


Contrasting the distribution of butterflies and termites in plantations and tropical forests

Yves Basset^{1,2,3}  · Héctor Barrios³ · José Alejandro Ramirez¹ · Yacksecari Lopez¹ · James Coronado¹ · Filonila Perez¹ · Stephany Arizala¹ · Ricardo Bobadilla¹ · Maurice Leponce⁴

Received: 28 May 2016 / Revised: 4 October 2016 / Accepted: 7 October 2016
© Springer Science+Business Media Dordrecht 2016

Abstract In the tropics vast areas of natural forests are being converted into plantations. The magnitude of the resulting loss in arthropod biodiversity and associated ecosystem services represents a significant topic of research. In this study we contrasted the abundance, species richness and faunal turnover of butterflies, resident butterflies (i.e., whose host plants were ascertained to occur in the habitats studied) and termites between small (average 4.3 ha) 20+ year old exotic plantations (teak and *Terminalia*), native plantations (Cedro espino), and an old growth forest in Panama. We used Pollard walks and manual search to quantify the abundance or occurrence of butterflies and termites, respectively. In 2014 we observed 4610 butterflies representing 266 species and 108 termite encounters (out of 160 quadrats) representing 15 species. Butterflies were more abundant and diverse in plantations than in the forest, whereas this pattern was opposite for resident butterflies and termites. There was marked faunal turnover between plantations and forest. We conclude that (a) the magnitude of faunal changes between forest and plantations is less drastic for termites than for butterflies; (b) resident butterfly species are more impacted by the conversion of forest to plantations than all butterflies, including transient species; and

Communicated by Akihiro Nakamura.

This article belongs to the Topical Collection: Forest and plantation biodiversity.

Electronic supplementary material The online version of this article (doi:[10.1007/s10531-016-1231-6](https://doi.org/10.1007/s10531-016-1231-6)) contains supplementary material, which is available to authorized users.

✉ Yves Basset
bassety@si.edu

¹ Smithsonian Tropical Research Institute, Apartado, 0843-03092, Panama City, Republic of Panama

² Faculty of Science, University of South Bohemia and Institute of Entomology, Biology Centre of Czech Academy of Sciences, Branišovská 31, 370 05 Ceske Budejovice, Czech Republic

³ Maestria de Entomologia, Universidad de Panamá, 080814 Panama City, Republic of Panama

⁴ Operational Directorate Natural Environment, Institut Royal DES Sciences Naturelles de Belgique, 1000 Brussels, Belgium

(c) species richness does not necessarily decrease in the series forest > native > exotic plantations. Whereas there are advantages of studying more tractable taxa such as butterflies, the responses of such taxa can be highly unrepresentative of other invertebrate groups responsible for different ecological services.

Keywords Barro Colorado Island · Cedro espino · Faunal turnover · Isoptera · Teak · *Terminalia*

Introduction

Throughout the tropics vast areas of natural forests (i.e., naturally regenerated) are being converted into plantations of exotic or indigenous trees (Brockerhoff et al. 2008). All these manipulations have influences on the habitats which tropical forest provide for animals and plants. Apart from change in species composition, the physical and botanical structure of the habitat may be severely altered, with consequences for ecosystem services (Speight et al. 2003; Brockerhoff et al. 2013). The relationship between biodiversity and the persistence of ecosystem services in agricultural landscapes has generated considerable interest and a range of experimental approaches (Swift et al. 2004; Cardinale et al. 2012). There is unequivocal evidence that biodiversity loss reduces the efficiency by which ecological communities capture biologically essential resources, produce biomass, decompose and recycle biologically essential nutrients (Cardinale et al. 2012). Moreover, although species may appear functionally redundant when one function is considered under one set of environmental conditions, many species are needed to maintain multiple functions at multiple times and places in a changing world (Isbell et al. 2011).

Most of terrestrial eukaryote diversity on Earth is represented by arthropods in tropical rainforests (Hamilton et al. 2013). Hence, assessing potential loss of arthropod species by converting natural forests into plantations in the tropics represents a significant topic of research, which is not devoid of controversies. For example, some studies reported a loss of biodiversity in plantations as compared to adjacent forests (Holloway et al. 1992; Barlow et al. 2007; Brockerhoff et al. 2008), while other studies observed the opposite pattern (Nummelin and Fuersch 1992; Davis and Sutton 1998; Speight et al. 2003). Most discrepancies can be explained with regard to differences in (1) insect ecology; (2) insect variables (e.g., species richness vs. abundance, species turnover or trophic guild structure: Gotelli and Chao 2013); (3) study methods (e.g., Sparrow et al. 1994); and (4) scale and timing of the study (Barlow et al. 2007). Hence, it is not surprising that little consensus exists as to whether the conversion of forests to plantations in the tropics depress or increase the local species richness of insect assemblages. Our contribution addresses item (1), above, as it is well-known that insect assemblages recruiting from different clades or with different ecology can have contrasted responses to habitat disturbance (Didham et al. 1996).

In the tropics, butterflies (Lepidoptera: Papilionoidea and Hesperioidea) are frequently used as indicators of environmental disturbance or environmental change because they offer a number of logistical advantages over other insect indicator taxa (Ghazoul 2002). Primarily, butterflies are more conspicuous than other insect groups and are active during the day, and many species can be identified in the field. Further, butterflies play important roles in ecosystem functioning and should be studied as targets of conservation in their

own right (Bonebrake et al. 2010). However, butterflies may not be good indicators of forest changes since their abundance is often marginal in deep forest by virtue of their halophilic lifestyles (Basset et al. 1998). For example, when the forest is opened by logging the subsequent invasion of heliophilous species from the canopy results in the understory butterfly community being more diverse and abundant than the original one. These differences are primarily caused by changes in the behaviour of butterflies rather than changes in their abundance (Spitzer et al. 1997). Hence, comparisons of butterfly abundance and diversity in plantations versus adjacent forests may not be forthright and may yield results different than if considering other insect assemblages.

Butterfly assemblages often differ between rainforest and tropical plantations. For example, Barlow et al. (2007) showed that in Brazil the species richness of fruit-feeding butterflies was highest in primary forest and lowest in eucalypt plantations, while butterfly abundance showed the opposite response. Koh and Wilcove (2008) observed that 83 % of butterfly species in forests were lost when the land was converted to oil palm plantations in Peninsular Malaysia and Borneo. Conversely Stephen and Sánchez (2014) collected more butterfly species in plantations than in forests in Costa Rica.

In tropical forests surveying adult butterflies remains far easier than surveying their caterpillars, which requires significant sampling effort (Novotny and Basset 2000). Yet, adult butterflies are rather mobile species, even if many tropical butterfly species have rather short dispersal distances (<200 m; Vlasanek et al. 2013). Hence, the diversity of adult butterflies may augment in plantations with increasing proximity to forest primarily due to spillover of 'transient' forest species (whose larval host plants do not occur in plantations; Lucey and Hill 2011). In contrast, the spatial distribution of 'resident' species (as opposed to transient species) from other insect assemblages less vagile than butterflies may be easier to assess in plantations.

Termites (Blattodea:Termitidae) may represent one group for which the diversity of resident species may be easily assessed in tropical plantations. Termites are dominant invertebrate decomposers of dead organic matter in tropical and subtropical terrestrial regions (Bignell and Eggleton 2000). Termite taxonomy is mostly based on the morphology of the soldier caste (Eggleton 1999). The apterous soldiers usually stay rather close to the nest, thus ascertaining with high confidence that they may be resident in a particular habitat, even if the nest is not observed. Jones et al. (2003) reported that in Sumatra termite species richness declines significantly from primary forest to plantations of rubber and of *Paraserianthes falcataria*. Attignon et al. (2005) also showed that in Benin (West Africa), termite species richness was significantly higher in forests than in teak plantations, but termite encounters were significantly lower. Conversely, in Cameroon, young plantations of *Terminalia ivorensis*, supported higher termite species richness than near primary forest (Eggleton et al. 1995). Similarly to butterflies, the extent to which termite diversity is affected by the conversion of forests to plantations is not entirely clear, although most studies suggest that termite diversity may be reduced (Jones et al. 2003; Luke et al. 2014).

In this study, we contrast the distribution of all adult butterflies observed, resident adult butterflies (with host plant occurring in the plantations) and soldier termites in three different plantations in Panama, and further compare the plantation data to those obtained with similar protocols in a nearby old growth forest. Our aims are to compare the abundance, species richness, composition and species turnover of these insect assemblages among two kinds of exotic plantations, one kind of native plantation and one old growth forest. Our working hypotheses are as follows. (a) Termites and butterflies have contrasting resilience to the conversion of forests to plantations, as a result of different ecology and

vagility. (b) The magnitude of change in insect variables from forest to plantations may be considerable when considering resident butterfly assemblages, as opposed to considering all butterflies observed, including transient species. (c) Species richness of butterflies and termites should decrease within the series old growth forest > native plantation > exotic plantations.

Methods

Study area and study sites

We studied the plantations of the Argos cement factory in the Colon Province, Panama (ca 9°15'40"N, 79°39'27"W, ca 100 m asl). This area is characterized by similar annual air temperature and rainfall than Barro Colorado Island (BCI), which is situated ca 25 km away and which represented our old growth forest site (see below). The Argos plantations include a mosaic of 228 ha including secondary forest and 74 plantations of timber trees between 0.3 and 13 ha, and planted between 1962 and 1999. Of those, we studied the three most abundant timber trees: teak (*Tectona grandis*, Lamiaceae, 30 parcels), 'Cedro espino' (*Pachira quinata* W.S. Alverson, Malvaceae, 18 parcels) and *Terminalia* (*T. ivorensis* A. Chev., Combretaceae, 5 parcels). Teak is an exotic species from India and SE Asia, whereas Cedro espino is native to Central America and NW South America. Most of the *Terminalia* parcels were planted with *T. ivorensis*, an exotic species from Africa, but some also included *T. amazonia* (J.F.Gmel.) Exell, which is native to the Neotropics (see description of parcels, below). Other timber trees in the Argos plantations included *Acacia*, *Melina*, *Casuarina*, *Pinus*, *Colubrina* and *Khaya*.

