BULLETIN DE L'INSTITUT ROYAL DES SCIENCES NATURELLES DE BELGIQUE

BULLETIN VAN HET KONINKLIJK BELGISCH INSTITUUT VOOR NATUURWETENSCHAPPEN

ENTOMOLOGIE
VOL. 77

BRUXELLES 2007 BRUSSEL

BULLETIN
DE L'INSTITUT ROYAL DES SCIENCES NATURELLES DE BELGIQUE
ENTOMOLOGIE

BULLETIN
VAN HET KONINKLIJK BELGISCH INSTITUUT VOOR NATUURWETENSCHAPPEN
ENTOMOLOGIE

Vol. 77 - 2007 ISSN 0374-6232

Publié, verschenen, *published*: 20.XII.2007

CONTENTS

IBISCA-Panama, a large-scale study of arthropod beta-diversity and vertical stratification in a lowland rainforest: rationale, study sites and field protocols

by Yves BASSET[1], Bruno CORBARA[2], Héctor BARRIOS[3], Philippe CUÉNOUD[4], Maurice LEPONCE[5], Henri-Pierre ABERLENC[6], Johannes BAIL[7], Darren BITO[8], Jonathan R. BRIDLE[9], Gabriela CASTAÑO-MENESES[10], Lukas CIZEK[11], Aydee CORNEJO[12], Gianfranco CURLETTI[13], Jacques H. C. DELABIE[14], Alain DEJEAN[15], Raphael K. DIDHAM[16], Marc DUFRÊNE[17], Laura L. FAGAN[18], Andreas FLOREN[19], Dawn M. FRAME[20], Francis HALLÉ[20], Olivier J. HARDY[21], Andrés HERNANDEZ[1], Roger L. KITCHING[8], Thomas M. LEWINSOHN[22], Owen T. LEWIS[23], Markus MANUMBOR[24], Enrique MEDIANERO[25], Olivier MISSA[26], Andrew W. MITCHELL[27], Martin MOGIA[24], Vojtech NOVOTNY[11, 24], Frode ØDEGAARD[28], Evandro Gama de OLIVEIRA[29], Jérôme ORIVEL[15], Claire M. P. OZANNE[30], Olivier PASCAL[31], Sara PINZÓN[32], Mathieu RAPP[12], Sérvio P. RIBEIRO[33], Yves ROISIN[21], Tomas ROSLIN[34], David W. ROUBIK[1], Mirna SAMANIEGO[1], Jürgen SCHMIDL[7], Line L. SØRENSEN[35], Alexey TISHECHKIN[36], Christian VAN OSSELAER[37] & Neville N. WINCHESTER[38]

Abstract

IBISCA-Panama ("Investigating the BIodiversity of Soil and Canopy Arthropods", Panama module) represents a large-scale research initiative to quantify the spatial distribution of arthropod biodiversity in a Neotropical forest, using a combination of (1) international collaboration, (2) a set of common research questions, and (3) an integrated experimental design. Here, we present the rationale of the programme, describe the study sites, and outline field protocols. In the San Lorenzo Protected Area of Panama, twelve 20 x 20 m sites, all less than 2 km apart, were surveyed for plants and arthropods, from the ground to the upper canopy. Access to the canopy and its fauna was facilitated by fogging, single-rope techniques and a variety of devices such as a canopy crane, the "SolVin-Bretzel" canopy raft, the canopy bubble and Ikos. IBISCA-Panama represented the first attempt to combine these complementary techniques of canopy access in a large-scale investigation. Such techniques provided spatial replication during initial field work performed in September-October 2003. Temporal replication across seasons consisted of subsequent field work of varying intensity during dry, early wet and late wet periods in 2004. Arthropods were surveyed using 14 different protocols targeting the soil, litter, understorey, mid-canopy and upper canopy habitats. These protocols included: Winkler sifting; Berlese-Tullgren; hand-collecting of galls and social insects; fogging; beating; wood-rearing; baits; and various types of traps such as pitfall, small and large flight-interception, sticky, light, and Malaise traps. Currently, analyses of arthropod distribution in this forest concentrate on a set of 63 focal taxa representing different phylogenies and life-histories. IBISCA-Panama may be considered as a model for large-scale research programmes targeting invertebrate biodiversity. Its collaborative *modus operandi* can be applied to answer a variety of pressing ecological questions related to forest biodiversity, as evidenced by the recent development of further IBISCA programmes in other parts of the world.

Key words: biodiversity, canopy, Panama, soil, tropical rainforests

Introduction

Without doubt, one of the fundamental questions in biology is "how many species are there on Earth"? Sadly, at the beginning of the 21st century, when most of the diverse ecosystems of our planet are increasingly threatened by widespread land-use modification, global climate change, pollution, biological invasions and over-harvesting (Sala *et al*., 2000), there is still no satisfactory answer to this basic question. A related, equally vital, but perhaps methodologically more tractable investigation is to assess where the greater part of this biodiversity is located. Understanding the distribution and ecology of species is also crucial to study the relationship between biodiversity and ecosystem function. By far the greatest fraction of terrestrial animal diversity is made up of arthropods. In recent years, there has been considerable debate as to whether or not most of arthropod biodiversity occurs either in the soil or in the canopy of tropical rainforests (Erwin, 1982; Stork, 1988; May, 1990). This issue lies at the heart of wildly varying, and hence hugely contentious, global estimates of arthropod species richness derived from surveys of arboreal arthropods on particular host-trees (Erwin, 1982; May, 1990, Ødegaard, 2000). Erwin (1982) contended that the canopy fauna was the most species-rich. Later, other authors championed the

opposing point of view, that the soil fauna was actually more species-rich (Hammond, 1990, 1995; André *et al*., 1992; Hammond *et al*., 1997; Walter *et al*., 1998). As yet, however, no data have been collected that are extensive enough to test this contention in a convincing manner, due principally to a lack of spatial replication and a restricted taxonomic focus.

There have been three previous attempts at a small-scale, restricted comparison of arthropod species richness in the soil-litter layer versus the canopy layer of a tropical rainforest that are worth mentioning. In the Brazilian Amazon, Adis & Schubart (1984) compared the fauna of different vertical strata with several techniques, but they focused primarily on estimates of the abundance and biomass of arthropod taxa, as opposed to species diversity. Similarly, in a 1-ha sampling plot in Seram, Stork (1988, 1996) compared the abundance and biomass of arthropods extracted from the soil and litter using Tullgren funnels, with those collected from the forest canopy using insecticide knockdown ('fogging'). Both studies focused on abundance and biomass, not on species richness and there was basically no spatial replication of sites. However, both studies indicated that most of the abundance and biomass of arthropods was concentrated in the soil, not in the canopy.

By contrast, the only study that has previously compared the diversity of ground versus canopy arthropod communities on a relatively large scale (accounting to some extent for seasonal variation) was performed in Sulawesi (Hammond, 1990; Hammond *et al*., 1997). This intensive sampling programme, utilizing multiple sampling methods, suggested that the soil-litter fauna was indeed richer than the canopy fauna, with perhaps as many as 70-80 % of species restricted to the soil-litter habitat (Hammond *et al*., 1997). Unfortunately, the study was restricted to beetles and there was little replication from which to allow a convincing extrapolation of these trends to tropical forests in general (see also Stork & Grimbacher, 2006, for a study targeting beetles with a single collecting method in Australia).

These pioneering studies have paved the way for more rigorous and intensive studies quantifying the spatial distribution of biodiversity by pointing out several impediments to clear interpretation of sampling data, and by highlighting possible strategies to circumvent them. First, although sampling arthropods in the soil-litter layer is far from easy (André *et al*., 2002), at least spatial replication and methodological 'repeatability' within this habitat are somewhat easier to achieve than in the canopy, where access and spatial patchiness of habitats is problematic. In fact, none of the studies indicated earlier have sampled canopy arthropods *in situ* with sufficient replication. Within the emerging discipline of canopy biology (Ozanne *et al*., 2003), the most challenging and rewarding scientific advances are likely to be made by studying the abundance, distribution and functional interactions among organisms *in situ*, within relatively undisturbed rainforest canopies (e.g. Lowman & Nadkarni, 1995; Stork *et al*., 1997; Linsenmair *et al*., 2001; Basset *et al*., 2003a, 2003b). Consequently, biodiversity studies (along with studies of atmospheric processes at the canopy interface) figure prominently on the global research agenda for canopy biology (Ozanne *et al*., 2003; Didham & Fagan, 2004). Although access *in situ* remains the main limitation, the range of available techniques to reach tree crowns is expanding (review in Mitchell *et al*., 2002) and now allows a freedom of spatial replication in the canopy that was previously unheard of.

Second, it is difficult to contrast ground and canopy arthropod faunas in a directly comparable way, since they are frequently (and sometimes unavoidably) sampled using different methods. For example, extremely high densities of springtails have been recorded in canopy habitats of certain tropical dry forests in Mexico (Palacios-Vargas *et al*., 1998), but how do these densities compare with springtail densities in the soil and litter? Habitat structure is very different and it might even be difficult to employ the same sampling method in a standardized fashion, making direct comparison of 'sample size' challenging. Two possible strategies to address this problem may be to standardize either to the number of individuals collected (species accumulation or rarefaction techniques), or to the volume of substrate or habitat sampled (or to the number of habitat units sampled). For the former strategy, see for example Lindo & Winchester (2006), comparing mite densities in ground and suspended soils of temperate rainforests.

Third, assessing the relative diversity of soil versus canopy arthropod communities evidently also depends on patterns of beta-diversity. Because of the relatively high specialization of insect herbivores on particular host-tree species (Novotny *et al*., 2002) and because of their associated specific predators and parasitoids, faunal turnover may be rather high in the canopy as compared to that in the soil. Thus, it may be inappropriate to compare the diversity of equivalent projected areas of canopy and soil, and extrapolate these to predicted estimates of global arthropod diversity. Monodominant stands aside, the beta-diversity of canopy communities may be higher than that of soil communities in tropical rainforests. For example, the beta-diversity (and "host

specificity") of soil mites is very low in Australia (Osler & Beattie, 2001). In temperate rainforests in Canada, Fagan *et al*. (2006) used experimental litter bags to control for microhabitat structure and resource quality, and found some evidence that while ground and canopy mite assemblages were similar in total biodiversity, it appeared that local mite richness (alpha diversity) was higher on the ground, whereas species turnover between sites (beta diversity) was higher in the canopy. Note, however, that at the appropriate (larger) spatial scale a correlation between below-ground and above-ground biodiversity may exist (Hooper *et al*., 2000). In particular, plant diversity, because of the production of diverse root exudates, can lead to increased diversity of mutualistic soil microflora, which represents the first link in a cascade of interactions resulting in increased diversity of other soil animals (Lavelle *et al*., 1995). These problems and interactions can be minimised and explored, respectively, by considering sampling protocols based on spatial replication among soil and canopy habitats at different sites.

Fourth, microarthropods such as mites are often dominant but underestimated in arboreal habitats (Walter & Behan-Pelletier, 1999), whereas they are relatively well sampled in soil and litter. Since Acari are diverse and numerically dominant in rainforest soils (Stork, 1988), comparison between the faunas of ground and canopy must ensure that mites have been well sampled in the latter. This, ideally, requires similar sampling procedures and samples obtained *in situ* in the canopy. However, this serves to illustrate the wider problem of the choice of focal taxa, since many groups of tropical arthropods have different ecological requirements and may be expected to follow different distributional patterns (Lawton *et al*., 1998). Hence, a multi-taxa approach is likely to be more powerful in drawing generalizations about the spatial distribution of biodiversity, than concentrating on a single taxon or a group of related taxa (see below).

Fifth, faunal comparisons rely on the taxonomic study of adult specimens, and immatures are rarely taken into account in biodiversity assessment, be they spiders or beetles. In these taxa, immatures may often develop near or in the soil, and then move up into the canopy as adults, and then feed and disperse from there (Hammond, 1990; Basset & Samuelson, 1996). Faunal comparisons are complicated in this case, but can be improved by evaluating differences among seasonal samples with emergence traps collecting the fauna that hatches and moves up from the soil (Pokon *et al*., 2005).

Finally, the massive scale of the sampling programmes necessary to address the aforementioned problems are likely to overwhelm investigators and saturate taxonomic experts with the sheer amount of material collected. Aside from the monumental logistical difficulties in handling the large numbers of specimens collected, the continuing crisis in biosystematics (Miller, 2000) makes the identification of described species, and the description of new species, collected in the soil or canopy an increasingly difficult task. For example, it took two weeks of field work for Stork (1991) to fog 15 Bornean trees, but more than a decade for him and his numerous collaborators to sort the collected material to morphospecies (unnamed species diagnosed by standard taxonomic procedures), without accounting for mites. Thus, one has to be extremely cautious about the expectations of mass collecting programmes and it is not realistic to expect that all the material collected will be studied in the foreseeable future. However, a careful selection of focal taxa (i.e., a multi-taxa approach), including different orders with differing life-history strategies, and a matching of taxa with motivated and committed investigators, may allow a robust test of whether spatial distribution patterns of diverse focal taxa converge or not. Subsidiary funding may also allow adequate storage of material residues that may be preserved for future studies.

Despite these obvious impediments, we believe that quantifying the spatial distribution of biodiversity in tropical rainforests and testing hypotheses about the origin and maintenance of this biodiversity are of fundamentally greater interest than the rather esoteric goal of knowing the exact number of species on Earth. The distribution of biodiversity within forests and the functional interactions between ground and canopy arthropods are also of central importance to a deeper understanding of ecosystem dynamics and estimating levels of redundancy in ecosystem function, and, hence, are a vital key to forest management for sustainable use. However, wresting high quality data from tropical forests is a slow and painstaking business, taking (optimistically) decades of careful study if carried out by traditional, small research groups (Basset *et al*., 2003a). It is this apparent dilemma – the urgent need for high quality results contrasted with the essentially long-term nature of obtaining such results – which led to the development of the IBISCA-Panama programme. Here, we detail the goals of IBISCA-Panama, provide descriptions of the study sites and techniques of canopy access, and outline the arthropod sampling protocols aimed at rigorously quantifying, for the first time, the spatial distribution of biodiversity in a lowland tropical rainforest. This paper is primarily intended to serve as

reference framework for future collective and individual contributions related to IBISCA-Panama.

1. Aims of IBISCA-Panama

IBISCA-Panama is a research programme that aims to quantify the degree of beta-diversity and vertical stratification of arthropods in a lowland tropical rainforest. The programme is based on a combination of (1) international collaboration including ecologists, taxonomists, students and parataxonomists; (2) a set of common research questions; and (3) an integrated experimental design. The large-scale approach is unusual in tropical biodiversity studies and includes complementary techniques of canopy access, diverse arthropod sampling protocols, a large number of focal taxa (a multi-taxa approach), substantial spatial and temporal replication, large numbers of experts working simultaneously in the field, as well as large numbers of taxonomic specialists studying the material collected and analyzing the associated distribution data. As such, IBISCA-Panama is an original attempt to overcome the severe impediments on measuring the distribution of tropical biodiversity, mentioned above. Field work was performed at 12 sites in a Panamanian rainforest, using 14 arthropod sampling protocols. Many of those methods allowed direct, comparative assessment of arthropod vertical stratification.

The key questions targeted by IBISCA-Panama are: (1) what is the relative contribution of vertical stratification, seasonality and degree of beta-diversity to the distribution of arthropod biodiversity in a closed-canopy tropical rainforest? and (2) how do life history traits of species, such as host specificity or feeding guild, influence the spatial and temporal partitioning of arthropod biodiversity in a closed-canopy tropical rainforest? To this end, one leading approach to consider is to partition diversity into its spatial and temporal components (Veech et al., 2002): total diversity consists of alpha diversity (within-sample units), horizontal beta-diversity, vertical beta-diversity and seasonal beta-diversity. The interaction between horizontal and vertical beta-diversity is of special interest. For the purposes of defining the arthropod entities among which to partition components of diversity, we consider three major spatio-temporal 'axes' of interest: (a) spatial turnover among sites, (b) vertical stratification (i.e., vertical turnover), and (c) temporal variation among repeated sampling intervals through time. Our aims are to contrast these biotic gradients in relation to potential ecological variables that might be driving the spatial gradients, rather than simply within arbitrary spatial categories. The most important of these environmental variables include: differences in floristic composition, tree basal area, or spatial heterogeneity in vegetation structure between sites (for spatial turnover among sites); light, canopy openness or leaf area index (for vertical stratification); and rainfall, temperature or tree phenology (for temporal variation). We attempt to predict arthropod distribution patterns from this set of variables measured at each site. Progress towards these aims has been updated periodically, as far as is possible, in published progress reports from IBISCA-Panama (Roslin, 2003; Bradbury, 2003; Didham & Fagan, 2003; Longino, 2004; Springate & Basset, 2004; Schmidl & Corbara, 2005; Pennisi, 2005; Corbara *et al*., 2006) and news bulletins are available at www.ibisca.net.

2. Study area and study sites

2.1. Study area (Plate 1)

The field sampling component of IBISCA-Panama took place in the San Lorenzo Protected Area (SLPA, Colón Province, Republic of Panama), which is situated on the Atlantic side of the Isthmus of Panama, between Lake Gatun and the Caribbean Sea, near sea level. This location was chosen because of (a) the presence of the Smithsonian Tropical Research Institute (STRI) canopy crane, which facilitated access to the forest canopy, in a track of little disturbed, though accessible forest; (b) the proximity of a STRI field station with essential laboratory facilities (Barro Colorado Island); and (c) its placement in the middle of the Mesoamerican Biological Corridor "hotspot", which is known to harbour relatively high levels of biodiversity (Weaver & Bauer, 2004).

This lowland wet forest is situated on a geological formation known as the Chagres sandstone, dating from the late Miocene/early Pliocene (Pyke *et al*., 2001). This location averages 3139 mm annual rainfall and an annual average air temperature of 26.0ºC (1998-2002 data). The climate is wet all year round, with a somewhat drier season between January and mid-April (average length of dry season = 125 days: Chave *et al*., 2004). Rainfall and temperature data during the field study periods (from September 2003 to November 2004) are summarized in Fig. 1. The forest is evergreen, with less than 3 % loss in canopy cover by the end of the dry season (Condit *et al*., 2000, 2004). The SLPA has been mostly free of severe disturbance for the past 150 years except for a few isolated spots. As an indication of this, individuals of slow growing tree-species such as

Brosimum utile (Kunth) Oken ex J. Presl var. *utile* have attained a large size.

The canopy crane stands in a six-hectare plot where all 21911 trees with a bole size of 10 mm in diameter at breast height (dbh) or greater have been identified (238 species), measured and mapped. Structurally, the forest can be characterized as having an average of 3676 stems per ha and a total basal area of almost 32 m^2 per ha with the tallest trees reaching 45 m in height. Liana abundance amounts to 2222 individuals and 0.776 m^2 basal area per ha (≥ 0.5 cm diameter; Schnitzer, 2005). At least 103 epiphyte species are present within the crane perimeter (Zotz, 2004) and 119 liana and vine species have been recorded from the 6 ha plot (S.J. Wright, unpublished data). The most common plant species include *Tovomita longifolia* (Rich.) Hochr., *Protium panamense* (Rose) I.M. Johnst., *Tachigali versicolor* Standl. & L.O. Williams and *Psychotria suerrensis* Donn. Sm. in the understorey; and *Brosimum utile* var. *utile, Aspidosperma spruceanum* Benth. ex Müll. Arg., *Manilkara bidentata* (A. DC.) A. Chev. and *Tapirira guianensis* Aubl. in the canopy.

