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Taxonomic and functional composition of arthropod assemblages across contrasting Amazonian forests

Greg P. A. Lamarre[1,2,3]*, Bruno Hérault[4], Paul V. A. Fine[5], Vincent Vedel[2,3], Roland Lupoli[3], Italo Mesones[5] and Christopher Baraloto[2,6]

[1] Université Antilles-Guyane, UMR Ecologie des Forêts de Guyane, 97310 Kourou, French Guiana; [2]INRA, UMR Ecologie des Forêts de Guyane, 97310, Kourou, French Guiana; [3]Société Entomologique Antilles-Guyane, 97354 Rémire-Montjoly, French Guiana; [4]CIRAD, UMR Ecologie des Forêts de Guyane, 97310 Kourou, French Guiana; [5]Department of Integrative Biology, University of California, Berkeley, 1005 Valley Life Sciences Building #3140, Berkeley, CA 94720, USA; and [6]International Center for Tropical Botany, Department of Biological Sciences, International Center for Tropical Botany, Florida International University, Miami, FL 33199, USA

Summary

1. Arthropods represent most of global biodiversity, with the highest diversity found in tropical rain forests. Nevertheless, we have a very incomplete understanding of how tropical arthropod communities are assembled.

2. We conducted a comprehensive mass sampling of arthropod communities within three major habitat types of lowland Amazonian rain forest, including *terra firme* clay, white-sand and seasonally flooded forests in Peru and French Guiana. We examined how taxonomic and functional composition (at the family level) differed across these habitat types in the two regions.

3. The overall arthropod community composition exhibited strong turnover among habitats and between regions. In particular, seasonally flooded forest habitats of both regions comprised unique assemblages. Overall, 17·7% (26 of 147) of arthropod families showed significant preferences for a particular habitat type.

4. We present a first reproducible arthropod functional classification among the 147 taxa based on similarity among 21 functional traits describing feeding source, major mouthparts and microhabitats inhabited by each taxon. We identified seven distinct functional groups whose relative abundance contrasted strongly across the three habitats, with sap and leaf feeders showing higher abundances in *terra firme* clay forest.

5. Our novel arthropod functional classification provides an important complement to link these contrasting patterns of composition to differences in forest functioning across geographical and environmental gradients. This study underlines that both environment and biogeographical processes are responsible for driving arthropod taxonomic composition while environmental filtering is the main driver of the variance in functional composition.

Key-words: Amazon, arthropod community, environmental filtering, forest habitat, French Guiana, functional composition, mass sampling, Peru, trophic cascades

Introduction

Arthropods represent most of the world's biodiversity, with the highest species richness totals found in tropical rain forests. Yet with less than 1·5 million species described out of the estimated 6 million insect species globally (Hamilton *et al.* 2011; Basset *et al.* 2012), we have hardly scratched the surface in our attempt to quantify arthropod diversity. Moreover, we have little idea how arthropod communities are structured across geographical and environmental gradients. In megadiverse tropical forests, an important component of plant diversity is the turnover of species composition across geographical regions and contrasting habitats (i.e. beta diversity, Condit et al. 2002; Tuomisto *et al.* 2003). Current evidence suggests that herbivorous insects may vary in abundance because of changing environmental conditions across habitat gradients (Novotny *et al.* 2005;

*Correspondence author. E-mail: greglamarre973@gmail.com

Rodriguez-Castañeda *et al.* 2010), or due to geographical variation in co-evolutionary dynamics (Thompson & Cunningham 2002). However, contrasting predictions have been made for the contribution of beta diversity to regional diversity within lowland tropical forests. For instance, Novotny *et al.* (2007) present evidence for a greater number of generalist herbivores resulting in a low species turnover across relatively large areas in Papua New Guinea. In contrast, Dyer *et al.* (2007) suggest that tropical lowland forests should have a high arthropod beta diversity because of higher host specificity than in temperate forests.

Pioneering attempts to study tropical insect assemblages involved fogging several individuals of a single tree species (Erwin 1982). Recently, studies have employed hand collections of known host plant lineages to estimate alpha and beta diversity and the degree of host specialization (Novotny *et al.* 2002, 2006; Ødegaard, Diserud & Ostbye 2005; Dyer *et al.* 2007; Rodriguez-Castañeda *et al.* 2010; Basset *et al.* 2012). While these studies have revealed important patterns of diversity and specificity of particular arthropod lineages, they are far from representative of complete arthropod communities (Ødegaard *et al.* 2000; Sobek *et al.* 2009; Rodriguez-Castañeda *et al.* 2010; De Vries *et al.* 2012) or are very restricted in geographical area (Novotny *et al.* 2005; Basset *et al.* 2012). A more comprehensive macroecological approach would sample entire arthropod communities at large geographical scales using a combination of traps in a wide variety of habitat types. Yet to our knowledge, no such community-level arthropod composition study has been conducted in tropical rain forests, and therefore, the factors governing assembly rules in tropical arthropod communities are still poorly understood.

In the Amazon basin, three broad types of lowland forest habitats have been distinguished based on soil texture and fertility and seasonal water stress, and associated forest structure (Baraloto *et al.* 2011): (i) nutrient-poor and dry soils of the white-sand forest (hereafter WS) that are often surrounded by (ii) *terra firme* clay forest with high soil nutrient content (TF); and, in low-lying areas nears rivers and streams (iii) seasonally flooded forests (SF) in which episodic flooding often submerges soil surfaces during periods of high precipitation or Andean snowmelt (Baraloto *et al.* 2007). A unique floristic composition among these three habitats has been detected, with a high spatial turnover among tree species (Baraloto *et al.* 2007; Fine *et al.* 2010; Wittmann, Schöngart & Junk 2010), including host plant species on which arthropods rely for nourishment and shelter (Price 2002). A recent study conducted among habitat-specialist tree species has shown contrasting patterns in leaf production and insect herbivory rates across habitats (Lamarre *et al.* 2014), with consistently higher rates of leaf production in seasonally flooded forests (Lamarre *et al.* 2012a). Contrasting environmental conditions may therefore select for different ecological strategies in tropical trees, including evolutionary trade-offs in allocation to growth and defence against herbivores (Fine, Mesones & Coley 2004; Fine *et al.* 2006). We therefore predict that arthropod community composition varies strongly among habitats types because of differences in resource availability, plant composition and habitat structure.

Complementary insights into the role of environmental filtering in community assembly can be gleaned using analyses of functional composition (Cadotte, Carscadden & Mirotchnick 2011). Most studies examining insect diversity have focused on species richness or taxonomic composition (Erwin 1982; Novotny *et al.* 2002, 2007; May 2010; Basset *et al.* 2012). Yet the literature on assembly rules in plant communities has underlined contrasts between patterns of taxonomic and functional diversity and composition (Baraloto *et al.* 2012; Lavorel *et al.* 2013). It is not uncommon for unrelated taxonomic groups of arthropods to share similar functions, such as the leaf-chewing habit of Nymphalidae larvae (Lepidoptera) and Chrysomelidae (Coleoptera). If food substrates vary across forest types, as suggested by studies showing denser leaf, stem and roots tissues in white-sand forests (Fortunel *et al.* 2014), then we would predict higher turnover in arthropod functional composition than might be expected from patterns of turnover in taxonomic composition. Turnover in functional composition may also provide a more meaningful assay of the role of arthropod communities in ecosystem processes such as decomposition (Lavorel *et al.* 2013). In this study, we sampled representative arthropod communities across white-sand, *terra firme* and flooded forests in lowland Amazonian rain forests of Peru and French Guiana. We then used these collections to investigate how taxonomic and functional composition varied across the three contrasted tropical forest habitats at broad geographical scales.