For each of the timber tree studied, we selected five parcels (sites) of similar age and size, although our final choice was limited by the availability of such parcels within the Argos grounds (Table 1; Fig. S1). Most of these parcels were about 23 years of age and their average size was 4.3 ha (Table 1). In each parcel, we delineated 100 m of trail, using as far as possible narrow trails already delimited. Distance between the mid-point of these trails varied between 71.5 and 3003.5 m. Hence, for each timber tree species studied, we delineated 500 m of disjoint trails that we used for butterfly and termite transects (see below). Because of the relatively small size of parcels, compared to the old growth forest (see below), our plantation data are replicated spatially for 100 m trails (five replicates in each plantation type) but not for 500 m trails. In each parcel, the vegetation was surveyed according to standard protocols of the Centre for Tropical Forest Science-ForestGEO (CTFS-ForestGEO, see below). This included surveying, identifying and measuring the height and DBH of all trees and shrubs ≥ 10 cm of DBH within plots of 25 × 25 m.

The old growth study area for comparison was Barro Colorado Island (9.15° N, 79.85° W, 120–160 m asl), which is a biological reserve. It receives an annual rainfall average of 2631 mm, with an annual average daily maximum air temperature of 28.5 °C. Around 1910, the Chagres River was dammed for the Panama Canal. Cerro Barro Colorado, cut off from the mainland by the rising water, became a 1542 ha island (M. Solano, pers. comm.). The island is currently 100 % forested, bar a few man-made clearings concentrated in the laboratory and housing area and one lighthouse clearing. A permanent botanical plot of 50 ha is located in the centre of the island. This plot is part of the network of forest dynamics plots monitored by CTFS-ForestGEO (Anderson-Teixeira et al. 2014). At all of these plots, each tree with a diameter at breast height (DBH) of 1 cm or greater is counted,

Table 1 Salient characteristics of the sites in plantations and forest

Site	Lat N	Long W	Elev	Age	Area	Hab	Stem	BA	DBH	H	Open	Tree	Gini	Host
Teak														
TK1	9°16'22"	79°39'12"	66	1993	5.1	3	336	1.4	59.5	21.7	2.08	2	0.472	1
TK2	9°16'31"	79°39'12"	80	1993	5.1	3	272	1.5	63.1	23.0	2.08	2	0.111	1
TK3	9°15'59"	79°39'24"	101	1993	5.1	3	272	1.5	63.1	23.0	2.08	2	0.111	1
TK4	9°16'45"	79°39'14"	157	1995	6.9	5	912	1.0	30.9	13.1	2.70	12	0.423	6
TK5	9°16'47"	79°39'28"	164	1995	6.9	5	1088	1.3	31.4	11.7	1.97	6	0.192	3
Cedro espino														
C37	9°16'21"	79°39'13"	110	1992	0.5	5	1520	3.0	33.2	15.8	3.01	23	0.840	11
C42	9°16'21"	79°39'16"	117	1992	0.5	4	1104	3.4	43.3	15.5	1.61	18	0.847	10
C48	9°15'40"	79°39'27"	108	1992	1.4	2	1792	2.5	24.2	17.5	2.23	21	0.808	13
C57	9°15'49"	79°39'23"	110	1992	2.7	3	1664	3.0	28.1	15.7	2.08	21	0.889	12
C64	9°16'46"	79°39'16"	155	1996	29.4	5	3872	6.6	30.7	13.7	1.87	22	0.858	12
Terminalia														
T38	9°14'37"	79°39'31"	119	1977	0.2	3	768	2.2	34.1	23.6	4.47	12	0.771	3
T39	9°14'39"	79°39'33"	111	1993	0.6	3	2976	3.1	26.7	13.7	3.74	16	0.711	5
T46	9°14'41"	79°39'32"	107	1993	0.2	3	528	1.2	49.8	13.4	6.44	6	0.485	3
T47	9°16'14"	79°39'09"	104	1993	0.1	1	1008	2.0	39.0	20.0	2.49	11	0.607	6
T61	9°16'13"	79°39'07"	126	1995	0.2	3	2048	1.8	19.2	20.1	3.53	19	0.834	11
Forest														
ARM1	9°09'14"	79°50'57"	155	1914	1542	0	4168	32.1	50.3	30.0	1.66	169	0.951	320
ARM2	9°09'07"	79°50'58"	168	-	-	-	-	-	-	-	1.14	-	-	-
ARM3	9°09'03"	79°51'10"	149	-	-	-	-	-	-	-	1.45	-	-	-
ARM4	9°08'56"	79°51'19"	127	-	-	-	-	-	-	-	1.66	-	-	-
BAL1	9°09'20"	79°50'41"	125	-	-	-	-	-	-	-	1.87	-	-	-
DRA1	9°08'58"	79°50'47"	115	-	-	-	-	-	-	-	1.87	-	-	-
WHE1	9°09'12"	79°50'52"	155	-	-	-	-	-	-	-	1.87	-	-	-

Table 1 continued

Site	Lat N	Long W	Elev	Age	Area	Hab	Stem	BA	DBH	H	Open	Tree	Gini	Host
WHE2	9°09'03"	79°50'46"	125	-	-	-	-	-	-	-	2.49	-	-	-
ZET1	9°09'11"	79°51'09"	158	-	-	-	-	-	-	-	1.66	-	-	-
ZET2	9°09'07"	79°51'24"	134	-	-	-	-	-	-	-	1.24	-	-	-
Site	Lia	Max	Div	Clo	Win	T	RH	Simil	Ab	AbR	S	Sest	SR	
Teak														
TK1	0	200	2	36.6	0.6	29.9	82.7	0.323	51	0	13	44.6	0	
TK2	0	150	5	36.1	0.3	30.6	81.8	0.594	56	4	22	181.4	4	
TK3	0	60	3	35.6	0.3	30.6	82.8	0.379	55	3	23	131.2	2	
TK4	10	150	4	31.6	0.4	30.8	84.4	0.455	129	6	25	58.44	5	
TK5	10	150	8	32.6	0.6	32.0	81.1	0.263	128	2	22	74.14	1	
Cedro espinoso														
C37	35	200	12	36.3	0.2	30.1	87.3	0.451	289	11	45	98.12	4	
C42	55	200	12	35.5	0.1	29.8	86.3	0.597	263	5	54	140.5	4	
C48	35	250	13	39.1	0.2	30.2	86.3	0.682	152	1	30	68.19	1	
C57	0	200	5	34.3	0.2	30.2	83.4	0.527	293	8	53	131.6	7	
C64	20	250	4	34.0	0.3	30.6	84.8	0.559	176	9	30	72.19	4	
Terminalia														
T38	10	250	11	36.4	0.2	30.6	85.7	0.384	355	1	62	229.8	1	
T39	5	250	13	37.3	0.2	30.4	85.6	0.575	380	1	61	144.2	1	
T46	0	150	7	34.2	0.2	30.5	85.3	0.369	310	5	48	112.2	1	
T47	5	250	3	33.6	0.5	33.6	84.5	0.487	206	4	50	130.5	4	
T61	10	150	6	37.6	0.2	30.2	81.7	0.391	281	19	57	143.4	9	
Forest														
ARM1	72	70	6	34.6	0.0	28.1	90.0	0.877	134	35	20	47.66	7	
ARM2	83	50	2	35.4	0.1	27.3	89.9	0.861	126	16	17	33.89	6	

Table 1 continued

Site	Lia	Max	Div	Clo	Win	T	RH	Simil	Ab	AbR	S	Sest	SR
ARM3	79	180	3	33.3	0.2	27.8	90.9	0.982	139	23	22	58.93	8
ARM4	87	100	4	33.3	0.2	28.4	87.4	0.957	212	49	24	60.4	10
BAL1	79	70	6	35.8	0.4	28.4	91.1	0.872	150	34	33	63.78	15
DRA1	73	200	2	37.9	0.1	28.9	90.3	0.934	169	36	18	47.03	7
WHE1	79	200	3	32.5	0.3	28.5	90.7	0.958	125	16	19	39.91	7
WHE2	83	200	3	30.0	0.2	28.7	89.9	0.914	120	22	24	76.28	9
ZET1	85	150	4	32.9	0.2	28.7	87.5	0.950	154	28	17	46.34	7
ZET2	70	200	4	34.2	0.1	28.3	86.2	0.990	157	34	23	65.72	12

For the forest, variables identical for all sites are detailed in the first entry, for comparison with plantations

Lat N, *Long W*, *Elev* latitude, longitude and elevation (m); *Age*, *Area* age (years) and area (ha) of the parcel; *Hab* no. of different habitats nearby; *Stem* no. of stems per ha; *BA* basal area (m² per ha); *DBH* average diameter at breast height (mm); *H* average tree height (m); *Open* canopy openness (%); *Tree*, *Gini*, *Hosi* no. of tree species, diversity of tree species (Gini-Simpson index) and no. of tree species host to butterfly species as measured in the 25 × 25 m plots; *Lia* Liana load (% of trees with liana); *Max* maximum height (cm) of the understorey vegetation; *Div* no. of main plant families present as understorey vegetation; *Clo*, *Win*, *T*, *RH* average cloudiness (% of sky obscured), wind velocity (m/sec), air Temperature (°C) and relative humidity (%) during transects performed at these sites; *Simil* faunal similarity (Morisita-Horn) with the assemblage of butterflies recorded on BCI during 2014; *Ab*, *AbR* Abundance of butterflies and of resident butterflies (total no. of individuals recorded); *S*, *Sest*, *SR* no. of butterfly species recorded, estimated (Chao2) and resident butterfly species

mapped, and identified to species. A detailed description of the BCI setting and of the CTFS-ForestGEO plot may be found in Windsor (1990) and Condit (1998). To survey butterflies on BCI (see below), we designated ten sites the shady understory of the forest, each consisting of 500 m of concatenated and established narrow trails within and near the CTFS-ForestGEO plot. The minimum distance between locations was 200 m and all of their salient characteristics are detailed in Basset et al. (2013; Table S2).