The arthropod fauna of Panama is relatively well known, owing to many surveys and studies performed at Barro Colorado Island (BCI; Quintero & Aiello, 1992). Since BCI is ca. 25 km distant of the San Lorenzo forest, we can expect some similarities in the fauna of these two locations, although San Lorenzo is wetter than BCI. Besides taxonomic and ecological studies listed in Quintero and Aiello (1992) and earlier references collated therein, which may be relevant to the arthropod fauna of San Lorenzo, a number of ecological studies have also been performed within the San Lorenzo forest. This trend has accelerated since the installation of the STRI canopy crane in 1997. In particular, recent studies focused on leaf miners and galling insects (Barrios & Medianero, 1999; Medianero *et al*., 2003); chrysomelids and other phytophagous beetles (Ødegaard, 2003 [relevant checklist], 2006; Charles & Basset, 2005; Ødegaard *et al*., 2005; Ødegaard & Frame, 2007); bees (Zayed *et al*., 2003; Wcislo *et al*., 2004); leaf-cutting ants (Villelsen *et al*., 2002; Geraldo *et al*., 2004: Kweskin, 2004) and insect assemblages feeding on particular plants (Basset, 2001; Schowalter & Ganio, 2003; Ødegaard, 2004). To this growing list, we can add some of the references listed in Section 4 of the present article and numerous manuscripts in preparation, all resulting from IBISCA-Panama

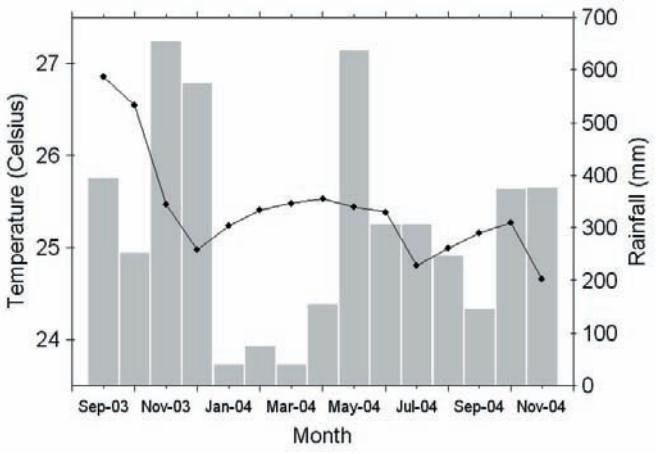

Fig. 1 — Monthly rainfall (bars) and average air temperature (line) for the study period (September 2003 to November 2004) at San Lorenzo (courtesy S. Paton, STRI).

2.2. Study sites

Overview

The IBISCA-Panama sampling protocols focused on 12 study sites, each 20 x 20 m in area. This 400 m^2 ground surface area was chosen to match the projected area of the canopy raft that would be sitting on the forest canopy (see Section 3). The 12 sites were situated in the surroundings of the STRI canopy crane (alt. 130m), on the top of a rather convex hill that slopes down towards the banks of the Rio Chagres, with the exception of one site (R1), which was located in the floodplain. Sites were selected so as to best represent the variety of the forest environment, with the distance between the most remote sites being less than 2 km (Table 1 and Fig. 2). To calculate distances between sites, geographic coordinates were converted to Cartesian coordinates by taking the relationship that 1° latitude = 2 x pi x r / 360 and 1° longitude = cos(lat) = 2 x pi x r / 360, with r = 6372.8 km (mean earth radius) and lat = 9°16.771 (average latitude of sites). Distances were then calculated using Pythagoras´ theorem (Table 1).

Sites were coded according to how the canopy was locally accessed (see Section 3, canopy access). Three "crane sites" (C1, C2 & C3) were located inside the crane perimeter. Two "bubble sites" (B1 & B2) were situated on either sides of the access road, ca. 1.5 km from the canopy crane. One "Ikos site" (I1), hosting the Ikos tree-house, was situated on a ridge not far from sites R2 and R3. Three "raft sites" (R1, R2 & R3) were far apart, with R1 located in the plain that borders Rio

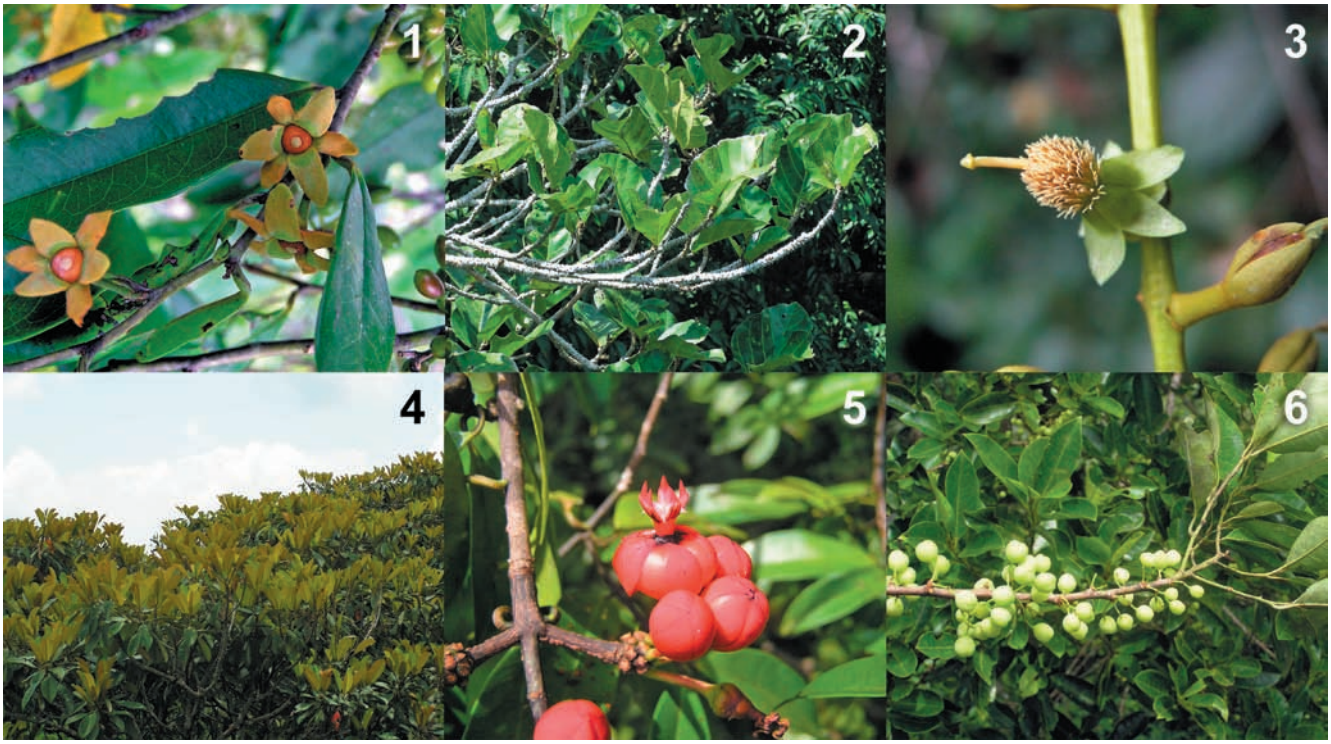

Plate 1 — [**A**] A selection of six plant species often encountered in the San Lorenzo forest, photographed from the canopy crane. (1) *Guatteria dumetorum* (Annonaceae), flowers and fruits; (2) branches of *Poulsenia armata* (Miq.) Standl. (Moraceae); (3) *Marila laxiflora* (Clusiaceae), flower; (4) tree crown of a large *Manilkara bidentata* (Sapotaceae); (5) *Symphonia globulifera* L. f. (Clusiaceae), flowers; (6) *Pera arborea* (Euphorbiaceae), branch with fruits. All photos by PC.

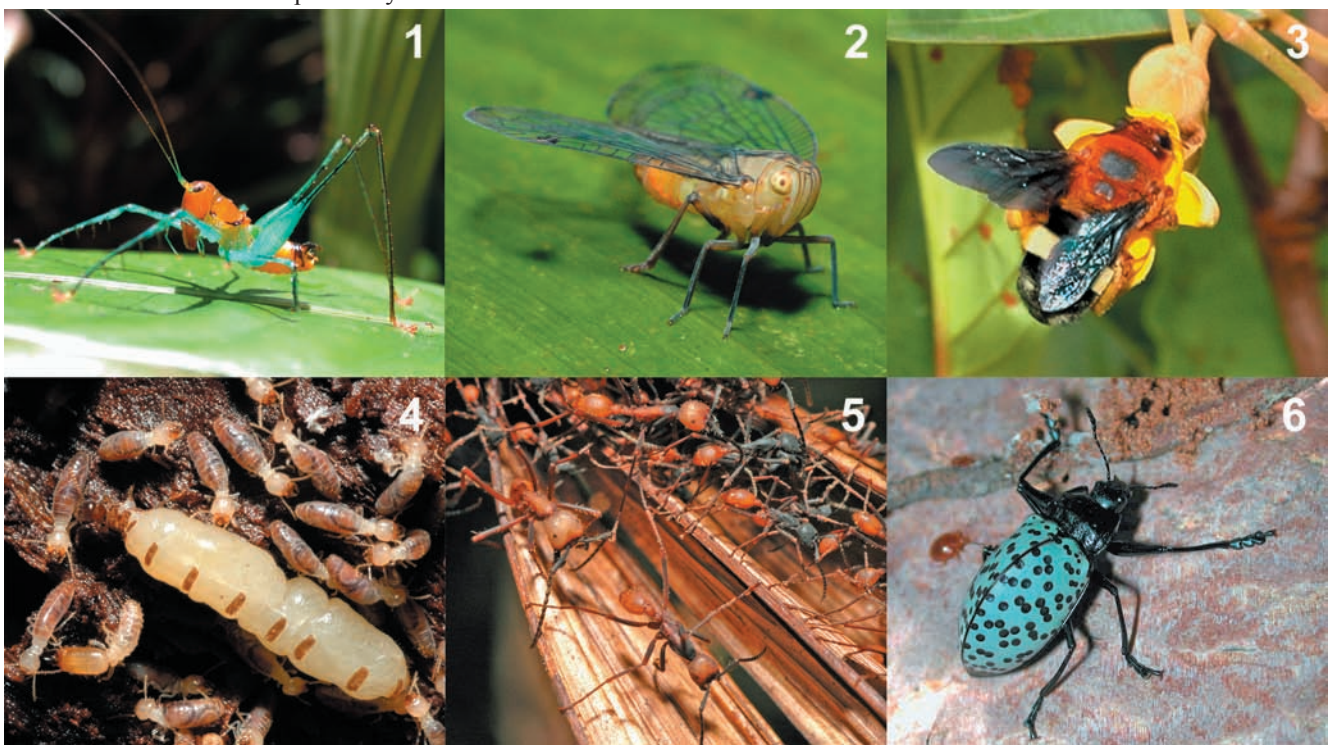

Plate 1 — [**B**] Insects from the San Lorenzo forest, representatives of various orders and feeding guilds. (1) *Arachnoscelis* sp. [Orthoptera Tettigoniidae, predator]; (2) *Biolleyana costalis* (Fowler) [Hemiptera Nogodinidae, sap-sucker]; (3) *Ptilotopus zonata* (Mocsáry) [Hymenoptera Apidae, pollinator], buzz-pollinating flowers of the canopy tree *Apeiba membranacea*; (4) *Cylindrotermes macrognathus* Snyder [Isoptera Termitidae, scavenger]; (5) *Eciton burchelli* Westwood [Hymenoptera Formicidae, predator]; (6) *Gibbifer impressopunctata* (Crotch) [Coleoptera Erotylidae, fungal-feeder]. Photos: ML (1-5), JS (6).

Table 1 — Geographic coordinates of the 12 IBISCA sites; lower matrix of geographic distances; Simpson index of diversity calculated for each site; number of species expected in a sample of 100 individuals, S(100); and lower matrix of floral similarity as calculated with NNESS(100) (see text for details).

Site code	Latitude (deg. N)	Longitude (deg. W)	Geographic distance between sites (m)									
				B1	**B2**	**C1**	**C2**	**C3**	**F1**	**F2**	**F3**	**I1**	**R1**	**R2**
B1	9°17.133	79°59.106	**B2**	338										
B2	9°17.146	79°59.290	**C1**	1303	1613									
C1	9°16.774	79°58.495	**C2**	1279	1592	36								
C2	9°16.793	79°58.499	**C3**	1342	1654	50	63							
C3	9°16.779	79°58.468	**F1**	1521	1750	653	683	683						
F1	9°16.453	79°58.642	**F2**	1548	1792	586	618	612	102					
F2	9°16.472	79°58.590	**F3**	1543	1789	564	596	589	122	24				
F3	9°16.482	79°58.582	**I1**	1644	1941	363	396	344	573	474	452			
I1	9°16.617	79°58.377	**R1**	1108	1426	1018	983	1014	1623	1579	1560	1338		
R1	9°17.322	79°58.533	**R2**	1592	1912	321	331	272	832	741	717	301	1097	
R2	9°16.769	79°58.320	**R3**	1415	1653	561	588	596	117	140	144	540	1512	771
R3	9°16.515	79°58.653												

NNESS(100) between sites

	Simpson	**S(100)**										
				B1	**B2**	**C1**	**C2**	**C3**	**F1**	**F2**	**F3**	**I1**	**R1**	**R2**
B1	0.855	35.67	**B2**	0.333										
B2	0.923	30.64	**C1**	0.416	0.397									
C1	0.985	59.03	**C2**	0.400	0.494	0.509								
C2	0.961	42.47	**C3**	0.329	0.528	0.624	0.586							
C3	0.973	44.26	**F1**	0.407	0.541	0.551	0.561	0.601						
F1	0.951	37.4	**F2**	0.419	0.500	0.486	0.622	0.602	0.699					
F2	0.930	37.91	**F3**	0.375	0.494	0.565	0.624	0.674	0.663	0.680				
F3	0.968	41.96	**I1**	0.439	0.494	0.554	0.619	0.604	0.543	0.638	0.599			
I1	0.977	52.33	**R1**	0.187	0.114	0.207	0.175	0.182	0.124	0.150	0.146	0.199		
R1	0.934	34.92	**R2**	0.395	0.515	0.426	0.570	0.575	0.534	0.566	0.620	0.593	0.061	
R2	0.961	37.47	**R3**	0.309	0.467	0.555	0.531	0.587	0.621	0.619	0.654	0.573	0.164	0.525
R3	0.930	35.8												

Chagres, at a lower elevation than the other sites, whilst R2 and R3 were located in the same area as sites I1 (and also the fogging sites F1-F3). Site R1 was surveyed with the canopy raft, whereas sites R2 and R3 were equipped with climbing ropes and the canopy accessed by single rope techniques. Finally, three "fogging sites" (see arthropod sampling, Section 4.3; F1, F2 & F3) were considered as "surrogate" sites for C1, C2 and C3, since fogging was not allowed within the crane perimeter.

In the following sections, the authors responsible for the botanical and arthropod protocols detailed in the text are identified by their initials in parentheses, and listed in alphabetical order.

Botanical description of sites (PC, FH, AH, OP & MS)

At all sites, plants >10 mm dbh were tagged and identified, and their dbh measured (including *Geonoma* palms, that remain small at adult age) before any arthropod collection. Appendix I details species abundance per site. Basal area was estimated by computing pi x $(dbh)^2$ / 4 for each tree and summing up the results for each site. A succession index was computed as the average of the specific fraction of recruits (sfr) in light gaps x number of conspecific individuals in each plot, where the sfr parameter was obtained from Welden et al. (1991), for available species (60 out of 165). Table 2 summarizes the main characteristics of the sites. Average canopy openness at the sites was 7% (Table 2 and see Fig. 7.15).

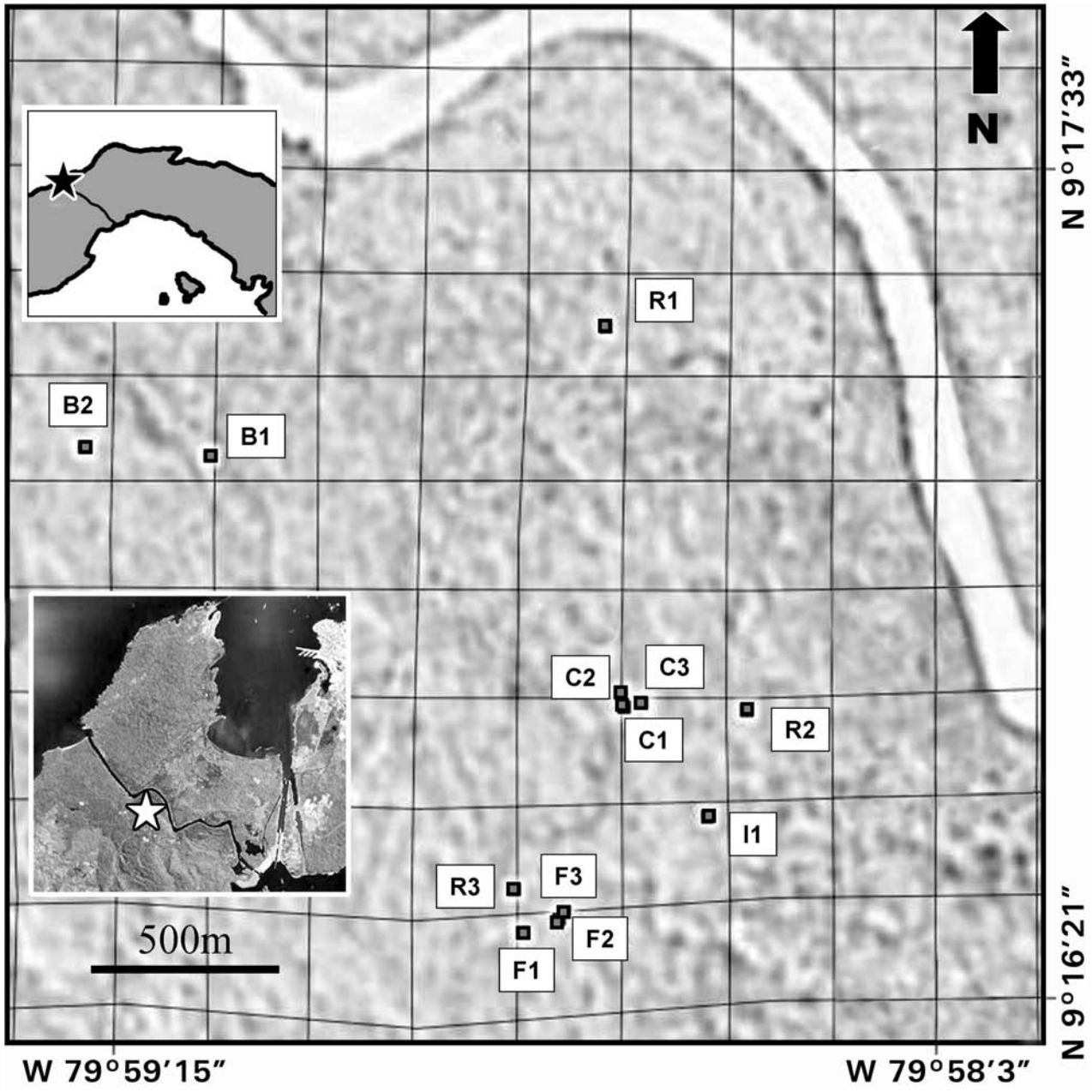

Fig. 2 — Map of the lower Rio Chagres, with the twelve IBISCA sites, coded as in Table 1. Upper inset: view of the Panama isthmus; lower inset: San Lorenzo protected area. The location of the study sites is indicated with a star.

