



# Influence of local illumination and plant composition on the spatial and seasonal distribution of litter-dwelling arthropods in a tropical rainforest

Enrique Medianero<sup>a,\*</sup>, Gabriela Castaño-Meneses<sup>b</sup>, Alexey Tishechkin<sup>c</sup>, Yves Basset<sup>d</sup>, Héctor Barrios<sup>a</sup>, Frode Ødegaard<sup>e</sup>, Andrew R. Cline<sup>f</sup>, Johannes Bail<sup>g</sup>

<sup>a</sup>Programa Centroamericano de Maestría en Entomología, Vicerrectoría de Investigación y Postgrado, Universidad de Panamá, Apartado 0824, Panama

<sup>b</sup>Ecología y Sistemática de Microartrópodos, Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, Universidad Nacional Autónoma de México, Ciudad Universitaria, 04510 México, D.F., Mexico

<sup>c</sup>Louisiana State Arthropod Museum, Dept Entomology, Louisiana State University, 400 Life Sciences Building, Baton Rouge, LA 70803-1710, USA

<sup>d</sup>Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancon, Panama City, Republic of Panama

<sup>e</sup>Norwegian Institute for Nature Research, Tungasletta 2, NO-7485 Trondheim, Norway

<sup>f</sup>California Department of Food and Agriculture-Plant Pest Diagnostics, 3294 Meadowview Road, Sacramento, CA 95832-1448, USA

<sup>g</sup>Ecology and Nature Conservation, Institute for Zoology I, Staudtstr. 5, D-91058 Erlangen, Germany

Received 30 October 2006; received in revised form 28 February 2007; accepted 8 March 2007

## KEYWORDS

Basal area;  
Canonical partitioning;  
Litter;  
Pitfall traps;  
Soil;  
Taxonomic resolution

## Summary

Using pitfall traps, we evaluated the spatial and seasonal variance in arthropod abundance, species richness, higher taxonomic and species composition, and guild structure within the ground litter of seven sites in a relatively undisturbed rainforest in Panama. We examined each of these five arthropod-dependent variables at two spatial scales (a few meters and a few hundred meters) and one temporal scale (a few months encompassing dry and wet periods), against environmental variables including local illumination and plant composition. Trap catches (9458 arthropods collected during 630 trap-days) were high compared to similar studies in temperate

\*Corresponding author. Departamento de Biodiversidad y Biología Evolutiva. Museo Nacional de Ciencias Naturales, c/ José Gutiérrez Abasca 2, 28006 Madrid, Spain.

E-mail addresses: [mcnem823@mncn.csic.es](mailto:mcnem823@mncn.csic.es), [medianero@yahoo.com](mailto:medianero@yahoo.com) (E. Medianero), [gcm@hp.fciencias.unam.mx](mailto:gcm@hp.fciencias.unam.mx) (G. Castaño-Meneses), [atishe1@lsu.edu](mailto:atishe1@lsu.edu) (A. Tishechkin), [bassety@si.edu](mailto:bassety@si.edu) (Y. Basset), [hbarrios@ancon.up.ac.pa](mailto:hbarrios@ancon.up.ac.pa) (H. Barrios), [frode.odegaard@nina.no](mailto:frode.odegaard@nina.no) (F. Ødegaard), [ACline@cdfa.ca.gov](mailto:ACline@cdfa.ca.gov) (A.R. Cline), [johannes\\_bail@hotmail.com](mailto:johannes_bail@hotmail.com) (J. Bail).

forests. We observed spatial and seasonal differences in abundance, species richness and composition of litter-dwelling arthropods. Often these differences appeared weakly related to geographical coordinates. They reflected forest structure (basal area) and local plant composition, and less so illumination patterns or seasonal changes in radiation. Seasonal variance was high and may relate to surrogate variables accounting for seasonal changes in litter moisture. The composition of higher taxa and species was often predicted by different independent variables at the three scales studied. Guild structure was difficult to predict. Our study lead us to expect that litter-dwelling arthropods may be more seasonal than soil microarthropods in tropical rainforests; and that tropical litter-dwelling arthropods may also be more spatially variable and seasonal than their temperate counterparts. We also recommend that conservation studies using pitfall traps in tropical rainforests should focus on: (1) taxonomic resolution to understand the functional complexity of soil organisms; (2) spatial replication to address subtle changes in plant composition throughout the study area; and (3) seasonal replicates to be commensurate with seasonal changes in litter moisture.

© 2007 Elsevier GmbH. All rights reserved.

## Introduction

The microgeographic distribution of arthropods, their sheer number and short generation span make them ideal organisms for biodiversity monitoring (Mattoni et al., 2000). The arthropod component of the soil/litter fauna appears particularly important in this context, since it is involved in crucial processes of ecosystem functioning, such as decomposition and nutrient cycling (Wolters, 2001). The soil/litter interface of tropical and temperate forests differ in several aspects: tropical soils are usually N-rich and P-poor, as opposed to the N-poor and P-rich soils of temperate forests; the amount of litterfall in tropical rainforests is usually high and may occur year-long; and decomposition rates are also twice as fast in tropical forests than in temperate forests, and the primary decomposers are predominantly fungi (Beck, 1971; Takeda and Abe, 2001; McGroddy et al., 2004). Thus, the organic layer of tropical forests is composed mainly of freshly fallen litter and a poorly developed humus horizon. In both tropical and temperate forests, food resources for soil/litter animals include mainly fresh litter, live fungi and dead organic matter; however, many animals feed on fungi in tropical forests (Beck, 1971; Takeda and Abe, 2001). As a result, litter and fungal feeders are more abundant in tropical than temperate forests, but densities of detritus-feeders in the soil are one-order of magnitude lower in tropical than in temperate forests (Beck, 1971; Takeda and Abe, 2001; Wiwatwitaya and Takeda, 2005). Therefore, separate studies of ground litter-dwelling and soil fauna should be conducted especially in the tropics.

The soil/litter fauna remains very poorly studied, particularly in the tropics (André et al., 2002). Studies of local differences in the composition of soil/litter arthropods within old-growth or relatively undisturbed tropical forests are few (Atkin and Proctor, 1988; Burgess et al., 1999; Goehring et al., 2002; Wiwatwitaya and Takeda, 2005). The paucity of studies is primarily due to: (a) the considerable variability in arthropod abundance and species richness, due to the substrate, its past history and disturbance regime, as well as to a suite of abiotic and biotic factors; and (b) the difficulty in extracting, identifying, studying and monitoring focal organisms (Brussaard et al., 1997).