For the sake of clarity, we hereafter use the following terms, defined as follows: habitats = the plantation types (teak, Cedro espino, *Terminalia*) and old growth forest (BCI); sites = spatial locations within habitats where butterflies were surveyed (parcels in Table 1 for plantations; Table S2 in Basset et al. 2013 for BCI); 500 and 100 m transects = butterfly transects ('walks', see below); surveys = butterfly transects replicated at each location and during different periods of the year (see below).

Insect surveys

To survey whole assemblages of butterflies, we used Pollard Walks to calculate indices of species abundance along a linear transect that was repeatedly sampled over a given time interval (Pollard 1977). During each transect, one observer walked at slow and constant pace along a 500 m trail in about 30 min while recording butterflies within 5 m of either side of the trail and to a height of 5–7 m. Butterflies were either identified 'on the wing' as accurately as possible (to species, genus or family); netted, identified with a home-made field guide and released; or collected for processing and identification in the laboratory (see below). Thus, the procedure avoided killing unnecessarily butterflies. Prior to the start of each transect, the observer recorded air temperature, relative humidity, wind velocity, percentage cloudiness and time of day. We use the term 'butterflies recorded' to mean butterflies both collected and observed within a particular sampling unit. At all sites, we avoided walks on days with inclement weather (high rainfall or wind). Transects were usually walked between 9:00 and 15:00 h, on different days, using a randomized sequence. Each 500 m transect was surveyed as three replicates in each of four surveys encompassing a weighted frequency of dry/wet periods: March (dry), May (wet), September (wet) and November (wet). Four observers (FP, RB, YL, JAR) walked transects in plantations and in the forest. The protocol is extensively detailed elsewhere (Basset et al. 2013; Appendix S5).

We used the above protocol without modifications in the old growth forest. Because the plantations were much smaller than the forest, we walked ten replicates of each 100 m transects during each survey. The rationale for the slightly different protocols between the forest and plantations is explained in Appendix S1. In sum, during year 2014 we performed 60 km of transects (or 60 h of observation) in each of the old growth forest and Argos plantations, organized as follows. For the forest, we performed 1 (habitat) \times 10 (sites, 500 m) \times 3 (replicates, 500 m) \times 4 (surveys) = 120 transects of 500 m. At Argos, we obtained either (a) 3 (habitats) \times 5 (parcels) \times 10 (replicates, 100 m) \times 4 (surveys) = 600 transects of 100 m; or (b) 3 (habitats) \times 1 (site, 500 m) \times 10 (replicates) \times 4 (surveys) = 120 transects of 500 m. We use both (a) and (b) to present plantation data. Butterflies were also netted opportunistically in the plantations to evaluate better local species richness. Reference collections were built before the onset of monitoring and used later to identify, whenever possible, butterflies in flight. However, an appreciable number of specimens sighted was also collected for verifying identifications ($n = 1104$ or 24 % of observed butterflies). Specimens were identified as indicated in Appendix S1.

Termite census were modeled after Jones and Eggleton (2000), with modifications as in Roisin and Leponce (2004). For both the forest and each of the plantations (teak, *Terminalia* and Cedro espino), one termite transect consisted of 40 quadrats of 5 m², 10 m distant from each other (transect length = 400 m, total 40 samples). Each quadrat was searched for 30 min by one person fragmenting wood, litter and searching for termite galleries up to 2 m in the vegetation. Transect were performed during 2014, at the beginning of the wet season in June. In the forest, one single transect was performed outside but near the CTFs permanent plot. In the plantations, transects were delineated as 8 quadrats parallel to each of 100 m butterfly transects, 10 m distant from the butterfly transects (i.e., each site was characterized by 8 quadrats). Thus, during 2014, we obtained four full termite transects of 40 quadrats for each of forest, teak, *Terminalia* and Cedro espino habitats. This protocol targeted wood-feeding termites (T. Bourguignon, pers. comm.). Termites were identified as indicated in Appendix S1. Following Donovan et al. (2001), we classified termites into the following feeding groups. Group I: lower termite dead wood and grass-feeders; group II: Termitidae with a range of feeding habits including dead wood, grass, leaf litter, and micro-epiphytes; group III: Termitidae feeding in the organic rich upper layers of the soil; group IV: Termitidae which are true soil-feeders, ingesting apparently mineral soil.

Statistical analyses

Abundance and species richness reported by transect were not normally distributed so we used non-parametric analyses to report our data. Plantation habitats were directly compared, with unit sampling being either 100 m transects walked in 10 min. or 500 m transects walked in 50 min. We computed randomized species accumulation curves and estimated the total number of species present in each habitat with the Incidence Coverage-based Estimator (ICE), both computed with EstimateS 8.50 (Colwell 2009; 100 permutations). Butterfly transects at BCI are not spatially autocorrelated (Basset et al. 2013). However, because of the smaller area studied in the Argos plantations, butterfly composition at each site was spatially autocorrelated (Mantel test between matrix of faunal composition and matrix of site coordinates, $r = 0.373$, $p < 0.05$, 10,000 permutations). We accounted for spatial autocorrelation by including geographic distance in our regression and multivariate analyses (see details in Appendix S1). We considered six log-transformed butterfly variables for each site: abundance of all species and of resident species only (see below); species observed and of resident species only; species richness estimated (ICE); and similarity with the whole butterfly assemblage in the forest during 2014 (Table 1). We modeled these variables with a lagged-predictor model of spatial autoregression (Anselin 1988) using the software SAM (Rangel et al. 2010). Four categories of predictor variables were used in our models: coarse features of the site (including cartesian coordinates), forest structure, forest diversity and heterogeneity, and variables related to the conditions of transects. Measurements of all of these variables are explained in Appendix S1 and they are detailed in Table 1.

We used Nonmetric multidimensional scaling (NMDS) to compare the faunal composition of sites. For this analysis we considered only species recorded with ≥ 4 individuals (i.e., to have a probability that at least one individual was collected in each habitat; matrix of 85 species \times 25 sites; Bray-Curtis distance). To explain the composition of butterfly assemblages among habitats, we performed a Canonical Correspondence Analysis (CCA) with the same data sets (either plantation and forest sites or only plantation sites), and the same predictor variables used for the spatial autoregression. We used the CANOCO

package and its module WinKyst 1.0 for all multivariate analyses (Ter Braak and Smilauer 2003). The similarity of assemblage composition was estimated with the Morisita-Horn index, considering all butterfly species (and termite species, see below), and calculated with the R-language function `vegdist` in the `vegan` library (Oksanen et al. 2011). The strength of relation between the two similarity matrices of butterfly and termite species occurring at plantation sites was assessed with a Mantel test also calculated with `vegan` (10,000 permutations). We also evaluated whether butterfly species preferred particular habitats and what were the probability of detection of butterflies across the habitats studied (i.e., naïve and true occupancy of sites). Details of these analyses are provided in Appendix S1.

Last, we tested whether the above regressions and ordinations were different in considering only “resident” butterfly species, as opposed to all butterfly species observed. We define a resident butterfly species for a specific site as feeding on a host plant species which grows within that site. Yet, both in the plantations and in the forest, our vegetation data only apply to trees and shrubs, not to lianas and herbs. Thus, we were only able to establish the residency status for butterfly species only if they feed on trees or shrubs (further details in Appendix S1).

Since social insects, such as termites, have strongly aggregated distributions, abundance data and estimates of variability may be highly dependent on the distance to colony and related factors, such as behaviour and speed. Hence, species occurrence in samples is usually used as a surrogate of species abundance (Longino 2000). Thus, for each species and transect, we report the number of quadrats occupied out of the 40 quadrats of the transect. As far as possible, we performed similar multivariate analyses (NMDS and CCA) with both termite and butterfly data (further details in Appendix S1). In contrast to butterflies, termite composition was not spatially autocorrelated among each site (Mantel test between matrix of faunal composition and matrix of site coordinates, $r = 0.022$, $p = 0.384$, 10,000 permutations).

Results

Abundance and species richness of butterflies

A total of 4610 butterflies were recorded in the plantations and forest during 2014, representing 266 species (Table 2; Appendix S2). Some 199 species were recorded in the plantation transects and a further 21 species were additionally recorded on Argos grounds, outside transects, most being represented by singletons. In contrast, only 88 species were recorded from the forest (Appendix S2). Butterfly abundance was significantly different among habitats (Kruskal–Wallis test, $U = 135.33$, $p < 0.001$; all pairs significantly different, Steel–Dwass tests, all with $p < 0.05$) and, irrespective of whether we considered uncorrected or time-corrected data, it decreased among habitats as follows: *Terminalia* > Cedro espino > forest (BCI) > teak. Overall, butterflies were more abundant in plantations than in the forest (Table 2).