"Crane sites" C1, C2, and C3. The largest trees were specimens of *Brosimum utile* var. *utile*. Other large trees of the three sites included specimens of *Andira inermis* (W. Wright) DC., *Cespedesia spathulata* Planch., *Inga pezizifera* Benth., *Jacaranda copaia* (Aubl.) D. Don, *Marila laxiflora* Rusby, *Sloanea* aff. *meianthera* Donn. Sm., *Tabernaemontana arborea* Rose, and *Vochysia ferruginea* Mart. The most abundant tree species were *Marila laxiflora*, *Perebea xanthochyma* H. Karst., *Tovomita longifolia*, *T. stylosa* Hemsl. and *Unonopsis panamensis* R.E. Fr. The understorey was dominated by the palms *Geonoma congesta* H. Wendl. ex Spruce and *G. cuneata* H. Wendl. ex Spruce.

"Fogging sites" F1, F2, and F3. As in the C1-C3 sites, the largest trees were *Brosimum utile* var. *utile*. Other large tree species included *Aspidosperma spruceanum*, *Carapa guianensis* Aubl., *Guatteria dumetorum* R.E. Fr., *Eugenia coloradoensis* Standl., *Humiriastrum diguense* Standl., *Marila laxiflora, Tovomita longifolia,* and *Virola multiflora* (Standl.) A.C. Sm. The most abundant tree species were the palm *Socratea exorrhiza* (Mart.) H. Wendl., as well as *Dendropanax arboreus* (L.) Decne. & Planch., *Tovomita longifolia, Unonopsis panamensis* and *Xylopia macrantha* Triana & Planch. *Geonoma congesta* and *G. cuneata* were widespread in the understorey.

Table 2 — Characteristics of the 12 IBISCA-Panama sites: number (No.) of stems (including those of a few unidentified trees); number of identified tree species; basal area; succession index (see text); canopy openness (proportion of visible sky (open) to closed in hemispherical pictures, analyzed by Hemiview 2.0); mean reflected light (average from 28 measurements within each site, cell facing down at dbh, measured with a digital lux meter LX-1010B, Kaito Electronics Inc., Montclair, USA); largest trees and most common species (*); dominant species with basal area (BA) or percentage occurrence (*); herbivory (mean percentage of leaves in samples with over 10 % of leaf area damaged, ± s.e.).

Site code	No. stems >10mm	No. tree species	Basal area (m^2)	Succession index	Canopy openness (%)	Mean reflected light (lux, n=28)	s.e.m.	Largest trees / Most common spp.	Dominant sp. BA (m^2), %	Herbivory
B1	211	51	1.01	14.13	7.55	7.96	2.19	Sap, Cal / Psy, Ing	Cal 0.46, 45	36.2 ± 5.6
B2	127	34	1.62	17.39	6.00	57.18	10.14	Ape, Per / Bro, Geo	Ape 0.34, 21	n/a
C1	141	71	1.21	19.62	6.80	57.57	25.36	Bro, And / Prb, Geo	Bro 0.68, 72	29.8 ± 4.2
C2	104	43	1.05	14.72	7.60	68.21	10.66	voc, Bro / Prb, Mar	Voc 0.15, 23	38.1 ± 5.0
C3	121	49	1.16	15.91	10.60	8.46	1.60	Bro, Jac / Tov, Geo	Bro 0.47, 46	39.4 ± 5.9
F1	116	40	1.41	13.83	7.10	n/a	n/a	Car, Mar / Geo, geu	Car 0.29, 41	n/a
F2	140	45	1.75	13.88	7.70	n/a	n/a	Bro, Vir / Geo, Geu	Bro 0.53, 44	n/a
F3	151	50	1.51	16.32	7.60	n/a	n/a	Bro, Hum / Geo, Den	Bro 0.58, 38	n/a
I1	124	59	1.13	16.33	6.90	21.61	5.05	Ape, Cal / Soc, Tov	Ape 0.23, 20	41.8 ± 4.3
R1	123	39	2.93	17.64	2.91	26.56	1.92	Lue, Spon / Rin, Far	Lue 1.08, 37	n/a
R2	134	43	0.98	15.67	6.70	14.96	1.97	Asp, Man / Pro, Tov	Asp 0.46, 47	n/a
R3	107	37	1.03	16.60	6.90	44.96	5.54	Car, Tap / Geo, Mar	Car 0.40, 39	n/a

* Plant names abbreviations: And = *Andira inermis*; Ape = *Apeiba membranacea*; Asp = *Aspidosperma spruceanum*; Bro = *Brosimum utile* var *utile*; Cal = *Calophyllum longifolium*; Car = *Carapa guianensis*; Den = *Dendropanax arboreus*; Far = *Faramea occidentalis*; Geo = *Geonoma congesta*; Jac = *Jacaranda copaia*; Lue = *Luehea seemannii*; Man = *Manilkara bidentata*; Mar = *Marila laxiflora*; Per = *Pera arborea*; Prb = *Perebea xanthochyma*; Pro = *Protium panamense*; Psy = *Psychotria horizontalis*; Rin = *Rinorea squamata*; Sap = *Sapium* sp. 'broadleaf"; Soc = *Socratea exorrhiza*; Spo = *Spondias mombin*; Tap = *Tapirira guianensis*; Tov = *Tovomita stylosa*; Vir = *Virola multiflora*; Voc = *Vochysia ferruginea.*

"Bubble sites" B1 and B2. Site B1 showed remains of past constructions at ground level, that were not noticed when the site was chosen and that were evidently part of past jungle warfare training by U. S. soldiers (Weaver & Bauer, 2004). The largest trees in B1 belonged to the species *Sapium* sp. "broadleaf" and *Calophyllum longifolium* Willd. Other large trees included *Terminalia amazonia* (J.F. Gmel.) Exell and *Lacmellea panamensis* (Woodson) Markgr. The most abundant woody species was *Psychotria horizontalis* Sw., with *Inga sertulifera* DC., *Piper colonense* C. DC. and *Sorocea affinis* Hemsl. being well represented. Only one specimen of *Geonoma congesta* was recorded on the site, and no *G. cuneata*. The largest trees at the B2 site were an *Apeiba membranacea* Spruce ex Benth. and a *Pera arborea* Mutis. *Tapirira guianensis*, *Laetia procera* (Poepp.) Eichler, *Brosimum utile* var. *utile* and *Virola sebifera* Aubl. also grew as large trees at this site. The most abundant species were *Brosimum utile* var. *utile*, *Perebea xanthochyma, Protium panamense* and the palms *Socratea exorrhiza* and *Oenocarpus mapora* H. Karst. *Geonoma congesta* was well represented in the understorey, but *G. cuneata* was not recorded at this site.

"Ikos site" I1. The largest trees at this site belonged to *Apeiba membranacea, Brosimum utile* var. *utile*, *Calophyllum longifolium, Dendropanax arboreus, Simarouba amara* Aubl., *Tovomita longifolia,* and *Virola sebifera*. The best represented species included *Brosimum utile* var. *utile*, *Matayba apetala* Radlk., *Protium panamense, Tovomita longifolia, Virola sebifera,* and the palm *Socratea exorrhiza. Geonoma congesta* and *G. cuneata* were present in the understorey.

"Raft sites" R1, R2, and R3. Two trees at the R1 site exceeded 1 m in diameter, one *Luehea seemannii* Triana & Planch. and one *Spondias mombin* L. *Anacardium excelsum* (Bert. & Balb. ex Kunth) Skeels and *Carapa guianensis* also grew there as large trees. The most abundant species were *Carapa guianensis*, *Desmopsis panamensis* (B.L. Rob.) Saff., *Faramea occidentalis* (L.) A. Rich., *Oxandra panamensis* R.E. Fr., and *Rinorea squamata* S.F. Blake. No *Geonoma* palms were recorded from the understorey at this site. The largest trees at site R2 were several *Aspidosperma spruceanum*. Other large trees included *Brosimum utile* var. *utile*, *Guatteria dumetorum*, *Manilkara bidentata*, *Marila laxiflora*, *Matayba apetala* and *Tapirira guianensis*. The most abundant species were *Maranthes panamensis* (Standl.) Prance & F. White, *Marila laxiflora*, *Perebea xanthochyma*, *Protium panamense*, *Tovomita longifolia*, and *T. stylosa.* Only one *Geonoma congesta* occurred at

this site, and no *G. cuneata*. The largest trees at the R3 site were *Carapa guianensis* and *Tapirira guianensis*. *Brosimum utile* var. *utile*, *Cecropia insignis* Liebm. and *Marila laxiflora* also grew as large trees at this site. The most abundant species were *Brosimum utile* var. *utile*, *Marila laxiflora, Perebea xanthochyma*, *Protium panamense*, *Xylopia macrantha* and the palms *Socratea exorrhiza* and *Synechanthus warscewiczianus* H. Wendl. In the understorey, *Geonoma congesta* was more abundant than *G. cuneata*.

Vegetation analysis (YB, PC, OJH, ML)

The 12 IBISCA sites included 1,556 individual trees of more than 10 mm dbh (including also adult *Geonoma* palms), representing 163 species, in a total area of 0.48 ha. The most abundant species was *Geonoma congesta* (129 individuals), followed by *Perebea xanthochyma, Psychotria horizontalis* and *Brosimum utile* var. *utile* (69, 69 and 65 individuals, respectively). The most diverse family was Fabaceae *s.l.* with 16 species, and three other families included ten or more species (Annonaceae: 10 spp., Arecaceae: 12 spp., Rubiaceae: 11 spp.). In terms of number of individuals, Arecaceae was the most abundant family (315 individuals, of which 175 belonged to one of the two *Geonoma* species). Four other families were represented by more than one hundred individuals (Annonaceae: 119 ind., Clusiaceae: 179 ind., Moraceae: 174 ind., Rubiaceae: 121 ind.). Locally abundant species are detailed in the description of sites and in Table 2.

The study sites were chosen in order to examine arthropod beta-diversity, and hence were not specifically designed to investigate vegetation changes according to distance. However, the floristic composition of sites is expected to be of prime importance in determining the distribution patterns of arthropod abundance and diversity. Hence, the following four analyses aimed to compare plant distributions between sites. First, the software EstimateS (Colwell, 2004) was used to compute rarefaction curves of plant species richness at each site based on individuals (Coleman method). We also computed Simpson diversity index for each site and the expected number of species occurring in a sub-sample of size k, with k representing the maximal value permitted to compare all pairs of samples (k = 100 in our case), with software provided by Hardy (2007). Species rarefaction indicated that site C1 was the richest and most diverse site, followed by I1, C3, C2, F3, F2, F1, R2, B1, R3, R1 and B2 (Fig. 3). Site B1 was the most densely populated site with trees (Fig. 3, Table 1).

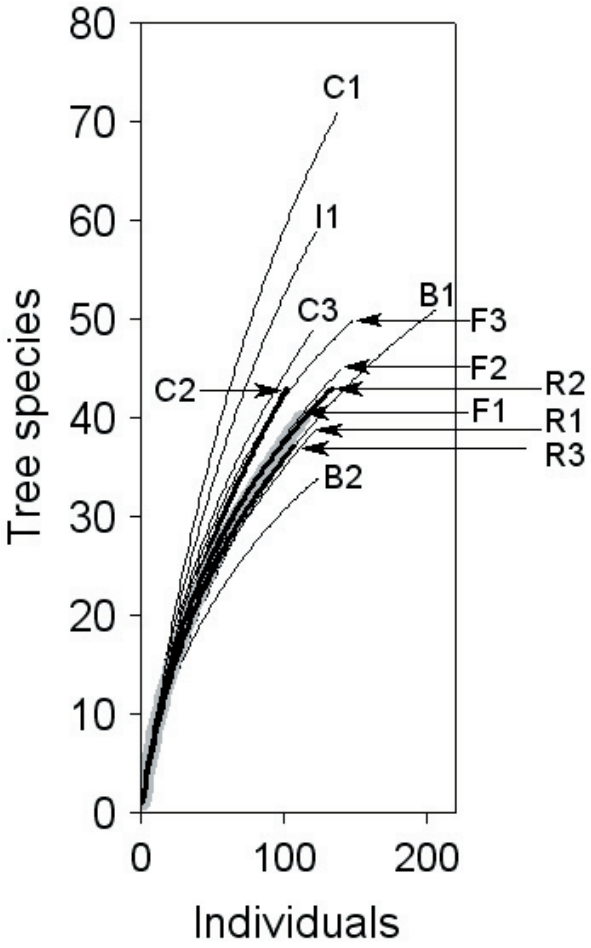

Fig. 3 — Comparison of tree species richness (individual-based rarefaction, Coleman method) and abundance in the twelve 400m² plots investigated during the IBISCA-Panama project. A few unidentified trees were not taken into account in this analysis.

Second, data on plant species-abundance at each site were compiled to build pair-wise measures of similarity between sites. For this purpose, we calculated two quantitative indices of species similarity, the Morisita-Horn index and the NNESS index, with software provided by Hardy (2007). NESS is a metric relatively insensitive to sample size but sensitive to rare and abundant species; NNESS is a modification of NESS to allow calculations with singletons. NNESS values were calculated with sample size parameter k set to 1 (identical to Morisita-Horn index, most sensitive to common species), to the maximal k for comparing all pairs of samples (most sensitive to rare species; in our case k = 100, hence the notations S(100) and NNESS(100) in Table 1; Grassle & Smith, 1976; Hardy, 2007). Both the plots of Morisita-Horn similarites (not presented here, $R^2 = 0.322$, Mantel test p=0.026)

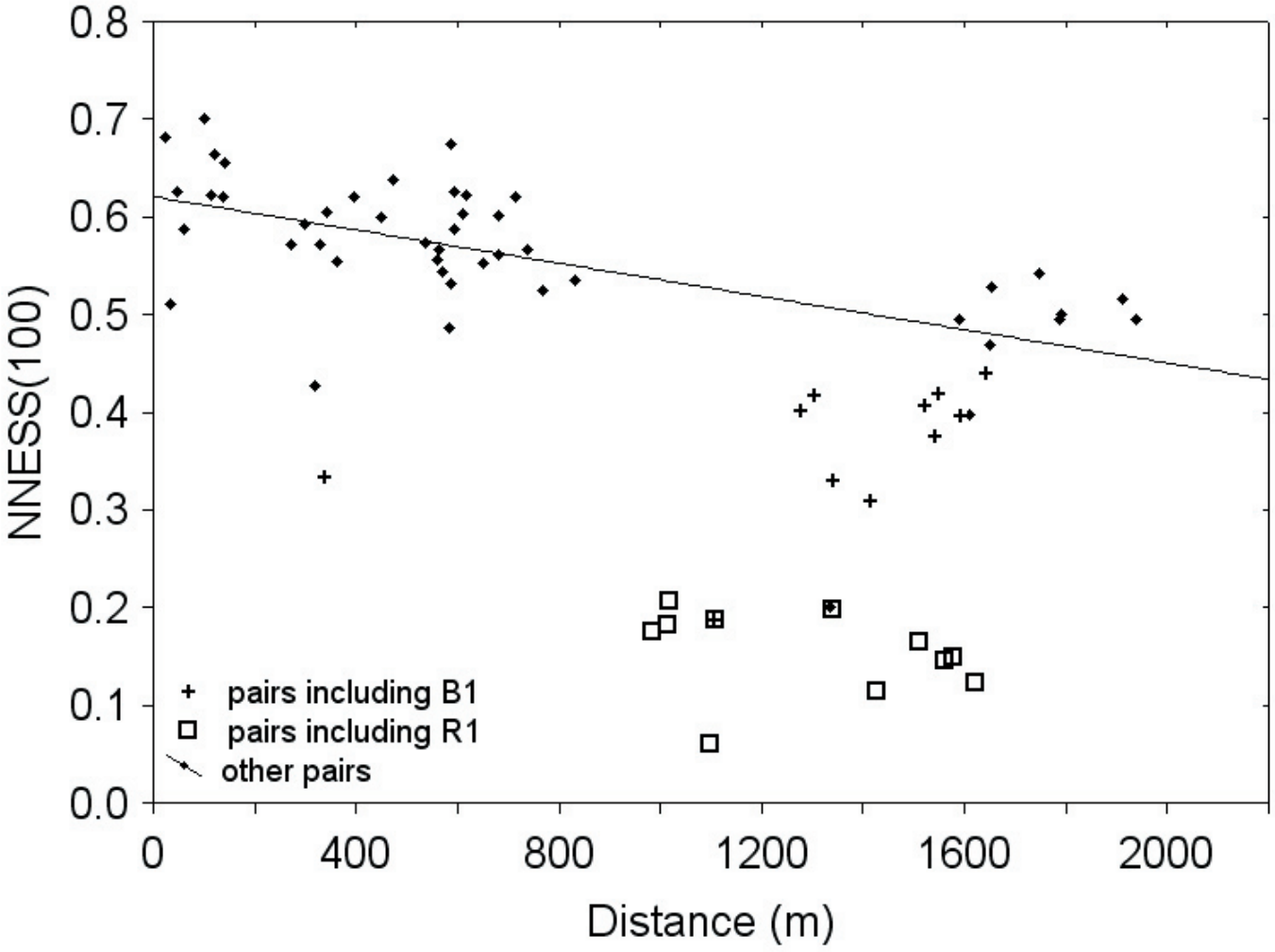

Fig. 4 — Scatter plot of pair-wise NNESS(100) tree species similarity between sites (vertical axis) plotted against straight-line geographic distances between sites (horizontal axis; metres), detailed for different pairs of sites (open squares = pairs including site R1; crosses = pairs including site R1; closed diamonds = pairs including other sites). The negative regression is significant both for pairs including all sites and for pairs with the exception of B1 and R1, as shown here (see text).

and NNESS(100) similarities were significantly and negatively correlated with geographic distances (Fig. 4, $R^2 = 0.334$, Mantel test p=0.018, including all pairs of sites). The similarities of B1 and R1 with other sites were low, but the correlation between similarity and distance remained similar when pairs including B1 and R1 are removed from the analysis (Fig. 4, $R^2 = 0.335$).