In temperate forests, variability in the distribution of soil/litter arthropods depends mostly on soil humidity, pH and the physical and chemical composition of litter produced by one or a few tree species (Burghouts et al., 1992). In tropical rainforests, similar variability can be explained at the regional scale by altitude, soil nutrients and disturbance regime (Atkin and Proctor, 1988; Burghouts et al., 1992; Olson, 1994; Thomas and Proctor, 1997). At the local scale, however, the situation may be confounded by many factors. Since tropical species are often thought to be more habitat-specific than their temperate counterparts (Stevens, 1989) and/or diversity of habitats and microhabitats are higher in tropical forests than in temperate forests (Novotny et al., 2006), highly variable distribution of tropical soil/litter arthropods may be expected, even at the scale of a few meters (Kaspari, 1996).

Soil/litter moisture content, illumination, topography, canopy structure (affecting illumination and evaporation), standing crop litter, litter fall

and canopy leachate from diverse tree species with complex phenologies, and predator-free space (particularly from army ants) are important variables that potentially influence the distribution of soil/litter arthropods (Levings, 1983; Levings and Windsor, 1984; Frith and Frith, 1990; Burghouts et al., 1992; Kaspari, 1996; Burgess et al., 1999; Hansen, 2000; Noti et al., 2003). In addition, seasonal variability of soil/litter arthropods also may be influenced by changes in rainfall, severity of dry season, and timing and periodicity of litterfall (Willis, 1976; Levings and Windsor, 1982, 1985; Frith and Frith, 1990). However, broad and unifying patterns are few.

One of the reasons for this relative lack of consensus of what the key factors in dictating distribution are, may be that most studies on tropical soil/litter arthropods were analyzed at higher taxon level or considered only total abundance (Lieberman and Dock, 1982; Levings and Windsor, 1984; Pearson and Derr, 1986; Atkin and Proctor, 1988; Frith and Frith, 1990; Burghouts et al., 1992; Thomas and Proctor, 1997; Burgess et al., 1999). Those concerned with species level analyses often included only a single taxon, usually ants or scarabs (Levings, 1983; Kaspari, 1996; Feener et al., 1998; Goehring et al., 2002). However, discriminating power for biological monitoring appears highest when considering different taxa at the species level (Basset et al., 2004). Here, we evaluate whether variables affecting distribution of litter-dwelling arthropods are similar when considering higher taxa, species or functional guilds.

Despite obvious shortcomings (Adis, 1979), pitfall traps are routinely used in conservation studies of litter-dwelling arthropods, as they are inexpensive and allow high spatial replication for habitat comparisons. Many studies concerned with forest fragmentation and edge effects have used unbaited or baited pitfall traps (Klein, 1989; Goehring et al., 2002; Şekerçioğlu et al., 2002; Quintero and Roslin, 2005). However, little is known about the variability in arthropod spatial distribution in relatively undisturbed forest tracks and away from edges. For example, changes in arthropod-dependent variables with plant composition irrespective of disturbance may represent a confounding factor.

Our specific objectives were to evaluate spatial and seasonal variance in arthropod (a) abundance; (b) species richness; (c) higher taxonomic composition; (d) species composition; and (e) guild structure within ground litter of a relatively undisturbed rainforest with pitfall traps. We considered each of these dependent variables at two spatial scales (a few meters and a few hundred meters) and one temporal scale (a few months encompassing dry

and wet periods). Whenever applicable, we tested the influence of variables such as spatial location, local illumination and plant composition. Our specific questions included: (i) Do overall patterns for dependent variables converge? (ii) Which variables best explain observed variability in the five dependent variables?

## Material and methods

### Study area

Field work was conducted in a lowland rainforest in San Lorenzo Protected Area (Colón Province, Republic of Panama), on Chagres sandstone (Late Miocene or early Pliocene; Pyke et al., 2001). Annual rainfall averages 3139 mm and mean annual air temperature is 26.0 °C (1998–2002 data; [http://striweb.si.edu/esp/physical\\_monitoring/descrip\\_fts.htm](http://striweb.si.edu/esp/physical_monitoring/descrip_fts.htm)). The climate is wet year-round, with a comparatively drier season between January and mid-April (average dry season length = 125 days; Chave et al., 2004). Study sites were located near a six-hectare plot where 22,400 trees (238 species) with a bole size of  $\geq 1$  cm dbh were identified, measured and mapped. Structurally, the forest can be characterized as including 3338 stems per ha ( $> 1$  cm dbh) with a total basal area of ca. 32 m<sup>2</sup> per hectare and the tallest trees being 45 m. The forest has been free of severe disturbance for 150 years and is predominantly evergreen, with  $< 3\%$  loss in canopy cover by the end of dry season (Condit et al., 2000, 2004).

The Investigating the Biodiversity of Soil and Canopy Arthropods (IBISCA) programme (Didham and Fagan, 2003) operated in this study area on 12 sites, each 20 m  $\times$  20 m in area, in which plants  $> 1$  cm dbh were tagged and identified. These sites were situated within a 2 km radius on top of a hill that slopes down toward the Rio Chagres, with the exception of site R1 located in the floodplain. Site B1 was disturbed by past US warfare training (Weaver and Bauer, 2004). Seven sites (Table 1) were surveyed in September 2003–October 2003 (wet season), sites C1 and C2 again in February 2004 (dry season) and May 2004 (early wet season) and sites C1, C2 and C3 in November 2004 (wet season; Table 2).

### Arthropod collecting and processing

We estimated the abundance and activity of litter arthropods with pitfall traps, i.e., plastic cylinders of 6 cm in diameter and 15 cm depth (0.424 l) containing a solution of 50 ml ethanol,

**Table 1.** Main characteristics of IBISCA sites (20 m × 20 m) surveyed with pitfall traps at San Lorenzo

Site code	Latitude (deg. N)	Longitude (deg. W)	No. stems > 10 mm	No. tree species	Basal area (m <sup>2</sup> )	Succession index <sup>a</sup>	Canopy openness (%) <sup>b</sup>	Mean reflected light (lux, n = 28)	Largest trees/Most common spp. <sup>c</sup>	Dominant sp. BA (m <sup>2</sup> ), % <sup>c</sup>
B1	9° 17.133	79° 59.106	207	51	1.01	14.13	7.55	8.0 ± 2.2	Sap, Cal/Psy, Ing	Cal 0.46, 45
B2	9° 17.146	79° 59.290	125	34	1.62	17.39	6.00	57.2 ± 10.1	Ape, Per/Bro, Geo	Ape 0.34, 21
C1	9° 16.774	79° 58.495	138	70	1.21	19.62	6.80	57.6 ± 25.4	Bro, And/Prb, Geo	Bro 0.68, 72
C2	9° 16.793	79° 58.499	102	43	1.05	14.72	7.60	68.2 ± 10.7	Voc, Bro/Prb, Mar	Voc 0.15, 23
C3	9° 16.779	79° 58.468	121	48	1.16	15.91	10.60	8.5 ± 1.6	Bro, Jac/Tov, Geo	Bro 0.47, 46
I1	9° 16.617	79° 58.377	123	59	1.13	16.33	6.90	21.6 ± 5.1	Ape, Cal/Soc, Tov	Ape 0.23, 20
R1	9° 17.322	79° 58.533	123	39	2.93	17.64	2.91	26.6 ± 1.9	Lue, Spon/Rin, Far	Lue 1.08, 37