Observed species richness was also significantly different among habitats (Kruskal–Wallis test, $U = 127.73$, $p < 0.001$) and followed a similar pattern than that of abundance (Table 2). Results were also similar for estimated species richness, with the highest value for *Terminalia* plantations (ICE, Table 2). The only discrepancy was the relatively high species richness for teak plantations when rarefied to 150 individuals (Table 2). The

Table 2 Abundance and species richness of butterflies surveyed in the four habitats studied

Variable	TEK	CED	TER	Plantations	Forest
Total individuals observed (120 transects)	419	1173	1532	3124	1486
Median of abundance per transect	9	28.5	33	26.5	11
Time-corrected median of abundance	5.4	17.1	19.8	15.9	11
Median of abundance of resident sp. per transect*	0 (18)	0 (24)	0 (11)	0 (52)	2 (88)
Median of species richness per transect	2	10	12	9	4
Time-corrected median of species richness	1.2	6.0	7.2	5.4	4
Median of species richness for resident species	0	0	0	0	1
Sobs for 40 transects	64	114	153	–	–
Sobs for 120 transects	–	–	–	199	88
Percentage of individuals identified to species	38	54	52	51	72
Percentage of individuals identified to genus	55	68	63	64	81
Dominance (Berger-Parker index)	0.12	0.12	0.12	0.11	0.24
Percentage of singletons recorded	59	48	49	41	49
ICE \pm SD	151.9 \pm 2.8	195.1 \pm 2.5	250.9 \pm 2.3	308.0 \pm 0.02	171.7 \pm 0.03
Species richness for 150/1000 individuals** \pm SD	61.6 \pm 5.9	52.8 \pm 4.2	59.5 \pm 4.5	163.2 \pm 7.5	85.4 \pm 6.1

Comparisons of teak (TEK), Cedro espino (CED), *Terminalia* (TER) plantations and of all plantations together versus forest (BCI). Unless otherwise stated, values are estimated for transects of 500 m

* No. of non empty transects in brackets

** For habitats and plantations/forest, respectively

species accumulation curve for teak plantations was also rather steep in comparison to other habitats (Fig. 1). In general, species accumulation curves for plantations were steeper than for the forest. The relatively low sample size in teak plantations was due to lower butterfly abundance (Table 2), but also to a relatively low percentage of individuals identified to species (Table 2). The percentage of individuals identified to species was higher in forest than in plantations, and rather low in teak plantations, and these differences were significant (Chi square test = 224.9, $p < 0.001$; Table 2).

There were significant differences between environmental variables recorded at plantation and forest sites (Table 1). In comparison with forest sites, plantation sites on average had a slightly lower elevation; their canopy was more open; their trees supported less lianas; their understory vegetation was more diverse; air temperature and wind velocity were higher, and relative humidity was lower than in forest (Table 1, Mann–Whitney tests all with $p < 0.05$). After accounting for spatial autocorrelation, the butterfly variables

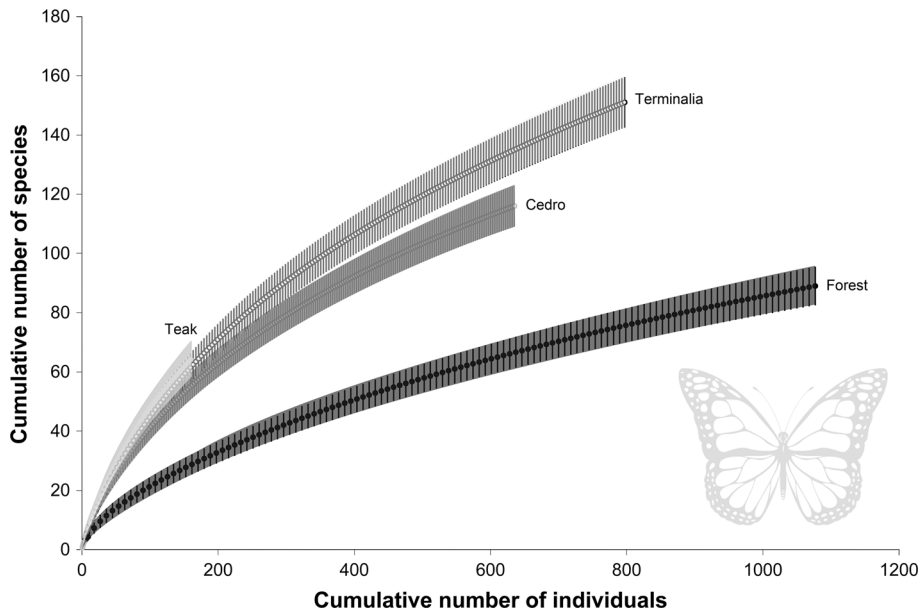


Fig. 1 Cumulative number of butterflies recorded plotted against the mean cumulative number of butterfly species recorded (\pm SD), for each habitat surveyed

describing abundance and species richness were often difficult to predict from the variables that we measured at the different sites. In general it was easier to predict butterfly variables among plantation sites than when we contrasted the plantation and forest sites (Table 3; note that more variables were available to characterize plantations than the forest). Variables such as wind velocity (negative coefficient) and air temperature (positive coefficient) were often significant in explaining differences in abundance or species richness between sites, particularly when contrasting plantation and forest sites. Differences in butterfly abundance among plantations were best explained by canopy openness (56 % of variance explained, Table 3). This variable was also significant in explaining butterfly similarity with forest assemblages among plantation sites.

Butterfly assemblages

Both the abundance and species richness of the six butterfly families were all significantly different among habitats (Kruskal–Wallis tests, all with $p < 0.0001$; Fig. S2). In particular, HesperIIDae, Nymphalidae, Papilionidae were abundant or species-rich in Cedro espino and, particularly, in *Terminalia* plantations. Lycaenidae were only well represented in *Terminalia* plantations, whereas Pieridae were best represented in the forest (Fig. S2). Some 158 butterfly species were recorded from plantations but not from the forest. In contrast, 46 butterfly species were recorded in the forest but not in plantations. The most common species of butterflies recorded in plantations are illustrated in Figs S3, S4, and S5, while common forest species are illustrated elsewhere (Basset et al. 2011). The NMDS ordination indicated that the composition of butterfly assemblages was distinct in the forest and in teak plantations, whereas assemblages in Cedro espino and *Terminalia* plantations were more difficult to differentiate between them, but distinct from the other two habitats

Table 3 Summary of the best lagged-predictor models of spatial autoregression fitting the log abundance (abund.) and species richness (sp. rich.) of butterflies among different sites (n = 15 sites; only plantations; n = 25 sites; plantations and forest)

Model/variable	$\rho \pm$ s.e.	$\gamma \pm$ s.e.	Coef. \pm s.e.	T	p	r ²	AIC
Log abund. (n = 15)							
Canopy openness	0.824 \pm 0.031	-0.042 \pm 0.995	0.313 \pm 0.077	4.07	0.002	0.56	-19.93
Log abund. resident spp. (n = 15)							
Not significant	-	-	-	-	-	-	-
Log abund. (n = 25)							
Elevation	0.807 \pm 0.045	0.649 \pm 0.205	-0.304 \pm 0.118	-2.59	0.017	0.35	-33.91
Wind	-	0.301 \pm 0.766	-0.186 \pm 0.085	-2.20	0.039	-	-
Log abund. resident spp. (n = 25)							
Not significant	-	-	-	-	-	-	-
Log sp. rich. (n = 15)							
Wind	0.654 \pm 0.184	0.175 \pm 0.913	-0.582 \pm -0.867	-4.23	0.001	0.61	-8.79
Temperature	-	-0.146 \pm 0.941	0.393 \pm 0.591	2.88	0.015	-	-
Log sp. rich. resident spp. (n = 15)							
Not significant	-	-	-	-	-	-	-
Log sp. rich. (n = 25)							
Not significant	-	-	-	-	-	-	-
Log sp. rich. resident spp. (n = 25)							
Not significant	-	-	-	-	-	-	-
Log estimated sp. rich. (n = 15)							
Wind	-0.271 \pm 0.809	0.175 \pm 0.913	-0.584 \pm -0.602	-2.72	0.019	0.36	-2.56
Log estimated sp. rich. (n = 25)							
Temperature	0.496 \pm 0.446	0.492 \pm 0.453	0.517 \pm 0.207	2.50	0.021	0.27	-4.87
Wind	-	0.301 \pm 0.766	-0.445 \pm 0.181	-2.46	0.023	-	-
Log similarity with forest (n = 15)							
Wind	-0.461 \pm 0.527	0.175 \pm 0.913	-0.661 \pm 0.130	-5.09	0.001	0.78	-9.99

Table 3 continued

Model/variable	$\rho \pm \text{s.e.}$	$\gamma \pm \text{s.e.}$	Coef. \pm s.e.	T	p	r^2	AIC
Canopy openness	-	0.230 \pm 0.852	0.491 \pm 0.126	3.91	0.003	-	-
Max understorey height	-	-0.042 \pm 0.995	-0.299 \pm 0.127	-2.35	0.040	-	-
Log similarity with forest (n = 25)							
Wind	0.704 \pm 0.137	0.301 \pm 0.766	-0.376 \pm 0.102	-3.69	0.001	0.51	-32.62
Canopy openness	-	0.339 \pm 0.709	-0.276 \pm 0.103	-2.69	0.014	-	-
Maximum understorey height	-	0.272 \pm 0.807	0.215 \pm 0.100	2.16	0.043	-	-

When several variables are significant, they are listed in order of decreasing standardized coefficients
AIC akaikie information criterion