Materials and methods

STUDY SITES AND ENVIRONMENT

This study was conducted in 12 plots within four representative sites (Fig. 1) that represent the entire range of variation in climatic, edaphic and forest structure factors observed in a larger plot network in lowland tropical forests of South America in Loreto, Peru, and French Guiana (Baraloto *et al.* 2011). Each plot consists of ten 10 × 50 m transects distributed throughout a 2-ha area that is chosen for homogeneity and to represent a given forest habitat in a given region. UTM coordinates for each plot (Universal Transverse Mercator system using WGS 1984 datum) were collected using handheld Garmin 60csx units. Environmental variables describing climate, soil and forest structure were used in order to define the environmental conditions of each studied plot (for complete details, see Baraloto *et al.* 2011). Soil physical and chemical descriptions were conducted on ten bulked samples of surface soil (0–20 cm depth) collected throughout each plot. Climatic variables were calculated using Météo-France data in French Guiana and from IIAP weather stations in Peru. Climate in the Guianas is driven by a marked seasonal alternation

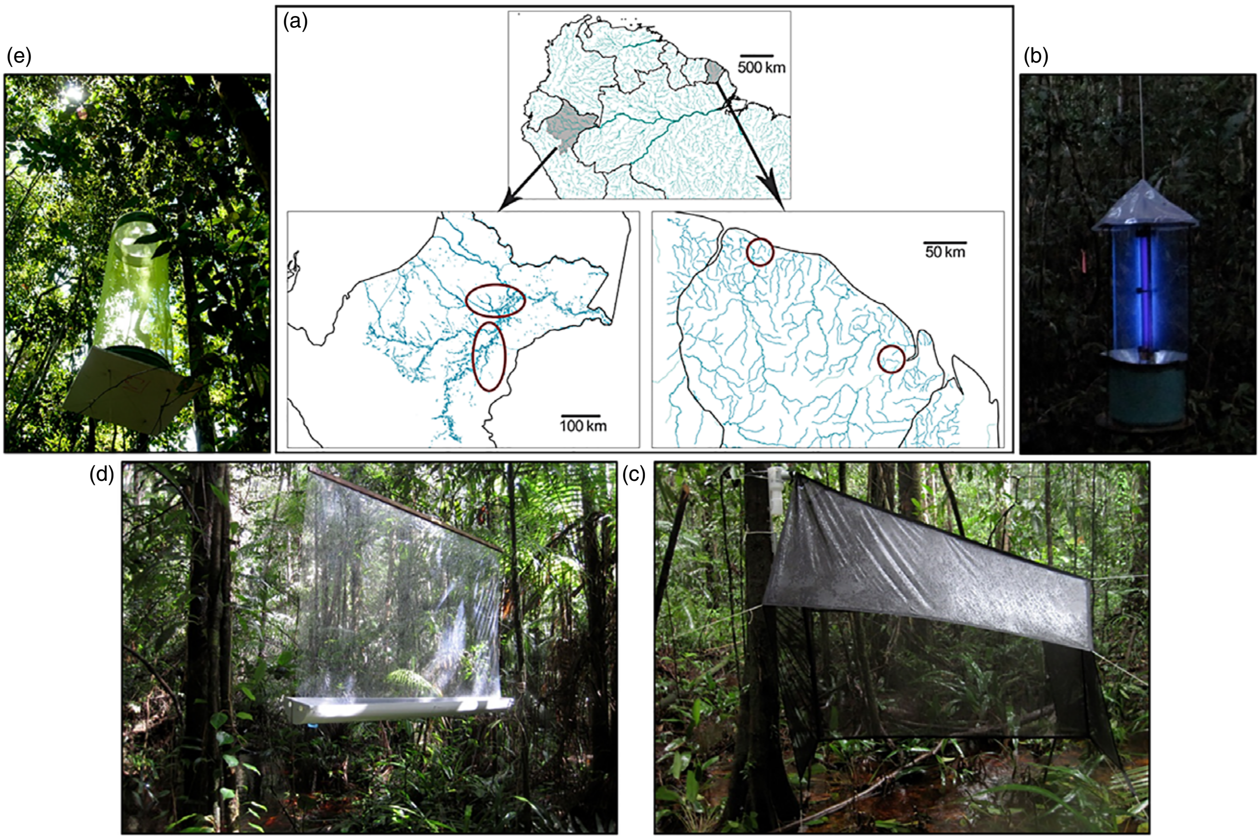

Fig. 1. Sampling sites and trap methods installed in the Amazon Basin. (a) Map of the Amazon region with major watersheds, illustrating sites (circles) and plots (dots) established in the northern (Porvenir) and southern (Jenaro Herrera) regions of Loreto, Peru; and the western (Laussat) and eastern (Regina) regions of French Guiana. (b) Automatic light trap. (c) Malaise trap. (d) The new type of windowpane trap developed in French Guiana. (e) Aerial fruit trap.

between a wet season (December to August) and a dry season (September to November). In French Guiana, the intertropical convergence zone results in heavy rains with up to 120 mm on some days in December to February and April to July. A marked and short dry season in March is also characteristic of the Guianas, in addition to a long dry period during August to November (Wagner *et al.* 2011). In contrast with the Guianas, there is no distinctive dry season in northern Peru, although it also can have short periods of heavy precipitation for several days (Marengo 1998). Each habitat type was separated by 1 km to avoid collecting specimens (i.e. avoiding the 'tourist' issue, see Ødegaard 2004) from adjacent habitats.

SAMPLING ARTHROPOD COMMUNITIES

Arthropod communities were sampled weekly in the twelve permanent plots from August to November 2010 in French Guiana and between May and September 2011 in Peru, corresponding to drier periods in each region. We employed a multiple trapping method composed of two types of flight interception trap (FIT), the malaise trap (MT) and the windowpane trap (WT); and two types of attractive traps: the fruit trap (FT) and the automatic light trap (ALT) (Fig. 1). For each plot, one pair of each FIT (2 MTs + 2 WTs) and two pairs of FT were installed within the forest understorey of the 2-ha surface area covered. Malaise and windowpane traps represent wide interception surfaces that are together collecting a representative portion of flying arthropods (Lamarre *et al.* 2012b). To capture multidirectional trajectories of insects flying through the forest understorey, we installed one pair of each MT and WT in or around gaps in each plot. These traps were collected every 6 days during the study period in each region.

Each fruit trap (4 FTs per plot) was installed and fixed in tree branches between 3 and 5 m high and collected every 2 days. These traps consist of a 1-m mosquito net cylinder in which a fermented mixture of banana, sugar and rum actively attract fruit-feeding butterflies and to a lesser extend nectar-feeding butterflies and a few other taxa (i.e. grasshoppers, beetles and wasps).

Finally, we installed one portable automatic light trap (ALT) with an 8-W backlight tube to collect light-attracted arthropods during each new moon of the study period (+/−2 days). We installed ALTs in the middle of each plot and trapped for a total of 24 sampling nights over the study period. Each of the trap types was separated by at least 20 m to avoid spatial interference both between and within traps. We employed equal sampling effort in terms of number of day–night periods for each trap in each plot and in each country.

TAXONOMIC SORTING AND COLLECTIONS

For each plot (aggregating the collections of multiple traps), adult arthropods including five important major insect orders in Insecta (Coleoptera, Lepidoptera, Hemiptera, Hymenoptera and Orthoptera) in addition to spiders (Araneae) were counted and identified to the family level. This level of taxonomic resolution has been found to be sufficient for detecting some significant patterns of community composition and beta diversity in temperate systems (Timms *et al.* 2013). Moreover, family-level identification has provided ecologically adequate surrogates for species in the study of functional diversity (see also Cardoso *et al.* 2011 for both temperate and tropical systems). Because of strong divergence in life histories within some family-level taxa, eight diverse groups were sorted further to the subfamily level (Lawrence *et al.* 1999): Ceratocanthinae (Hybosoridae), Colydiinae (Zopheridae), Malachiinae (Melyridae), Paussinae (Carabidae), Platypodinae, Scolytinae (Curculionidae), Noctuinae (Erebiidae) and Scydmaeninae (Staphylinidae). Three hymenopteran taxa (Chalcidoidea, Ichneumonoidea and Proctotrupoidea) could be identified only to the super-family due to our inability to consistently separate them further. Due to the lack of knowledge in identification and classification of some groups, we excluded all Diptera, Odonata and specimens in small orders (Phasmatodea, Mantodea). Most specimens in Gryllacrididae, Anostostomatidae, Rhaphidophoridae and Gryllidae families (Orthoptera) were highly damaged because of the windowpane trap collecting methods and were therefore excluded from the analysis. Because of their important functional role in ecosystems (Cardoso *et al.* 2011), we included spiders in our sample and were able to capture a representative portion of them with our flight interception traps (Vedel, Camus & Lamarre 2011). Samples were sent to taxonomists that are collaborating along with the *Société Entomologique Antilles-Guyane* (SEAG) representing hundreds of taxonomists from institutes, universities and museums world-wide. Distribution records were added to the lists of French Guiana (SEAG, Labex CEBA) and Peru (IIAP Iquitos).