Third, the matrices of geographic distance and floral similarity (Morisita-Horn index) were used to compute a dendrogram using Ward's algorithm (Fig. 5). This analysis confirmed the previous one and, in particular, the low floristic similarities of sites B1 and R1 with other sites. Site B1 was, overall, not much different floristically from other sites but was heavily dominated in frequency by a single species, *Psychotria horizontalis*, absent from other sites. This shade-tolerant shrub species does not recruit highly from light gaps (Welden et al., 1991), but it can be propagated easily in the forest from sterns, leaves, or leaf fragments (Sagers & Coley, 1995). Hence, the past constructions at ground level observed at site B1 seem overall to have little altered the floral composition of site B1 and its canopy openness (as evidenced by low succession index and canopy openness values of site B1 in Table 2), but we cannot discount that the local spread of *P. horizontalis* has been promoted by this past disturbance. On the other hand, site R1 was clearly floristically different from other sites, with several plant species not shared with other sites, due the location of this site in the floodplain of the Rio Chagres. The dendrogram also suggested that sites F1-F3 could not be considered as true surrogates of sites C1-C3 (Fig. 5).

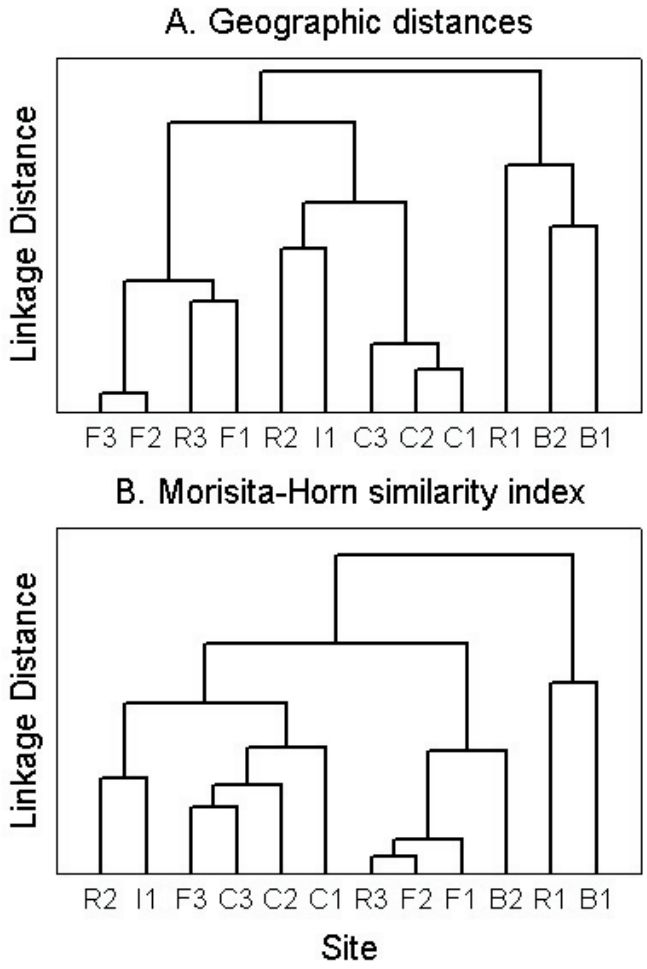

Fig. 5 — Cluster analysis (Ward's method) of similarity in geographic distances between sites (A) and with Morisita-Horn similarity of plant species composition between sites (B).

Fourth, Hubbell (2001) discussed the possible signification of dominance-diversity curves in the framework of his neutral theory of biodiversity and biogeography. From various simulations, it appears that steep curves tend to be associated with early states that are still far from dynamic equilibrium, or with systems having low θ values (a biodiversity parameter encapsulating the size of the source community - a.k.a the meta-community - and the rate of speciation), whereas S-shaped curves are indicative of systems close to equilibrium and with high θ values. Dominance-diversity curves are obtained by ranking species in order from the most abundant to the rarest, and plotting the log of each species relative abundance against its rank. The curves were computed for (a) the 6 ha plot (see description earlier in the text), (b) all IBISCA sites pooled together and (c) the IBISCA sites averaged (the relative abundance of species was averaged for species occupying the same rank in different samples). Hubbell (2001, p. 150) used a similar approach, with the pooled sites considered a surrogate for the meta-community, and the 'averaged sites' used as an estimate of dominance-diversity curves at a smaller scale. Fig. 6 shows the curves obtained for the IBISCA sites and the 6 ha plot. The curve for the pooled sites was not too different from the 6 ha plot curve, as was expected from two samples closer to the meta-community than individual plots. On the other hand, the averaged curve looked distinctly steeper (i.e. the rarest species in the plots appeared on average rarer than in the approximated meta-community). A similar pattern was found by Hubbell (2001), who attributed it to dispersal limitation at a small scale, a reason that is possibly applicable to the IBISCA sites as well.

3. Canopy access (Plate 2)

During IBISCA-Panama, different techniques (canopy fogging, single rope techniques) and devices (canopy crane, canopy raft, canopy bubble and Ikos) allowed field participants to survey arthropods in the upper canopy, either *in situ* or indirectly. This was the first time that these complementary techniques and devices had been deployed in parallel (Roslin, 2003). Canopy fogging may be considered as a sampling technique, yielding indirect access to the canopy (see Section 4.3). Single rope techniques (SRT) are undoubtedly the cheapest way to reach the canopy. Although SRT requires training and a reasonable level of physical fitness, it is used by increasing numbers of canopy researchers (Barker & Stanridge, 2002). A minority of IBISCA-Panama participants were trained climbers. Most of participants relied on the assistance of professional climbers, but used SRT to access the canopy raft and Ikos. Two sites were mainly accessed with SRT.

Canopy cranes are currently the most appropriate devices allowing long-term research on canopy biodiversity (Basset *et al*., 2003b). The Smithsonian Tropical Research Institute first developed the idea of using construction cranes to access the forest canopy in Panama (Parker *et al*., 1992). The first permanent canopy crane was installed in 1992 in the Parque Natural Metropolitano, near the capital of Panama. In 1997, STRI installed a second crane in the San Lorenzo Protected Area (Wright *et al*., 2003). A metal basket called the gondola, in which observers stand, is hoisted above the forest by the crane and lowered to research locations within the canopy. Canopy cranes enable

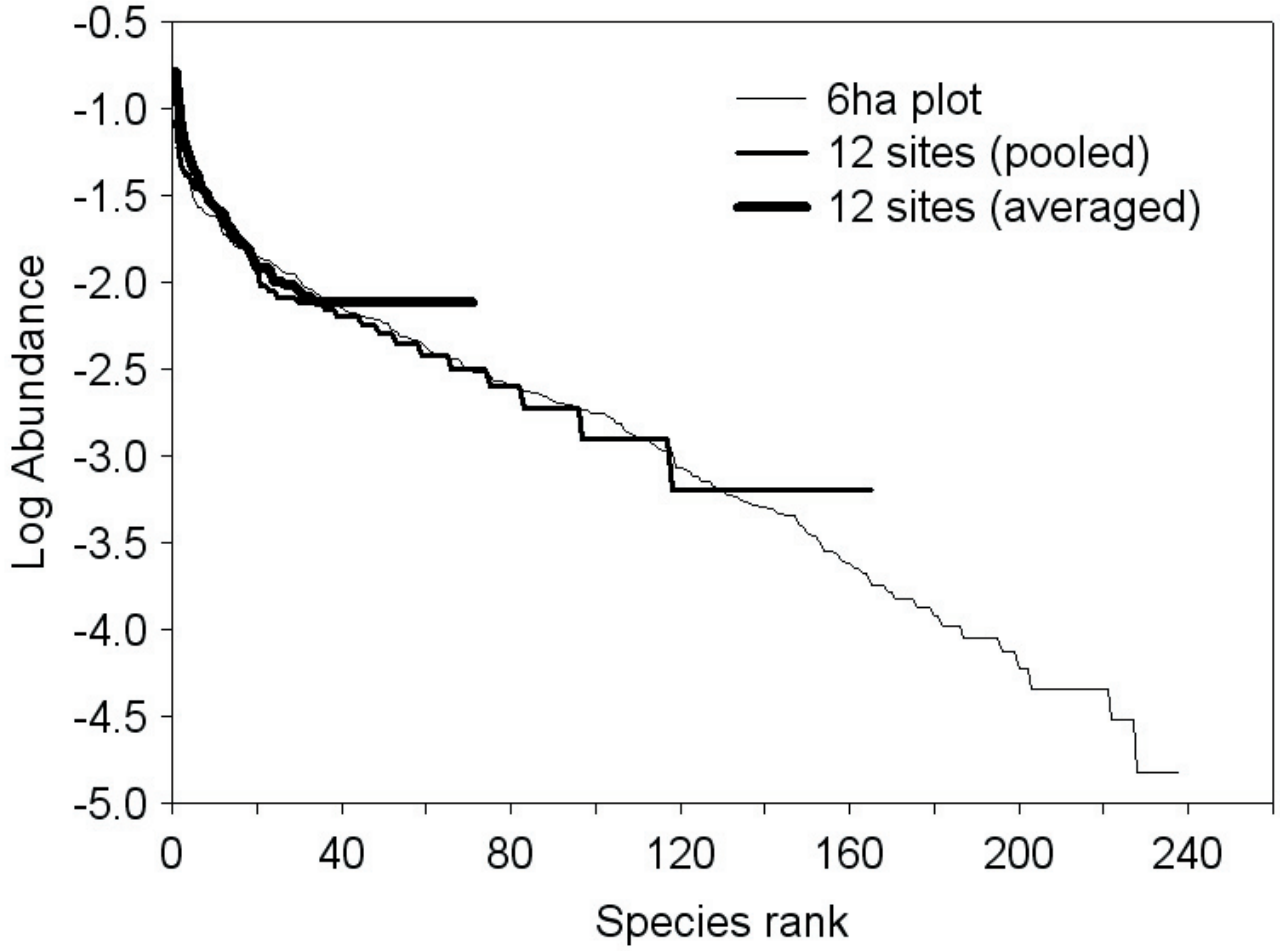

Fig. 6 — Dominance-diversity curves for the plant species of the 12 IBISCA-Panama sites, averaged and pooled, compared with the curve obtained for the 6 ha plot next to the San Lorenzo canopy crane.

easy and safe three-dimensional access to the canopy. The movement of the crane and gondola is controlled through radio communication with a crane operator. The tower height of the San Lorenzo crane is 52 m, its jib length 54 m, the maximum height reached by the gondola is 49.5 m and the area of accessed forest 0.92 ha. During IBISCA-Panama this crane was used to access the upper canopy of three sites.

The SolVin-Bretzel canopy raft corresponds to the 4th generation of canopy raft ("radeau des cimes" in French; Hallé, 2000). It is a 400 m^2 platform of 500 kg, shaped like a pretzel and consisting of air-inflated beams and Aramide™ (PVC) netting that rests on the top of canopy trees. It was first used in the Masoala National Park (Madagascar) in 2001 and for the second time during IBISCA-Panama. Access to the raft is provided by single rope techniques. Researchers can walk on the net from one side to the other and may collect specimens by leaning over and collecting from the tree tops within reach. Compared with canopy cranes, the mobile canopy raft allows comparisons between remote sites. Usually an air-inflated dirigible raises the raft and sets it upon the canopy. During IBISCA-Panama a Bell-212 helicopter from the Servicio Aero Nacional was used for this purpose. The helicopter carried the canopy raft at the end of an array of ca. 60 m cables, in order to cause minimal disturbance to the canopy. Unfortunately, due to unexpected maintenance problems with the helicopter, the canopy raft was only installed at one site.

The canopy bubble (or "bulle des cimes" in French) is an individual 180 m^3 helium balloon of 6 m in diameter which runs along a fixed line set up in the upper canopy. The observer is seated in a harness suspended below the balloon and moves along the line by hands or with the aid of mechanical jumars. The canopy bubble was first used in Gabon (1999) and Madagascar (2001). One such device is permanently installed in the Nouragues station

Plate 2 — Canopy access devices, clockwise: SolVin-Bretzel canopy raft, canopy bubble, Ikos tree house and canopy crane. Photos: S. Bechet, R. Le Guen, JO, ML.

in French Guiana, with a 5 km guide-rope network. In Panama the guide ropes were installed by helicopter and allowed access to the upper canopy of two sites.

The Ikos is an icosahedral unit (i.e., twenty sides), 3.2 m in diameter, installed in the fork of a large tree, which is designed primarily for long-term observations (a canopy tree-house). It can be assembled in the tree or partially built on the ground and then hoisted up. Single rope techniques provided access to the Ikos. Researchers can work on a platform, which is attached to the top of the structure. The Ikos was first used in the Forêt des Abeilles (Gabon) in 1999 (Hallé, 2000) and then in Masoala National Park (Madagascar) in 2001. During IBISCA-Panama the Ikos allowed access to the upper canopy of one site.

4. Outline of arthropod sampling protocols

4.1. Timeframe, seasonal replications and overview

A first six-week field study during the late wet season of 2003 (22 September to 31 October) concentrated on all 12 sites, using 14 arthropod protocols. It was attended by 45 participants from 15 countries, including entomologists, botanists, students (University of Panama, Maestria de Entomologia) and 10 technical staff (professional tree climbers, consultants and photographers). Repeated seasonal replicated sampling in 2004 included shorter periods of field work, focusing on a restricted number of study sites with a restricted number of arthropod protocols:

Seasonal replicate 1: 1 February- 15 March 2004: five weeks; dry season; 7 participants who concentrated on 2-6 sites with five protocols.

Seasonal replicate 2: 10-31 May 2004: three weeks; onset of the wet season; 27 participants (including two parataxonomists) who concentrated on 2-8 sites with 14 protocols.

Seasonal replicate 3: 15 October - 22 November 2004: five weeks; late wet season; 9 participants who concentrated on 2-6 sites with six protocols.

Thus, seasonal replicates were conducted three times at least at the three crane sites. One full replication (all sampling protocols) took place in May 2004. Arthropods were collected from inside the 400 m^2 area of each site after completion of the vegetation survey, unless sampling protocols necessitated a larger surface (e.g., hand collection of ants and termites). We detail below the scope of each arthropod sampling protocol (Fig. 7) and Table 3 summarizes the sampling effort for each protocol. In total, 1386 traps and other protocols produced 9402 samples, equivalent to 24354 trap-days (or person-days) of sampling effort. A substantial part of this sampling effort focused on the upper canopy of the forest. The spatial replication achieved with protocols such as light, flight-interception and sticky traps, and Berlese-Tullgren was high and has little or no equivalent in the published literature, particularly when considering the vertical dimension. The advantages and limitations of each sampling protocol are discussed in Southwood (1978), Muirhead-Thomson (1991) and Basset *et al*. (1997).

4.2. Soil and litter samples

Winkler sifting (HPA, BC, AD, ML, JO & YR)

This method collected active and passive arthropods in ground litter. The leaf litter was sifted and then extracted for 48 hours using a mini-Winkler apparatus (as detailed in Fisher, 1998) to obtain all arthropods. In September-October 2003, 8 sites were surveyed, from which 51 samples of 1 m^2 of leaf litter were extracted per site. In May 2004, three sites were re-surveyed, yielding 153 additional samples of 1 m^2 of leaf litter. Such sampling intensities yield a representative estimate of the local structure of ant assemblages (Leponce *et al*., 2004)

Berlese-Tullgren (GCM, NNW)

This method collected microarthropods in ground soil and in suspended debris accumulations in the canopy. At each site, three trees were sampled and 16 cores (3 x 5 cm each) were obtained from each tree: 8 from the ground and 8 from suspended debris accumulations in the tree. Each soil core (sample) was extracted for 48 hours in a Berlese-Tullgren apparatus and the resulting arthropod specimens were collected into 75 % ethanol (see Winchester & Behan-Pelletier, 2003 for more details). In 2003, 8 sites were surveyed, yielding 384 samples. In May 2004, 4 sites were surveyed, yielding 176 additional samples. Sub-samples of the Collembola material were studied by Castaño-Meneses *et al*. (2006).

Hand collecting: social insects (BC, AD, ML, JO & YR)

Hand collecting for social insects (ants and termites) was performed on the ground, in the understorey and in the mid- and upper canopy, with substantial help from

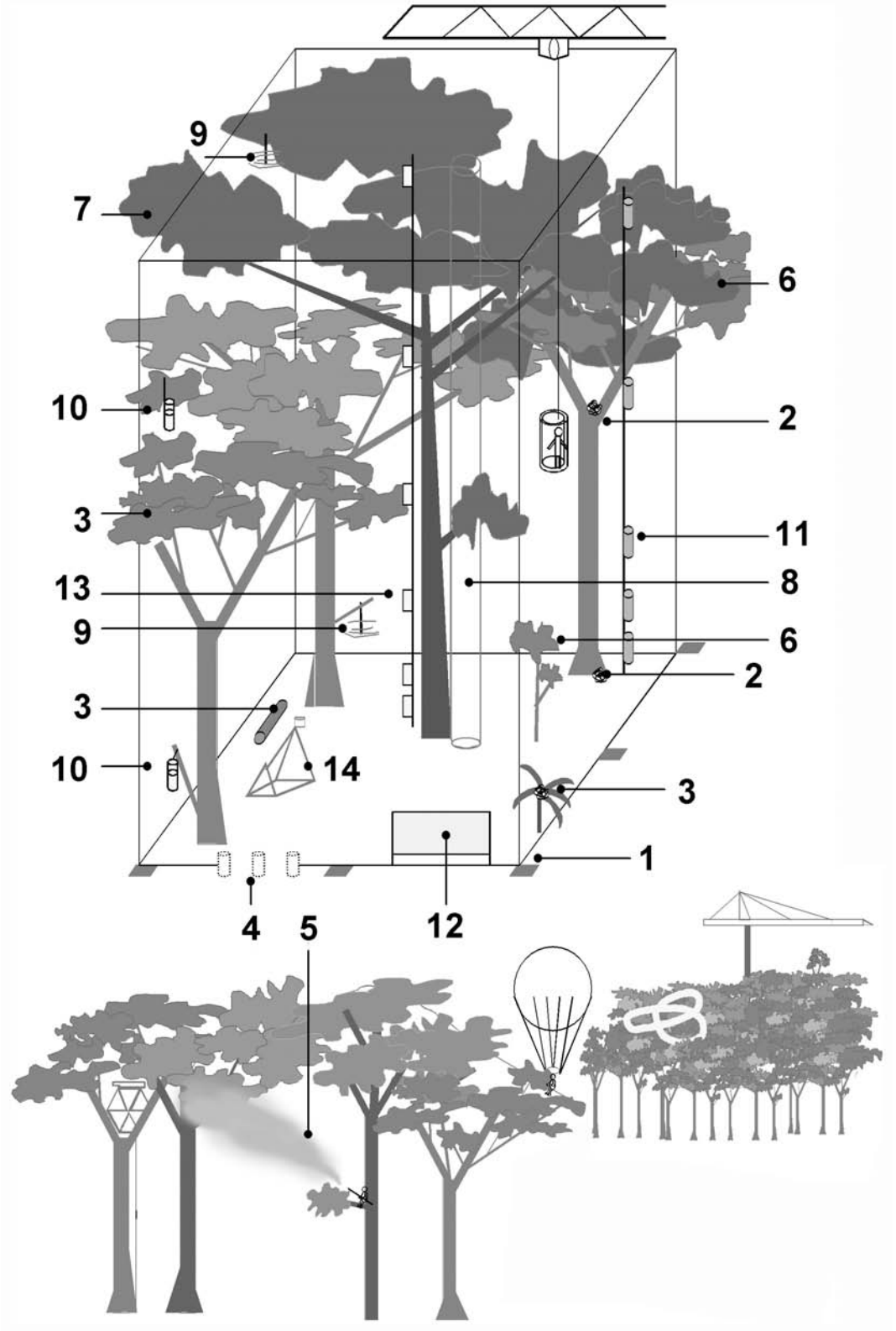

Fig. 7 — Sampling protocols used: (1) collection of the leaf-litter fauna and extraction with a mini-Winkler apparatus; (2) collection of ground and suspended soils, extraction with Berlese-Tullgren funnels; (3) hand collecting for ants and termites; (4) pitfall traps; (5) canopy fogging; (6) beating of vegetation and dead branches; (7) baits and netting; (8) gall sampling within the volumetric space of a vertical cylinder; (9) wood rearing; (10) light traps; (11) aerial composite flight-interception traps; (12) ground flight-interception traps; (13) sticky traps; (14) ground Malaise traps; (15) aerial view of San Lorenzo forest. Photos by ML (1-2,4-6,13), N. Baiben (3,15), JS (7), SR (8), M. Janda & J. Patera (9), RLK (10), NW(11), CE Carlton (12), SP(14). **(Fig. 7 continued on opposite page)**


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15

professional climbers. In 2003, 8 sites were surveyed, yielding 160 samples of 10 m² on the ground and 45 samples in the canopy (termites); as well as two 170 x 40 m transects and approximately 300 samples in the canopy and understorey each (ants). In 2004, ground termites were collected from 40 quadrats of 5 m² located at intervals of 10 m along a transect line (yielding approximately 100 samples). Canopy samples were collected from 40 emergent trees along a transect line (n = 32 samples collected); arboreal termites were collected from nests, galleries and pieces of dead wood observed in the canopy; and arboreal ants were collected from live branches (approximately 100 samples; Roisin *et al.*, 2006).

