H is the Shannon diversity index and S the number of species in the community. Evenness ranges from 0 to 1.

In addition to these indices, we also used a similarity index for a closer examination of the species composition in different forest types. The percent similarity (P) shows the proportion of species in common between sites (Krebs, 1989). The index is relatively insensitive to sample size and species diversity and is calculated by the equation:

$$\mathbf{P = \sum minimum\ (P_{1\mathit{i}}, P_{2\mathit{i}}) \times 100}$$

where P is the percentage similarity between sites 1 and 2, P_{1i} is the proportion of species *i* in community sample one and P_{2i} is the proportion of species *i* in community sample two.

One way analysis of variance (ANOVA) was used to compare diversity and richness indices and the environmental variables canopy cover: undergrowth vegetation cover, tree species richness, undergrowth plant species richness and tree height among forest types. Parametric tests were used when the data were normally distributed, followed by Student Newman-Keuls multiple comparison of means if the ANOVA revealed significance. Data transformations were made for all diversity indices, using the natural logarithm. However, normalisation of the data was only achieved for species richness.

For the remaining indices, we used non-parametric Kruskal-Wallis analysis of variance followed by the Nemenyi *post hoc* test. Non-parametric analysis were necessary because the data presented high variance heterogeneity.

We pooled data of all disturbed forest habitats (*A. leiocarpus* dry forest, abandoned settlements and *C. odorata* thicket) and all undisturbed forest habitats (semi-deciduous forest and *C. megalophylla* lowland forest) from within the *Noyau Central* and compare Heteroptera species richness, Shannon diversity index and Berger-Parker dominance, using unbalanced one way analysis of variance (ANOVA).

Simple correlations between habitat characteristics and Heteroptera abundance and diversity indices were determined using the SPSS 11.0 software. These analyses allowed testing for the effect of abiotic factors on diversity.

When the same data were used repeatedly the errors was adjusted using Bonferroni adjustment.

Indicator species include species restricted to a particular type of forest and those more widely distributed yet especially abundant in a particular type of forest. We used the method of Dufrêne and Legendre (1997) to determine Heteroptera indicator species for the different habitats. This method combines data on the concentration of species abundance in a particular group of sites (habitats) and the faithfulness of occurrence of species in a particular group. Indicator species analysis was performed as described by Lachat et al. (2004). The significance of indicator values was tested using Monte Carlo randomisation (1,000 runs). The threshold level was set to 25% and the significance level to $P \leq 0.01$, as proposed by Dufrêne and Legendre (1997).

Results

Composition of bug assemblages

A total of 893 adult specimens comprising 104 species were recorded in the nine habitats (Tables 1 & 2). These species belong to 16 families of which Alydidae made up the largest proportion of the total catch (35.9%), followed by Lygaeidae (21.3%), Reduviidae (16.2%), Pentatomidae (6.9%), Pyrrhocoridae (4%), Coreidae (3.9%), Plataspidae (3.8%), Cydnidae (3.4%) and Largidae (2.9%). The greatest number of species was found in the Reduviidae family (26), followed by Lygaeidae (19), Pentatomidae (19), Coreidae (13), Plataspidae (6) and Alydidae (5). Thirty four percent of all Heteroptera specimens were singletons (Table 2).

Both species richness (n = 49) and the number of families (n = 14) were highest in isolated forest fragments (Table 3). Species richness was lowest in semi-deciduous forest (n = 21), whereas the lowest number of families was found in young teak plantations (n = 8). Bug abundance was highest in lowland forest, with a total of 290 adult bugs, and lowest in young teak plantations (48 adult bugs). Each habitat had at least one unique species. Fifteen species were restricted to isolated forest fragments, six species to *Anogeissus leiocarpus* dry forest, six species to abandoned settlements and four species to *Chromolaena odorata* thicket. Old teak plantations, *Cynometra megalophylla* lowland forest and firewood plantations had three unique species each, and young teak plantations and semi-deciduous forest two and one species, respectively (Table 4).