ARTHROPOD FUNCTIONAL CLASSIFICATION

Each arthropod family was described using 21 functional and ecological traits belonging to three trait categories (Table 1, Appendix S3, Supporting Information). Based on these functional attributes, we constructed a matrix of binary functional traits using the literature (Gauld & Bolton 1988; Delvare & Aberlenc 1989; Browne & Scholtz 1999; Lawrence *et al.* 1999) and confirmed by experts of the SEAG network. First, in order to extend the designation of arthropods into major ecological guilds, we classified each group by its most frequent food source. Secondly, we described the general type of insect mouthparts as a complementary measure of feeding mode and morphological feature that emphasizes resource use. We recognize that insect mouthparts represent a complex structure in which variation may be contributed to by at least 34 fundamental mouthpart types (Labandeira 1997). Nevertheless, we chose to distinguish three major types of mouthparts (siphoning, piercing–sucking and mandibulates) that represent the ecological attributes of insect feeding strategy among our studied arthropod taxa. Thirdly, we described the different habitats and microhabitats inhabited by each taxa. We classified 'free-living' insects in this third category because these taxa are believed to be 'tourist insects' as defined by Morán & Southwood (1982), implying high mobility across a wide range of habitats. Some generalization of ecological characteristics was made because detailed trait information is not yet available for some invertebrate taxa and/or not in South America. In some cases, when information was missing in the Amazon for a given family, we used the data available for the same family in another part of the world or those available for other related taxonomic group. Despite the coarse taxonomic resolution of our data set (i.e. mostly family level), this approach focussed on resource-capture and resource-use traits that are expected to capture most of the evolutionarily conserved functional attributes at the family level (see Timms *et al.* 2013 for discussion on optimal taxonomic resolution).

Table 1. List of the 21 functional traits used in this study

Categories	Functional traits	Details[b]
Feeding source	Leaf	Leaf-feeding insect
	Sap	Including phloem, xylem and mesophyll cell sucker
	Wood-related	Including decayed vegetation (saproxylophagous)
	Invertebrates	Predator and parasitoid
	Organic matter	Including dung
	Fruit and Flower	Including seed, nectar and pollen feeder
	Fungi-related	Fungivore
	Scavenge	Insects that scavenge as resource-use
Mouthparts	Mandibulates	An insect having mandible
	Piercing–sucking	Insect with mouthpart modified for piercing and sucking
	Siphoning	Insect with mouthpart modified for siphoning
Habitats	Terrestrial	Insects that have terrestrial habit
	Aquatic	Insects that have aquatic or semi-aquatic habit
	Riparian	Living in river shore, sand and muddy habitat
	Litter	Insects inhabiting the first layer of soil profile
	Wood	Xylophage insects including insect inhabiting under bark
	Endophagy	Insects performing leaf mining, stem boring, gall forming
	Dead tree	Decaying wood
	Free-living	Defined as 'tourist' insect[a]
	Dung and carrion	Insects inhabiting dung and carrion matter

[a] Definition from Morán & Southwood (1982)
[b] We tried to add all details concerning functional attributes for both adult and larvae when information was available.

STATISTICAL ANALYSES

A taxonomic approach was first constructed based on the sum of the relative abundance of each collected arthropod taxa for each plot (i.e. mostly at the family level, in addition to seven subfamilies and three super-families). Dissimilarity in community-level arthropod abundance among plots – that is community turnover – was measured using Bray–Curtis indices. Correlations between taxonomic arthropod dissimilarity among habitat and countries were visualized with a NMDS ordination and tested for significant differences among habitats and across country with analysis of variance (ANOVA on NMDS coordinates). We then explored how arthropod taxa differ in abundance among the three different forest habitats and between countries. The impact of habitats and countries was modelled using a generalized linear model framework. Because our response variable, *that is* the number of individuals recorded in a plot, was discrete with positive values, we modelled them with a Poisson distribution. The significance of both habitat and country effects was assessed through the Wald statistic Z (R software; R Development Core Team, 2013):

$$\log(E(Ind_{ch})) = \theta_0 + \theta_c + \theta_h$$

where Ind_{ch} is the number of individuals of a given taxa in country c and habitat h and θ the model parameters. To counteract the problem of multiple comparisons, we used the Holm–Bonferroni method (Holm 1979) to correct the significance values. Secondly, in order to evaluate the degree of arthropod habitat associations across the studied forests, we calculated indicator taxa values (IndVal) for each arthropod taxon after Dufrene & Legendre (1997).

The trait-based approach integrated the matrix of 21 functional traits (Table 1) to create a pairwise functional dissimilarity matrix for the studied plots. Functional distances between all taxa were computed according to their trait value using the Gower's metric (Gower 1966). Then, we constructed a functional typology of the overall arthropod community using Ward's method (Everitt *et al.* 2011). We then computed the KGS penalty function (Kelley, Gardner & Sutcliffe 1996) to decide where to prune the tree in order to delimit arthropod functional groups. The minimum of this function represents the suggested pruning size. The consistency of each arthropod taxon's membership to a given functional group (i.e. suggested pruning) was computed and validated using a silhouette plot (Rousseeuw 1987). We then tested for differences in functional group abundances among the three habitats using a GLM Poisson model in the same way as for the taxonomic approach.

Finally, we partitioned the degree to which spatial variation in community composition (taxonomic and functional group composition) was explained by environmental and geographical components using a canonical partitioning procedure (Legendre, Borcard & Peres-Neto 2005). We used geographical distances between pairs of plots calculated from the UTM coordinates of each permanent plot. An environmental distance matrix of the 24 environmental variables (i.e. forest stand, climatic and edaphic variables, see Baraloto *et al.* 2011) was calculated for each plot pair following a principal component analysis of the environmental data set of the entire 74 plot network. We first calculated two principal coordinates of neighbour matrices (PCNM), the first one on the community composition and the second one on the geographical distance matrices. We then extracted the first five eigenvectors of each PCNM and used these eigenvectors in two partial constrained correspondence analyses (pCCA), the first in which community composition was constrained by environmental eigenvectors while partitioning out the effect of geographical eigenvectors, and the second in which community composition was constrained by geographical eigenvectors while partitioning out the effect of environmental eigenvectors. We were able to partition the variance in community composition that is solely attributable to environmental effects, to geographical effects and to 'shared' variation among environment and geography (Table 2).

Results

CHANGES IN ARTHROPOD TAXONOMIC COMPOSITION

In total, 60 123 specimens of arthropods were collected and assigned to 147 taxonomic groups, representing 108 super-families in seven arthropod orders (Appendix S1). Variance partitioning showed that geographical distances and environmental dissimilarity among plots explained most of the variation in arthropod community taxonomic composition (Table 2). Geographical distance (controlling for environment) explained slightly more (39% vs 34%) of the variation in community composition than environmental distance (controlling for geography).

These results can be visualized in the ordinations presented in Fig. 2, which show a clear separation in arthropod composition between SF forest and the two other forest habitats (axis 2; $F_{(1,\ 6)} = 41{\cdot}8$; $P = 0{\cdot}0003$). We also

Table 2. Partitioning the effect of environment and geography on variation in arthropod community taxonomic and functional composition. We used partial canonical correspondence analyses. A first correspondence analysis (CA) was run on the taxonomic and functional composition matrices to quantify all variation in the data. Then, canonical correspondence analyses (CCA) were run to decipher the part variance that can be explained by one constraint (environment or geography) while controlling for the other. The first 5 axes summarize more than 99% of the observed variation in constraints

	Inertia[a]	Axis 1[b]	Axis 2[b]	Axis 3[b]	Axis 4[b]	Axis 5[b]	MSC[c]
Taxonomic composition							
CA	0·88						
CCA Environment	0·30	0·11	0·07	0·06	0·03	0·02	34·3%
CCA Geography	0·35	0·12	0·10	0·08	0003	0·02	39·3%
Functional composition							
CA	0·27						
CCA Environment	0·12	0·10	0·01	0·01	0·00	0·00	42·6%
CCA Geography	0·07	0·03	0·03	0·01	0·00	0·00	26·0%

[a] sum of eigenvalues.

[b] eigenvalues.

[c] MSC = (inertia of CCA/inertia of CA)*100; it provides an indication of the proportion of the variance accounted for by environment or geography.