Pitfall traps (EM & AT)

Pitfall traps collected active arthropods in the ground litter. Traps were made of plastic cylinders of 6 cm in diameter and 15 cm depth (0.424 l) containing a solution of 50 ml ethanol, 10 ml of liquid detergent and 5 g salt. Traps were covered with an 18 cm raised plastic plate to protect them from rainfall. At each study site, 15 traps were buried flush with the soil surface, in a straight line at 1.3 m intervals. Traps were surveyed after three days, for a total sampling effort of 630 trap-days, obtained from seven sites (Medianero *et al*., 2007).

4.3. Understorey and/or canopy samples
Canopy fogging (JB, AF, & JS)

A wide range of arthropods was collected with this method, which consisted of dispersing knockdown insecticide up into trees with a fogging machine operated from the ground or from a tree. The stunned arthropods fell on to collecting trays installed at 1 m height above ground (for more details, see Adis *et al*., 1998 and Kitching *et al*., 2002). A Swingfog ® SN1 machine was used with a 1 % natural Pyrethrum solution, dissolved in white oil Essobayol ® 82. At each fogged site, six samples were obtained, corresponding to the arthropods that fell onto six distinct 4 x 5 m plastic sheets installed at 1 m height. In 2003, eight sites were fogged (48 samples), whereas six sites were re-fogged in May 2004 (36 samples) and October 2004 (36 samples).

Beating of vegetation and dead branches (HB & FØ)

Beating collects passive foliage arthropods and was

Table 3 — Sampling effort for each arthropod protocol: number (no.) of traps (if relevant), no. of sites surveyed, no. of seasonal replicates, types of habitats surveyed (s = soil, l = litter, u = understorey, m = mid-canopy, c = upper canopy), no. of samples, no. of trap-days (or person-days, whichever is relevant), and no. of arthropod individuals collected. NA= not available.

Protocol[#]	Traps	Sites	Replicates	Habitats	Samples	Trap-days	Individuals (x1000)
Winkler	—	8	2	l	561	44	24
Berlese Tullgren	—	8	2	sc	528	22	30
HC: social insects	—	10	2	lumc	848	129	1.5
Pitfall traps	210	7	4	l	210	630	10
Fogging	—	8	3	m	120	19	81
Beating	—	8	4	uc	560	11	3.5
Baits	—	8	2	uc	59	28	1.3
HC: galls	—	5	2	umc	231	14	5
Wood rearing	—	—	2	uc	2303	1213	NA
Light traps	48	8	4	uc	90	90	55
Aerial FITs	90	5	4*	lumc	1659	16244	69
Ground FITs	36	9	2	u	173	248	15
Sticky traps	993	8	4	lumc	1986	4965	56
Malaise traps	9	9	3	u	74	697	165
TOTAL	1386	12	4*	slumc	9402	24354	>500

[#]HC = hand collecting; FIT = flight-interception trap
*Aerial FITs ran continously from October 2003 to October 2004

performed during day-time either on live vegetation or dead branches. For the former, arthropods were collected on square beating sheets of 0.4 m^2 in area, of conical shape, ending in a circular aperture (7 cm in diameter), which was fitted with a removable plastic bag. Sheets were inserted below the foliage so that one layer of leaves above occupied approximately the entire area of the sheet. Arthropods were dislodged from the foliage with three good strokes, and gently brushed inside the plastic bag, which was then closed and replaced by a new one. A total of 560 beating samples were obtained from the vegetation at 7 sites, half from the understorey and half from the upper canopy (sites C1 and C2 were replicated in February, May and October 2004).

To compare the vertical stratification of saproxylic beetles within and between different plant species, another protocol was used. Cut branches of 16 tree species were first suspended in their parent tree. For each tree species, four branches were placed in the canopy (15-25 m above ground) and four in the understorey (1 m above ground). All branches were beaten regularly, approximately every second day over a three-week period starting five days after branches were cut. A total of 304 and 268 samples from the understorey and canopy were obtained, respectively. All Coleoptera associated with dead wood and senescing leaves were collected. This protocol was initiated in 2003 and replicated in May 2004.

Baits and netting (DMF & DWR)

Using honey water as bait for meliponines and Cineol™ for euglossines, bees were netted in the understorey (approximately at breast height) and in the upper canopy at eight sites in 2003 and six sites in May 2004. The baits were left for two hours at each location, meliponines were sampled and euglossines systematically caught. A total of 59 samples were obtained.

Hand-collecting: gall-forming insects and herbivory (SPR)

This protocol aimed at quantifying galling performance and free-feeding herbivory. It consisted of sampling galls on leaves observed within the volumetric space of a vertical cylinder 1 m diameter, established from the upper canopy to the understorey (up to three meters above the ground). At each site, three vertical "transects" were chosen randomly, within the range of reachable spaces. An additional horizontal 30m-long transect was surveyed in the understorey of each site. Within each transect, the following measurements were recorded: height of branches; number of leaves; number of dead or active insect galls; number of leaves with more than 10 % of leaf area lost by chewing insects; and number of active meristems. Five sites were surveyed in 2003 and re-surveyed in May 2004, totaling 43994 leaves inspected in 231 branch samples from 73 tree and liana species (Ribeiro & Basset, 2007).

Wood rearing (HB, LC, GC, FØ & MR)

Xylophagous insects were reared from baits of cut branches of 15 tree species, collected from outside the study sites. All timber baits included about 15 kg of fresh wood. For each tree species, a minimum of eight timber baits were placed as follows, shortly after being cut: two baits in the shade, understorey; two baits in the sun, understorey; two baits in the shade, upper canopy; and two baits in the sun, upper canopy. After one month of exposure to ovipositing females of saproxylic insects, all baits were removed and enclosed in emergence bags of fine black mesh, fitted with a 'Malaise-type' collecting bottle at the upper corner, and filled with a 5 % formaldehyde-ethylene glycol solution. Pilot studies were initiated in 2004 but all samples (n = 2303) were collected during additional field work in 2005. To date, not all reared specimens have been processed and databased.

Light traps (AC, RLK, MMa, MMo & EGO)

Our light traps surveyed insects that are attracted to light, including moths. We used a commercially available design based on the so-called Pennsylvania (or Texas) trap (Frost, 1957). Essentially this comprised a vertically-mounted 'black light' fluorescent tube with three transparent plastic vanes mounted equidistantly around it. These vanes were shaped to fit within a funnel and the funnel sat within a replaceable bucket in which the catch accumulated. The light operated using a 12 Volt gel battery. To this commercially available model we added a rain protector of a size larger than the bucket (we used an alloy dustbin lid around 60 cm diameter) and a sandwich of wooden boards beneath in which the battery could be mounted. These modifications ensured that: (a) the trap could be used in wet to very wet conditions; and (b) the trap and its battery could be hauled into the canopy by rope. We used a block of Dichlorvos™ impregnated plastic as a killing agent placing it in the bucket together with torn baking paper to provide resting places for captured insects (for more details see Kitching *et al*., 2000).

The upper canopy traps were hung from tree branches

(ca. 25-35 m above ground). The understorey traps were hung at approximately 2 m above ground from ropes tied to two adjacent tree trunks. Each site was equipped with three canopy and three understorey traps, which were run for a night. The traps were usually set at about 5-6:30 PM (sunset) and removed the following morning around 6-7:00 AM (sunrise). In 2003, eight sites were surveyed (48 samples). In 2004, sites C1 and C2 were re-surveyed in February, May and October (36 samples). An additional site was also surveyed in May 2004 (6 samples).

Aerial composite flight-interception traps (RKD, LLF & MR)

These traps collected large flying insects in the understorey and canopy. Each consisted of a rain cover and two 60 cm tall, perpendicular perspex intercept sheets above a 23 cm diameter collecting funnel and preserving jar (active collecting area = 0.55 m^2, double sided). At each study site, three vertical trap transects were installed. Each transect consisted of six traps set up at different heights (0 m, 1.3 m, 7 m, 14 m, 21 m and 28 m). Ground traps (0 m) were placed near the base of each tree and were dug into the ground level with the top of the collecting funnel, and in this way they acted as combined pitfall and flight traps (for more details see Ewers *et al*., 2007). Traps were usually surveyed every ten days. They ran more or less continuously from October 2003 to October 2004 on 4-5 sites, yielding 1659 samples.

Ground flight-interception traps (AT)

These traps were erected on the ground as large rectangular fences (3 x 1 m) made of fine plastic mesh (active collecting area = 6 m^2, double-sided). They collected large flying insects, which impacted the fence and fell into the collecting trays disposed below the fence, which were filled with water and ethanol. Three such traps were run per site, each for an exposure period of 1-2 days. Eight sites were surveyed in 2003 and May 2004, yielding 120 samples. In addition, traps were run at other locations in the study area as part of a study of myrmecophilous Histeridae (Coleoptera) and yielded an additional 53 samples.

Sticky traps (HPA, HB, YB, LC & GC)

Sticky traps collected small flying insects in the understorey and canopy. They consisted of small (29 x 12.5 cm, active collecting area = 0.0725 m^2, double-sided), yellow-colored, plastic cardboard coated with glue (Kollant Temo-O-Cid Colortrap, Kollant Padova, Italy). At each site, 25 traps were placed in the understorey (at dbh, 1.3 m) and 25 traps in the upper canopy (treetops, usually 30-35 m). In addition, three vertical transects, consisting of seven traps placed at 0 m, 1.3 m, 7 m, 14 m, 21 m, 28 m and the treetops (upper canopy), were surveyed at each site. Thus, in total 71 traps were set up at each site and each left for five days. Overall, nine sites were surveyed and 993 traps were used, with sites C1 and C2 being replicated three times in 2004. In addition, sticky traps were also installed specifically to collect wood-boring *Agrilus* (Coleoptera, Buprestidae) near dead trees in the study area (Curletti, 2005; Curletti *et al*., 2006).

Ground Malaise traps (SP & Neil D. Springate)

Our Malaise traps collected various insects flying in the understorey. We used a model from Harris House Nets (B&S Entomological Services, Portadown, N. Ireland) with an active collecting area of ca. 4 m^2 (double-sided), based on the basic design of Townes (1972). Malaise traps were emplaced on the ground at nine sites in 2004 and later reduced to six sites, due to human interference. Traps were surveyed every 10 days during three seasonal replicates in 2004, yielding 74 samples.

4.4. Processing of material

During IBISCA-Panama, each participating entomologist in the field was responsible for a particular sampling protocol and the study of 1-2 focal taxa (= 'supervisor'). Initial sorting at the ordinal or familial level was facilitated by students from the University of Panama and by parataxonomists from the New Guinea Binatang Research Center (for a discussion on parataxonomist duties in biodiversity projects, see Basset *et al*., 2004). The supervisors collaborated with taxonomic authorities for the formal study of the material (88 additional participants), first pre-sorting the material into morphospecies, then identifying them as far as current knowledge allowed. In total, IBISCA-Panama will evaluate patterns of spatial distribution for 63 focal taxa, representing different lineages and life history strategies (Table 4).

Thorough taxonomic study of this material is essential for at least two reasons. First, morphospecies need to be cross-checked both among study sites and between levels within the forest (from the soil to the upper canopy) in order to be able to include them in cross-site comparisons and beta-diversity estimates.

Second, the Latin binomials of identified species provide access to additional ecological information available from the published literature. For specific focal taxa, the entomological fauna of Panama is reasonably well known, in comparison with other tropical countries, so that information can be extracted from a relatively large literature.

A special database with a MS-Access 97 core was developed in order to register conveniently all arthropod records. The definition of a common set of codes for samples, higher taxa (i.e., taxa ranking above genus level), guilds and host plants prevented problems of duplication. The individual data files from each supervisor responsible for a taxonomic group or protocol were merged in a master database. This collective data matrix summarizes interactions at eight main sites between five main habitats (soil, litter, understorey, mid-canopy and upper canopy), 14 sampling protocols, 9402 samples, four seasonal replicates, 315 plant species. We estimate that the final product should shed light on the spatial and seasonal distribution of approximately half a million specimens belonging to ca 5500 species, distributed among 63 focal groups of different phylogeny and ecology. No comparable dataset exists for arthropods of tropical rainforests.

Many species collected during IBISCA-Panama appear to be new to science and will be described in due course. So far, 26 new species have been described from tenebrionid and buprestid material alone, including one species named in honour of the programme, *Lenkous ibisca* Ferrer & Ødegaard (Curletti, 2005; Ferrer & Ødegaard, 2005). New species often included specimens originating from the upper canopy, but not always. New species were often cryptic, such as the many species of Anobiidae (Coleoptera) collected by fogging. Inevitably, this probably represents but a fraction of the task awaiting taxonomists. The material collected by IBISCA-Panama may also be instrumental in documenting the spread of alien species, as shown by Kirkendall and Ødegaard (2007) for some scolytine species.

5. Significance of IBISCA-Panama and perspectives

In some sense, it is puzzling to observe that scientists have managed to focus public attention on complex problems of gas exchange and nutrient cycling involving many processes that are invisible to the naked eye, whereas they have largely failed to focus public attention on the fundamental and unanswered questions of how many species inhabit the Earth, what proportion of these have been named and described, and how widely are they distributed! Perhaps one of the main reasons for this is that sufficient primary research has been conducted to a point where global cycles of gases and nutrients can now be relatively well explained by extrapolation from observations at smaller-spatial scales. In contrast, the magnitude and determinants of biodiversity are far from being reasonably well understood. For example, knowledge of local food webs, especially in the tropics, is still rudimentary (Godfray *et al*., 1999; Kitching, 2006). In short, the inability of the scientific community to document species diversity, let alone alterations brought about by global environmental change, is hugely detrimental to the credibility of the conservation movement (Mann, 1991). The magnitude of the effort and cost necessary for adequate surveys of biodiversity and implementation of conservation policies may also be overwhelming to many individuals, organizations and institutions.

The new *modus operandi* of IBISCA involves team work (ecologists, taxonomists, students, parataxonomists), international collaboration and complementary skills, both in the field and laboratory. There have been major multi-scientist studies of tropical nature before, but these have seldom been coordinated within a strong, single experimental design that will generate an accurate picture of the spatial distribution of arthropods within the study area. Specifically, with IBISCA-Panama, it will be possible to compare, for the first time, faunal samples obtained *in situ* from the canopy with those obtained from the understorey or soil-litter of a tropical rainforest with sufficient taxonomic, spatial and temporal replication. Such data were collected in the field at a fraction of the cost associated with recent research initiatives in other life sciences. All fieldwork-related expenses amounted to less than US$ 300,000. Although acquiring raw data in the field was relatively inexpensive, the costs of processing, identifying and databasing IBISCA specimens may easily double the overall expenses of IBISCA-Panama. Still, this investment appears low in comparison to budgets of large-scale genetic research programmes, and a small price to pay to stimulate innovative lines of research in tropical ecology.

Multi-protocol, multi-habitat and multi-taxa studies, such as IBISCA, are essential if statements are to be made about the overall arthropod diversity of forests. The assumption, tacit since Erwin & Scott's (1980) article, that the species richness of the forest is totally canopy-dominated is certainly not true. IBISCA-Panama may be considered as a model for large-scale investigative programmes focusing on arthropod

Table 4 — Current status of taxonomic knowledge for the major focal taxa studied by IBISCA-Panama, as of August 2007: order; feeding guild; supervisors (abbreviated by initials); number of individuals databased (Ind.), total number of species or morphospecies databased (Spp.), percentage of species so far identified to species level (Id.). To put these preliminary data in perspective, the estimated number of known species from Panama is also indicated (Panama), compiled from various sources. In total 63 focal taxa are studied under the responsibility of 27 supervisors and 109 taxonomists.