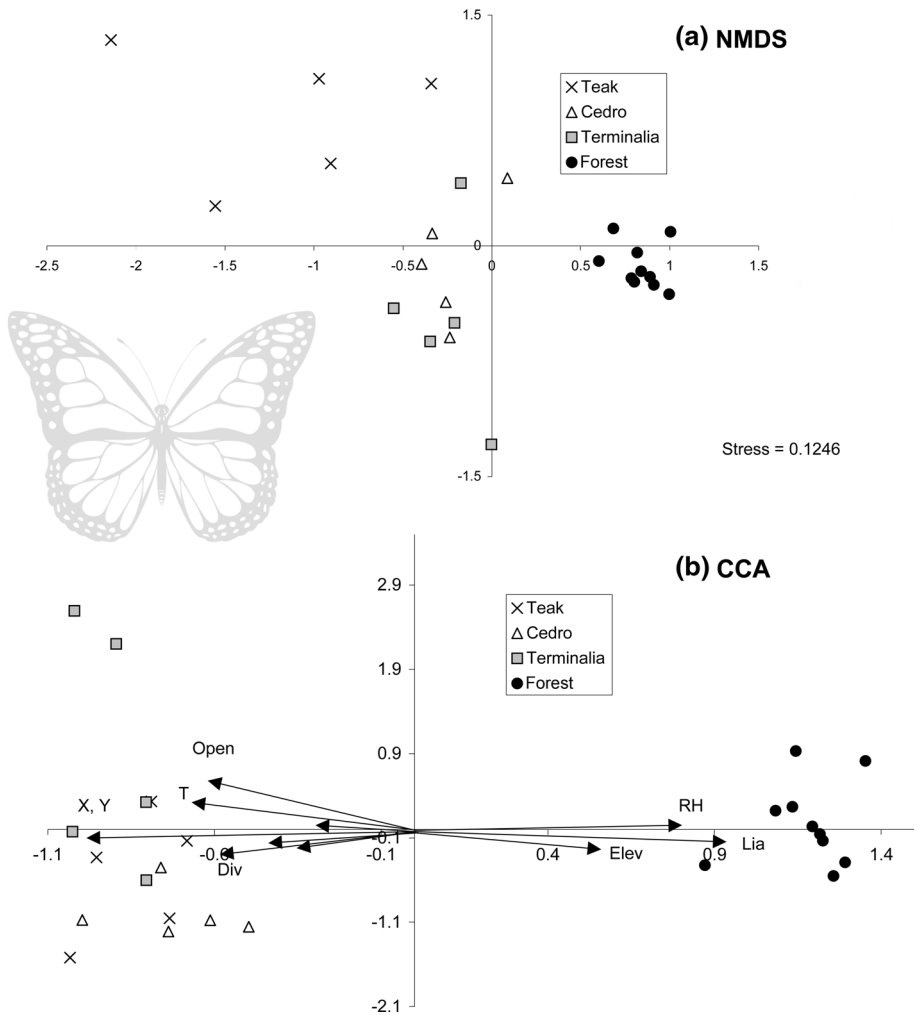


Fig. 2 Multivariate analyses considering 85 butterfly species recorded at 25 sites (plantations and forest), detailed by habitat. Plot of the scores of the sites in Axes 1, 2 of the **a** NMDS and **b** CCA (with plot of environmental variables, the main ones abbreviated as in Table 1)

(Fig. 2a). The significant CCA including both plantation and forest sites explained 45.2 % of the total inertia (2.230; Fig. 2b). Four canonical axes were significant (Monte-Carlo test, $F = 2.00$, $p < 0.01$, 999 permutations). They were best explained by geographical coordinates ($r = 0.98$, $p < 0.05$) for Axis 1 and canopy openness ($r = 0.51$, $p < 0.05$) for Axis 2. Axis 3 could be also explained by the diversity of understorey vegetation ($r = -0.49$, $p < 0.05$). The significant CCA including only plantation sites explained a higher proportion of variance than the CCA including both plantation and forest sites (62.5 % of a total inertia of 1.655). The first axis of the CCA was best explained by geographical coordinates ($r = -0.68$, $p < 0.05$), the second axis by site area ($r = 0.82$, $p < 0.05$; Fig. S6). Morisita-Horn indices confirmed that the highest faunal similarity was between the *Terminalia* and Cedro espino plantations, whereas the lowest similarity was between

the teak plantations and the forest (Table S1). Forty-four butterfly species out of 85 common species tested could be considered as indicator species for one habitat (Appendix S2). Few species were indicators for teak plantations (two Nymphalinae) or for the forest (two Pierinae, one Satyrinae and one Pyrginae).

Influence of species detectability and seasonality on butterfly assemblages

Our estimates of true occupancy for the ten very common butterfly species and, particularly, of the bias between naive and true occupancy were significantly different between habitats (percentage difference, Kruskal–Wallis test, $W = 11.17$, $p < 0.05$; Table S2). Bias in occupancy increased from the series Cedro espino < *Terminalia* < teak plantations < forest. Bias appeared most obvious in the forest, for small species less abundant, such as *Mesosemia lamachus* and *Calycopis thama* (Table S2). In general, differences in butterfly abundance and species richness among seasons were not well marked, with the exception of teak plantations, which were more variable than other habitats (Fig. S6). A Friedman test (equivalent to a non-parametric two-way analysis of variance with repeated measures) confirmed that the effect of habitat (treatment) was significant on butterfly abundance and species richness despite seasonality (blocking variable; Friedman tests = 9.90, $p < 0.05$ and 10.85, $p < 0.05$, respectively). Teak plantations supported higher abundance and species richness of butterflies in September, as compared to other surveys (Kruskal–Wallis test, $W = 15.22$, $p < 0.05$; Fig. S6). Further, whereas the percentage of individuals identified to species was always >36–40 % or higher for during all surveys in plantations and in the forest, this proportion was very low for transects performed in March in teak plantations (14.1 %).

Resident butterflies and their host plants

The composition of resident butterfly assemblages at each plantation site was not spatially autocorrelated (Mantel test, $r = -0.155$, $p = 0.823$, 10,000 permutations). Out of all butterfly species recorded in plantations and forest, 68 had a tree or shrub as host-plant species, as recorded in the literature (Appendix S2). However, out of those, only 25 butterfly species had a recorded tree or shrub as host in the plantations. No butterfly species feed on host trees teak and Cedro espino, whereas 3 species feed on *Terminalia*, two hesperides and one riordinid. The number of tree and shrub species present and recorded as hosts for butterflies was highest in Cedro espino plantations, then in *Terminalia* plantations and lowest in teak plantations (Kruskal–Wallis test, $W = 10.01$, $p = 0.007$; Table 1). When considering only butterfly resident species, abundance in plantations was very low (one order of magnitude lower than overall abundance). Despite this, the abundance of resident species was significantly higher in Cedro espino than in teak plantations (Table 2; Kruskal–Wallis test, $W = 8.30$, $p < 0.05$; Steel–Dwass test, $p < 0.05$). These patterns were similar for species richness (Table 2; Kruskal–Wallis test, $W = 8.12$, $p < 0.05$; Steel–Dwass test, $p < 0.05$). However, the abundance and species richness of species considered as resident were higher in the forest than in plantations (Table 2; Mann–Whitney tests, $U = 43.8$, $p < 0.001$ and $U = 28.6$, $p < 0.001$, respectively). After accounting for spatial autocorrelation, none of the variables that we measured were significant in explaining the abundance or species richness of resident species among plantation and forest sites (Table 3). The NMDS ordination for resident species indicated that transects were rather distinct in the forest and more difficult to differentiate among plantation transects (analysis not shown here for the sake of brevity). However, the CCAs

for resident butterfly species, either for plantation and forest sites or restricted to plantation sites, were not significant. Similarity for resident species was very low between the forest and the different plantations, and was highest between the teak and *Terminalia* plantations (Table S1). Many resident species could be considered as indicator species for a particular plantation (40 % of the total resident species; Appendix S2).

Termite occurrence and assemblages

Termite occurrence in quadrats decreased from the series forest (BCI) > teak > Cedro espino > *Terminalia* plantations (Table 4). In the forest 90 % of quadrats were occupied by termites, whereas this proportion was overall lowest in the plantations (60 %). Termite occurrence (all species) was significantly different between habitats (Kruskal–Wallis test, $W = 22.07$, $p < 0.001$), with obvious differences between the forest and Cedro espino/*Terminalia*, and teak and *Terminalia* (Dwass–Steel tests, $p < 0.05$). The percentage of termite occurrences that could be identified with soldiers (without accounting for Apicotermitinae spp.) was high (teak: 95.1 %; Cedro espino: 78.8 %; *Terminalia*: 100 %; forest: 84.9 %). In total, 15 species of termites were recorded from transects performed in plantations and in the forest. Eight species occurred in teak plantations, 7 in Cedro espino plantations, 6 in *Terminalia* plantations and 12 in the forest (transect 2014). In contrast to butterfly data, species accumulation curves (based on occurrence in quadrats) for termites were steeper for the forest than for plantations, with lowest accumulation of species in *Terminalia* plantations (Fig. 3). These curves also suggested that most termite species had been collected in plantations, whereas more species could be discovered in the forest (about 40 species of termites are known to occur on BCI, Y. Roisin et al. unpubl. data). All termite species recorded from the Argos plantations were also recorded from BCI during the period 2009–2014.

In comparison to butterfly assemblages, termite assemblages appeared less distinct in the forest when compared to plantations. The NMDS ordination indicated that the composition of termite assemblages was rather different in the forest than in plantations, but this was apparent only on the first axis of the ordination (Fig. 4a; Kruskal–Wallis test between scores on axis 1 of forest versus plantation sites, $W = 7.09$, $p < 0.01$). The significant CCA including plantation and forest sites explained 42.4 % of the total inertia (2.486). Its first axis was best explained by geographical coordinates ($r = -0.58$, $p < 0.05$) and its second axis by canopy openness ($r = 0.70$, $p < 0.05$; Fig. 4b). The significant CCA including only plantation sites explained 66.1 % of the total inertia (2.141). Its first axis was best explained by canopy openness ($r = 0.80$, $p < 0.05$) and its second axis by average DBH ($r = -0.66$, $p < 0.05$; Fig. S8).

There was no correlation between the NMDS scores of plantation sites as characterized by butterfly and termite assemblages neither in Axis 1 ($r_s = 0.168$, $p > 0.50$) nor in Axis 2 ($r_s = 0.529$, $p > 0.05$). Morisita–Horn indices of similarity between habitats were lower for termite than for butterfly assemblages (averages 0.619 and 0.672, respectively), but not when resident butterflies were considered (average similarity 0.236). The lowest faunal similarity was the Cedro espino plantations and the forest (Table S1). There was no significant relation between the two matrices of similarity of butterfly and termite assemblages occurring at plantation sites (Mantel test, $r = 0.285$, $p = 0.248$). The distribution of termites assigned to feeding group II among habitats was not significantly different from that of termites assigned to other feeding groups (number of encounters, G test, $G = 7.50$, $p = 0.058$).