<sup>a</sup>Average of [specific fraction of recruits (SFR) in light gaps × no. of conspecific individuals in the plot]. SFR extracted from Weiden et al. (1991), when known (60 species out of 165, 36%).  
<sup>b</sup>Proportion of visible sky (open) to closed in hemispherical pictures, analyzed by Hemiview 2.0.

<sup>c</sup>And = *Andira inermis* (W. Wright) DC.; Ape = *Apeiba membranacea* Spruce ex Benth.; Asp = *Aspidosperma spruceanum* Benth. ex Müll. Arg.; Bro = *Brosimum utile* (Kunth) Pittier; Cal = *Calophyllum longifolium* Willd.; Car = *Carapa guianensis* Aubl.; Den = *Dendropanax arboreus* (L.) Decne. and Planch.; Far = *Farama occidentalis* (L.) A. Rich.; Geo = *Geonoma congesta* H. Wendl. Ex Spruce; Geu = *Geonoma cuneata* H. Wendl. Ex Spruce; Hum = *Humiriastrum diguense* (Cuatrec.) Cuatrec.; Ing = *Inga sertifera* DC.; Jac = *Jacaranda copaia* (Aubl.) D. Don.; Lue = *Luehea seemannii* Triana and Planch.; Man = *Manilkara bidentata* (A. DC.) A. Chev.; Mar = *Marrla laxiflora* Rusby; Per = *Pera arborea* Mutis; Prb = *Perebea xanthochryma* H. Karst.; Pro = *Protium panamense* (Rose) I. M. Johnston.; Psy = *Psychotria horizontalis* Sw.; Rin = *Rinorea squamata* S.F. Blake; Sap = *Sapium* sp. 'broadleaf'; Soc = *Socratea exorrhiza* (Mart.) H. Wendl.; Spo = *Spondias mombin* L.; Tap = *Tapirira guianensis* Aubl.; Tov = *Tovomita stylosa* Hemsl.; Vir = *Virola multiflora* (Standl.) A.C. Sm.; Voc = *Vochysia ferruginea* Mart.

10 ml of liquid detergent and 5 g salt. Traps were covered with a 18 cm plastic plate to protect from rainfall. In each study site, 15 traps were buried flush with the soil surface, in a straight line at 1.3 m intervals. All traps were set > 300 m from forest edges. Traps were surveyed after 3 days, for a total sampling effort of 630 trap-days.

Arthropods were sorted to higher taxonomic categories (Hexapoda to families, other classes to orders: Appendix A), and later identified to species or morphospecies (unnamed but diagnosed entities; hereafter known as 'species'). The following taxa, were well represented in trap catches: Scolytinae, Scarabaeidae, Scydmaenidae, Carabidae, Nitidulidae, Curculionidae, Tenebrionidae and other Cucujoidea, Gryllidae and Auchenorrhyncha (mostly Cixiidae). This material contained different guilds (Appendix A), and included 74 species and 801 individuals (Appendix B). Taxa were assigned to the following guilds (following Moran and Southwood, 1982): chewers, sap-suckers, predators, parasitoids, wood-eaters, scavengers, ants, epiphyte grazers, fungal-feeders, tourists and 'unknown'. Higher taxa were assigned 'unknown' when including representatives of different guilds.

## Environmental variables and statistical analyses

Our five dependent variables were arthropod (a) abundance; (b) species richness; (c) higher taxonomic composition; (d) species composition; and (e) guild structure. The variance of each variable was examined at two spatial scales and one temporal scale. The 'micro-scale' considered data at a few meters (i.e., variance among pitfall traps), whereas 'local scale' considered data at a few hundred meters (i.e., variance among study sites). The 'seasonal' scale considered variance among seasonal replicates, a few month distant and encompassing dry and wet periods. In each category, higher taxonomic composition and guild structure included number of individuals instead of number of species, as the latter type of analysis is less robust due to possible influx of transient species (Basset et al., 1996).

We used ANOVA and the post hoc Tukey-test to assess differences in arthropod abundance and species richness between sites and seasonal replicates (repeated measures ANOVA in the latter case). We employed linear correlations and stepwise multiple regressions to evaluate the effects of several independent variables on these dependent variables. Abundance data were  $\sqrt{(x + 0.5)}$  transformed prior to analyses, to satisfy normality assumptions.

**Table 2.** Dependent variables for each combination of site and seasonal replicates

Sample	Date	Rainfall (mm) <sup>a</sup>	Degree-days (°C) <sup>b</sup>	Wind (km/h) <sup>c</sup>	Radiation (moles m <sup>-2</sup> ) <sup>d</sup>	Litter fall (g dry weight) <sup>e</sup>
C1-1	22–25 Sep. 2003	396.7	273.6	4.8	884.0	14.3
C1-2	3–6 Feb. 2004	39.6	210.7	9.7	988.9	64.5
C1-3	6–9 May 2004	358.7	223.2	8.4	968.8	17.0
C1-4	18–21 Oct. 2004	147.6	230.1	4.6	915.1	39.7
C2-1	25–28 Sep. 2003	406.4	272.7	4.6	914.7	14.3
C2-2	3–6 Feb. 2004	39.6	210.7	9.7	988.9	64.5
C2-3	6–9 May 2004	358.7	223.2	8.4	968.8	17.0
C2-4	18–21 Oct. 2004	147.6	230.1	4.6	915.1	39.7
C3-1	28 Sep.–1 Oct. 2003	432.5	273.1	4.6	914.7	15.9
C3-4	18–21 Oct. 2004	147.6	230.1	4.6	915.1	39.7
B1-1	6–9 Oct. 2003	423.7	271.9	4.4	939.4	20.4
B2-1	1–4 Oct. 2003	402.1	273.4	4.6	924.9	15.9
I1-1	11–14 Oct. 2003	357.6	273.9	4.1	958.0	20.4
R1-1	14–17 Oct. 2003	354.1	271.1	4.0	939.9	25.8

<sup>a</sup>Sum of rainfall for 30 preceding days; sum of rainfall for year 2003 = 3478 mm, for year 2004 = 2696 mm; sum of rainfall during dry season in 2003 = 254 mm, in 2004 = 308 mm.