The most abundant species was *Stenocoris southwoodi* Ahmad, comprising 304 individuals (34%). The second most abundant species was Lygaeidae sp. 12 (n = 51, 5.7%), followed by Pyrrhocoridae sp. 1 (n = 35, 3.9%), Lygaeidae sp. 11 (n = 32, 3.6%), Cydnidae sp. 1 (n = 29, 3.2%), *Lisarda crudelis* (n = 27, 3%), Largidae sp. 1 (n = 26, 2.9%), Lygaeidae sp. 14 (n = 24, 2.7%), Lygaeidae sp. 6 (n = 18, 2%) and *Oncocephalus* sp. 1 (n = 16, 1.8%) (Table 5). Only one species (Lygaeidae sp. 12) occurred in all nine forest types. Another four species occurred in eight forest types. *Stenocoris southwoodi* Ahmad and Cydnidae sp. 1 were found in all forest types except in *Chromolaena* thicket and young teak plantations respectively, and *Lisarda crudelis* and Largidae sp. 1 were only absent in firewood plantations. Fifty species (48.1%) collected in this study were identified to morphospecies only, and some species are probably new to Benin.

Table 1. Heteroptera collected in the Lama forest reserve in Benin

Taxon	Forest types									
	SF	LF	DF	AS	CT	YT	OT	FP	IF	Totals
Alydidae										
Stenocoris southwoodi Ahmad	16	246	3	5		1	23	1	9	304
? Tupalus maculatus Distant		1								1
Sjostedtina sp.			2	1						3
Riptortus dentipes Fabricius	1			4				6		11
Daclera punctata Signoret				1			1			2
Totals										321
Aradidae										
Meriza sp.					1					1
Aradus flavicornis Dalman									1	1
Totals										2
Berytidae										
Berytidae sp. 1									1	1
Totals										1
Coreidae										
Acanthocoris collarti Schouteden			2							2
Coreidae sp. 1				1			1		1	3
Coreidae sp 2		1							2	3
Anoplocnemis curvipes Fabricius	4						3		2	9
Clavigralla curvipes Stål		1								1
Cletus pronus Berger			1							1
Anoplocnemis curvipes Fabricius						1			1	2
Hydara tenuicornis Westwood									2	2
Phyllogonia biloba Signoret			1							1
Coreidae sp. 3							1			1
Coreidae sp. 4	1		1						1	3
Coreidae sp. 5							1	2		3
Homoeocerus pallens Fabricius							1	2	1	4
Totals										35
Cydnidae										
Cydnidae sp. 1	5	5	1	1	1		1	2	13	29
Cydnidae sp. 2	1								1	2
Totals										31
Dinidoridae										
Coridius remipes Stål		1			1					2
Totals										2
Largidae										
Largidae sp. 1	2	4	4	4	2	4	3		3	26
Totals										26
Lygaeidae										
Lygaeidae sp. 1	1		1			1	1		3	7
Lygaeidae sp. 2		1			2	2		1		6
Lygaeidae sp. 3		1					1	5	1	8
Lygaeidae sp. 4		1				1			1	3
Lygaeidae sp. 5		1		2			2			5
Lygaeidae sp. 6		1	3	3		2	5	1	3	18
Lygaeidae sp. 7					1					1
Lygaeidae sp. 8					1					1
Lygaeidae sp. 9							1			1
Lygaeidae sp. 10								1		1

Taxon	Forest types									
	SF	LF	DF	AS	CT	YT	OT	FP	IF	Totals
Aspilocoryphus fasciativentris Stål			2	1				1	1	5
Lygaeidae sp. 11	4	1	17	6	2				2	32
Lygaeidae sp. 12	7	1	12	8	9	3	1	9	1	51
Lygaeidae sp. 13				1						1
Lygaeidae sp. 14			5	9	3	4	1		2	24
Lygaeidae sp. 15		1	1				3			5
Lygaeidae sp. 16		1		1		2	4	1		9
Lygaeidae sp. 17		1	3			1	1		1	7
Lygaeidae sp. 18	1	1	3							5
Totals										190
Miridae										
Miridae sp. 1									1	1
Miridae sp. 2									1	1
Miridae sp. 3				1						1
Totals										3
Nabidae										
Nabidae sp. 1						1		1		2
Totals										2
Pentatomidae										
Pentatomidae sp. 1	1									1
Durmia haedula Stål				1						1
Aspavia hastator Fabricius	4			3	3		2	1		13
Stenozygum alienatum Fabricius						1				1
Carbula sp.			1							1
Pentatomidae sp. 2									2	2
Aspavia accuminata							8	4	1	13
Aspavia brunnea Signoret									1	1
Lerida punctata (Palisot de Beauvois)							2		1	3
Sepontia misella Stål								2	1	3
Leptolobus murrayi Signoret				3						3
Aspavia sp.			1							1
Pentatomidae sp. 3									1	1
Pentatomidae sp. 4						3			2	5
Pentatomidae sp. 5				1					4	5
Macrorhaphis acuta Dallas									1	1
Pentatomidae sp. 6									1	1
Nezara viridula Linnaeus		1					2		1	4
Acrosternum rinapsis Dallas							2			2
Totals										62
Plataspidae										
Plataspidae sp. 1	1	1				1	1	2	2	8
Plataspidae sp. 2				1			1	1		3
Plataspidae sp. 3					2			2	1	5
Plataspidae sp. 4		4		1	3		1	2		11
Plataspidae sp. 5			1		2		1			4
Coptosoma nigriceps Signoret					1		2			3
Totals										34
Pyrrhocoridae										
Pyrrhocoridae sp. 1	1	1	17	1	4		1		10	35
Probergrothius sexpunctatus Laporte									1	1
Totals										36