Focal area	Order	Guild	Supervisor(s)	Ind.	Spp.	Id. %	Panama
Oribatei	Acari	varia	NNW	>16,000	>139	33	ca. 200
Araneae	Araneae	Predator	JS	>5,000	>200	0	-
Opiliones	Arachnida	Predator	JS	>400	36	0	-
Ricinulei	Arachnida	Predator	JS	17	2	0	6
Collembola	Collembola	Scavenger	GCM	11,603	50	4	23
Curculionoidea	Coleoptera	varia	HB	ca. 7,000	548	35	ca. 4,000
Cucujoidea/Tenebrionoidea (part)	Coleoptera	varia	LC	2,000	210	0	-
Chrysomelidae (part)	Coleoptera	Chewer	AF	>400	>115	21	-
Cerambycidae	Coleoptera	Wood-eater	FØ	>150	57	68	-
Ceratocanthidae	Coleoptera	Fungal-feeder	AT	313	24	15	40
Histeridae	Coleoptera	Predator	AT	1648	173	33	250
Pselaphidae	Coleoptera	Predator	AT	1402	142	22	508
Scolytinae & Plarypodinae	Coleoptera	Wood-eater	FØ	>5,000	144	34	-
Scarabaeoidea	Coleoptera	Scavenger	FØ	>300	48	96	541
Scydmaenidae	Coleoptera	Predator	FØ	>250	63	3	-
Buprestidae: Agrilus	Coleoptera	Wood-eater	GC	44	22	18	28
Nitidulidae	Coleoptera	Varia	AT	ca. 2,500	45	35	92
Erotylidae & Endomychidae	Coleoptera	Fungal-feeder	LC & JS	>500	103	0	-
Cleridae	Coleoptera	Predator	JS	>600	46	0	-
Eucnemidae	Coleoptera	Wood-eater	JS	>500	79	0	-
Elateridae	Coleoptera	Various	JS	>1,000	99	28	-
Empididae	Diptera	Predator	RKD & LLF	>300	-	0	-
Scatopsidae	Diptera	Various	RKD & LLF	>100	-	0	-
Mycetophilidae	Diptera	Fungal-feeder	RKD & LLF	>100	-	0	-
Phoridae	Diptera	Various	RKD & LLF	>5,000	-	0	-
Sphaeroceridae	Diptera	Various	RKD & LLF	>2,000	-	0	-
Ceratopogonidae	Diptera	Various	RKD & LLF	>8,000	-	0	-
Dolichopodidae	Diptera	Predator	RKD & LLF	>2,000	-	0	-
Drosophilidae	Diptera	Various	RKD & LLF	>2,000	-	0	-
Membracoidea	Hemiptera	Sap-sucker	YB	1460	57	58	137
Fulgoroidea	Hemiptera	Sap-sucker	YB	5400	180	31	500-1,000
Psylloidea	Hemiptera	Sap-sucker	YB	1953	27	59	ca. 150
Cicadellidae	Hemiptera	Sap-sucker	YB	3827	160	33	-
Meliponini & Euglossini	Hymenoptera	Pollinator	DMF & DWR	1363	42 / 22	98	? / 35
Braconidae	Hymenoptera	Parasitoid	EM	2,500	ca. 80	31	-
Formicidae	Hymenoptera	Ant	BC, AD, ML & JO	ca. 50,000	291	57	301
Isoptera	Isoptera	Scavenger	YR & ML	ca. 15,000	60	55	50
Geometroidea	Lepidoptera	Chewer	RLK	>313	>108	77	ca. 1,500
Pyraloidea	Lepidoptera	Chewer	RLK	>994	>241	50	ca. 3,500
Arctiidae	Lepidoptera	Chewer	RLK	>432	>74	74	ca. 600
Psocoptera	Psocoptera	Epiphyte-grazer	PC	212	66	2	112
Orthoptera	Orthoptera	Various		>2,500	130	0	-

biodiversity. In particular, international collaboration based on an integrated experimental design allows the investigation of crucial ecological questions in unprecedented ways. Since the Panamanian experience, IBISCA participants have decided that the IBISCA model should be expanded to sites in other geographic regions, so as to address more effectively a range of issues of pressing importance related to biodiversity.

IBISCA-Queensland began in eastern Australia in April 2006 at 20 sites (now referred to as "standard" 20 x 20 m IBISCA-plots). Four plots were each located at five different altitudes between 300 m and 1100 m within the continuum of forest in Lamington National Park. Three main field periods are scheduled: September 2006, March 2007 and January 2008. Two of these have been completed to date. IBISCA-Santo took place in October-December 2006 in Vanuatu, as part of the "Forests, Mountains and Rivers" component of the Santo 2006 Global Biodiversity Survey. As with IBISCA-Queensland, IBISCA-Santo will examine distribution patterns of arthropods and plants along an altitudinal gradient (100 m to 1200 m in the case of IBISCA-Santo). Two other IBISCA projects are currently in preparation: one in a temperate deciduous forest (Forêt de la Comté d'Auvergne, France); and the second in a coastal tropical dry forest in Northern Mozambique (see www.ibisca.net for up-to-date information related to IBISCA programmes).

We urgently need these projects, and many more like them, to understand how arthropod biodiversity originated, how it is currently distributed and maintained in temperate and tropical forests, and to address biodiversity issues in an ecological context. Politicians and funding agencies should recognize that biodiversity research is no less technically challenging than is gene discovery, astrophysics, or other large-scale scientific endeavours. The costs of protecting ecosystems under study and of developing research infrastructure must be judged to be as justified as the development and massive use of 'cutting edge' molecular tools. Knowledge to be gained from understanding the evolution and functioning of a tropical forest or coral reef is every much as powerful as that associated with the sequencing of a genome. The intense spatial focus and collegial synergies of projects such as IBISCA cannot be underestimated. We are calling for institutional mechanisms that will better facilitate and support such teamwork in the future. We know the key questions. We have the methods to answer them. We need wider appreciation of the challenges faced by biodiversity research and the resources to face them. We trust that the former will lead to the latter.

Acknowledgements

IBISCA-Panama is an initiative of Pro-Natura International, Océan Vert, l'Université Blaise Pascal, la Universidad de Panama and the Smithsonian Tropical Research Institute (STRI), with core funding from SolVin-Solvay SA, STRI, the United Nations Environment Programme, the Smithsonian Institution (Walcott fund), the European Science Foundation and the Global Canopy Programme. The Canopy Crane team (José Herrera, Edwin Andrade) and Joe Wright at STRI; the tree climbers from "Les ACCRO-branchés" (Nouï Baiben, Stéphane Bechet & Julien Belleguic) as well as Thierry Aubert and Kevin Jordan; "Océan Vert" (Gilles Ebersolt, Dany Cleyet-Marrel & Laurent Pyot); and Patrick Basset & Eric Bauhaus helped with logistics in the field. Anovel Barba, Rosario Cabrera, Isella Díaz, Mario Gonzalez, Jorge Herrera, Betzi Perez and Oldemar Valdez helped with initial sorting of the arthropod and plant material. Lawrie Springate kindly checked botanical nomenclature. Roger Le Guen and Laurent Pyot provided free use of their photos. Isabelle Bachy helped to edit the figures and plates. IBISCA is greatly honoured to be under the patronage of Professor E.O. Wilson of Harvard University. We dedicate this article to the late Professor Joachim Adis, tropical ecologist, entomologist, colleague and friend.

References

Adis, J., Basset, Y., Floren, Hammond, P.M. & Linsenmair, K.E., 1998. Canopy fogging of an overstorey tree - recommendations for standardization. *Ecotropica*, 4: 93-97.

Adis, J. & Schubart, H.O.R., 1984. Ecological research on arthropods in Central Amazonian forest ecosystems with recommendation for study procedures. In: Cooley, J. & Golley, F.B. (eds.). Trends in Ecological Research for the 1980's. Plenum Press, New York, pp. 111-144.

André, H.M., Ducarme, X. & Lebrun, P., 2002. Soil biodiversity: myth, reality or conning? *Oikos*, 96: 3-24.

André, H.M., Lebrun, P. & Noti, M.-I., 1992. Biodiversity in Africa: a plea for more data. *Journal of African Zoology,* 106: 3-15.

Barker, M. & Standridge, N., 2002. Ropes as mechanisms for canopy access. In: Mitchell, A.W., Secoy, K. & Jackson, T. (eds.). The Global Canopy Handbook. Global Canopy Programme, Oxford, pp. 13-23.

Barrios, H. & Medianero, E., 1999. Riqueza de insectos formadores de agallas en nueve zonas de vida de la República de Panamá. *Scientia (Panamá)*, 14: 39-58.

Basset, Y., 2001. Communities of insect herbivores foraging on mature trees vs. seedlings of Pourouma bicolor (Cecropiaceae) in Panama. *Oecologia*, 129: 253-260.

Basset, Y., Aberlenc, H.-P., Springate, N.D. & Delvare, G., 1997. A review of methods for collecting arthropods in tree canopies. In: Stork, N.E., Adis, J.A. & Didham, R.K. (eds.). Canopy Arthropods. Chapman & Hall, London, pp. 27-52.

Basset, Y., Horlyck, V. & Wright, S.J. (eds.), 2003b.

Studying forest canopies from above: The International Canopy Crane Network. Smithsonian Tropical Research Institute and UNEP, Panama.

Basset, Y., Novotny, V., Miller, S.E. & Kitching, R.L. (eds.), 2003a. Arthropods of Tropical Forests. Spatio-temporal Dynamics and Resource Use in the Canopy. Cambridge University Press, Cambridge.

Basset, Y., Novotny, V., Miller, S. E., Weiblen, G. D., Missa, O. & Stewart, A.J.A., 2004. Conservation and biological monitoring of tropical forests: the role of parataxonomists. *Journal of Applied Ecology*, 41: 163-174.

Basset, Y. & Samuelson, G.A., 1996. Ecological characteristics of an arboreal community of Chrysomelidae in Papua New Guinea. In: Jolivet, P.H.A. & Cox, M.L. (eds.). Chrysomelidae Biology. Volume 2. Ecological Studies. SPB Academic Publishing, Amsterdam, pp. 243-262.

Bradbury, J., 2003. Surveying Panama's treetops. *Frontiers in Ecology and Environment*, 9: 457.

Castaño-Meneses, G., Basset, Y., Winchester, N. & Barrios, H., 2006. Colembolos (Hexapoda: Collembola) del dosel en la selva tropical de San Lorenzo, Provincia de Colon, Panama. *Entomologia mexicana*, 5: 486-490.

Charles, E. & Basset, Y., 2005. Stratification of leaf beetle assemblages (Coleoptera: Chrysomelidae) in two forest types in Panama. *Journal of Tropical Ecology*, 21: 329-336.

Chave, J., Condit, R., Aguilar, S., Hernandez, A., Lao, S. & Pérez, R., 2004. Error propagation and scaling for tropical forest biomass estimates. *Philosophical Transactions of the Royal Society, Series B*, 359: 409-420.

Colwell, R.K., 2004. EstimateS, Version 7: Statistical Estimation of Species Richness and Shared Species from Samples. User's Guide and application published at: http://purl.oclc.org/estimates.

Condit, R., Aguilar, S., Hernandez, A., Pérez, R., Lao, S., Angehr, G., Hubbell, S.P. & Foster, R.B., 2004. Tropical forest dynamics across a rainfall gradient and the impact of an El Niño dry season. *Journal of Tropical Ecology*, 20: 51–72.

Condit, R. & Pérez, R. 2002. Tree Atlas of the Panama Canal Watershed. Center for Tropical Forest Science, Panama. http://ctfs.si.edu/webatlas/maintreeatlas.html.

Condit, R., Watts, K., Bohlman, S.A., Pérez, R., Foster, R.B. & Hubbell, S.P., 2000. Quantifying the deciduousness of tropical forest canopies under varying climates. *Journal of Vegetation Science*, 11: 649-658.

Corbara, B., Basset, Y. & Barrios, H. 2006. IBISCA: a large-scale study of arthropod mega-diversity in a neotropical rainforest. In: Segers, H., Desmet, P. & Baus, E. (eds.). Tropical Biodiversity: Science, Data, Conservation. Proceedings of the 3rd GBIF Science Symposium, Brussels, 18-19 April 2005. Belgian Biodiversity Platform, Brussels, pp. 61-64.

Curletti, G., 2005. Notes about the genus *Agrilus* Curtis, 1825 in Panama. *Lambillionea*, 105: 545-571.

Curletti, G., Aberlenc, H.-P. & Basset, Y., 2006. Progetto IBISCA in Panama: considerazioni sul genere *Agrilus* Curtis, 1825. *Rivista Piemontese di Storia Naturale*, 27: 339-348.

Didham, R.K. & Fagan, L.L., 2003. Project IBISCA – Investigating the biodiversity of soil and canopy arthropods. *The Weta*, 26: 1-6.

Didham, R.K. & Fagan, L.L., 2004. Forest canopies. *In*: Burley, J., Evans, J. & Youngquist, J. (eds.). Encyclopaedia of Forest Sciences. Academic Press, Elsevier Science, London, pp. 68-80.

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

Erwin, T.L. & Scott, J.C., 1980. Seasonal and size patterns, trophic structure and richness of Coleoptera in the tropical arboreal ecosystem: the fauna of the tree *Luehea seemannii* Triana and Planch in the Canal Zone of Panama. *The Coleopterists Bulletin*, 34: 305-322.

Ewers, R.M., Thorpe, S. & Didham, R.K., 2007. Synergistic interactions between edge and area effects in a heavily fragmented landscape. *Ecology*, 88: 96-106.

Fagan, L.L., Didham, R.K., Winchester, N.N., Behan-Pelletier, V., Clayton, M., Lindquist, E. & Ring, R.A., 2006. An experimental assessment of biodiversity and species turnover in terrestrial vs canopy leaf litter. *Oecologia*, 147: 335-347.

Ferrer, J. & Ødegaard, F., 2005. New species of darkling beetles from Central America with systematic notes (Coleoptera: Tenebrionidae). *Annales Zoologici*, 55: 633-661.

Fisher, B.L., 1998. Ant diversity patterns along an elevational gradient in the réserve spéciale d'Anjanaharibe-Sud and on the western Masoala peninsula, Madagascar. *Fieldiana Zoology (n.s.)*, 90: 39-67.

Frost, S.W., 1957. The Pennsylvania light trap. *Journal of Economic Entomology*, 50: 287-292.

Gerardo, N.M., Mueller, U.G., Price, S.L. & Currie, C.R., 2004. Exploiting a mutualism: parasite specialization on cultivars within the fungus-growing ant symbiosis. *Proceedings of the Royal Society of London, Series B*, 271: 1791-1798.

Godfray, H.C., Lewis, O.T. & Memmott, J., 1999. Studying insect diversity in the tropics. *Philosophical Transactions of the Royal Society, Series B*, 354: 1811-1824.

Grassle, J.F. & Smith, W., 1976. A similarity measure sensitive to the contribution of rare species and its use in investigation of variation in marine benthic communities.

Oecologia, 25: 13-22.

Hallé, F. (ed.), 2000. Biologie d'une Canopée de Forêt Tropicale - IV. Rapport de la Mission du Radeau des Cimes à la Makandé, Forêt des Abeilles, Gabon, Janvier-Mars 1999. Pro-Natura International & Opération Canopée, Paris.

Hammond, P.M., 1990. Insect abundance and diversity in the Dumoga-Bone National Park, N. Sulawesi, with special reference to the beetle fauna of lowland rain forest in the Toraut region. *In*: Knight, W.J. & Holloway, J.D. (eds.). Insects and the Rain Forests of South East Asia (Wallacea). The Royal Entomological Society of London, London, pp. 197-254.

Hammond, P.M., 1995. Magnitude and distribution of biodiversity. In: Heywood, V.T. & Watson, R.T. (eds.). Global Biodiversity Assessment. Cambridge University Press, Cambridge, pp. 113-138.

Hammond, P.M., Stork, N.E. & Brendell, M.J.D., 1997. Tree-crown beetles in context: a comparison of canopy and other ecotone assemblages in a lowland tropical forest in Sulawesi. In: Stork, N.E., Adis, J.A. & Didham, R.K. (eds.). Canopy Arthropods. Chapman & Hall, London, pp. 184-223.

Hardy, O.J., 2007. BiodivR 1.0. A program to compute statistically unbiased indices of species diversity within samples and species similarity between samples using rarefaction principles. Published at: http://www.ulb.ac.be/sciences/ecoevol/biodivr.html.

Hooper, D.U., Bignell, D.E., Brown, V.K., Brussaard, L., Dangerfield, J.M., Wall, D.H., Wardle, D.A., Coleman, D.C., Giller, K.E., Lavelle, P., Van der Putten, W.H., De Ruiter, P.C., Rusek, J., Silver, W.L., Tiedje, J.M. & Wolters, V., 2000. Interactions between aboveground and belowground biodiversity in terrestrial ecosystems: patterns, mechanisms, and feedbacks. *BioScience,* 50: 1049-1061.

Hubbell, S.P., 2001. The Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press, Princeton.

Kweskin, M.P., 2004. Jigging in the fungus-growing ant *Cyphomyrmex costatus*: a response to collembolan garden invaders? *Insectes Sociaux*, 51: 158–162.

Kirkendall, L.R. & Ødegaard, F. 2007. Ongoing invasions of old-growth tropical forests: establishment of three incestuous beetle species in southern Central America (Curculionidae: Scolytinae). *Zootaxa*, in press.

Kitching, R.L., 2006. Crafting the pieces of the biodiversity jigsaw. *Science*, 313: 1055-1057.

Kitching, R.L., Basset, Y., Ozanne, C. & Winchester, N., 2002. Canopy knockdown techniques for sampling canopy arthropod fauna. In: Mitchell, A.W., Secoy, K. & Jackson, T. (eds.). The Global Canopy Handbook. Techniques of Access and Study in the Forest Roof. Global Canopy Programme, Oxford, pp. 134-139.

Kitching, R.L., Orr, A.G., Thalib, L., Mitchell, H., Hopkins, M.S. & Graham, A.W., 2000. Moth assemblages as indicators of environmental quality in remnants of upland Australian rain forest. *Journal of Applied Ecology*, 37: 284-297.

Lavelle, P., Lattaud, C., Trigo, D. & Barois, I., 1995. Mutualism and biodiversity in soils. *Plant & Soil,* 170: 23-33.

Lawton, J.H., Bignell, D.E., Bolton, B., Bloemers, G.F., Eggleton, P., Hammond, P.M., Hodda, M., Holt, R.D.,

Larsen, T.B., Mawdsley, N.A., Stork, N.E., Srivastava, D.S. & Watt, A.D., 1998. Biodiversity inventories, indicator taxa and effects of habitat modification in a tropical forest. *Nature*, 391: 72-76.

Leponce, M., Theunis, L., Delabie, J.H.C. & Roisin, Y., 2004. Scale dependence of diversity measures in a leaf-litter ant assemblage. *Ecography*, 27: 253-267.

Lindo, Z. & Winchester, N.N., 2006. A comparison of microarthropod assemblages with emphasis on oribatid mites in canopy suspended soils and forest floors associated with ancient western redcedar trees. *Pedobiologia*, 50: 31-41.

Linsenmair, K.E., Davis, A.J., Fiala, B. & Speight, M.R. (eds.), 2001. Tropical Forest Canopies: Ecology and Management. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Longino, J.T., 2004. Arthropods of the tropical canopy (and elsewhere). *Ecology*, 85: 1170-1171.

Lowman, M.D. & Nadkarni, N.M. (eds.), 1995. Forest Canopies. Academic Press, San Diego.

May, R.M., 1990. How many species? *Philosophical Transactions of the Royal Society, Series B*, 330: 293-304.

Mann, C.C., 1991. Extinction: are ecologists crying wolf? *Science*, 253: 736-738.

Medianero, E., Castaño-Meneses, G., Tishechkin, A., Basset, Y., Barrios, H, Ødegaard, F., Cline, A.R. & Bail, J., 2007. Influence of local illumination and plant composition on the spatial and seasonal distribution of litter-dwelling arthropods in a tropical forest. *Pedobiologia*, 51: 131-145.

Medianero, E., Valderrama, A. & Barrios, H., 2003. Diversidad de insectos minadores de hojas y formadores de agallas en el dosel y sotobosque del bosque tropical. *Acta Zoológica Mexicana (n.s.)*, 89: 153-168.