<sup>b</sup>Sum of degree-days for 30 preceding days, see Methods and materials.

<sup>c</sup>Average wind speed over 30 preceding days.

<sup>d</sup>Sum of solar radiation of daily total of 30 preceding days.

<sup>e</sup>Sum of average weekly litterfall (20 traps of 0.25 m<sup>2</sup>) over 30 preceding days.

To compare species diversity in different sized samples, the expected number of species occurring in a subsample of size  $k$  was calculated, with  $k$  representing the maximal value permitted to compare all pairs of samples (Hardy, 2005).

The independence between faunal composition (higher taxa and species data)/guild structure and spatial location (e.g. at micro- and local scales) was tested by canonical partitioning. This method is more appropriate and robust than Mantel tests for explaining variance in community composition among sites (Legendre et al., 2005). Ecological variance in canonical partitioning is broken down into four fractions using partial ordination methods (Borcard et al., 2004): (a) a non-spatially structured component explained by environmental variables in the model, (b) a spatially structured component of environmental variance, (c) a fraction of spatially structured variance not explained by environmental variables, and (d) a residual fraction (unexplained variance). This method uses geographic coordinates as explanatory variables in constrained ordinations. Further, instead of using coordinates  $X$ ,  $Y$  as geographic coordinates, Borcard and Legendre (2002) proposed an approach to identify spatial patterns across the whole range of scales perceptible with a given data set. This method is based on computation of principal coordinates of a matrix of geographic neighbors (PCNM) among sampling sites. The advantage of

PCNM is that spatial dependence can be detected over a wider range of scales. PCNM variables were extracted from grid transect data using Space-Maker2 (Borcard and Legendre, 2004), and partial ordinations were performed with CANOCO (ter Braak and Smilauer, 1998). Linear ordinations, Principal Component Analysis (PCA) and Redundancy Analysis (RDA) were used in lieu of unimodal ordinations (i.e., Detrended Correspondence Analysis and Canonical Correspondence Analysis), since the length of detrending segments in our data sets was rather short (i.e., low number of spatial and seasonal replicates and concomitant short gradients: ter Braak and Smilauer, 1998).

Specifically, unconstrained ordinations (PCA) were performed at the micro-, local and seasonal scales for higher taxa, species and guilds to examine grouping of different sites and seasonal replicates. We further performed constrained ordinations (RDA) to evaluate effects of independent variables on composition and guild structure at the same scales. Selection of environmental variables was guided by a stepwise forward selection procedure in CANOCO. Finally, different partial RDA's enabled canonical partitioning. At the micro-scale, the influence of trap illumination over composition of trap catches was evaluated by performing a RDA in which trap illumination was the sole explanatory variable. All seasonal replicates were considered and this analysis was

performed with higher taxa (109 taxa, 210 traps), species (74 species, 162 traps) or guilds (11 guilds, 210 traps). Incident light on each trap was measured when surveying traps with a digital lux meter LX-1010B (Kaito Electronics Inc., Montclair, CA 91763, USA).

At the local scale, the influence of several variables was evaluated with faunal composition (higher taxa,  $n = 75$  and species,  $n = 43$ ) and guild structure ( $n = 11$ ) at the seven sites during the first replicate (i.e., masking seasonal effects) with RDA. Explanatory variables included the number of woody stems ( $\text{dbh} \geq 10 \text{ mm}$ ), the number of woody plant species, basal area, reflected light (average from 28 measurements within each site, cell facing down at dbh), canopy openness (proportion of visible sky open to closed, measured with Hemi-view 2.0 software from hemispherical pictures), and an index of vegetational succession (Welden et al., 1991) based on floristic composition (Table 1).

At the local scale, the influence of plant species composition on arthropod higher composition, species composition and guild structure was tested using predictive co-correspondence analysis (CO-CA; ter Braak and Schaffers, 2004). CO-CA attempts to relate one assemblage data set to another in a direct predictive way, and seeks to identify ecological gradients common to both assemblages. Plant composition was used within study sites as predictor data sets and taxa/species/guild data relevant to the first seasonal replication as dependent matrices. These analyses were performed with the cocorresp package of R Project software (R Development Core Team, 2006; Simpson, 2005).

To test seasonal variables with sufficient replicates, we considered seasonal replication at each study site as samples ( $n = 14$ ) and tested the influence of seasonal variables such as rainfall, air temperature (degree-days), solar radiation, wind speed and litterfall amount (Table 2) on the composition of higher taxa ( $n = 109$ ), species ( $n = 74$ ) and guilds ( $n = 11$ ) with RDAs. The first four variables were derived from meteorological data collected at the San Lorenzo canopy crane ([http://striweb.si.edu/esp//physical\\_monitoring/descrip\\_fts.htm](http://striweb.si.edu/esp//physical_monitoring/descrip_fts.htm)). Degree-days represent a better predictor than maximum air temperature for arthropods and were calculated with the rectangle method (Arnold, 1960):

Degree-days = ((Maximum temperature + Minimum temperature)/2) – Minimum threshold,

with minimum threshold set to  $18^\circ\text{C}$  (i.e., minimum temperature at night in the tropics). Litterfall was

estimated by weekly censuses of 40 litter traps located in the botanical plot ( $0.25 \text{ m}^2$  each, S.J. Wright, unpubl. data 1998–2005; methods as in Wright et al., 2004). The sum or average of these seasonal variables was considered over the 30 preceding days prior survey of pitfall traps, as this time lag has been shown to be relevant to tropical litter arthropods (Thaiutsa and Granger, 1979).

The floral/faunal (higher taxa and species only) similarities with the NNESS index between different combinations of sites and seasonal replications also was calculated. NNESS 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), and to an intermediate  $k$ -value expressed on a log distribution in base 2 (Grassle and Smith, 1976; Hardy, 2005).