Taxon	Forest types									
	SF	LF	DF	AS	CT	YT	OT	FP	IF	Totals
Reduviidae										
Ectmetacanthus annulipes Reuter				1						1
Petalocheirus (Platychiria) murrayi Signoret	4	2			1				1	8
Oncocephalus pilicornis Herrich-Schaeffer		1						1		2
Vestula lineaticeps Signoret		1			1					2
Peirates (Cleptocoris) sp.		3				3				6
Cleptria (Cleptriola) togoana Schouteden			4		2				4	10
Sphedanolestes lamottei Villiers				1				2	1	4
Rhynocoris bicolor Fabricius					1					1
Peprius nodulipes Signoret			3	1	1	3	5		2	15
Santosia dahomeyana Villiers		2								2
Tribelocephala tristis Breddin						1				1
Haematochares obsuripennis discalis Schouteden									1	1
Reduviidae sp. 1	1			1						2
Pisilus tipuliformis Fabricius				1						1
Nagusta praecatoria Fabricius									1	1
Reduviidae sp. 2						1	1			2
Lisarda crudelis	4	1	6	6	2	4	1		3	27
Microcarenus clarus Bergroth			3							3
Oncocephalus sp.1			4		1			11		16
Lisarda vandenplasi Schouteden	1	3			3			1		8
Ectomocoris cruciger Fabricius			1	3	2			1		7
Reduviidae sp. 3	1				1	6	1			9
Ectrichodia lucida Lepeletier & Audinet-Serville					1	1	3	1		6
Sphedanolestes sp.								1		1
Rhynocoris crudellis Stål			3	1	1				1	6
Microstemma atrocyanea Signoret	1				1	1				3
Totals										145
Rhopalidae										
Leptocoris sp.								1		1
Peliochrous nigromaculatus Stål									1	1
Totals										2
Tingidae										
Tingidae sp. 1									1	1
Totals										1

Table 2. Species richness and abundance of Heteroptera

Family	Species richness	Abundance	Singletons
Reduviidae	26	145	7
Lygaeidae	19	190	5
Pentatomidae	19	62	9
Coreidae	13	35	3
Plataspidae	6	34	0
Alydidae	5	321	1
Miridae	3	3	3
Aradidae	2	2	2
Cydnidae	2	31	0
Pyrrhocoridae	2	36	1
Rhopalidae	2	2	2
Berytidae	1	1	1
Dinidoridae	1	2	0
Largidae	1	26	0
Nabidae	1	2	0
Tingidae	1	1	1
Total	104	893	35

Table 3. Richness, abundance and diversity indices of various forest habitats of the Lama forest reserve

Forest type	Species richness	Family richness	Abundance	Unique species	Shannon index	Berger Parker index	Evenness
SF	21	9	62	1	2.59	0.26	0.85
LF	29	10	290	3	0.90	0.85	0.27
DF	28	9	106	6	2.88	0.16	0.86
AS	31	10	75	6	3.10	0.12	0.90
CT	29	9	56	4	3.14	0.16	0.93
YT	23	8	48	2	2.94	0.13	0.94
OT	34	9	88	3	2.98	0.26	0.84
FP	28	10	67	3	2.94	0.16	0.88
IF	49	14	101	15	3.50	0.13	0.90