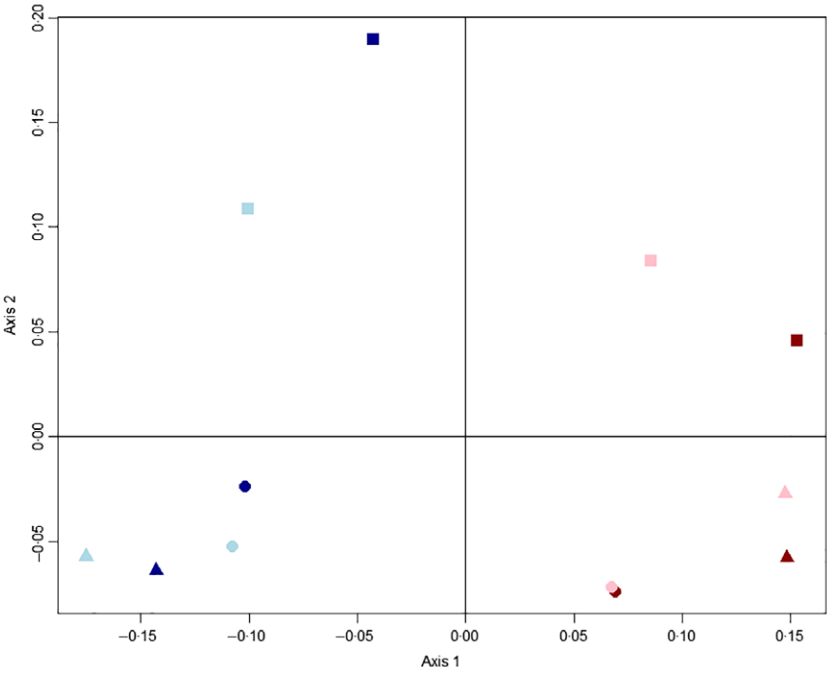

Fig. 2. Non-metric dimensional scaling (NMDS) ordinations illustrating similarity in arthropod taxonomic composition among plots of different habitats, regions and countries. French Guiana plots are coloured in blue and Peruvian plots in red. Habitats include *terra firme* clay forest (circles), white-sand forest (triangles) and seasonally flooded forest (squares). Light and dark blue symbols represent the Laussat and Regina regions of French Guiana, respectively. Light and dark red symbols represent the Porvenir and Jenaro Herrera regions of Peru, respectively (see Fig. 1). The colour version of this figure is available online.

found convergent patterns of dissimilarity among habitat types between Peru and French Guiana. In particular, overall community composition in SF forest was remarkably similar in the two countries, mainly because of a consistent dominance of aquatic insect communities in these habitats (Appendix S1 and Table 3). We observed a high similarity in taxonomic composition in *terra firme* clay forest and to a lower extent in white-sand forest habitats within each country (Fig. 2). Taxonomic composition was strongly and significantly differentiated between Peru and French Guiana (axis 1; $F_{(1,\ 6)} = 200{\cdot}4$; $P < 0{\cdot}001$). The partitioning analysis clearly showed that the effect of geographical variation in community taxonomic composition was stronger than the effect of environment (Table 2), a pattern also confirmed by the visual inspection of the NMDS ordination.

ARTHROPOD HABITAT ASSOCIATIONS

Overall, arthropod taxa exhibited striking contrasts in habitat associations across the studied forest communities, with more than 17% (26 out of 147) of arthropod taxonomic groups having significant preferences for a single habitat type (Table 3). Arthropod families that showed clear habitat associations were mostly detected in high-resource habitats (e.g. TF and SF). Nevertheless, white-sand forest communities were preferred habitats for two moth families (Dalceridae and Nolidae), in addition to two Auchenorrhyncha families (Delphacidae and Fulgoridae). Ground beetles (i.e. Carabidae) were the beetle family exhibiting the strongest association with a particular forest habitat, with nearly two-thirds of all individuals collected in SF forests. We also found that more than 60% of the individuals in Mordellidae flower beetles were collected in TF forest (see Table 1). These patterns are consistent with the results of the generalized linear model (Appendix S1) in which we found

Table 3. Arthropod taxa with significant associations with each of the studied forest habitats. Indicator taxa values after Dufrene & Legendre (1997) and the probability of obtaining as great an indicator value as observed over 1000 iterations

Order	Taxa	Preferred forest habitat	Indicator value	*P*
Coleoptera	Carabidae	Flooded	0·738	0·007
Coleoptera	Cicindelidae	Flooded	0·912	0·013
Coleoptera	Heteroceridae	Flooded	0·891	0·013
Coleoptera	Hydrophilidae	Flooded	0·805	0·016
Coleoptera	Hydrochidae	Flooded	0·864	0·019
Coleoptera	Dytiscidae	Flooded	0·967	0·066
Hemiptera	Gerridae	Flooded	0·933	0·006
Isoptera	Termitidae	Flooded	0·852	0·008
Lepidoptera	Hesperiidae	Flooded	0·593	0·047
Coleoptera	Scarabaeidae	*terra firme*	0·681	0·007
Coleoptera	Ptilodactylidae	*terra firme*	0·588	0·019
Coleoptera	Nitidulidae	*terra firme*	0·63	0·038
Coleoptera	Phengodidae	*terra firme*	0·7	0·05
Coleoptera	Curculionidae	*terra firme*	0·483	0·067
Coleoptera	Erotylidae	*terra firme*	0·579	0·089
Coleoptera	Mordellidae	*terra firme*	0·656	0·006
Hemiptera	Cicadellidae	*terra firme*	0·46	0·071
Hemiptera	Flatidae	*terra firme*	0·7	0·073
Lepidoptera	Nymphalidae	*terra firme*	0·496	0·01
Lepidoptera	Saturniidae	*terra firme*	0·611	0·01
Orthoptera	Acrididae	*terra firme*	0·567	0·02
Araneae	Salticidae	*terra firme*	0·634	0·045
Hemiptera	Delphacidae	White sand	0·824	0·013
Hemiptera	Fulgoridae	White sand	0·81	0·019
Lepidoptera	Dalceridae	White sand	1	0·007
Lepidoptera	Nolidae	White sand	0·675	0·059