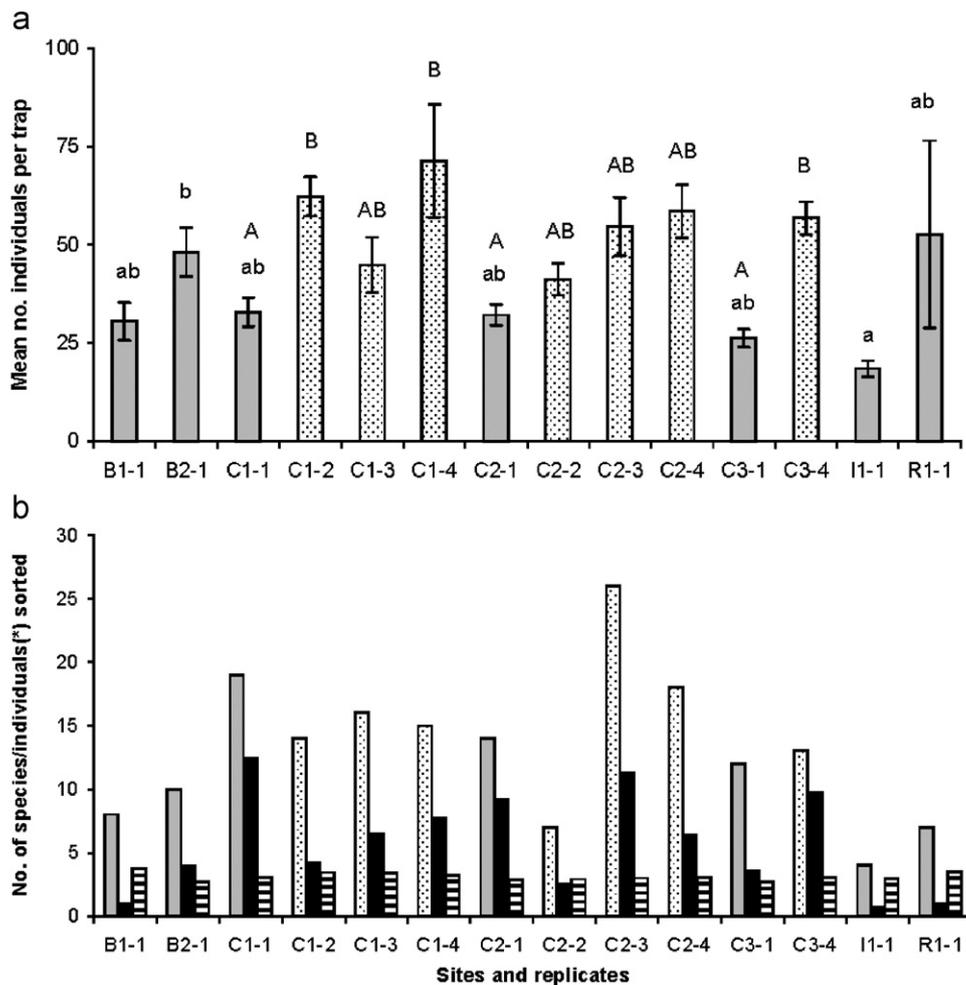
## Results

### Faunal considerations

In total, 9458 arthropods were collected, including 109 taxa (mean catch per trap =  $45.0 \pm 2.5$  individuals (SE),  $n = 210$ ). The most abundant arthropod families were Formicidae, Phoridae, Entomobryidae, Sminthuridae, Gryllidae and Isoptomidae (Appendix A). Within the sorted material, the most speciose families included Curculionidae-Scolytinae, Gryllidae, Scarabaeidae and Nitidulidae (Appendix B). Most collected material belonged to the scavenger guild (46.6%), followed by the 'unknown' category (22.3%), ants (14.3%) and predators (4.6%; Appendix A).

### Arthropod abundance and species richness

Trap catches ranged from 3 to 384 arthropods per sample and from 2 to 26 species sorted per sample. Arthropod abundance varied significantly among sites during the first temporal replication ( $F_{6,98} = 2.80$ ,  $P < 0.05$ ), with notable high and low values at sites B2 and I1, respectively (Fig. 1a). Variability in arthropod abundance among temporal replications was higher ( $F_{3,84} = 7.07$ ,  $P < 0.001$ ), with notable differences between September 2003 and October 2003 and October 2004 replications (Fig. 1a). The number of species sorted at different



**Figure 1.** (a) Mean number ( $\pm$ SE) of individuals and (b) number of species collected at study sites (gray bars) and during time replicates (stippled bars; coded as in Tables 1 and 2). For individuals, different letters indicate significant differences between sites (small capitals) or time replicates at a particular site (large capitals; Tukey's tests,  $P < 0.05$ ). For species, open bars represent number of species sorted; closed (black) bars, the number of individuals represented by these species, for comparison ([\*] divided by 10 for clarity); and hatched bars the expected number of species occurring in a subsample of size 4, the common sample size (see methods).

sites and temporal replications was highly correlated with number of individuals sorted (sample size;  $r = 0.85$ ,  $P < 0.001$ ). The number of expected species  $S(k)$  from these combinations of sites and seasonal replicates varied relatively little, despite the sometimes quite large numbers of sorted individuals (Fig. 1b).

A simple correlation test showed no relationship between arthropod abundance and incident light in the trap, neither when considering only the first replicate in September 2003–October 2003 nor all seasonal replicates ( $r_{105} = 0.14$  and  $r_{210} = 0.06$ ,  $P > 0.05$ ). However, a weak positive correlation between the number of species sorted in traps and incident light was determined ( $r_{162} = 0.183$ ,  $P < 0.05$ ,  $R^2$  of regression = 0.033). At the local scale, the best predictor (as tested by

stepwise multiple linear regression) of arthropod abundance was basal area (positive coefficient,  $F_{1,5} = 9.37$ ,  $P < 0.05$ ,  $R^2 = 0.65$ ). At the seasonal scale, arthropod abundance was best predicted with degree-days and wind speed (both with negative coefficients,  $F_{3,10} = 5.32$ ,  $P < 0.05$ ,  $R^2 = 0.50$ ). Predicting the number of species sorted from traps at the local or seasonal scale proved more difficult, with no significant multiple regressions ( $P > 0.05$ ). However,  $S(k)$ , the expected number of species in a subsample  $k (= 4)$ , could be predicted at the local scale by number of plant stems and canopy openness (the former with positive coefficient, the latter with negative coefficient,  $F_{1,5} = 8.06$ ,  $P < 0.05$ ,  $R^2 = 0.80$ ). At the seasonal scale,  $S(k)$  could not be predicted with the variables measured ( $P > 0.05$ ).