Table 4. List of Heteroptera species found exclusively in specific habitats

Species per habitat	Number of unique species per habitat
Semi-deciduous forest	1
Pentatomidae sp1	
***Cynometra megalophylla* lowland forest**	
? Tupalus maculatus Distant	3
Clavigralla curvipes Stål	
Santosia dahomeyana Villiers	
***Anogeissus leiocarpus* dry forest**	6
Cletus pronus Berger	
Phyllogonia biloba Signoret	
Microcarenus clarus Bergroth	
Acanthocoris collarti Schouteden	
Carbula sp.	
Aspavia sp.	
Abandoned settlement	6
Miridae sp. 3	
Durmia haedula Stål	
Leptolobus murrayi Signoret	
Ectmetacanthus annulipes Reuter	
Pisilus tipuliformis Fabricius	
Lygaeidae sp. 3	
***Chromolaena odorata* thickets**	4
Meriza sp.	
Lygaeidae sp. 7	
Lygaeidae sp. 8	
Rhynocoris bicolor Fabricius	
Young teak plantation	2
Stenozygum alienatum Fabricius	
Tribelocephala tristis Breddin	
Old teak plantation	3
Coreidae sp. 3	
Lygaeidae sp. 9	
Acrosternum rinapsis Dallas	
Firewood plantation	3
Lygaeidae sp. 10	
Sphedanolestes sp.	
Leptocoris sp.	
Isolated forest fragment	15
Hydara tenuicornis Westwood	
Miridae sp. 1	
Miridae sp. 2	
Aspavia brunnea Signoret	
Pentatomidae sp. 4	
Macrorhaphis acuta Dallas	
Pentatomidae sp.7	
Probergrothius sexpunctatus Laporte	
Haematochares obsuripennis discalis Schouteden	
Nagusta praecatoria Fabricius	
Peliochrous nigromaculatus Stål	
Tingidae sp. 1	
Pentatomidae sp. 2	
Aradus flavicornis Dalman	
Berytidae sp. 1	

Table 5. ist of the most abundant heteropterans

			Number of individuals per habitat								
Species	Abundance	Percentage	SF	LF	DF	AS	CT	YT	OT	FP	IF
Stenocoris southwoodi Ahmad	304	34.0	16	246	3	5		1	23	1	9
Lygaeidae sp. 12	51	5.7	7	1	12	8	9	3	1	9	1
Pyrrhocoridae sp. 1	35	3.9	1	1	17	1	4		1		10
Lygaeidae sp.11	32	3.6	4	1	17	6	2				2
Cydnidae sp. 1	29	3.2	5	5	1	1	1		1	2	13
Lisarda crudelis	27	3.0	4	1	6	6	2	4	1		3
Largidae sp. 1	26	2.9	2	4	4	4	2	4	3		3
Lygaeidae sp. 14	24	2.7			5	9	3	4	1		2
Lygaeidae sp. 7	18	2.0		1	3	3		2	5	1	3
Oncocephalus sp.1	16	1.8			4		1			11	
Peprius nodulipes Signoret	15	1.7			3	1	1	3	5		2
Aspavia hastator Fabricius	13	1.5	4			3	3		2	1	
Aspavia accuminata	13	1.5							8	4	1
Riptortus dentipes Fabricius	11	1.2	1			4				6	
Plataspidae sp. 4	11	1.2		4		1	3		1	2	
Cleptria (Cleptriola) togoana Schouteden	10	1.1			4		2				4

Diversity of Heteroptera

Species richness was highest in isolated forest fragments, *A. leiocarpus* dry forest and abandoned settlement, with 15.7 ± 0.8, 13.2 ± 2.8 and 12.0 ± 2.0 (mean ± standard error) species, respectively, and lowest in semi-deciduous forest (8.0 ± 0.9), young teak plantations (8.2 ± 1.4) and firewood plantations (8.7 ± 0.7). The remaining habitats had intermediate levels of species richness, ranging from 9.0 ± 0.6 in lowland forest to 11.2 ± 4.1 in old teak plantations. However, differences in species richness among forest types were not statistically significant (ANOVA: $F_{8,27} = 1.6$, $P = 0.168$).

The highest Shannon diversity was found in isolated forest fragments (2.5 ± 0.1) and the smallest Berger-Parker index too (0.17 ± 0.03) (least dominance by a single species), followed by *A. leiocarpus* dry forest, abandoned settlement and *C. odorata* thicket. These habitats had similar evenness (0.9).

Although the nine habitats did not differ significantly in species richness (see above) and evenness (Kruskal-Wallis: $\chi^2 = 10.5$, d.f. = 8, $P = 0.231$), some differences in abundance (Kruskal-Wallis: $\chi^2 = 17.5$, d.f. = 8, $P = 0.025$), Shannon diversity (Kruskal-Wallis: $\chi^2 = 19.2$, d.f. = 8, $P = 0.014$) and Berger-Parker dominance (Kruskal-Wallis: $\chi^2 = 10.5$, d.f. = 8, $P = 0.017$) were found (Fig. 2). All normally significant indices are significant at $P < 0.05$ after Bonferroni adjustment.