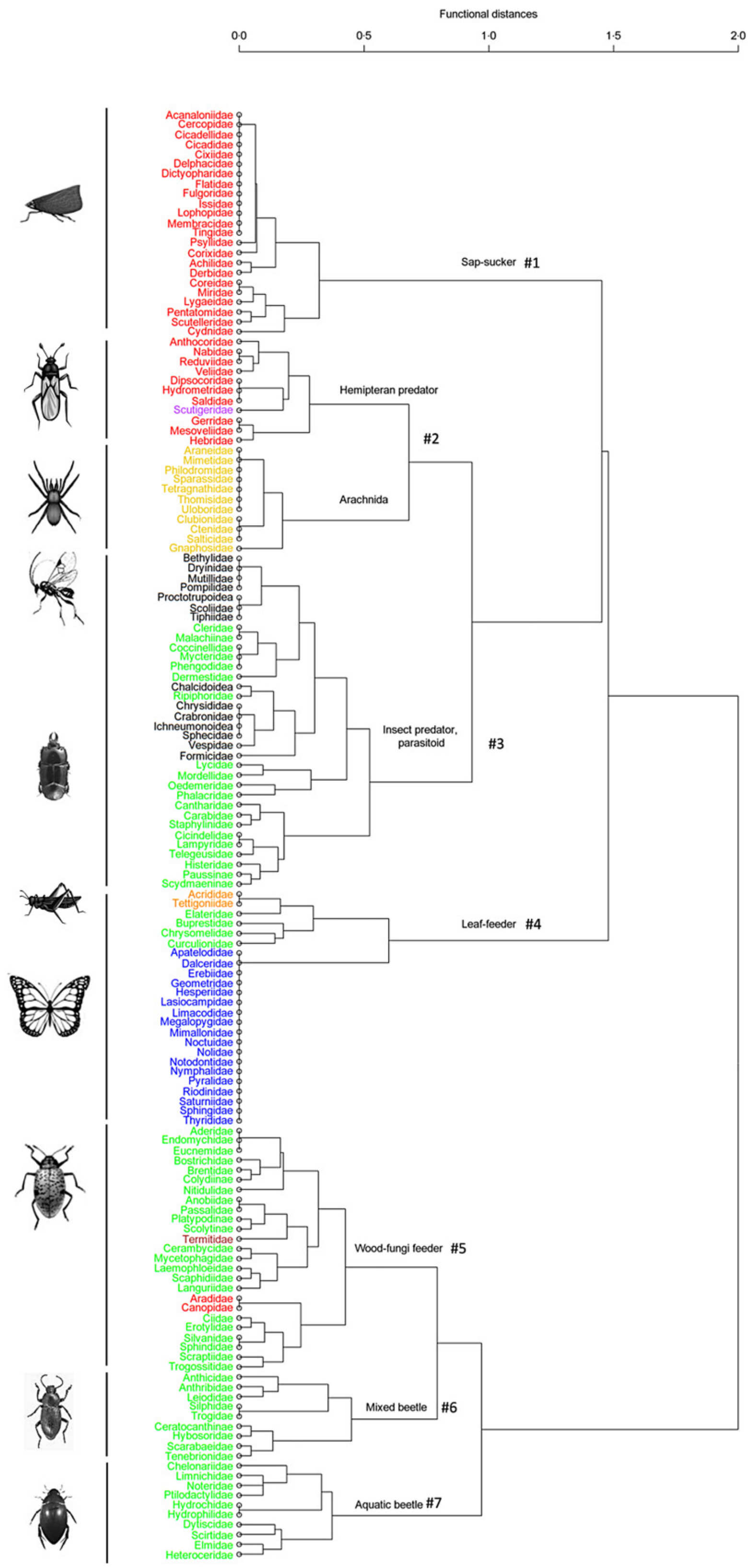

Fig. 3. Cluster functional dendrogram of the overall arthropod community. Results for the functional-based approach integrated the matrix of 21 functional traits to create a pairwise functional dissimilarity matrix. Functional distances between all taxa were computed according to their trait value using the Gower's metric. Arthropod orders are coloured to visualize phylogenetic conservatism in functional attributes; red = Hemiptera, green = Coleoptera, blue = Lepidoptera, yellow = Araneae, orange = Orthoptera, black = Hymenoptera, purple= Scutigeromorpha and burgundy = Isoptera. The colour version of this figure is available online.

that 82 out of 147 taxonomic groups (i.e. 55·8 %) differed significantly in their abundance among the three studied forest habitats.

CHANGES IN ARTHROPOD FUNCTIONAL COMPOSITION

The functional typology of the 147 taxa identified seven distinct functional groups (Fig. 3), or clusters of taxonomic groups sharing similar ecological and functional attributes and that are therefore likely to be similar in their response to their environment and/or their effects on ecosystem functioning (Diaz & Cabido 2001). Figure 3 illustrates the clear separation between arthropod groups related to leaf resources (groups 1 and 4), those represented by predators and parasitoids (groups 2 and 3) and those feeding on wood and fungi (groups 5 and 6). Our approach also discriminated different feeding sources (e.g. groups 1 and 4 feed on leaf tissue) from morphological traits related to foraging (hemipterans from Group 1 but also Group 2 harbour the same piercing–sucking stylet).

Each of the seven functional groups had contrasting distributions across the three forest habitat types (Fig. 4). Most groups exhibited higher abundance in high-resource environments (i.e. SF and/or TF). Herbivores (leaf feeders

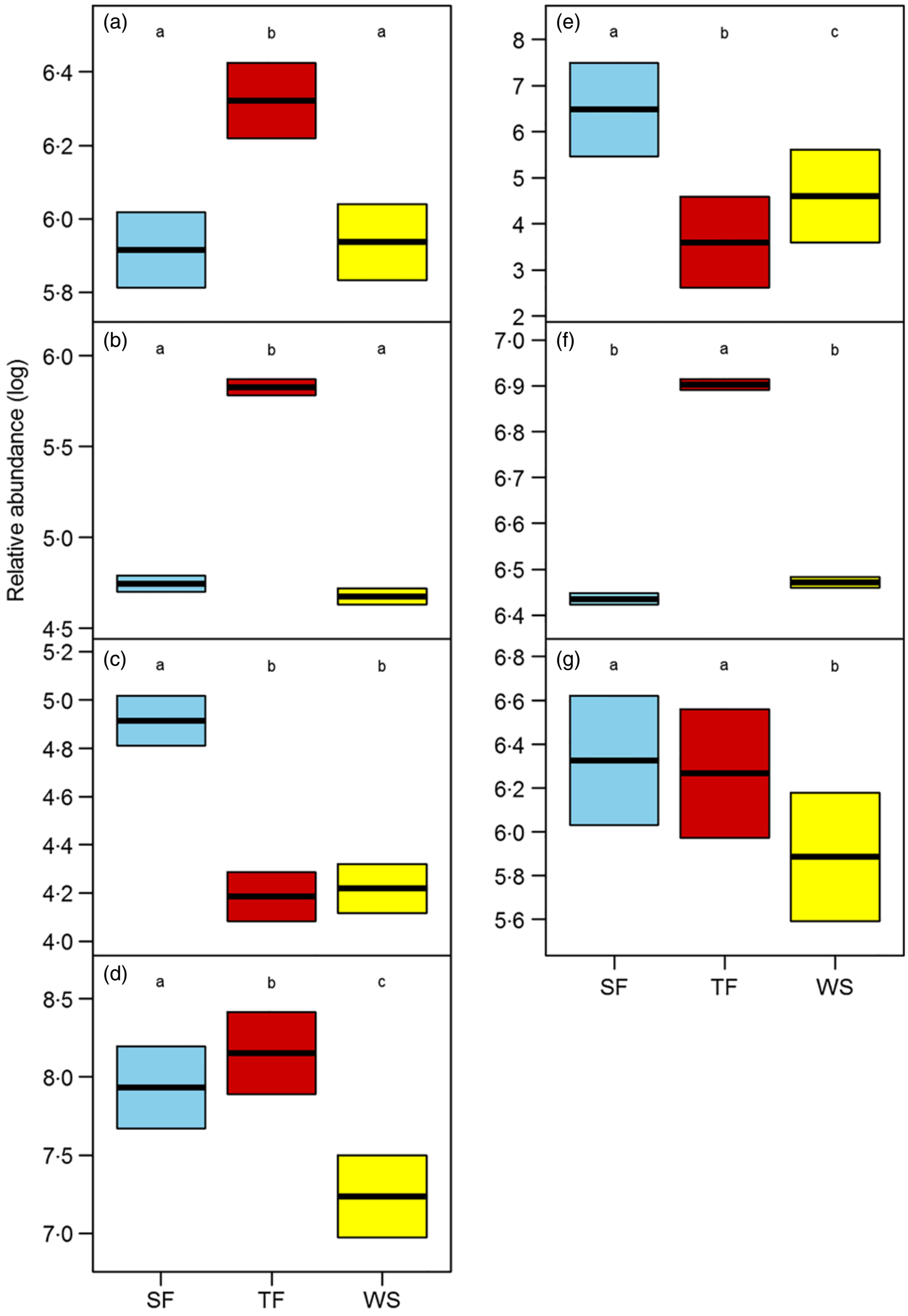

Fig. 4. Relative abundances of arthropod functional groups differ among contrasted types of habitats (TF = *terra firme* clay forest, SF = seasonally flooded forest, WS = white-sand forest). (a) Sap-sucker; (b) leaf-feeder; (c) wood–fungi feeder; (d) mixed beetle; (e) aquatic beetle; (f) hemipteran predator (+Araneae) and (g) insect predator and parasitoid. Different letters indicate significant differences in mean abundance among habitats at $P < 0{\cdot}05$.

and sap suckers), mixed beetles and insect predators showed a higher abundance of individuals in TF than in both SF and WS forests. Wood–fungi feeders and aquatic insects were most abundant in SF forests.

Variance partitioning showed that geographical distance and environmental dissimilarity among plots also explained most of the variation in arthropod community functional composition (Table 2). However, functional composition was much more clearly linked to environmental effects than to geographical distance. Geographical distance (controlling for environment) explained only 26% of the variation in community functional composition, whereas environmental distance (controlling for geography) explained 43% of variation in arthropod community functional composition.

Discussion

HABITAT FILTERING SHAPES ARTHROPOD TAXONOMIC COMPOSITION

In our study, arthropod community composition varied markedly across contrasting tropical forest habitats. This strong pattern of turnover among habitat types is concordant with the few previous studies of arthropod community composition in tropical forests (Smith, Hallwachs & Janzen 2014). For instance, Novotny *et al.* (2005) found a high turnover in caterpillars associated with the host plant genus *Ficus* along altitudinal gradients. Rodriguez-Castañeda *et al.* (2010) also found high beta diversity in both plant and insect communities across a tropical montane gradient in four distinct elevation zones (see also Smith, Hallwachs & Janzen 2014 for ants). Our study therefore confirms that marked shifts in environmental conditions can strongly influence spatial patterns in arthropod communities, here in lowland Neotropical forests. We sampled a limited number of sites as comprehensively as possible. Nevertheless, our statistical approach allowed us to compare the relative contributions of geography and environment in shaping arthropod community composition, which were relatively equal and explained most of variation (Table 2).