Table 4 Occurrence of termite species in transects performed in 2014, detailed by habitats

Taxa	Teak			Cedro espino			Terminalia			Forest			FG	BIN
	Q	Occ	95 % CL	Q	Occ	95 % CL	Q	Occ	95 % CL	Q	Occ	95 % CL		
Kalotermitidae														
<i>Rugitermes panamae</i>	-	-	-	-	-	-	-	-	-	1	0.025	0.001, 0.132	I	-
Rhinotermitidae														
<i>Heterotermes convexinotatus</i>	3	0.075	0.016, 0.204	4	0.100	0.028, 0.237	6	0.150	0.057, 0.298	15	0.375	0.227, 0.542	I	AAP9551
Termitidae														
Apicotermitinae														
Apicotermitinae spp. (workers)*	3	0.075	0.016, 0.204	2	0.050	0.006, 0.169	5	0.125	0.042, 0.268	6	0.150	0.057, 0.298	III, IV	-
Apicotermitinae sp. 2YB (alates)	-	-	-	-	-	-	-	-	-	1	0.025	0.001, 0.132	III, IV	AAQ0786
Apicotermitinae sp. 6YB (alates)	4	0.100	0.028, 0.237	-	-	-	-	-	-	-	-	-	III, IV	-
Nasutitermitinae														
<i>Nasutitermes corniger</i>	16	0.400	0.249, 0.567	5	0.125	0.042, 0.268	3	0.075	0.016, 0.204	4	0.100	0.028, 0.237	II	AAP9620
<i>Nasutitermes ephratae</i>	7	0.175	0.073, 0.328	6	0.150	0.057, 0.298	1	0.025	0.001, 0.132	1	0.025	0.001, 0.132	II	AAP9619
<i>Nasutitermes guayanae</i>	-	-	-	-	-	-	4	0.100	0.028, 0.237	3	0.075	0.016, 0.204	II	AAP9712
<i>Nasutitermes nigriceps</i>	3	0.075	0.016, 0.204	-	-	-	-	-	-	2	0.050	0.006, 0.169	II	AAP9617
<i>Nasutitermes</i> sp. 7YB	-	-	-	2	0.050	0.006, 0.169	-	-	-	-	-	-	II	AAP9618
<i>Obtusitermes panamae</i>	1	0.025	0.001, 0.132	5	0.125	0.042, 0.268	-	-	-	3	0.075	0.016, 0.204	II	AAP9645
<i>Velocitermes barrocoloradensis</i>	-	-	-	-	-	-	-	-	-	1	0.025	0.001, 0.132	II	-
Synermitinae														
<i>Amitermes beaumonti</i>	-	-	-	-	-	-	-	-	-	4	0.100	0.028, 0.237	II	AAQ1330
<i>Cornitermes walkeri</i>	-	-	-	-	-	-	-	-	-	2	0.050	0.006, 0.169	II, III, IV	AAP9751
Termitinae														
<i>Microcerotermes arboreus</i>	5	0.125	0.042, 0.268	4	0.100	0.028, 0.237	4	0.100	0.028, 0.237	8	0.200	0.091, 0.356	II	AAP582
Unidentified workers	2	0.050	0.006, 0.169	7	0.175	0.073, 0.328	-	-	-	2	0.050	0.006, 0.169	-	-
Occupied samples	32	0.800	0.643, 0.909	21	0.525	0.361, 0.685	19	0.475	0.315, 0.639	36	0.900	0.763, 0.972	-	-

Table 4 continued

Taxa	Teak			Cedro espino			Terminalia			Forest			FG	BIN
	Q	Occ	95 % CL	Q	Occ	95 % CL	Q	Occ	95 % CL	Q	Occ	95 % CL		
Empty samples	8	0.200	0.091, 0.356	19	0.475	0.315, 0.639	21	0.525	0.361, 0.685	4	0.100	0.028, 0.237	-	-

Q number of occupied quadrats, Occ Occurrence, CL 95 % confidence limits of occurrence. For the definition of feeding groups (FG), see Methods. BIN barcode index number, when available

* Including at least 7 genera and species (R. Scheffrahn, pers. comm.), and 2, 2, 4 and 3 species recorded in Teak, Cedro espino, Terminalia plantations and forest, respectively

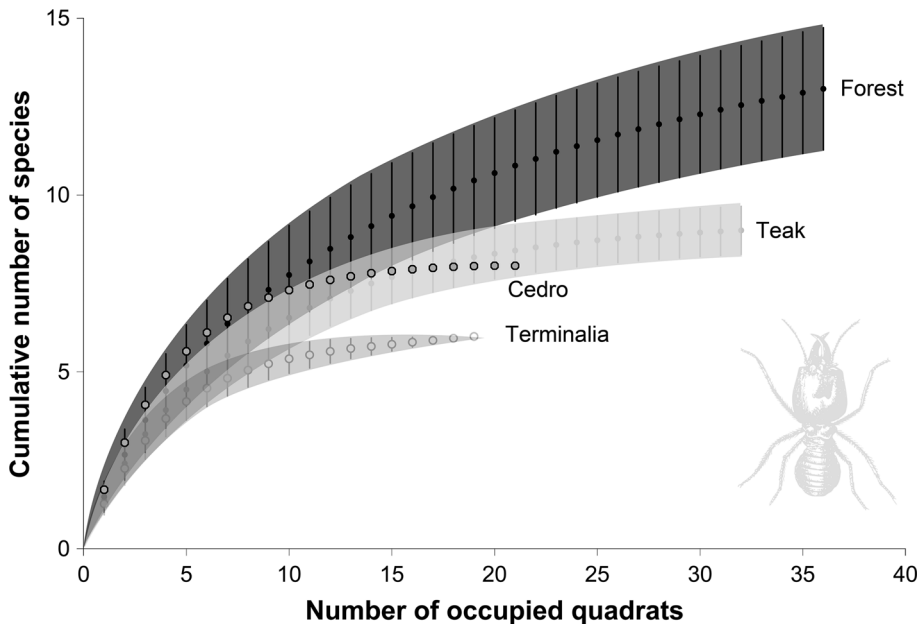


Fig. 3 Cumulative number of quadrats occupied by termites plotted against the mean cumulative number of termite species recorded (\pm SD), for each habitat surveyed

Discussion

Interpreting butterfly and termite data

Land-use studies such as ours are inevitably faced with limited availability of treatment replicates, with concomitant pseudoreplication (more obvious in the case of our teak parcels). In our analyses, we explicitly included spatial variables to account for this spurious effect, but we acknowledge that this is not the perfect solution. Three issues are related to the spatial constraints that we faced when planning our study: parcel area, matrix effects and study area. Parcel area and matrix effects (number of different habitats adjoining the parcel) had no significant effects in our lagged-predictor models of spatial autoregression describing butterfly abundance and species richness. However, we cannot discount the probable large edge effects associated with the smaller parcels that displayed high butterfly diversity (*Terminalia* and Cedro espino). Resident butterfly data are therefore more likely to be representative of the actual butterfly diversity within these plantations than overall butterfly data. The study area is also not ideally suited for our study. Within a radius <15 km, our plantation sites are surrounded by forests in the West, North and South-East, whereas our control (forest) sites, in the West, are more distant (25 km) and not interspersed with our plantation sites. However, these forests all experience similar amount of rainfall and, as a result, differences in vegetation are few (Condit et al. 2005). Thus, we can consider the BCI forest as a representative surrogate of forests that have been replaced by plantations within the Argos study area.

Whereas comparison of termite transects were rather straightforward, several potential factors may complicate comparisons of butterfly transects. First, the factor that we used to

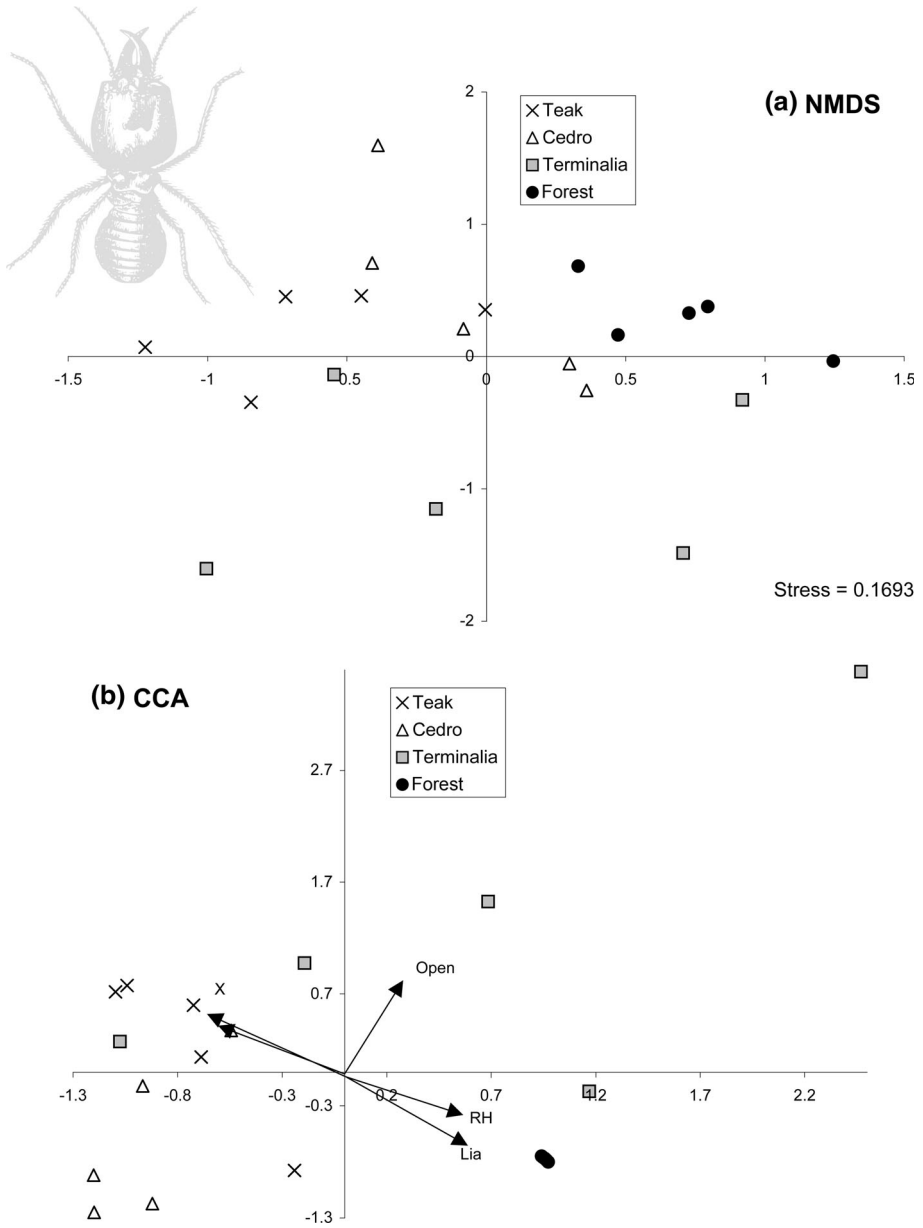


Fig. 4 Multivariate analyses considering 15 termite species recorded at 20 sites (plantations and forest), detailed by habitat. Plot of the scores of the sites in Axes 1, 2 of the **a** NMDS and **b** CCA (with plot of environmental variables, the main ones abbreviated as in Table 1)

correct for different time duration in transects within plantations and the forest was rather drastic (see Appendix S1). Nevertheless, corrected and uncorrected values indicated similar decreasing butterfly abundance and species richness from the series *Terminalia* plantation > Cedro espino plantations > forest > teak plantations.