## Higher taxa and species composition

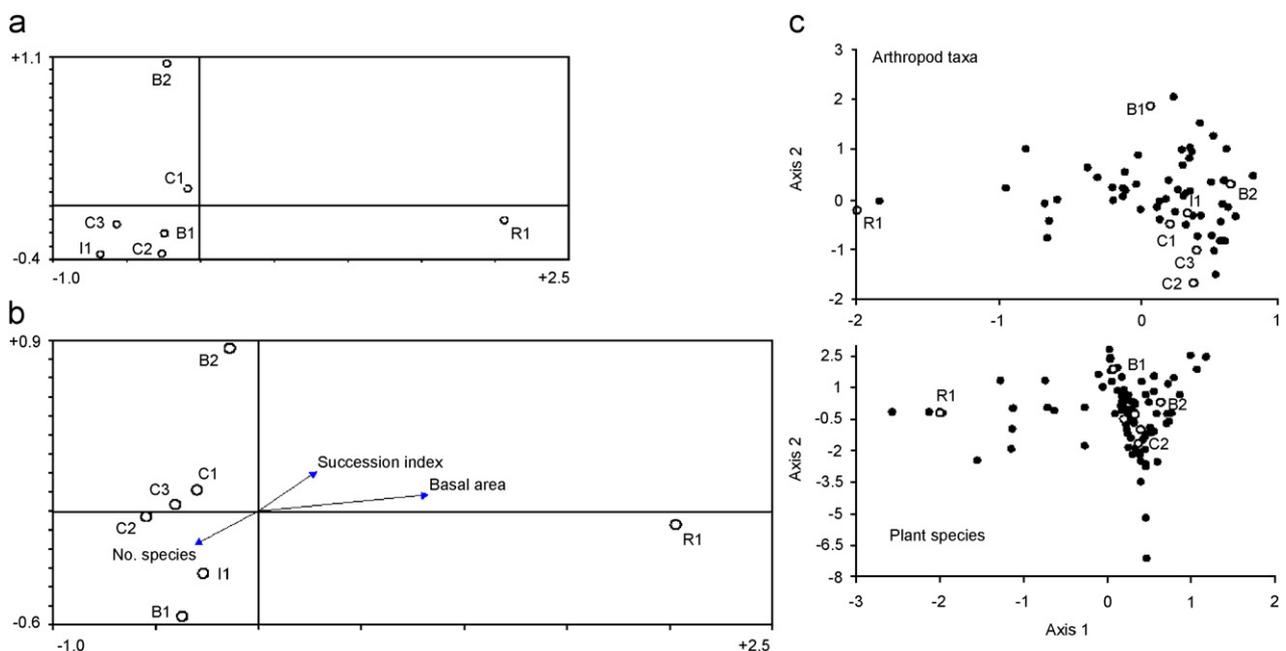
At the micro-scale, the first axis extracted by PCA on higher arthropod taxa explained 65% of total variance, but the explanation for this result remains obscure. The RDA with trap illumination as sole explanatory factor was not significant (overall Monte-Carlo test  $P > 0.05$  with 1000 permutations), but geographical coordinates of the traps explained 4% of the variance in trap composition ( $P < 0.05$  with 1000 permutations). Patterns were different when considering species composition: trap illumination significantly affected trap composition, but explained little of the variance (2.6%; RDA,  $P < 0.05$  with 1000 permutations). Further, geographical coordinates of the traps did not affect trap composition at the species level.

At the local scale (sites), axes 1 and 2 combined of PCA for higher arthropod taxa explained 95.3% of the variance. Study sites were not clearly clustered with regard to distance (note the position of closest sites, C1–C2–C3, in Fig. 2a). Patterns were similar for the arthropod species data set. Other explanatory variables in the RDA that allowed examination of higher faunal composition at different sites included basal area, number of plant species and succession index. Canonical axes 1 and 2 combined explained 86.6% of the variance (69.9% explained by axis 1), with basal area best explaining axis 1 ( $r = 0.98$ ; overall Monte-Carlo test  $P < 0.05$  with 1000 permutations; Fig. 2b). A similar analysis using

species instead of higher taxa yielded different patterns: canonical axes 1 and 2 combined explained 63.8% of the variance, with light best explaining axis 1 ( $r = 0.77$ , explained 55% of the variance; overall Monte-Carlo test of significance  $P < 0.05$  with 1000 permutations).

Geographical coordinates explained a significant amount of variance for arthropod higher composition and species composition (RDA, 82.2% and 14.9%, respectively; overall Monte-Carlo test of significance  $P < 0.05$  with 1000 permutations). Most of the explained variance in arthropod higher composition derived from spatially structured environmental variance, whereas explained variance in species composition derived from non-spatial environmental variance (Table 3). The first axis of CO-CA predicting composition of arthropod taxa from composition of plant species at different sites was significant (permutation test,  $F = 0.539$ ,  $P = 0.01$ , percentage fit = 35.0; Fig. 2c), whereas others were not ( $P > 0.05$ ). The taxa-derived and plant-derived scores of sites on CO-CA axis 1 were highly correlated ( $r = 0.981$ ,  $P < 0.001$ ). However, all axes of CO-CA predicting arthropod species from plant species matrix were not significant (permutation tests, all with  $P > 0.05$ ).

PCA of higher arthropod taxa ordered by seasonal replicates clearly segregated the October 2003–September 2003 and October 2004 replications (Fig. 3a). Axes 1 and 2 combined of PCA explained 62% of total variance. Seasonal variables