The low overlap in overall arthropod composition between highly contrasted forest habitats may be driven by differences in habitat structure, changes in host plant species richness and composition and host plant functional traits. The three forest habitats we studied differ markedly in forest structure and soil texture and fertility (Baraloto *et al.* 2011), with potential consequences for arthropod community composition. For instance, forests with less limiting mineral nutrients and a more rapid turnover of plant tissue (Lamarre *et al.* 2012a, 2014) support higher abundances of herbivorous insects and associated predators. A recent study showed that a single tree species may host different assemblages of insect herbivores in white-sand and *terra firme* sites and that this pattern might be directly linked to variations in soil nutrient availability (Fine *et al.* 2013). Because of higher resources and presumably greater niche partitioning (food, seasonality and space), we also found significant differences in cascading trophic level structure with higher abundances in high-resource habitats than low-resource habitats (e.g. white-sand forest). For example, rove beetles (Staphylinidae) had nearly five times more individuals in high-resource habitats (both SF and TF) than in white-sand forests (Appendix S1).

Previous studies have shown that plant species composition shows strong turnover among local communities (Tuomisto *et al.* 2003) and across different habitats types in the Amazon (Fine *et al.* 2010). Indeed, each habitat considered in our study harbours a unique floristic composition (Baraloto *et al.* 2007; Fine *et al.* 2010) that includes many habitat specialists (Lamarre *et al.* 2012a). Finally, we believe that host plant functional traits may be influencing herbivore community structure. Leaf traits promoting higher resource conservation are expected in low-resource habitats, whereas *terra firme* tree species are allocating, in turn, more resources into growth with higher specific leaf area and higher nutrient concentrations (Baraloto *et al.* 2010; Fortunel *et al.* 2014; Lamarre *et al.* 2014). We would therefore expect strong turnover in arthropod communities dependent on plant community composition, especially host-specialist herbivores (Novotny *et al.* 2006). In general, we found a high turnover of arthropod communities across forest communities with different floristic composition (Fine *et al.* 2010). For instance, leaf beetle (Chrysomelidae) and weevil (Curculionidae), which are the most diverse insect families, support, respectively, 2·7 and 2·1 more individuals in TF forests than in WS forests (Appendix S1). Furthermore, moth and butterfly communities also showed striking differences in abundance between habitat types with a clear dominance in high-resource habitats (for Nymphalidae, Notodontidae, Saturniidae, Sphingidae and Noctuidae).

ARTHROPOD HABITAT ASSOCIATION

Most arthropod families in both regions showed striking differences in their relative abundances among the three studied habitats. In particular, we found strong differences in arthropod composition between seasonally flooded forests and the two other forest habitats (Fig. 2). In particular, the ground beetle family (Carabidae) exhibited 4·3 more individuals in SF than in TF forests (Appendix S1). Seasonally flooded forests exhibited a convergent effect on overall community composition that was remarkably similar in the two countries. A recent study found a high rate of treefall disturbances in French Guianan flooded forests, resulting in a more rapid forest turnover than in *terra firme* forests (Ferry *et al.* 2010). We speculate that the more rapid forest dynamics in flooded forests may increase resources available for specific feeding guilds such as predators. Disturbance caused by water-table fluctuation in seasonally flooded forests is likely to influence arthropod community composition (Ellis *et al.* 2001; Baccaro *et al.* 2013). Additional explanations to the trend observed may lie in physiological stressors among host plant assemblages subjected to regular flooding regimes that may drive herbivore and associated higher trophic level in lowland tropical forests.

TOWARDS A FUNCTIONAL CLASSIFICATION OF TROPICAL ARTHROPODS

Several authors first described the guild concept for arthropods based on feeding strategy (Morán & Southwood 1982). As a novel application to the feeding guild approach, we propose a functional composition approach based on feeding, habitat and mouthpart traits that are inherent to each arthropod family. Although we recognize that the functional traits assigned in our study (e.g. at the family level) may be a simplistic representation of insect ecological niches, we believe this is a novel approach that may help investigating arthropod community patterns. Based on trait-based similarity, each of the 147 taxa was classified and grouped into seven functional groups. The visual inspection of the silhouette plot, a graphical aid for validation of cluster analysis, showed high consistency of affiliation for each taxon within each functional group (Appendix S2). Such a functional tree can be considered as a first step towards describing more accurately the roles of arthropods in ecosystem functioning. For instance, the functional clustering obtained from our data set highlights that Coleoptera (in green), one of the most diverse groups of arthropods, comprise taxa with highly contrasting functional roles in lowland tropical forests. We believe that a refined approach to functional characterizations (Flynn *et al.* 2009; Moretti *et al.* 2009), in concert with phylogenetic data (Smith, Hallwachs & Janzen 2014; Lamarre *et al.* in press), will allow enhancing and generalizing this functional approach for future studies of arthropods.

CONTRASTING FUNCTIONAL COMPOSITION ACROSS LOWLAND TROPICAL FORESTS

Overall, our functional approach using simple functional and ecological traits at the family level reveals strong patterns of dissimilarity in functional structure among arthropod communities collected in *terra firme*, flooded forest and white-sand forest plots (Fig. 4). Environmental filtering should translate taxonomic turnover into functional turnover across these steep habitat gradients (e.g. low functional redundancy, see Flynn *et al.* 2009; but see Villéger *et al.* 2012). In our study, we observed that taxonomic turnover was accompanied by marked changes in functional composition. Most of the functional groups showed greatest abundance in high-resource habitats compared to low-resource habitats (Fig. 4). This result is consistent with previous studies that have reported greater herbivory rates in high-resource habitats (Fine *et al.* 2006; Lamarre *et al.* 2014). For example, insects associated with wood and fungi resource uses are found to be more common in seasonally flooded forest, in which more forest dynamics, microclimate (e.g. moisture) and natural perturbation occur and are favourable for specific insect guilds. Our results are thus consistent with recent research conducted in some of the same forest sites that showed a significantly lower wood density in seasonally flooded plant specialists (Fortunel *et al.* 2014). The pattern found on functional Group 5 (see Fig. 3) would not have been detected unless using a functional approach (Group 5 includes 21 taxonomically distinct beetle families).

The strength of environmental filtering on functional community composition may be even stronger because we included white-sand forests that are characterized by vegetation with pronounced sclerophylly, low diversity and high endemism in plant species (Medina, Garcia & Cuevas 1990; Fine *et al.* 2010). We predicted that a unique assemblage of insect herbivores would be able to feed on the thicker and tougher leaves, for example the white-sand habitat specialists such as Delphacidae and Fulgoridae (Table 3). Our functional approach confirmed this generally as we found that functional composition in leaf-chewer and sap-sucker taxa clearly differed in relative abundance among the three contrasted habitats with a higher abundance in *terra firme* clay forest (Fig. 4 and Table 2). A high allocation to secondary compounds restricts the relative abundance of leaf and sap feeders, and these properties are more characteristic of white-sand forests (Coley, Bryant & Chapin 1985; Fine *et al.* 2006). Further investigations are needed on the functions of different plant tissues (resource conservation and/or defence) that would allow us to test whether plant functional trade-offs are directly influencing arthropod functional community structure in tropical forests. We envision a bottom-up model by which herbivore species and associated natural enemies are filtered among habitat types based on shifts in host plant community functional composition correlated with environmental changes.

PARTITIONING EFFECTS ON ARTHROPOD COMMUNITY COMPOSITION

The NMDS ordination clearly suggests that arthropod taxonomic assemblages are partitioned in two regions, Loreto, Peru, and French Guiana, representing distinct biogeographical regions that differ in geological and edaphic histories in addition to highly contrasted rainfall seasonality (Hoorn *et al.* 2010). The considerable turnover found between countries is also consistent with the results of the generalized linear model in which we found that nearly 47% of the arthropod taxonomic groups (69 out of 147) differed significantly in their abundance between French Guiana and Peru (Appendix S1). We believe this pattern is particularly evident because of the contrast in soil profiles at both ends of the Amazon that are expected to influence both host plant and associated arthropod community composition (Radtke, da Fonseca & Williamson 2007; Lamarre *et al.* in press). In our study, we attempt to quantify the degree to which the effect of environment and geography explain the variation in community composition using both taxonomic and functional approaches (Table 2). Our results showed that the variation in community taxonomic composition is explained by both geography and the environment while community functional composition is chiefly explained by the effect of environment. Very few studies have disentangled the relative contribution of biogeographical processes driving community composition in tropical arthropods, and the study of several additional sites would be required to understand general patterns of biogeographical processes driving arthropod composition. This result is rather interesting as the strong turnover found between French Guiana and Peru may be explained by the Amazonian rivers and Guiana shield that act as a major barrier to dispersal (Wallace 1852). Furthermore, the variation in community functional composition is largely driven by the environment (43% of the variance explained), a pattern consistent with the greatest abundance of functional groups found in high-resource habitats (Fig. 4). This finding reinforces the idea that habitat filtering is shaping functional attributes in arthropod assemblages that allow a species to persist (or not) in a given habitat and confirms the importance to attempt arthropod functional classification across contrasting tropical rain forests.