Second, species detectability may depend on gross features of the vegetation (Pellet 2008). Bias in species detectability appeared higher in the forest than in plantations, probably because of the significant lower canopy openness in the forest and concomitant lower illumination. In highly illuminated plantations (as compared to the forest), bias in species detectability increased in the series Cedro espino < *Terminalia* < teak plantations, in parallel with a decrease in the density of vegetation and, particularly, a decrease in the diversity of the understorey vegetation (Table 1). This suggests that butterfly detectability is highest in well lit habitats but with rather dense vegetation that may hinder butterfly flight and improve the probability of detection and identification. In turn, this suggests that butterfly abundance and species richness may be underestimated in teak plantations and in the forest. However, differences are large enough so that we can still conclude that abundance and species richness are lower in teak plantations and in the forest than in *Terminalia* and Cedro espino plantations.

Contrasting results for butterflies and termites

Butterflies are well-studied insects, which represent a diverse group as compared to termites (in Panama: butterflies: ca 1550 species: Robbins 1982; termites: 85 species: R. Scheffrahn pers. comm.). However, high butterfly species means that it is typically difficult to survey whole assemblages (compare Figs. 1, 3). Therefore our conclusions regarding butterflies most likely pertain to common species only. Termites are less affected by seasonality than butterflies and can be easily surveyed year-round. Assemblages were not spatially autocorrelated at the scale of our study and we probably collected most of wood-eating species (feeding groups I and II of Donovan et al. 2001) present in plantations. While time investment in the field was superficially similar to survey butterflies and termites (ca 60 persons-hours for each), 57 different dates during 2014 were necessary to survey the former, against 9 dates for the latter. Time investment in the field is thus lower for termites than for butterflies. Analyses of species richness may not be very sensitive or robust because of the overall low diversity of termite assemblages. Comparisons based on termite trophic structure may be more relevant than those based on species richness (Attignon et al. 2005). This is conditional to a suitable knowledge of the ecology of species, which appears more difficult to obtain than that of the better-known butterflies. In our study, assigning termite species to the feeding categories of Donovan et al. (2001) did not result in improved comparisons between plantations, but more subtle analyses may be pertinent, particularly if including data on soil-feeding species.

One of the main similarity between butterfly and termite assemblages was the difference in faunal composition between plantations and the forest, more marked for butterflies than for termites. Canopy openness was often a good predictor of these faunal differences. Many butterfly species were observed in plantations but not in the forest, whereas more termite species were surveyed in the forest than in plantations. If we consider abundance or species richness, the better habitat for butterflies was the *Terminalia* plantations, whereas it was the forest for termites and resident butterflies. As for termites, the inclusion of soil-feeding termites would have further increased the difference in species diversity among forests and plantations. This is due to the large proportion of soil-feeding species in forest habitats and their sharp decline with land-use intensity (Jones et al. 2003). Teak plantations represented the worst plantation habitat for butterflies but the best one for wood-feeding termites. Thus, as an overall result, there was no correlation between the scores of sites on the axes of the NMDS for butterflies and termites, emphasizing that different variables may be important for butterflies and termites, respectively. Among the potentially meaningful

variables not measured in this study, one may cite nectar resources for butterflies and amount of dead wood for termites.

Resident versus transient butterfly species

Since butterflies are vagile species, their data are more likely to be spatially autocorrelated and to depend on the scale of the study (Barlow et al. 2007) than that of termites. In our study, data for resident butterfly species were not spatially autocorrelated, which suggests that data could be easier to interpret. However, these data were only relevant to species feeding on host trees or shrubs (ca one-third of all butterfly species). Typically herb and liana hosts are difficult to survey with standard methods in tropical rainforests (Condit 1998), so that suitable data on resident butterfly species may be hard to obtain for most tropical studies. It is well-known that the influence of transient species can confound the assessment of habitat value (Ghazoul 2002). This cautions from jumping to the conclusion that plantations may be richer in species than the forest, since the number of resident species was higher in the forest than in plantations. The occurrence of transient species in plantations may depend on the local matrix of habitats and the size of the plantations (Horner-Devine et al. 2003; Barlow et al. 2007). Still, these variables did not account for differences in species richness among our sites, which were better explained by local variables such as canopy openness or air temperature, probably more relevant in the case of our rather small plantations.

Conservation value of plantations

As demonstrated by several authors (Hamer and Hill 2000; Barlow et al. 2007), the spatial scale of a study can affect its conclusion, as, for example, small spatial scales may fail to sample the increased heterogeneity at larger scales in undisturbed forests. This argument is relevant to our study, as we compared small plantations (0.13–13 ha) with a 1542 ha forest. Estimates of projected species richness for plantations (Table 1) were far lower than the overall 390 species of butterfly breeding on BCI (Basset et al. 2015). Therefore, it is well possible that higher sampling effort accounting for the heterogeneity of the forest would have provided a more balanced view of differences in species richness between plantations and the forest. Comparing butterfly and termite species richness among plantation sites may be more straightforward than comparing plantations and the forest, as plantations are smaller and more homogeneous than the forest. In terms of faunal composition, the most similar plantations to the forest for butterflies and termites were Cedro espino and *Terminalia* (Figs. 2, 4; Table S1). These habitats also supported more butterfly species (overall and resident species) than teak plantations.

Attignon et al. (2005) suggest that the high termite species richness and densities in forests as compared to plantations are influenced by soil water and leaf biomass. Teak plantations represented a better habitat for termites than other plantations, but these differences, particularly in terms in species richness, were small. Within plantations, the wood of teak and Cedro espino is resistant to termites (Rudman et al. 1958; Castellanos and Stevenson 2011), whereas that of *T. ivorensis* is “moderately resistant” to termite attack (Orwa 2010). Hence, wood resistance or wood density are unlikely to explain differences in the occurrence of termites within the different plantations. In teak plantations, leaf litter is usually higher than in the forest, so it may be possible that in these plantations leaf litter may be more important than the amount of dead wood available for termites (Attignon et al. 2005). Overall, we conclude that Cedro espino and *Terminalia* plantations represent a

better habitat than teak plantations. At least for butterflies, targeted management to increase host plant availability in these plantations is likely to translate into higher carrying capacity for these habitats (Curtis et al. 2015).

Conclusions and implications

To return to our working hypotheses, we conclude that (a) the magnitude of faunal changes between forest and plantations is less drastic for termites than for butterflies. (b) Resident butterfly species are more impacted by the conversion of forest to plantations than all butterfly species (including transient species). (c) Variables related to species richness do not necessarily decrease in the series forest > native > exotic plantations; it depends whether we consider all butterflies, resident butterflies or termites.

There are at least two implications of our results. First, not surprisingly, it is more difficult to detect butterflies in forest than in open plantations. However, this does not preclude long-term monitoring of butterflies in tropical rainforests, as long as good reference collections allow identifying accurately a high proportion of species observed in the forest, as was the case in this study (>70 % of individuals). Further, if host-plants for the majority of butterfly species are known and have been surveyed in the habitats studied, data about resident species may be pertinent to estimate the conservation value of habitats for these vagile species, especially when plantations are small, such as in this study.

Second, it is well-known that invertebrates are often neglected in conservation studies, as compared to vertebrates and plants. This “taxonomic chauvinism” (Leather 2009) is also evident within insect conservation studies with, for example butterflies featuring prominently as study subjects (Bonebrake et al. 2010). Hamer and Hill (2000) cautioned that invertebrate responses to forest conversion may depend on taxon mobility and the concomitant relationship between scale and diversity. Our study supports this contention as evidenced by the different conclusions reached when considering all butterflies, resident butterflies or termites. Whereas there are clear advantages of studying more tractable taxa such as butterflies, our study has shown that the responses of such taxa can be highly unrepresentative of other invertebrate groups responsible for different ecological services, such as termites. These taxa should not be neglected for a more comprehensive view of the effects of forest conversion on invertebrates.

Acknowledgments Bob Robbins, Andy Warren, Annette Aiello, Yves Roisin, Thomas Bourguignon and Rudolf Scheffrahn provided expert opinions on butterfly and termite taxonomy. Jefferson Hall and Estrella Yanguas kindly helped to organize the project and shared their vegetation data. Fieldwork was funded by Argos and ForestGEO, collecting permits were granted by the Autoridad Nacional del Ambiente de Panamá. Grants from the Smithsonian Institution Barcoding Opportunity FY012, FY013, FY014 and in-kind help from the Canadian Centre for DNA Barcoding via Paul Hebert and Alex Borisenko at the Biodiversity Institute of Ontario allowed the sequencing of the butterfly and termite specimens. YB was supported by Czech Science foundation GACR grant 14-36098G. YB and HB are members of the Sistema Nacional de Investigación, SENACYT, Panama. Isabelle Bachy helped with the preparation of the figures. Cecilia Dahlsjö, Alan Andersen and an anonymous reviewer greatly helped to improve the manuscript.