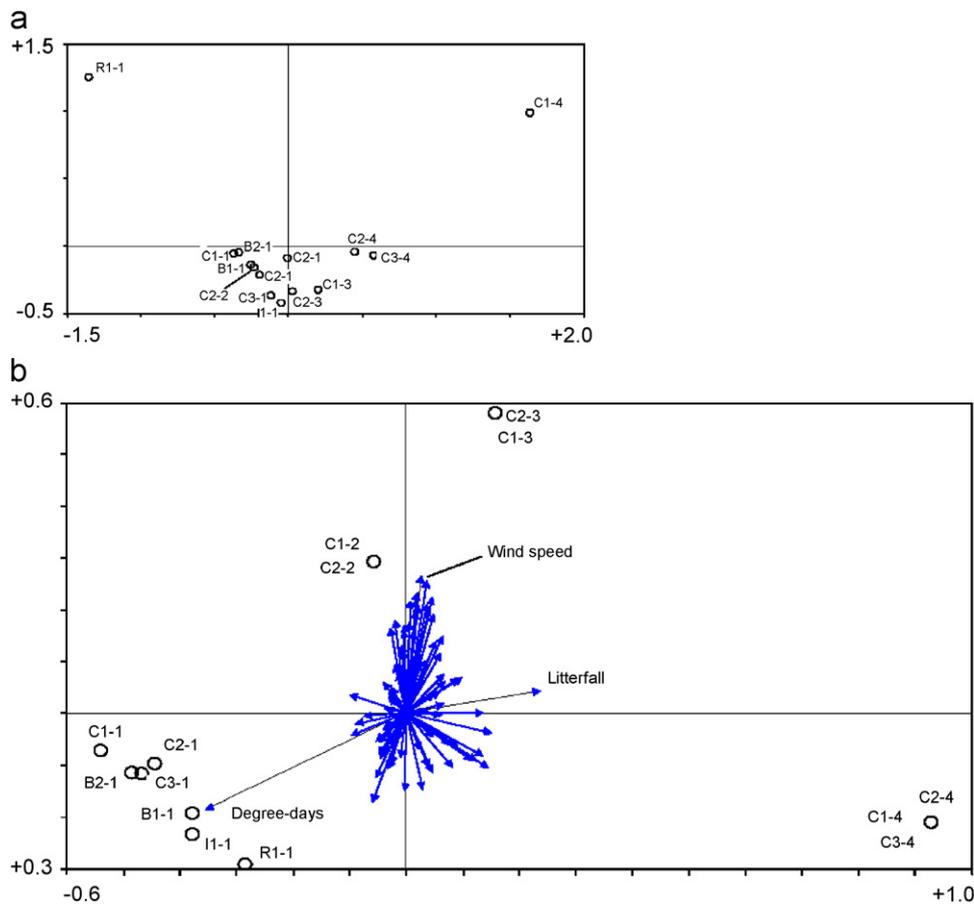


**Figure 2.** Multivariate analyses of higher arthropod taxa at local scale: (a) PCA, plot of study sites on axes 1 and 2; (b) RDA, biplot of sites and environmental variables on axes 1 and 2; and (c) Co-CA, biplot of arthropod taxa and plant species. Closed circles = taxa/species, open circles = study sites.

**Table 3.** Results of canonical partitioning for arthropod higher taxa and species composition considered at micro- and local scales (traps and sites, respectively)

Source of variance	Micro-scale (traps)		Local scale (sites)	
	Taxa	Species	Taxa	Species
(a) Environmental variance non-spatially structured	n.s.	<2.6	15.6	60.6
(b) Environmental variance spatially structured	<4.0	n.s.	72.7	3.2
(c) Spatially structured not explained by envir. var.	<4.0	n.s.	9.5	11.8
(d) Unexplained	96.0	97.4	2.2	24.4

Percentage of variance explained by (a) environmental variables non-spatially structured; (b) environmental variables spatially structured; (c) spatially structured variance not explained by environmental variables; and (d) unexplained. None of the ordinations with guild structure were significant. n.s. = not significant.

**Figure 3.** Multivariate analyses of higher arthropod taxa at seasonal scale: (a) PCA, plot of seasonal replicates (coded as in Table 2) on axes 1 and 2; (b) RDA, triplot of taxa (vectors), variables (labeled vectors) and seasonal replicates (open circles) on axes 1 and 2.

in RDA of higher taxa ordered by combinations of sites and seasonal replicates included degree-days, wind speed and litterfall. Canonical axes 1 and 2 combined explained 36.8% of the variance, with degree-days best explaining axis 1 ( $r = -0.67$ ) and wind speed best correlated to axis 2 ( $r = 0.90$ ; overall Monte-Carlo test of significance  $P < 0.05$  with 1000 permutations; Fig. 3b). A similar RDA

with species data yielded different results: canonical axes 1 and 2 combined explained 48.2% of the variance, with radiation best explaining axis 1 ( $r = -0.89$ ) and wind speed best correlated to axis 2 ( $r = 0.48$ ; overall Monte-Carlo test of significance  $P < 0.01$  with 1000 permutations).

Similarities calculated with arthropod higher taxa or species among study sites or combinations

of sites and seasonal replicates confirmed the limited influence of distance at the local scale (Appendices C-1, C-4; note the often low similarities between sites C1–C2–C3). In contrast, the effect of distance was obvious when calculating similarities between sites with an emphasis on common plant species (Appendix C-2, NNESS [ $k = 1$ ]). For higher taxa and species, similarities between seasonal replicates of wet and dry seasons (i.e., replicates 1 and 2, for example) were often low, suggesting high faunal turnover between seasonal replications (Appendices C-3, C-5).

## Guild structure

The micro- and local scale guild structure was impossible to predict from environmental variables, and geographical coordinates did not explain a significant amount of variance in guild structure (RDAs, permutation tests, all  $P > 0.05$ ). However, at the seasonal scale, guild structure could be best predicted from degree-days (correlation with axis 1 of the RDA,  $r = 0.75$ ) and litter fall (correlation with axis 2,  $r = 0.89$ ). Canonical axes 1 and 2, when combined, explained 45.0% of the total variance (overall Monte-Carlo test of significance  $P < 0.05$  with 1000 permutations). The first axis of CO-CA predicting guild structure from composition of plant species at different sites was significant (permutation test,  $F = 1.396$ ,  $P = 0.02$ , percentage fit = 58.2), whereas others were not ( $P > 0.05$ ). The

taxa- and plant-derived scores of sites on CO-CA axis 1 were highly correlated ( $r = 0.976$ ,  $P < 0.001$ ). Table 4 summarizes significant factors affecting various arthropod-dependent variables, at different scales.

## Discussion

### Limitations and faunal composition

Our study was designed to contribute to project IBISCA by investigating beta diversity and vertical stratification of arthropod taxa in the San Lorenzo forest. Further, our design allowed examination of the relative influence of illumination, plant composition and other environmental variables on litter-dwelling arthropods over three different scales (micro-, local and seasonal scales), as determined with pitfall traps. Pitfall trapping has limitations, in particular an intensity of activity is measured, not actual organism density (Adis, 1979). In addition, soil disturbance and concomitant increase of CO<sub>2</sub> production around the traps may benefit certain taxa such as Collembola or Formicidae (Joosse, 1965; Adis, 1979). This digging-in effect, which lasts about 2 days in temperate conditions, may artificially increase trap catch. However, the magnitude of this potential artifact should have been similar among study sites and temporal replications. The relative small number of