CONCLUSION

Our broad sampling approach in concert with the first attempt of arthropod functional classification reveals the importance of environmental filtering and biogeographical processes in shaping patterns of arthropod community assembly in lowland Amazonian forests. Multiple taxonomic groups share similar functions in these forests, and functional groups have markedly different abundances across habitat gradients. Nevertheless, we recommend more detailed taxonomic information in such broad surveys across multiple sites and for refined descriptions of important functional traits across arthropod groups. We believe this will require improved collaborations between taxonomists and ecologists. Further coordinated study will be necessary to examine the consistency of patterns we observed by combining mass sampling, metabarcoding and host specialization approaches across multiple habitats throughout tropical regions that differ in seasonality and geological history. Then, we will be able to more precisely disentangle biogeographical processes and environmental determinants that drive regional patterns of arthropod diversity across tropical forests.

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Data accessibility

All data for relative abundance of the taxonomic groups in each habitat are listed in Appendix S1. Data are available from the Dryad Digital Repository http://dx.doi.org/10.5061/dryad.mv60m (Lamarre *et al.* 2015).

References

Baccaro, F.B., Rocha, I.F., del Aguila, B.E.G., Schietti, J., Emilio, T., Pinto, J.L.P.D.V. *et al.* (2013) Changes in Ground-dwelling Ant Functional Diversity are Correlated with Water-Table Level in an Amazonian *Terra Firme* Forest. *Biotropica*, **45**, 755–763.

Baraloto, C., Morneau, F., Bonal, D., Blanc, L. & Ferry, B. (2007) Seasonal water stress tolerance and habitat associations within four Neotropical tree genera. *Ecology*, **88**, 478–489.

Baraloto, C., Paine, C.E., Poorter, L., Beauchene, J., Bonal, D., Domenach, A.M. *et al.* (2010) Decoupled leaf and stem economics in rain forest trees. *Ecology letters*, **13**, 1338–1347.

Baraloto, C., Rabaud, S., Molto, Q., Blanc, L., Fortunel, C., Herault, B. *et al.* (2011) Disentangling stand and environmental correlates of aboveground biomass in Amazonian forests. *Global Change Biology*, **17**, 2677–2688.

Baraloto, C., Hérault, B., Paine, C.E.T., Massot, H., Blanc, L., Molino, J.F. *et al.* (2012) Contrasting taxonomic and functional responses of a tropical tree community to selective logging. *Journal of Applied Ecology*, **49**, 861–870.

Basset, Y., Cizek, L., Cuénoud, P., Didham, R.K., Guilhaumon, F., Missa, O. *et al.* (2012) Arthropod diversity in a tropical forest. *Science*, **338**, 1481–1484.

Browne, J. & Scholtz, C.H. (1999) A phylogeny of the families of Scarabaeoidea (Coleoptera). *Systematic Entomology*, **24**, 51–84.

Cadotte, M.W., Carscadden, K. & Mirotchnick, N. (2011) Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*, **48**, 1079–1087.

Cardoso, P., Pekar, S., Jocqué, R. & Coddington, J.A. (2011) Global patterns of guild composition and functional diversity of spiders. *PLoS ONE*, **6**, e21710.

Coley, P.D., Bryant, J.P. & Chapin, F.S.I.I.I. (1985) Resource availability and plant antiherbivore defense. *Science*, **230**, 895–899.

Condit, R., Pitman, N., Leigh, E.G. Jr, Chave, J., Terborgh, J., Foster, R.B., *et al.* (2002) Beta-diversity in tropical forest trees. *Science*, **295**, 666–669.

Delvare, G. & Aberlenc, H.P. (1989) *Les insectes d'Afrique et d'Amérique tropicale. Clés pour la reconnaissance des familles*. CIRAD-GERDAT, Montpellier, France.

DeVries, P.J., Alexander, L., Chacon, I.A. & Fordyce, J.A. (2012) Similarity and difference among rainforest fruit-feeding butterfly communities in Central and South America. *Journal of Animal Ecology*, **81**, 472–482.

Diaz, S. & Cabido, M. (2001) Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution*, **16**, 646–655.

Dufrene, M. & Legendre, P. (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, **67**, 345–366.

Dyer, L.A., Singer, M.S., Lill, J.T., Stireman, J.O., Gentry, G.L., Marquis, R.J. *et al.* (2007) Host specificity of Lepidoptera in tropical and temperate forests. *Nature*, **448**, 696–699.

Ellis, L.M., Crawford, C.S. & Molles, M.C. Jr (2001) Influence of annual flooding on terrestrial arthropod assemblages of a Rio Grande riparian forest. *Regulated Rivers: Research & Management*, **17**, 1–20.

Erwin, T.L. (1982) Tropical forests, their richness in Coleoptera and other arthropod species. *The Coleopterists Bulletin*, **36**, 74–75.

Everitt, B.S., Landau, S., Leese, M. & Stahl, D. (2011) *Cluster Analysis*, 5th edn. John Wiley & Sons, Chichester, UK.

Ferry, B., Morneau, F., Bontemps, J.D., Blanc, L. & Freycon, V. (2010) Higher tree fall rates on slopes and waterlogged soils result in lower stand biomass and productivity in a tropical rain forest. *Journal of Ecology*, **98**, 106–116.

Fine, P.V.A., Mesones, I. & Coley, P.D. (2004) Herbivores promote habitat specialization by trees in Amazonian forests. *Science*, **305**, 663–665.

Fine, P.V.A., Miller, Z.J., Mesones, I., Irazuzta, S., Appel, H.M., Stevens, M.H.H. *et al.* (2006) The growth defense trade-off and habitat specialization by plants in Amazonian forests. *Ecology*, **87**, S150–S162.

Fine, P.V.A., Garcia-Villacorta, R., Pitman, N., Mesones, I. & Kembel, S.W. (2010) A floristic study of the white sand forests of Peru. *Annals of the Missouri Botanical Garden*, **97**, 283–305.

Fine, P.V.A., Metz, M.R., Lokvam, J., Mesones, I., Zuniga, J.M.A., Lamarre, G.P.A. *et al.* (2013) Insect herbivores, chemical innovation, and the evolution of habitat specialization in Amazonian trees. *Ecology*, **94**, 1764–1775.

Flynn, D.F.B., Gogol-Prokurat, M., Nogeire, T., Moliinari, N., Richers, B.T., Lin, B.B. *et al.* (2009) Loss of functional diversity under land use intensification across multiple taxa. *Ecology Letters*, **12**, 22–33.

Fortunel, C., Paine, C.E.T., Fine, P.V.A., Kraft, N.J.B. & Baraloto, C. (2014) Environmental factors predict community functional composition in Amazonian forests. *Journal of Ecology*, **102**, 145–155.

Gauld, I. & Bolton, B. (1988) *The Hymenoptera*. Oxford University Press, Oxford, UK.

Gower, J.C. (1966) Some distance properties of latent root and vector methods used in multivariate analysis. *Biometrika*, **53**, 325–333.

Hamilton, A.J., Basset, Y., Benke, K.K., Grimbacher, P.S., Miller, S.E., Novotny, V. *et al.* (2011) Quantifying uncertainty estimation of tropical arthropod species richness. *The American Naturalist*, **176**, 90–95.

Holm, S. (1979) A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics*, **6**, 65–70.

Hoorn, C., Wesselingh, F.P., ter Steege, H., Bermudez, M.A., Mora, A., Sevink, J. *et al.* (2010) Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. *Science*, **330**, 927–931.