Miller, S.E., 2000. Taxonomy for understanding biodiversity - the strengths of the BioNet International model. In: Jones, T. & Gallagher, S. (eds.). Proceedings of the Second BioNet-International Global Workshop (BIGW2). BioNet International, Egham, Surrey, England, pp. 13-18.

Mitchell, A.W., Secoy, K. & Jackson, T. (eds.), 2002. Global Canopy Handbook. Techniques of Access and Study in the Forest Roof. Global Canopy Programme, Oxford.

Muirhead-Thomson, R.C., 1991. Trap Responses of Flying Insects. Academic Press, London.

Novotny, V., Basset, Y., Miller, S.E., Weiblen, G.D., Bremer, B., Cizek, L. & Drozd, P., 2002. Low host specificity of herbivorous insects in a tropical forest. *Nature*, 416: 841-844.

Ødegaard, F., 2000. How many species of arthropods? Erwin's estimate revised. *Biological Journal of the Linnean Society*, 71: 583-597.

Ødegaard, F., 2003. Taxonomic composition and host specificity of phytophagous beetles in a dry forest in Panama. In: Basset, Y., Novotny, V., Miller, S.E. & Kitching, R.L. (eds.). Arthropods of tropical forests: Spatio-temporal dynamics and resource use in the canopy. Cambridge University Press, Cambridge, pp. 220-236.

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., 2006. Host specificity, alpha- and beta-diversity of phytophagous beetles in two tropical forests in Panama. *Biodiversity and Conservation*, 15: 83-105.

Ødegaard, F., Diserud, O.H. & Østbye, K., 2005. The importance of plant relatedness for host utilization among phytophagous insects. *Ecology Letters*, 8: 612-617.

Ødegaard, F. & Frame, D., 2007. Generalist flowers and phytophagous beetles in two tropical canopy trees: resources for multitudes. *Taxon*, 56: 696-706.

Osler, G.H.R. & Beattie, A.J., 2001. Contribution of oribatid and mesostigmatid soil mites in ecologically based estimates of global species richness. *Austral Ecology,* 26: 70-79.

Ozanne, C.M.P., Anhuf, D., Boulter, S.L., Keller, M., Kitching, R.L., Körner, C., Meinzer, F.C., Mitchell, A.W., Nakashizuka, T., Silva Dias, P.L., Stork, N.E., Wright, S.J. & Yoshimura, M., 2003. Biodiversity meets the atmosphere: a global view of forest canopies. *Science*, 301: 183-186.

Palacios-Vargas, J.G., Castaño-Meneses, G. & Gómez-Anaya, J.A., 1998. Collembola from the canopy of a Mexican tropical decidous forest. *Pan-Pacific Entomologist,* 74: 47-54.

Parker, G.G., Smith, A.P. & Hogan, K.P., 1992. Access to the upper forest canopy with a large tower crane. *BioScience,* 42: 664-670.

Pennisi, E., 2005. Sky-high experiments. *Science*, 309: 1314-1315.

Pokon, R., Novotny, V. & Samuelson, G.A., 2005. Host specialization and species richness of root-feeding chrysomelid larvae (Chrysomelidae, Coleoptera) in a New Guinea rain forest. *Journal of Tropical Ecology*, 21: 595-604.

Pyke, C.R., Condit, R., Aguilar, S. & Lao, S., 2001. Floristic composition across a climatic gradient in a neotropical lowland forest. *Journal of Vegetation Science*, 12: 553–566.

Quintero, D., & Aiello, A. (eds.), 1992. Insects of Panama and Mesoamerica: Selected studies. Oxford University Press, Oxford and New York.

Ribeiro, S.P. & Basset, Y., 2007. Gall-forming and free-feeding herbivory along vertical gradients in a lowland tropical rainforest: the importance of leaf sclerophylly. *Ecography*, in press.

Roisin, Y., Dejean A., Corbara B., Orivel J., Samaniego, M. & Leponce, M., 2006. Vertical stratification of the termite assemblage in a neotropical rainforest. *Oecologia*, 149: 301-311.

Roslin, T., 2003. Not so quiet on the high frontier. *Trends in Ecology and Evolution*, 18: 376-379.

Sagers, C.L. & Coley, P.D., 1995. Benefits and costs of defense in a Neotropical shrub. *Ecology*, 76: 1835-1843.

Sala, O.E., Chapin, F.S., III, Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., LeRoy Poff, N., Syrkes, M. T., Walker, B.H., Walker, M. & Wall, D.H., 2000. Global biodiversity scenarios for the year 2100. *Nature,* 287: 1770-1774.

Schmidl, J. & Corbara, B., 2005. IBISCA – Artenvielfalt der Boden- und Baumkronen-Arthropoden in einem tropischen Regenwald (San Lorenzo NP, Panama). *Entomologische Zeitschrift*, 115: 104-108.

Schnitzer, S.A., 2005. A mechanistic explanation for global patterns of liana abundance and distribution. *The American Naturalist*, 166: 262-276.

Schowalter, T.D. & Ganio, L.M., 2003. Diel, seasonal and disturbance-induced variation in invertebrate assemblages. *In*: Basset, Y., Novotny, V., Miller, S.E. & Kitching, R.L. (eds.). Arthropods of tropical forests: Spatio-temporal dynamics and resource use in the canopy. Cambridge University Press, Cambridge, pp. 315-328.

Southwood, T.R.E., 1978. Ecological Methods, with Particular Reference to the Study of Insect Populations. 2nd ed. Chapman and Hall, London.

Springate, N.D. & Basset, Y., 2004. IBISCA 2003-2005, Panama: progress report. *Bulletin of the British Ecological Society*, 35: 21-23.

Stork, N.E., 1988. Insect diversity: facts, fiction and speculation. *Biological Journal of the Linnean Society,* 35: 321-337.

Stork, N.E., 1991. The composition of the arthropod fauna of Bornean lowland rain forest trees. *Journal of Tropical Ecology,* 7: 161-180.

Stork, N.E., 1996. Tropical forest dynamics: the faunal components. In: Edwards, D.S., Booth, W.E. & Choy, S.C. (eds.). Tropical Rainforest Research - Current Issues. Kluwer Academic Publishers, Amsterdam, pp. 1-20.

Stork, N.E., Adis, J.A. & Didham, R.K. (eds.), 1997. Canopy Arthropods. Chapman & Hall, London.

Stork, N.E., & Grimbacher, P.S., 2006. Beetle assemblages from an Australian tropical rainforest show that the canopy and the ground strata contribute equally to biodiversity. *Proceedings of the Royal Society of London*, *Series B*, 273: 1969-1975.

Townes, H., 1972. A light-weight Malaise trap. *Entomological News*, 83: 239-247.

Veech, J.A., Summerville, K.S., Crist, T.O. & Gering, J.C., 2002. The additive partitioning of species diversity: recent revival of an old idea. *Oikos*, 99: 3-9.

Villelsen, P., Schultz, T.R. & Boomsma, J.J., 2002. Identifying the transition between single and multiple mating in attine ants. *Proceedings of the Royal Society of London, Series B*, 269: 1541-1548.

Walter, D.E., & Behan-Pelletier, V., 1999. Mites in forest canopies: Filling the size distribution shortfall? *Annual Review of Entomology*, 44: 1-19.

Walter, D.E., Seeman, O., Rodgers, D. & Kitching, R.L., 1998. Mites in the mist: how unique is a rainforest canopy-knockdown fauna? *Australian Journal of Ecology,* 23: 501-508.

Wcislo, W.T., Arneson, L., Roesch, K., Gonzalez, V., Smith, A.M. & Fernandez-Marin, H., 2004. The evolution of nocturnal behaviour in sweat bees, *Megalopta genalis* and *M. ecuadoria* (Hymenoptera: Halictidae): an escape from competitors and enemies? *Biological Journal of the Linnean Society*, 83: 377-387.

Weaver, P.L. & Bauer, G.P., 2004. The San Lorenzo Protected Area: A Summary of Cultural and Natural Resources. International Institute of Tropical Forestry, San Juan, PR.

Welden, C.W., Hewett, S.W., Hubbell, S.P. & Foster, R.B., 1991. Sapling survival, growth and recruitment: relationship to canopy height in a Neotropical forest. *Ecology*, 72: 35-50.

Winchester, N.N. & Behan-Pelletier, V., 2003. Fauna of suspended soils in an *Ongokea gore* tree in Gabon. In: Basset, Y., Novotny, V., Miller, S.E. & Kitching, R.L. (eds.). Arthropods of Tropical Forests. Spatio-temporal Dynamics and Resource Use in the Canopy. Cambridge University Press, Cambridge, pp. 102-109.

Wright, S.J., Horlyck, V., Basset, Y., Barrios, H., Bethancourt, A., Bohlman, S.A., Gilbert, G.S., Goldstein, G., Graham, E.A., Kitajima, K., Lerdau, M.T., Meinzer, F.C., Ødegaard, F., Reynolds D.R. , Roubik, D.W., Sakai, S., Samaniego, M., Sparks, J.P., Van Bael, S., Winter K. & Zotz, G., 2003. Tropical Canopy Biology Program, Republic of Panama. In: Basset, Y., Horlyck, V. & Wright S.J. (eds.). Studying Forest Canopies from Above: The International Canopy Crane Network. Smithsonian Tropical Research Institute and UNEP, Panama City, pp. 138-158. Available on-line at: http://www.stri.org/english/research/facilities/terrestrial/cranes/canopy_crane_network.php.

Zayed, A., Roubik, D.W. & Packer, L., 2003. Use of diploid male frequency data as an indicator of pollinator decline. *Proceedings of the Royal Society of London, Series B*, 271: S9-S12.

Zotz, G., 2004. How prevalent is crassulacean acid metabolism among vascular epiphyes? *Oecologia*, 138: 184-192.

[1]Smithsonian Tropical Research Institute, Panama City, Republic of Panama, basset@si.edu (YB, author for correspondence), hernande@bci.si.edu (AH), samaniem@si.edu (MS) & roubikd@si.edu (DWR)

[2]Université Blaise Pascal, Clermont-Ferrand, France, Bruno.Corbara@univ-bpclermont.fr

[3]Universidad de Panamá, Panama City, Republic of Panama, hbarrios@ancon.up.ac.pa

[4]Muséum d'histoire naturelle de la Ville de Genève, Genève, Switzerland, philippecuenoud@bluewin.ch

[5]Royal Belgian Institute of Natural Sciences, Brussels, Belgium, Maurice.Leponce@naturalsciences.be

[6]CIRAD, Montpellier, France,henri-pierre.aberlenc@cirad.fr

[7]University of Erlangen, Erlangen, Germany, johannes_bail@hotmail.com (JB) & jschmidl@biologie.uni-erlangen.de (JS)

[8]Griffith University, Brisbane, Australia, darren.Bito@student.griffith.edu.au (DB) & r.kitching@griffith.edu.au (RLK)

[9]University of Bristol, Bristol, U. K., jon.bridle@bristol.ac.uk

[10]Universidad Nacional Autónoma de México, México, gcm@hp.fciencias.unam.mx

[11]Biological Centre, Czech Academy of Sciences, Ceske Budejovice, Czech Republic, cizek@entu.cas.cz (LC) & novotny@entu.cas.cz (VN)

[12]Movimiento de Investigaciones Biológicas de Panamá, Panama City, Republic of Panama, aydcornejo@yahoo.com (AC) & mateo@heidimail.com (MR)

[13]Museo Civico di Storia Naturale, Carmagnola, Italy, giancurletti@tiscalinet.it

[14]Centro de Pesquisas do Cacau, Itabuna, Brazil, delabie@cepec.gov.br

[15]EDB, UMR-CNRS 5174, University Toulouse III, Toulouse, France, dejean@cict.fr (AD) & orivel@cict.fr (JO)

[16]University of Canterbury, Christchurch, New Zealand, r.didham@canterbury.ac.nz

[17]Ministère de la Région Wallonne, Gembloux, Belgium, M.Dufrene@mrw.wallon.be

[18]Crop and Food Research, Lincoln, New Zealand, FaganL@crop.cri.nz

[19]Universität Würzburg, Würzburg , Germany, floren@biozentrum.uni-wuerzburg.de

[20]University of Montpellier, Montpellier, France, aurora@isem.univ-montp2.fr (DF) and francishalle@wanadoo.fr (FH)

[21]Université Libre de Bruxelles, Brussels, Belgium, ohardy@ulb.ac.be (OJH) & yroisin@ulb.ac.be (YR)

[22]Universidade Estadual de Campinas, São Paulo, Brazil, thomasl@unicamp.br

[23]University of Oxford, Oxford, U. K., owen.lewis@zoology.ox.ac.uk

[24]The New Guinea Binatang Research Center, Madang, Papua New Guinea, binatangi@datec.com.pg

[25]Museo Nacional de Ciencias Naturales, Madrid, Spain, mcnem823@mncn.csic.es

[26]University of York, York, U. K, om502@york.ac.uk

[27]Global Canopy Programme, Oxford, U. K., andrew.m itchell@zoology.ox.ac.uk

[28]Norwegian Institute for Nature Research, Trondheim, Norway, frode.odegaard@nina.no

[29]Conservation International (TEAM), Brazil, evandro@icb.ufmg.br

[30]Roehampton University, London, U. K., c.ozanne@roehampton.ac.uk

[31]Pro Natura International, Paris, France, ol.pascal@freesurf.fr

[32]Imperial College, London, U. K., sara_vpn@yahoo.com.mx

[33]Universidade Federal de Ouro Preto, Ouro Preto, Brazil, spribeiro@iceb.ufop.br

[34]University of Helsinki, Helsinki, Finland, tomas.roslin@helsinki.fi

[35]Natural History Museum of Denmark, Copenhagen, Denmark, llsorensen@snm.ku.dk

[36]Lousiana State Arthropod Museum, Baton Rouge, USA, atishe1@lsu.edu

[37]Biotrac SPRL, Brussels, Belgium, cvo@floridienne.be

[38]University of Victoria, Victoria, Canada, winchest@uvic.ca

Appendix 1 — Frequency of 165 tree species occurring at the 12 IBISCA sites, listed by species. Nomenclature follows Condit and Pérez (2002), further checked against resources at http://mobot.mobot.org/W3T/Search/vast.html, http://www.ipni.org/index.html and the Royal Botanic Garden, Edinburgh, by Lawrie Springate.

Code	Plant Species	Family	B1	B2	C1	C2	C3	F1	F2	F3	I1	R1	R2	R3
PIT1BA	*Abarema barbouriana* (Standl.) Barneby & J.W. Grimes	Fabaceae:Mimos.	-	-	-	-	-	-	-	-	-	-	1	-
ACALDI	*Acalypha diversifolia* Jacq.	Euphorbiaceae	-	-	-	-	-	-	-	-	-	1	-	-
AEGIPA	*Aegiphila panamensis* Moldenke	Verbenaceae	-	-	-	-	-	-	-	-	-	-	-	1
ALCHLA	*Alchornea latifolia* Pax & K. Hoffm. in Engl.	Euphorbiaceae	-	-	1	-	-	-	-	-	-	-	-	-
AMAICO	*Amaioua corymbosa* Kunth	Rubiaceae	-	-	-	-	-	-	-	1	-	-	-	-
ANACEX	*Anacardium excelsum* (Bert. & Balb. ex Kunth) Skeels	Anacardiaceae	-	-	-	-	-	-	-	-	-	1	-	-
ANDIIN	*Andira inermis* (W. Wright) DC.	Fabaceae:Papil.	-	-	2	-	1	-	-	-	1	-	-	-
APEIME	*Apeiba membranacea* Spruce ex Benth.	Tiliaceae	-	1	1	-	1	-	-	-	2	-	-	-
APEITI	*Apeiba tibourbou* Aubl.	Tiliaceae	-	-	1	-	-	-	-	-	-	-	-	-
ARDIBA	*Ardisia bartlettii* Lundell	Myrsinaceae	-	-	-	-	-	-	-	-	1	-	1	-
ASPICR	*Aspidosperma cruentum* Benth. *ex* Müll.Arg.	Apocynaceae	-	-	-	-	6	1	1	5	1	-	4	1
AST1ST	*Astrocaryum standleyanum* L.H. Bailey	Arecaceae	-	-	-	-	-	-	-	-	-	4	-	-
BACTC1	*Bactris coloniata* L. H. Bailey	Arecaceae	-	2	1	-	2	2	-	-	2	1	-	3
BACTC2	*Bactris coloradonis* L.H. Bailey	Arecaceae	-	1	-	2	1	-	1	4	1	-	-	-
BACTMA	*Bactris major* Jacq.	Arecaceae	-	-	-	-	-	1	-	-	-	-	-	1
BACTPA	*Bactris panamensis* de Nevers & Grayum	Arecaceae	-	-	-	1	-	-	-	-	-	-	-	-
BEILPE	*Beilschmiedia pendula* (Sw.) Hemsl.	Lauraceae	-	-	-	-	-	-	-	-	-	-	-	1
BROSGU	*Brosimum guianense* (Aubl.) Huber	Moraceae	1	1	-	3	-	-	-	3	3	-	3	-
BROSUT	*Brosimum utile* var. *utile* (Kunth) Pittier	Moraceae	6	21	1	2	5	7	2	5	8	-	4	4
BYRSCR	*Byrsonima crassifolia* (L.) Kunth	Malpighiaceae	1	-	-	-	-	-	-	-	-	-	-	-
CALOLO	*Calophyllum longifolium* Willd.	Clusiaceae	4	-	-	1	-	1	1	1	2	-	2	-
CARAGU	*Carapa guianensis* Aubl.	Meliaceae	2	2	3	1	1	4	6	4	1	6	-	3
CASECO	*Casearia commersoniana* Cambess.	Flacourtiaceae	-	5	-	-	1	1	-	1	-	-	1	1
CASESY	*Casearia sylvestris* Sw.	Flacourtiaceae	-	-	-	-	-	-	-	-	1	1	-	-
CASSEL	*Cassipourea elliptica* (Sw.) Poir.	Rhizophoraceae	-	-	-	1	-	-	-	1	-	-	-	-
CECRIN	*Cecropia insignis* Liebm.	Cecropiaceae	-	-	2	-	-	-	-	-	-	-	-	1
CECRPE	*Cecropia peltata* L.	Cecropiaceae	-	-	1	-	-	-	-	-	-	-	-	-
CESPMA	*Cespedezia spathulata* Planch.	Ochnaceae	1	-	2	1	1	1	-	1	-	-	1	-
CESTME	*Cestrum megalophyllum* Dunal	Solanaceae	-	-	-	-	-	-	-	-	-	1	-	-
CHA1TE	*Chamaedorea tepejilote* Liebm. ex Mart.	Arecaceae	-	-	-	-	-	-	-	-	-	1	-	-
CHR2AR	*Chrysophyllum argenteum* Jacq.	Sapotaceae	2	-	1	-	1	-	-	-	1	-	-	-
COCCPA	*Coccoloba padiformis* Meisn. in A. DC.	Polygonaceae	-	-	-	-	-	-	-	-	1	-	-	-
COURPA	*Couratari guianensis* Aubl.	Lecythidaceae	-	-	-	-	-	-	2	2	-	-	-	-
CREMPA	*Cremastosperma panamense* Maas	Annonaceae	-	1	2	-	-	1	1	1	-	-	-	2
CUPASC	*Cupania scrobiculata* Rich.	Sapindaceae	-	3	1	-	-	1	-	-	1	-	5	-
CYM1LA	*Cymbopetalum lanugipetalum* Schery	Annonaceae	-	-	1	-	1	-	1	-	3	-	-	-
DENDAR	*Dendropanax arboreus* (L.) Dec. & Planch	Araliaceae	3	-	2	-	4	3	3	11	4	-	2	2
DES2PA	*Desmopsis panamensis* (B.L. Rob.) Saff.	Annonaceae	-	-	-	-	1	-	-	-	1	8	-	-
DIO2AR	*Diospyros artanthifolia* Mart. ex Miq.	Ebenaceae	-	-	1	-	-	-	-	-	-	-	1	-
DISCGU	*Discophora guianensis* Miers	Icacinaceae	-	-	-	-	2	-	-	4	-	-	1	-
DUSS1	*Dussia* sp.1	Fabaceae:Papil.	1	-	1	1	1	-	-	-	-	-	-	-
ERY1CO	*Erythrina costaricensis* Micheli	Fabaceae:Papil.	2	-	-	-	-	-	-	-	-	-	-	-
ERY2MA	*Erythroxylum macrophyllum* Cav.	Erythroxylaceae	-	-	-	-	-	-	-	-	-	-	-	1
EUGECO	*Eugenia coloradoensis* Standl.	Myrtaceae	-	-	-	-	-	-	1	-	1	-	-	1
EUGESP	*Eugenia* sp.	Myrtaceae	-	-	-	-	-	-	-	-	1	-	-	-
EUTEPR	*Euterpe precatoria* Mart.	Arecaceae	-	-	-	-	-	-	-	-	1	-	2	-
FARAOC	*Faramea occidentalis* (L.) A. Rich.	Rubiaceae	-	-	-	-	-	-	-	-	-	10	-	-
FICUOB	*Ficus obtusifolia* Kunth *in* Humb., Bonpl. & Kunth	Moraceae	-	-	-	-	-	-	1	-	-	-	-	-
FICUTO	*Ficus tonduzii* Standl.	Moraceae	-	-	1	-	-	-	-	-	-	-	-	-
GAR2MA	*Garcinia madruno* (H. B. K.) Hammel	Clusiaceae	-	-	-	1	-	-	1	-	1	-	4	-
GEONCO	*Geonoma congesta* H. Wendl. ex Spruce	Arecaceae	1	21	7	8	8	16	31	14	4	-	1	24
GEONCU	*Geonoma cuneata* H. Wendl. ex Spruce	Arecaceae	-	-	4	4	6	12	13	3	2	-	-	2
GUARGU	*Guarea guidonia* (L.) Sleumer	Meliaceae	1	-	-	-	-	-	-	-	-	1	-	-
GUAR2	*Guarea* sp. ‘sherman’	Meliaceae	-	-	-	1	-	-	-	-	-	2	-	-
GUATAM	*Guatteria amplifolia* Triana & Planch.	Annonaceae	-	-	1	-	1	1	-	2	-	-	1	-
GUATDU	*Guatteria dumetorum* R.E. Fr.	Annonaceae	2	-	2	-	-	3	1	2	-	-	1	2
GUETFO	*Guettarda foliacea* Standl.	Rubiaceae	-	-	-	-	-	-	-	-	-	1	-	-