The Nemenyi-tests revealed four significant differences. The Shannon index was significantly higher in isolated forest fragments than in *C. megalophylla* lowland forest, and the mean number of individuals of Heteroptera was significantly higher in *C. megalophylla* lowland forest than in young teak plantations. The Berger-Parker dominance index was significantly higher in *C. megalophylla* lowland forest than in isolated forest fragments and abandoned settlements (Fig. 2.).

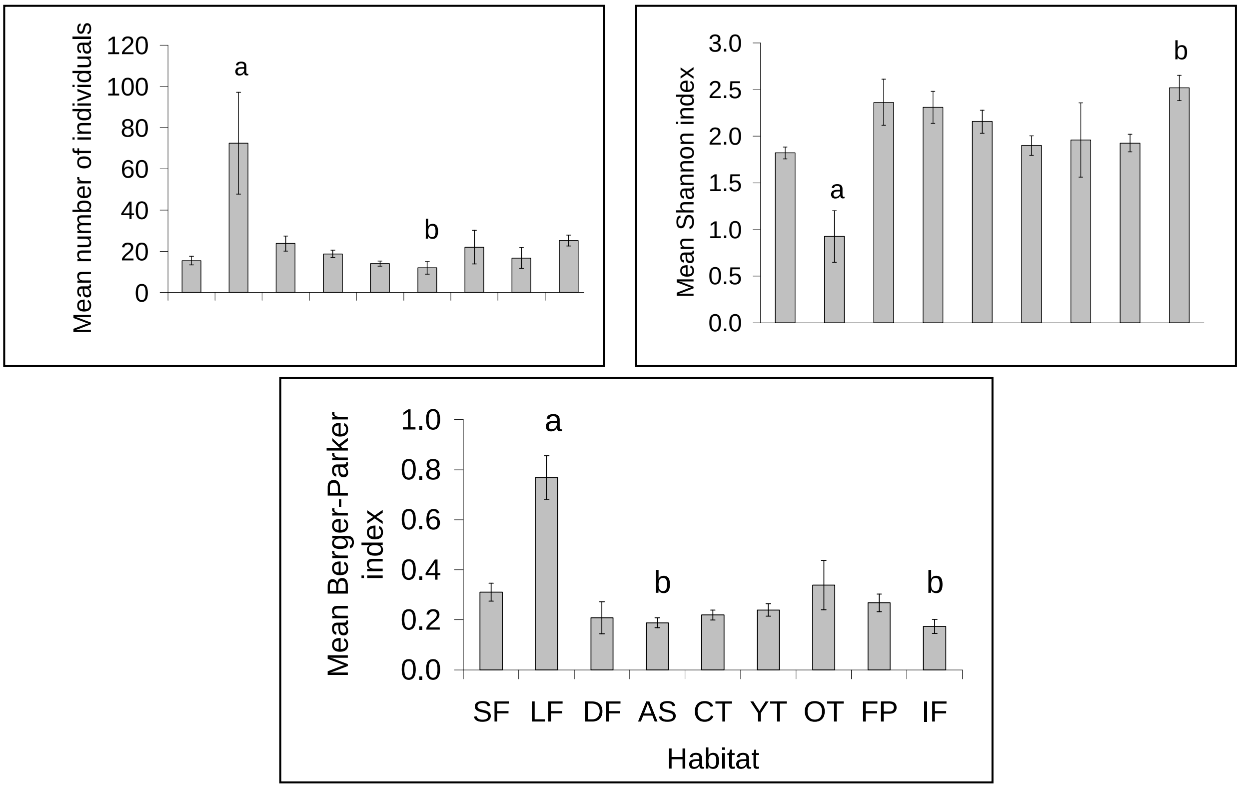

Figure 2. Mean number of individuals, Shannon diversity and Berger-Parker dominance (n = 4; ± standard error) for nine different forest habitats

Means not sharing the same letter are significantly different at *P* < 0.05 all remaining differences are not significant

Comparison between disturbed and undisturbed forest within the *Noyau Central* showed that differences in species richness, Shannon index and Berger-Parker index among forest types were statistically significant (ANOVA: $F_{1,18} = 4.8$, $P = 0.0426$; $F_{1,18} = 17.9$, $P = 0.0005$ and $F_{1,18} = 16.5$, $P = 0.0007$ respectively. Disturbed forest had higher species richness and Shannon diversity but lower Berger-Parker dominance than undisturbed forest (Fig. 3).