References

- Anderson-Teixeira KJ, Davies SJ, Bennett AC et al (2014) CTFS-ForestGEO: a worldwide network monitoring forests in an era of global change. *Glob Change Biol*. doi:[10.1111/gcb.12712](https://doi.org/10.1111/gcb.12712)
- Anselin L (1988) *Spatial econometrics: methods and models*. Kluwer Academic Publishers, Boston
- Attignon SE, Lachat T, Sinsin B et al (2005) Termite assemblages in a West-African semi-deciduous forest and teak plantations. *Agric Ecosyst Environ* 110:318–326

- Barlow J, Overal WL, Araujo IS et al (2007) The value of primary, secondary and plantation forests for fruit-feeding butterflies in the Brazilian Amazon. *J Appl Ecol* 44:1001–1012
- Basset Y, Novotny V, Miller SE et al (1998) Assessing the impact of forest disturbance on tropical invertebrates: some comments. *J Appl Ecol* 35:461–466
- Basset Y, Eastwood R, Sam L et al (2011) Comparison of rainforest butterfly assemblages across three biogeographical regions using standardized protocols. *J Res Lep* 44:17–28
- Basset Y, Eastwood R, Sam L et al (2013) Cross-continental comparisons of butterfly assemblages in rainforests: implications for biological monitoring. *Insect Conserv Divers* 6:223–233
- Basset Y, Barrios H, Segar S et al (2015) The butterflies of Barro Colorado Island, Panama: local extinction since the 1930s. *PLoS One* 10:e0136623. doi:10.1371/journal.pone.0136623
- Bignell DE, Eggleton P (2000) Termites in ecosystems. In: Abe T, Bignell DE, Higashi M (eds) *Termites: evolution, sociality, symbiosis, ecology*. Kluwer Academic Publishers, Dordrecht, pp 363–387
- Bonebrake TC, Ponisio LC, Boggs CL et al (2010) More than just indicators: a review of tropical butterfly ecology and conservation. *Biol Conserv* 143:1831–1841
- Brockerhoff EG, Jactel H, Parrotta JA et al (2008) Plantation forests and biodiversity: oxymoron or opportunity? *Biodiv Conserv* 17:925–951
- Brockerhoff EG, Jactel H, Parrotta JA et al (2013) Role of eucalypt and other planted forests in biodiversity conservation and the provision of biodiversity-related ecosystem services. *For Ecol Manag* 301:43–50
- Cardinale BJ, Duffy JE, Gonzalez A et al (2012) Biodiversity loss and its impact on humanity. *Nature* 486:59–67
- Castellanos MC, Stevenson PR (2011) Phenology, seed dispersal and difficulties in natural recruitment of the canopy tree *Pachira quinata* (Malvaceae). *Rev Biol Trop* 59:921–933
- Colwell RK (2009) EstimateS: statistical estimation of species richness and shared species from samples. version 8.50. user's guide and application. University of Connecticut, Storrs
- Condit R (1998) *Tropical forest census plots*. Springer, Texas
- Condit R, Perez R, Lao S et al (2005) Geographic ranges and b-diversity: discovering how many tree species there are where. *Biologiske Skrifter* 55:57–71
- Curtis RJ, Brereton TM, Dennis RL et al (2015) Butterfly abundance is determined by food availability and is mediated by species traits. *J Appl Ecol* 52:1676–1684
- Davis AJ, Sutton SL (1998) The effects of rainforest canopy loss on arboreal dung beetles in Borneo: implications for the measurement of biodiversity in derived tropical ecosystems. *Divers Distrib* 4:167–173
- Didham RK, Ghazoul J, Stork NE et al (1996) Insects in fragmented forests: a functional approach. *Tree* 11:255–260
- Donovan SE, Eggleton P, Bignell DE (2001) Gut content analysis and a new feeding group classification of termites. *Ecol Entomol* 26:356–366
- Eggleton P (1999) Termite species description rates and the state of termite taxonomy. *Insects Soc* 46:1–5
- Eggleton P, Bignell DE, Sands WA et al (1995) The species richness of termites (Isoptera) under differing levels of forest disturbance in the Mbalmayo Forest Reserve, southern Cameroon. *J Trop Ecol* 11:85–98
- Ghazoul J (2002) Impact of logging on the richness and diversity of forest butterflies in a tropical dry forest in Thailand. *Biodiv Conserv* 11:521–541
- Gotelli NJ, Chao A (2013) Measuring and estimating species richness, species diversity, and biotic similarity from sampling data. In: Levin SA (ed) *Encyclopedia of biodiversity*, 2nd edn. Academic Press, Waltham, pp 195–211
- Hamer KC, Hill JK (2000) Scale-dependent effects of habitat disturbance on species richness in tropical forests. *Conserv Biol* 14:1435–1440
- Hamilton AJ, Novotny V, Waters EK et al (2013) Estimating global arthropod species richness: refining probabilistic models using probability bound analysis. *Oecologia* 171:357–365
- Holloway JD, Kirk-Spriggs AH, Chey VK (1992) The response of some rain forest insect groups to logging and conversion to plantation. *Philos Trans R Soc Lond B* 335:425–436
- Horner-Devine MC, Daily GC, Ehrlich PR, Boggs CL (2003) Countryside biogeography of tropical butterflies. *Conserv Biol* 17:168–177
- Isbell F, Calcagno V, Hector A et al (2011) High plant diversity is needed to maintain ecosystem services. *Nature* 477:199–202
- Jones DT, Eggleton P (2000) Sampling termite assemblages in tropical forests: testing a rapid biodiversity assessment protocol. *J Appl Ecol* 37:191–203
- Jones DT, Susilo FX, Bignell DE et al (2003) Termite assemblage collapse along a land-use intensification gradient in lowland central Sumatra, Indonesia. *J Appl Ecol* 40:380–391

- Koh LP, Wilcove DS (2008) Is oil palm agriculture really destroying tropical biodiversity? *Conserv Lett* 1:60–64
- Leather SR (2009) Taxonomic chauvinism threatens the future of entomology. *Biologist* 56:10–13
- Longino JT (2000) What to do with the data? In: Agosti D, Majer JD, Alonson LE, Schultz TR (eds) *Ants. Standard methods for measuring and monitoring biodiversity*. Smithsonian Institution Press, Washington, pp 186–203
- Lucey JM, Hill JK (2011) Spillover of insects from rain forest into adjacent oil palm plantations. *Biotropica* 44:368–377
- Luke SH, Fayle TM, Eggleton P et al (2014) Functional structure of ant and termite assemblages in old growth forest, logged forest and oil palm plantation in Malaysian Borneo. *Biodiv Conserv* 23:2817–2832
- Novotny V, Basset Y (2000) Rare species in communities of tropical insect herbivores: pondering the mystery of singletons. *Oikos* 89:564–572
- Nummelin M, Fuersch H (1992) Coccinellids of the Kibale Forest, Western Uganda: a comparison between virgin and managed sites. *Trop Zool* 5:155–166
- Oksanen J, Blanchet FG, Kindt R et al (2011) *Vegan: community ecology package*. R package version 1.17-6. R Foundation for Statistical Computing, Vienna
- Orwa C (2010) *Agroforestry Database 4.0: a tree reference and selection guide*. World Agroforestry Centre. <http://www.worldagroforestry.org/treedb/>. Accessed 8 Nov 2015
- Pellet J (2008) Seasonal variation in detectability of butterflies surveyed with Pollard walks. *J Insects Conserv* 12:155–162
- Pollard E (1977) A method for assessing changes in the abundance of butterflies. *Biol Conserv* 12:115–153
- Rangel TF, Diniz-Filho JAF, Bini LM (2010) SAM: a comprehensive application for spatial analysis in macroecology. *Ecography* 33:1–5
- Robbins RK (1982) Comparison of butterfly diversity in the Neotropical and Oriental regions. *J Lep Soc* 46:298–300
- Roisin Y, Leponce M (2004) Characterizing termite assemblages in fragmented forests: a test case in the Argentinian Chaco. *Aust Ecol* 29:637–646
- Rudman P, Da Costa EWB, Gay FJ et al (1958) Relationship of tectoquinone to durability in *Tectona grandis*. *Nature* 181:721–722
- Sparrow HR, Sisk TD, Ehrlich PR et al (1994) Techniques and guidelines for monitoring Neotropical butterflies. *Conserv Biol* 8:800–809
- Speight MR, Intachat J, Khen CV et al (2003) Influences of forest management on insects. In: Basset Y, Novotny V, Miller SE, Kitching RL (eds) *Arthropods of tropical forests: spatio-temporal dynamics and resource use in the canopy*. Cambridge University Press, Cambridge, pp 380–393
- Spitzer K, Jaros J, Havelka J et al (1997) Effect of small-scale disturbance on butterfly communities of an Indochinese montane rainforest. *Biol Conserv* 80:9–15
- Stephen C, Sánchez R (2014) Species richness and relative species abundance of Nymphalidae (Lepidoptera) in three forests with different perturbations in the North-Central Caribbean of Costa Rica. *Rev Biol Trop* 62:919–928
- Swift MJ, Izac AM, van Noordwijk M (2004) Biodiversity and ecosystem services in agricultural landscapes—are we asking the right questions? *Agric Ecosyst Environ* 104:113–134
- Ter Braak CJF, Smilauer P (2003) *CANOCO reference manual and user's guide to canoco for windows: software for canonical community ordination (version 4.52)*. Microcomputer Power, Ithaca
- Vlasanek P, Sam L, Novotny V (2013) Dispersal of butterflies in a New Guinea rainforest: using mark-recapture methods in a large, homogeneous habitat. *Ecol Entomol* 38:560–569
- Windsor DM (1990) *Climate and moisture variability in a tropical forest: long-term records from Barro Colorado Island, Panama*. Smithsonian Institution Press, Washington