Kelley, L.A., Gardner, S.P. & Sutcliffe, M.J. (1996) An automated approach for clustering an ensemble of NMR-derived protein structures into conformationally-related subfamilies. *Protein Engineering*, **9**, 1063–1065.

Labandeira, C.C. (1997) Insect mouthparts: ascertaining the paleobiology of insect feeding strategies. *Annual Review of Ecology and Systematics*, **28**, 153–193.

Lamarre, G.P.A., Baraloto, C., Fortunel, C., Davila Cardozo, N., Mesones, I., Grandez Rios, J. *et al.* (2012a) Herbivory, growth strategies and habitat specialization in tropical tree lineages: implications for Amazonian beta-diversity. *Ecology*, **93**, S195–S210.

Lamarre, G.P.A., Molto, Q., Fine, P.V.A. & Baraloto, C. (2012b) A comparison of common flight interception traps to survey tropical arthropods. *ZooKeys*, **216**, 43–55.

Lamarre, G.P.A., Mendoza, I., Fine, P.V.A. & Baraloto, C. (2014) Leaf synchrony and insect herbivory among tropical tree habitat specialists. *Plant Ecology*, **215**, 209–220.

Lamarre, G.P.A., Hérault, B., Fine, P.V.A., Vedel, V., Lupoli, R., Mesones, I. *et al.* (2015) Data from: Taxonomic and functional composition of arthropod assemblages across contrasting Amazonian forests. *Dryad Digital Repository*, http://dx.doi.org/10.5061/dryad.mv60m.

Lamarre, G.P.A., Salazar Amoretti, D., Baraloto, C., Bénéluz, F., Mesones, I. & Fine, P.V.A. (in press) Phylogenetic overdispersion in Lepidoptera communities of Amazonian white-sand forests. *Biotropica*.

Lavorel, S., Storkey, J., Bardgett, R.D., de Bello, F., Berg, M.P., Le Roux, X. *et al.* (2013) A novel framework for linking functional diversity of plants with other trophic levels for the quantification of ecosystem services. *Journal of Vegetation Science*, **24**, 942–948.

Lawrence, J.F., Hastings, A.M., Dallwitz, M.J., Paine, T.A. & Zurcher, E.J. (1999) *Beetles of the World: Key and Information System for Families and Subfamilies*. CSIRO, Collingwood, Canada.

Legendre, P., Borcard, D. & Peres-Neto, P.R. (2005) Analyzing beta diversity: partitioning the spatial variation of community composition data. *Ecological Monographs*, **75**, 435–450.

Marengo, J.A. (1998) Climatología de la zona de Iquitos, Perú. *Geoecología y desarrollo amazónico: Estudio integrado de la zona de Iquitos, Perú*, (eds R. Kalliola & S.P. Flores), pp. 35–57. Annales Universitatis Turkensis Ser A II. Turun Yliopisto, Turku.

May, R.M. (2010) Tropical Arthropod species, more or less? *Science*, **329**, 41–42.

Medina, E., Garcia, V. & Cuevas, E. (1990) Sclerophylly and oligotrophic environments: relationships between leaf structure, mineral nutrient content, and drought resistance in tropical rain forests of the upper Rio Negro region. *Biotropica*, **22**, 51–64.

Morán, V.C. & Southwood, T.R.E. (1982) The guild composition of arthropods communities in trees. *Journal of Animal Ecology*, **51**, 289–306.

Moretti, M., de Bello, F., Roberts, S.P.M. & Potts, S.G. (2009) Taxonomical vs. functional responses of bee communities to fire in two contrasting climatic regions. *Journal of Animal Ecology*, **78**, 98–108.

Novotny, V., Basset, Y., Miller, S.E., Weiblen, G.D., Bremer, B., Cizek, L. *et al.* (2002) Low host specificity of herbivorous insects in a tropical forest. *Nature*, **416**, 841–844.

Novotny, V., Miller, S.E., Basset, Y., Cizek, L., Darrow, K., Kaupa, B. *et al.* (2005) An altitudinal comparison of caterpillar (Lepidoptera) assemblages on *Ficus* trees in Papua New Guinea. *Journal of Biogeography*, **32**, 1303–1314.

Novotny, V., Drozd, P., Miller, S.E., Kulfan, M., Janda, M., Basset, Y. *et al.* (2006) Why are there so many species of herbivorous insects in tropical rainforests? *Science*, **313**, 1115–1118.

Novotny, V., Miller, S.E., Hulcr, J., Drew, R.A.I., Basset, Y., Janda, M. *et al.* (2007) Low beta diversity of herbivorous insects in tropical forests. *Nature*, **448**, 692–695.

Ødegaard, F. (2004) Species richness of phytophagous beetles in the tropical tree *Brosimum utile* (Moraceae): the effects of sampling strategy and the problem of tourists. *Ecological Entomology*, **29**, 76–88.

Ødegaard, F., Diserud, O.H. & Ostbye, K. (2005) The importance of plant relatedness for host utilization among phytophagous insects. *Ecology Letters*, **8**, 612–617.

Ødegaard, F., Diserud, O.H., Engen, S. & Aagaard, K. (2000) The magnitude of local host specificity for phytophagous insects and its implications for estimates of global species richness. *Conservation Biology*, **14**, 1182–1186.

Price, P.W. (2002) Resource-driven terrestrial interaction webs. *Ecological Research*, **17**, 241–247.

R Development Core & Team. (2013) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.

Radtke, M.G., da Fonseca, C.R.V. & Williamson, G.B. (2007) The old and young Amazon: Dung beetle biomass, abundance, and species. *Biotropica*, **39**, 725–730.

Rodriguez-Castañeda, G., Dyer, L.A., Brehm, G., Connahs, H., Forkner, R.E. & Walla, T.R. (2010) Tropical forests are not flat: how mountains affect herbivore diversity. *Ecology Letters*, **13**, 1348–1357.

Rousseeuw, P.J. (1987) Silhouettes: a graphical aid to the interpretation and validation of cluster analysis. *Computational & Applied Mathematics*, **20**, 53–65.

Smith, A.M., Hallwachs, W. & Janzen, D.H. (2014) Diversity and phylogenetic community structure of ants along a Costa Rican elevational gradient. *Ecography*, **37**, 720–731.

Sobek, S., Steffan-Dewenter, I., Scherber, C. & Tscharntke, T. (2009) Spatiotemporal changes of beetle communities across a tree diversity gradient. *Diversity and Distribution*, **15**, 660–670.

Thompson, J.N. & Cunningham, B.M. (2002) Geographic structure and dynamics of coevolutionary selection. *Nature*, **417**, 735–738.

Timms, L.L., Bowden, J.J., Summerville, K.S. & Buddle, C.M. (2013) Does species-level resolution matter? Taxonomic sufficiency in terrestrial arthropod biodiversity studies. *Insect Conservation and Diversity*, **6**, 453–462.

Tuomisto, H., Ruokolainen, K., Aguilar, M. & Sarmiento, A. (2003) Floristic patterns along a 43-km long transect in an Amazonian rain forest. *Journal of Ecology*, **91**, 743–756.

Vedel, V., Camus, D. & Lamarre, G.P.A. (2011) Malaise and glass traps: useful means of catching canopy-dwelling spiders? *Newsletter of the British Arachnology Society*, **122**, 12–15.

Villéger, S., Miranda, J.R., Hernandez, D.F. & Mouillot, D. (2012) Low functional b-diversity despite high taxonomic b-diversity among tropical estuarine fish communities. *PLoS ONE*, **7**, e40679.

Wagner, F., Hérault, B., Stahl, C., Bonal, D. & Rossi, V. (2011) Modeling water availability for trees in tropical forests. *Agricultural and Forest Meteorology*, **151**, 1202–1213.

Wallace, A.R. (1852) On the monkeys of the Amazon. *Proceedings Zoological Society of London*, **20**, 107–110.

Wittmann, F., Schöngart, J. & Junk, W.J. (2010) Phytogeography, species diversity, community structure and dynamics of Central Amazonian floodplain forests. *Amazonian Floodplain Forests: Ecophysiology, Biodiversity and Sustainable Management* (eds W.J. Junk, M.T.F. Piedade, P. Parolin, F. Wittmann & J. Schöngart), pp. 57–97. Springer Verlarg, Heidelberg.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Arthropod taxonomic structure illustrated by the total abundance in each habitat and country.

Appendix S2. Silhouette plot showing the consistency of each arthropod taxon memberships into each of the seven arthropod functional clusters.

Appendix S3. Taxon-by-functional-trait matrix (supplementary data in an online Excel file)