The similarity of Heteroptera assemblages varied among habitats. The highest similarity was observed between *Anogeissus leiocarpus* dry forest and *Chromolaena odorata* thicket (45 %), semi-deciduous forest and abandoned settlements (43%), semi-deciduous forest and old teak plantations (41%), and *Anogeissus leiocarpus* dry forest and isolated forest fragments (38%) (Table 6).

Two indicator species were identified for two forest types. *Stenocoris southwoodi* Ahmad (Alydidae) was an indicator for *C. megalophylla* lowland forest and Lygaeidae sp. 11 for *A. leiocarpus* dry forest. However, we found no indicator species for the remaining forest habitats.

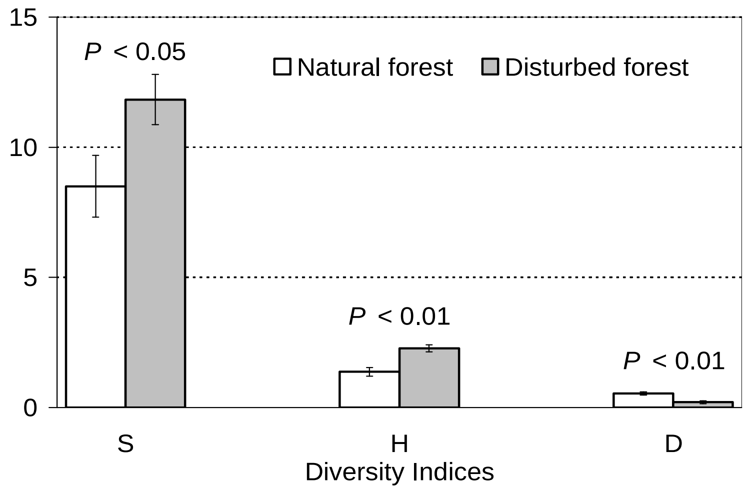

Figure 3. **Mean species richness, Shannon diversity and Berger-Parker dominance for undisturbed forest of the Noyau Central (n = 4; ± standard error) and disturbed forest (n = 12; ± standard error)**

Mean species richness is significant at P < 0.05, and Shannon diversity and Berger-Parker dominance P < 0.01 after Bonferroni adjustment

Table 6. **Percent similarity of Heteroptera assemblages among forest habitats.**

	SF	LF	DF	AS	CT	YT	OT	FP	IF
SF		32.70	34.92	43.08	37.04	24.46	41.53	21.98	35.68
LF			7.81	13.13	8.62	7.26	33.24	8.04	16.50
DF					45.13	30.60	19.88	20.99	37.67
AS					40.98	36.67	30.38	29.97	29.82
CT						29.46	18.99	31.93	28.15
YT							29.55	17.29	24.96
OT								21.39	31.57
FP									15.87

Difference in habitat characteristics and correlation with bug diversity

Canopy cover and undergrowth vegetation cover were significantly different between habitats (ANOVA: $F_{8,27}$ = 8.9, P < 0.001 and $F_{8,27}$ = 3.3, P = 0.009, respectively), as were tree species richness and tree height (Kruskal-Wallis: χ^2 =24.6, d.f. = 8, P = 0.002 and χ^2 =16.8, d.f. = 8, P = 0.032, respectively). But undergrowth plants species richness was not significantly different (ANOVA: $F_{8,27}$ = 2.1, P = 0.070).

Student Newman Keuls tests showed that canopy cover was significantly lower in *Chromolaena odorata* thicket than in the others habitats. In contrast, in young teak plantations the undergrowth vegetation cover was significantly lower than in the other habitats, but did not differ significantly from old teak plantations (Table 7).

Non-parametric Nemenyi post hoc tests showed that tree species richness was significantly higher in isolated forest fragments than in the old teak plantations, and that tree height was significantly higher in old teak plantations than abandoned settlements (Table 7).

Age of the forest habitats was the only parameter significantly correlated with Heteroptera community diversity and/or structure. The correlations were significant for Heteroptera abundance (*r*= 0.410, *P* = 0.013), Berger-Parker dominance, (*r* = 0.436, *P* = 0.008) and Shannon evenness (*r* = -0.452, *P* = 0.006) (Table 8).