HEISAC	*Heisteria acuminata* (Humb. & Bonpl.) Engl.	Olacaceae	1	-	-	1	3	-	1	1	-	-	1	-
HENRSU	*Henriettea succosa* (Aubl.) DC.	Melastomataceae	-	-	-	-	-	-	-	-	-	-	1	-
HIRTRA	*Hirtella racemosa* Lam.	Chrysobalanaceae	-	-	-	-	-	-	-	2	1	-	-	-
HIRTTR	*Hirtella triandra* Sw.	Chrysobalanaceae	-	-	1	-	-	-	-	-	-	5	-	-
HUMIDI	*Humiriastrum diguense* (Cuatrec.) Cuatrec.	Humiriaceae	-	-	-	-	-	-	2	1	-	-	-	-
HYERAL	*Hyeronima alchorneoides* Allemão	Euphorbiaceae	1	-	-	-	-	-	-	-	-	-	-	-
HYM1ME	*Hymenolobium mesoamericanum* H.C. Lima	Fabaceae:Papil.	-	-	1	-	-	1	-	-	-	-	-	-
INGACO	*Inga cocleensis* Pittier	Fabaceae:Mimos.	-	-	1	-	-	-	-	-	1	-	-	-
INGAGO	*Inga goldmanii* Pittier	Fabaceae:Mimos.	1	-	1	-	-	-	-	-	-	-	-	-
INGAMA	*Inga marginata* Willd.	Fabaceae:Mimos.	1	-	-	-	-	-	-	-	-	-	-	-
INGAM2	*Inga multijuga* Benth.	Fabaceae:Mimos.	2	-	-	-	-	1	-	-	1	-	-	-
INGAPE	*Inga pezizifera* Benth.	Fabaceae:Mimos.	3	-	3	1	-	2	1	-	2	-	-	-
INGASE	*Inga sertulifera* DC.	Fabaceae:Mimos.	11	-	2	-	-	-	-	-	-	-	-	-
JAC1CO	*Jacaranda copaia* (Aubl.) D. Don	Bignoniaceae	-	1	-	-	1	-	-	1	-	-	-	-
LACIAG	*Lacistema aggregatum* (P.J. Bergius) Rusby	Flacourtiaceae	1	-	1	-	3	-	-	2	1	3	3	1
LACMPA	*Lacmellea panamensis* (Woodson) Markgr.	Apocynaceae	7	-	1	-	-	-	-	1	-	-	-	-
LAETPR	*Laetia procera* (Poepp.) Eichler	Flacourtiaceae	-	2	-	-	-	-	-	-	-	-	-	-
LICAHY	*Licania hypoleuca* Benth.	Chrysobalanaceae	-	2	1	1	-	1	-	-	-	-	-	-
LONCLA	*Lonchocarpus latifolius* (Willd.) DC.	Fabaceae:Papil.	-	-	2	-	-	-	-	-	-	-	1	-
LOZAPI	*Lozania pittieri* (S.F. Blake) L.B. Sm.	Flacourtiaceae	5	-	1	1	-	-	-	-	1	-	1	2
LUEHSE	*Luehea semannii* Triana & Planch.	Tilliaceae	-	-	-	-	-	-	-	-	-	1	-	-
MALMSP	*Malmea* sp.	Annonaceae	-	-	-	-	-	-	-	-	-	1	-	-
MANIBI	*Manilkara bidentata* (A. DC.) A. Chev.	Sapotaceae	-	2	-	1	2	-	1	-	1	-	4	-
MAQUCO	*Maquira guianensis* subsp. *costaricana* (Standl.) C.C.Berg	Moraceae	2	-	1	-	-	-	-	-	-	-	-	-
MARAPA	*Maranthes panamensis* (Standl.) Prance & F. White	Chrysobalanaceae	-	-	-	-	-	-	2	1	2	-	9	-
MAR1LA	*Marila laxiflora* Rusby	Clusiaceae	-	2	6	8	7	5	3	5	-	-	8	10
MATAAP	*Matayba apetala* Radlk.	Sapindaceae	2	-	-	1	-	1	2	-	5	-	1	-
MICOAF	*Miconia affinis* DC.	Melastomataceae	-	1	-	-	-	-	-	-	-	-	-	-
MICOLI	*Miconia ligulata* Almeda	Melastomataceae	-	-	3	3	5	-	-	1	-	-	-	-
MICONE	*Miconia nervosa* (Sm.) Triana	Melastomataceae	-	-	1	-	-	-	-	-	-	-	-	-
MICOSI	*Miconia simplex* Triana	Melastomataceae	-	-	-	5	1	1	1	2	1	-	-	2
MICOSP	*Miconia* sp. 1	Melastomataceae	-	-	4	-	-	-	-	-	-	-	-	-
MICO3	*Miconia* sp. 3	Melastomataceae	-	-	1	-	1	-	-	-	-	-	-	-
MOLLDA	*Mollinedia darienensis* Standl.	Monimiaceae	-	-	-	-	-	2	3	-	-	-	-	-
MORTAN	*Mortoniodendron anisophyllum* (Standl.) Standl. & Steyerm.	Tiliaceae	-	-	2	-	1	-	-	-	-	-	-	-
MOURMY	*Mouriri myrtilloides* subsp. *parvifolia* (Benth.) Morley	Melastomataceae	-	-	1	-	-	-	-	1	1	-	-	-
MYRCGA	*Myrcia gatunensis* Standl.	Myrtaceae	-	-	-	-	-	-	-	-	-	-	1	-
MYRCZE	*Myrcia zetekiana* (Standl.) B.Holst	Myrtaceae	1	-	1	-	2	-	1	-	-	1	-	-
MYR22	*Myrciaria* sp. 2	Myrtaceae	-	-	-	-	1	-	-	-	-	-	-	-
NECTPU	*Nectandra purpurea* (Ruiz & Pav.) Mez	Lauraceae	3	-	-	1	-	-	1	-	1	-	1	-
NEEAAM	*Neea amplifolia* Donn. Sm.	Nyctaginaceae	1	-	-	-	-	-	-	-	1	-	-	-
OCOTDE	*Ocotea dendrodaphne* Mez	Lauraceae	-	-	-	-	-	-	2	-	1	1	-	1
OCOTIR	*Ocotea insularis* (Meisn.) Mez	Lauraceae	-	-	2	1	1	-	-	-	-	-	-	1
OCOTPU	*Ocotea puberula* (Rich.) Nees	Lauraceae	-	-	1	-	-	-	-	-	-	-	-	-
OENOMA	*Oenocarpus mapora* H. Karst.	Arecaceae	1	7	-	3	2	5	2	2	2	-	2	2
OURACO	*Ouratea prominens* Dwyer	Ochnaceae	-	-	1	1	-	-	1	2	-	2	-	-
OXANLO	*Oxandra longipetala* R.E. Fr.	Annonaceae	-	-	-	-	-	-	-	1	-	-	-	-
OXANPA	*Oxandra panamensis* R.E. Fr.	Annonaceae	-	-	-	-	-	-	-	-	-	7	-	-
PENTMA	*Pentagonia macrophylla* Benth.	Rubiaceae	-	-	1	1	-	-	-	1	2	4	-	1
PERAAR	*Pera arborea* Mutis	Euphorbiaceae	-	1	-	-	-	-	-	-	-	-	-	-
PEREXA	*Perebea xanthochyma* H. Karst.	Moraceae	4	13	9	12	2	1	3	5	2	5	8	5
PICRLA	*Picramnia latifolia* Tul.	Picramniaceae	-	-	-	-	-	-	-	-	-	4	-	-
PIPEA1	*Piper arboreum* subsp. *arboreum* Aubl.	Piperaceae	-	-	1	-	-	-	-	-	-	-	-	-
PIPECU	*Piper colonense* C. DC.	Piperaceae	9	-	-	-	-	-	-	-	-	-	-	-
PIPECO	*Piper cordulatum* C. DC.	Piperaceae	-	-	-	-	-	-	1	-	-	-	-	-
PIPERE	*Piper reticulatum* L.	Piperaceae	3	-	-	-	-	-	-	-	-	-	-	-
PIPESP	*Piper* sp. 1	Piperaceae	2	-	-	-	-	-	-	-	-	-	-	-
PIPE5	*Piper* sp. 5	Piperaceae	-	-	1	-	-	-	-	-	-	-	-	-
PIT1RU	*Pithecellobium* sp.	Fabaceae:Mimos.	1	-	-	-	-	-	-	-	-	-	-	-
POSOLA	*Posoqueria latifolia* (Rudge) Roem. & Schult.	Rubiaceae	-	-	-	-	-	-	-	-	-	2	-	-
POULAR	*Poulsenia armata* (Miq.) Standl.	Moraceae	-	-	2	-	-	-	-	-	-	-	-	-
POURBI	*Pourouma bicolor* Mart.	Cecropiaceae	1	1	1	-	-	-	-	1	1	-	-	-
POUTRE	*Pouteria reticulata* (Engl.) Eyma	Sapotaceae	-	-	2	1	1	1	-	1	-	1	-	-
PRI2CO	*Prioria copaifera* Griseb.	Fabaceae:Caesal.	-	-	-	-	-	-	-	-	-	1	-	-

PROTGL	*Protium glabrum* (Rose) Engl.	Burseraceae	-	-	2	-	-	-	-	-	1	-	-	-
PROTPA	*Protium panamense* (Rose) I.M. Johnst.	Burseraceae	4	7	1	1	3	3	3	7	7	-	14	6
PROTTE	*Protium tenuifolium* Engl.	Burseraceae	-	-	-	-	-	-	-	-	-	2	-	-
PSE2SP	*Pseudolmedia spuria* (Sw.) Griseb.	Moraceae	1	5	-	-	-	-	-	-	-	-	-	-
PSYCCH	*Psychotria chagrensis* Standl.	Rubiaceae	2	-	-	-	-	-	-	-	-	-	-	-
PSYCG3	*Psychotria grandis* Sw.	Rubiaceae	-	-	-	-	-	-	-	-	-	1	-	-
PSYCHO	*Psychotria horizontalis* Sw.	Rubiaceae	76	-	-	-	-	-	-	-	-	-	-	-
PSYCSU	*Psychotria suerrensis* Donn. Sm.	Rubiaceae	-	-	3	-	1	1	1	3	2	-	-	1
QUIISC	*Quiina schippii* Standl.	Quiinaceae	-	1	-	-	-	-	-	-	-	-	-	-
RANDAR	*Randia armata* (Sw.) DC.	Rubiaceae	-	-	-	-	-	-	-	-	-	5	-	-
RINOSQ	*Rinorea squamata* S.F. Blake	Violaceae	-	-	-	-	-	-	-	-	-	26	-	-
SAPISP	*Sapium* sp. 'broadleaf'	Euphorbiaceae	1	-	-	-	-	-	-	-	-	-	-	-
SIMAAM	*Simarouba amara* Aubl.	Simaroubaceae	1	2	1	-	-	-	-	-	1	-	-	-
SLOAM1	*Sloanea* sp.aff.*meianthera* Donn. Sm.	Elaeocarpaceae	-	-	2	1	-	-	-	2	1	-	1	1
SOCREX	*Socratea exorrhiza* (Mart.) H. Wendl.	Arecaceae	-	7	3	3	2	5	8	7	9	-	5	6
SOROAF	*Sorocea affinis* Hemsl.	Moraceae	8	-	2	-	1	-	-	-	1	1	-	-
SPONMO	*Spondias mombin* L.	Anacardiaceae	-	-	-	-	-	-	-	-	-	1	-	-
STEMGR	*Stemmadenia grandiflora* (Jacq.) Miers	Apocynaceae	-	-	-	-	-	-	-	-	-	-	1	-
SWARS2	*Swartzia simplex* var. *continentalis* Urb.	Fabaceae:Papil.	-	1	1	1	4	-	2	-	1	-	1	1
SYMPGL	*Symphonia globulifera* L. f.	Clusiaceae	-	-	1	-	1	1	1	1	1	-	-	-
SYNEWA	*Synechanthus warscewiczianus* H. Wendl.	Arecaceae	-	-	3	3	5	-	-	3	2	-	3	4
TAB2AR	*Tabernaemontana arborea* Rose in Donn. Sm.	Apocynaceae	-	-	-	-	1	-	-	-	-	-	-	-
TACHVE	*Tachigali versicolor* Standl. & L.O. Williams	Fabaceae:Caesal.	1	-	2	1	-	-	1	1	2	-	-	1
TALIPR	*Talisia princeps* Oliv.	Sapindaceae	-	-	-	-	-	-	-	-	-	1	-	-
TAPIGU	*Tapirira guianensis* Aubl.	Anacardiaceae	2	1	5	-	1	4	3	2	-	-	5	3
TERMAM	*Terminalia amazonia* (J.F. Gmel.) Exell	Combretaceae	3	-	-	-	-	-	-	-	-	-	-	-
TERNTE	*Ternstroemia tepezapote* Schltdl. & Cham.	Theaceae	1	-	-	-	-	-	-	-	-	-	-	-
TET4JO	*Tetrathylacium johansenii* Poepp. in Poepp. & Endl.	Flacourtiaceae	-	-	-	-	-	-	-	-	-	1	-	-
THEOBE	*Theobroma bernoullii* Pittier	Sterculiaceae	-	1	-	1	3	-	-	-	2	-	2	-
TOCOPI	*Tocoyena pittieri* (Standl.) Standl.	Rubiaceae	-	-	-	-	-	-	-	-	-	-	1	-
TOVOLO	*Tovomita longifolia* (Rich.) Hochr.	Clusiaceae	3	3	1	6	6	2	3	11	8	-	12	-
TOVOST	*Tovomita stylosa* Hemsl.	Clusiaceae	-	1	3	8	8	5	4	2	3	-	8	1
TRATAS	*Trattinnickia aspera* (Standl.) Swart	Burseraceae	-	2	-	-	-	-	-	-	-	-	-	-
TRI2PL	*Trichilia pleeana* (A. Juss.) C. DC.	Meliaceae	-	-	-	-	-	-	-	-	-	1	-	-
TRI2TU	*Trichilia tuberculata* (Triana & Planch.) C. DC.	Meliaceae	-	-	-	-	-	-	-	-	-	4	-	-
UNONPA	*Unonopsis panamensis* R.E. Fr.	Annonaceae	-	2	5	3	5	2	9	6	2	-	2	3
VIROEL	*Virola elongata* (Benth.) Warb.	Myristicaceae	-	-	3	-	1	1	1	-	-	-	-	-
VIROSP	*Virola multiflora* (Standl.) A.C. Sm.	Myristicaceae	5	1	-	1	-	1	5	-	1	1	-	-
VIROSE	*Virola sebifera* Aubl.	Myristicaceae	3	1	1	1	1	1	1	5	5	-	3	1
VIROSU	*Virola surinamensis* (Rol. ex Rottb.) Warb.	Myristicaceae	5	-	2	-	-	-	-	-	-	3	-	-
VISMBA	*Vismia baccifera* (L.) Tr. & Pl.	Clusiaceae	-	-	-	-	-	1	-	1	-	-	-	-
VOCHFE	*Vochysia ferruginea* Mart.	Vochysiaceae	-	-	-	1	-	1	-	-	-	-	-	-
XYL1MA	*Xylopia macrantha* Triana & Planch.	Annonaceae	-	-	2	2	1	9	5	2	3	-	-	4
ZANTPR	*Zanthoxylum acuminatum* subsp. *juniperinum* (Poepp.) Reynel	Rutaceae	1	-	-	-	-	-	-	-	-	-	-	-
???	Unidentified trees		4	2	3	2	-	3	-	2	1	-	-	-