Table 7. **Site characteristics of the different habitat types studied. Values are means ± standard errors (n = 4). Means in columns not sharing the same letter are significantly different at P < 0.05. All remaining differences are not significant. Asterisks denote levels of significance following Bonferroni adjustment: * P < 0.05 and ** = P < 0.01. Capital letters indicate parametric, small letters non-parametric post hoc test.**

Habitat	Age (year)	Canopy cover (%)	**	Undergrowth vegetation cover (%)	*	Tree species richness	**	Undergrowth plant species richness	Tree height (m)	*
SF	> 100	56.7 (3.6)	A	74.0 (12.8)	A	7.0 (0.4)		37.7 (5.1)	18.0 (1.1)	
LF	> 100	71.0 (3.3)	A	66.7 (4.4)	A	7.0 (1.8)		41.7 (4.0)	21.0 (0.8)	
DF	25	58.2 (4.2)	A	67.2 (13.2)	A	7.7 (1.0)		41.5 (5.9)	17.7 (0.9)	
AS	15	60.5 (5.5)	A	67.2 (7.7)	A	7.7 (0.9)		36.7 (3.2)	17.0 (0.9)	b
CT	15	18.2 (9.7)	B	69.0 (17.8)	A	9.0 (2.3)		25.2 (6.0)	18.2 (4.2)	
YT	15	76.7 (4.4)	A	19.5 (6.1)	B	2.2 (0.3)		37.7 (5.6)	17.7 (1.7)	
OT	40	63.2 (5.9)	A	43.0 (10.8)		1.2 (0.3)	a	35.5 (0.6)	24.0 (0.9)	a
FP	10	61.7 (2.4)	A	61.7 (5.7)	A	2.7 (0.8)		32.7 (5.5)	15.0 (1.8)	
IF	>100	55.5 (6.8)	A	83.0 (6.6)	A	9.2 (0.6)	b	50.7 (4.6)	23.7 (2.1)	

Table 8. **Correlations between habitat characteristics and Heteroptera diversity and dominance indices; N = number of individuals, S = species richness, H = Shannon diversity, E = evenness, D = Berger-Parker dominance. Note that, due to a high number of comparisons, correlations which are normally significant are only significant at P < 0.15 after Bonferroni adjustment.**

Habitat's characterisrics	Diversity indices				
	N	S	H	E	D
Age					
Pearson correlation	0.41	0.067	-0.284	-0.452	0.436
Significance	0.013	0.698	0.094	0.006	0.008
n	36	36	36	36	36
Canopy cover					
Pearson correlation	0.198	-0.16	-0.251	-0.18	0.258
Significance	0.248	0.353	0.139	0.293	0.128
n	36	36	36	36	36
Undergrowth vegetation cover					
Pearson correlation	0.141	0.24	0.109	-0.113	0.047
Significance	0.413	0.159	0.527	0.511	0.783
n	36	36	36	36	36
Tree species richness					
Pearson correlation	-0.065	0.253	0.29	0.128	-0.149
Significance	0.707	0.137	0.086	0.457	0.384
n	36	36	36	36	36
Undergrowth plant species richness					
Pearson correlation	0.177	0.209	0.06	-0.082	0.072
Significance	0.307	0.22	0.727	0.634	0.676
n	36	36	36	36	36
Tree height					
Pearson correlation	0.203	0.184	-0.014	-0.155	0.161
Significance	0.234	0.284	0.933	0.368	0.35
n	36	36	36	36	36

Discussion

Heteroptera assemblages

This is the first study on the diversity of Heteroptera assemblages in natural and plantation forests in Benin. The study yields an understanding of how bug community structure varies with various types of habitat and forest use. Our data demonstrate no difference in Heteroptera species richness between natural, degraded and plantation forests of the Lama forest reserve. These results confirm those of Kalif *et al.* (2001) who found similar species richness yet different composition of ant assemblages in degraded (logged) and natural forest in eastern Amazonia. However, we found that Shannon diversity was significantly higher in isolated forest fragments than lowland forest. This seems to be due to the low species richness and uneven distribution of dominant bugs in lowland forest, where a single species, *Stenocoris southwoodi* Ahmad, represented 84.9% of all specimens, but only 8.9% in isolated forest fragments. Roedel and Braendle (1995) reported that *Stenocoris elegans*, the second most common species of this genus, occurred in island and riverine forest of the Comoe National Park in Côte d'Ivoire. They also observed aggregations of millions of individuals. *Stenocoris southwoodi* is found in high number in most forests in Benin, independent of their size (Goeorgen, personal communication). Species in isolated forest fragment were more evenly distributed (E = 0.90) than in *C. megalophylla* lowland forest (E = 0.27). Shannon diversity decreased in lowland forest, an area which may be heavily flooded during the long rainy season. In addition, the decrease in bug species corresponds to increased domination by one species in the community (*Stenocoris southwoodi* Ahmad). This phenomenon has been previously observed by Samways (1983) in a study of ant community structure in a series of habitats associated with citrus.

Isolated forest fragments, *A. leiocarpus* dry forest and abandoned settlement had higher levels of dominant species (Berger-Parker dominance index) than lowland forest. Higher diversity of Heteroptera in isolated forest fragments can be attributed to higher habitat diversity and heterogeneity. Most isolated forest fragments are located outside of the Lama forest reserve, and are bordering to open degraded savannah or farmland. Based on results of this study, we assume that the proximity to colonizing sources may be important. Paoletti (1999) found that true bugs are distinct indicators of farmland. This could explain the high species richness found in isolated forest fragments. *A. leiocarpus* dry forest and abandoned settlements are secondary forests in degraded areas of the *Noyau central* and showed higher Heteroptera diversity compared to undisturbed natural forest (semi-deciduous and lowland forest).

Even though differences among the various forest types within the *Noyau central* were not significant (probably due to insufficient statistical power), the high diversity in disturbed forest may indicate the important role of secondary forest as a habitat for heteropterans. Dunn (2004) reviewed studies on the recovery of animal species in tropical forest and found that secondary forest may play an important role in biodiversity conservation. Our result confirms common knowledge that Heteroptera diversity is high in open landscapes.

Heteroptera are distinct indicators in farmland (Paoletti, 1999). In agricultural landscapes, their diversity has been found to correlate closely with total insect diversity. Yet we found only two indicator species for forest habitats. Our results suggest that Heteroptera may be inappropriate indicators in tropical forests. However, more data need to be collected to improve the understanding of Heteropteran diversity in tropical forest ecosystems before drawing such strong conclusions.

Similarity between habitats

Even though α-diversity was similar across habitats in the Lama forest reserve, similarity was highest between *Anogeissus leiocarpus* dry forest and *Chromolaena odorata* thicket, between *A. leiocarpus* dry forest and isolated forest fragments and between semi-deciduous forest and abandoned settlements. *C. odorata* thicket shared 45% of the species with *A. leiocarpus* dry forest but only 8.6% with *C. megalophylla* lowland forest, although these habitats are closer to each other. In contrast old teak plantations shared most species with semi-deciduous forest, despite of lying far from each other. Open forest with low canopy cover and isolated forest surrounded by farmland showed a high similarity in Heteroptera communities. It is difficult to explain the similarity between semi-deciduous forest and abandoned settlements as both of these two habitats exhibit a high number of unique species (5 to 13). Degraded habitats such as *Chromolaena odorata* thicket have significantly lower canopy cover due to low tree species densities. However, canopy cover and plant diversity that have been demonstrated to affect the diversity of insects in previous studies (Levings, 1983, Lynch et al., 1988) were not correlated to Heteroptera diversity in our study. This may be explained by the strong spatial heterogeneity of habitats within the *Noyau central* of Lama forest, which forms a small-scale mosaic of natural and degraded forest. Even though, our results showed that the abundance, evenness and Berger-Parker dominance structure of Heteroptera assemblages were strongly related to the successional stage (age) of the forest habitats. This suggests that the abundance and dominance of individual bug species increase as the forests mature, whereas species richness would be expected to decrease.

Conclusion

This paper assessed the diversity and community structure of true bugs in various habitats of the Lama forest reserve in Benin. The bug fauna consisted of 16 families of which the Reduviidae, Lygaeidae, Pentatomidae and Coreidae were the most species-rich. We found few differences in species richness and diversity of Heteroptera. However, lowland forest was characterized by the lowest species richness and diversity whereas isolated forest presented the highest species richness and diversity, but the lowest dominance of individual species. We found significant difference between disturbed and undisturbed forest within the *Noyau central* and this reflects common knowledge that Heteroptera diversity is high in open landscapes. The total abundance of Heteroptera was a function of habitat age, but habitat characteristics such as canopy cover, undergrowth vegetation cover and plant species richness did not influence species richness and diversity of bug assemblages in Lama forest reserve. Our study suggests that contrary to agricultural landscapes true bugs may not be suitable bioindicators for tropical forest habitats. However, we are aware that our study is only a first approach and that it is limited in scale and sampling effort, so more studies have to be conducted before final conclusions can be drawn.

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