**Table 4.** Summary of factors tested on arthropod dependent variables, at different scales

Dependent variable	Micro-scale (traps)	Local scale (study sites)	Seasonal scale (replicates)
Abundance	High variance Light n.s.	Intermediate variance Basal area* (65%)	High variance Degree-days* Wind speed* (50%)
Species richness	$S_{\text{obs}}$ : high variance Light* (3%) $S(k)$ not tested (too low)	$S_{\text{obs}}$ : high variance, n.s. $S(k)$ : low variance No. stems* Canopy openness* (80%)	$S_{\text{obs}}$ : high variance, n.s. $S(k)$ : low variance, n.s.
Higher taxa composition	Light n.s. Geographical coord.* (4%) Plant composition not tested	Basal area* (70%) Geographical coord.* (10%) CO-CA:Plant composition* (35%)	Degree-days* Wind speed* (37%)
Species composition	Light* (3%) Geographical coord. n.s. Plant composition not tested	Light* (55%) Geographical coord.* (12%) CO-CA: Plant composition n.s.	Radiation* Wind speed* (48%)
Guild structure	Light n.s. Geographical coord. n.s. Plant composition not tested	Envir. var. n.s. Geographical coord. n.s. CO-CA:Plant composition* (58%)	Degree-days* Litterfall* (45%)

\*Significant with  $P < 0.05$ ; n.s., not significant.

% Refers to percent variance explained;  $S_{\text{obs}}$ , species observed (sorted) and  $S(k)$ , expected number of species in subsample  $k$ .

study sites and temporal replications was likely more problematic. Furthermore, we were only able to sort 8.5% of the collected material to species level, in part due to taxonomic barriers. This effort nevertheless compares favorably with many previous studies of tropical litter-dwelling arthropods.

Collembola dominated pitfall trap catches at San Lorenzo, as in a Costa Rican forest (Goehring et al., 2002). Other tropical studies reporting ants as dominant in pitfall traps (Lieberman and Dock, 1982; Burgess et al., 1999) may have discounted microarthropods. When compared with studies targeting beetles with pitfall trapping in tropical rainforests (Goehring et al., 2002), our material included more Scolytinae, Ptiliidae and Nitidulidae; and less Scarabaeidae, Erotylidae and Carabidae. Species developing in fallen fruits could account for the high occurrence of Scolytinae in our study (e.g. *Araptus laevigatus* and *Coccotrypes* spp.: Wood, 1982). The distribution of these species may reflect fallen fruit density, which was not measured.

### Dependent variables and converging patterns

Variability in arthropod abundance, which was rather high at the micro-scale, was notably higher among seasonal replicates than among study sites. The number of species observed,  $S_{\text{obs}}$ , proved to be the most difficult variable to predict.  $S_{\text{obs}}$  was affected by light at the micro-scale but the amount of variance explained was very low. The rarefied number of species,  $S(k)$ , was easier to predict, at least at the local scale among study sites. The composition of higher taxa and species was often predicted by different (and significant) independent variables at the three scales. Illumination (of traps, sites, seasonal radiation) appeared important in determining species composition at the three scales. In general, guild structure was difficult to predict, likely as a result of problematic guild assignments (Stork, 1987). In our samples, this concerned many Acari, Collembola, Nitidulidae and Staphylinidae, which may be assigned to different guilds according to the level of taxonomic resolution achieved. For example, Collembola may be considered as 'scavengers' overall (Moran & Southwood, 1982; Stork, 1987), even though species feeding on fungi, pollen, mosses, and decaying plants and debris are included (Castaño-Meneses et al., 2004; Wiwatwitaya and Takeda, 2005).

Also, there were salient differences worth examining when analyzing data at the micro-, local and seasonal scales. Despite the high variability in trap catches, it was difficult to record potential

factors explaining the variance, beside light and geographical coordinates of traps, which had little influence on arthropod-dependent variables. At the local scale, the influence of forest structure (variables such as basal area and canopy openness) and local plant composition was apparent, suggesting that standing litter (Lieberman and Dock, 1982; Wiwatwitaya and Takeda, 2005) and composition, variables not measured in our study, are important for litter-dwelling arthropods. Our analyses further confirmed that a substantial amount of variance in arthropod composition was either spatially structured or related to environmental variables that are spatially structured. As for seasonal replicates, two variables were important in predicting various arthropod-dependent variables: number of degree-days and wind speed. We believe both variables influence litter moisture (see below).

### Environmental variables

At the scale of a few meters (distance between traps 1.3 m), there was high variance in arthropod abundance, species richness and composition, which emphasizes the patchiness of arthropod distribution in tropical rainforests (Kaspari, 1996). This variance, largely unexplained in our study (Table 3), probably relates to the heterogeneity of the forest but the environmental variables predominantly affecting it remain obscure. Both trap catch abundance and composition were weakly or not significantly affected by trap illumination. Light had a weak influence on number of species observed and species composition in trap catches. The influence of geographical location of traps also was weak or not significant. This suggests that many environmental variables affecting arthropod distribution at the micro-scale operate at a distance greater than 1.3 m. Among these, the composition (leaves, flowers, fruits, wood of different plant species) and quality of litter fall (particularly the C:N ratio; Noti et al., 2003) originating from large trees may represent variables of particular interest for future studies (Willis, 1976). Large sun flecks resulting from tree fall gaps and their seasonal changes may represent another variable of interest (Feener and Schupp, 1998), as may be the occurrence of herbs and wooden debris (Willett, 2001).

In general, study sites with higher basal area or number of plant stems had more abundant and species-rich (as reported with  $S(k)$ ) catches. While basal area may represent a surrogate for local standing litter, there was probably also a relation between local canopy openness and litter moisture

(Levings and Windsor, 1984), which may have affected several dependent variables. There were significant spatial differences among biomass collected by litter traps within the San Lorenzo botanical plot (ANOVA,  $P < 0.001$ ), and standing litter doubtlessly varied locally and among study sites. As with basal area, standing litter may influence higher taxa composition of litter-dwelling arthropods among study sites (Willis, 1976). Plant composition within the study sites significantly influenced higher taxa composition and guild structure, but not species composition (CO-CAs). Most species sorted from trap catches were scavengers (Appendices A and B) and less likely to be influenced by local composition of live vegetation.

For higher taxa and species, the fraction of spatially structured variance not explained by environmental variables at the local scale was similar. However, most of the variance explaining higher taxa composition originated from environmental variance that was spatially structured. Conversely, most of the variance explaining species composition originated from non-spatially structured environmental variance (Table 3). This distinction is important, as many pitfall studies of tropical arthropods report the spatial distribution of higher taxa, not species (cf. Introduction). Interspecific competition, predation and parasitism may further affect species composition at local and seasonal scales. Other variables likely to locally influence trap catches include occurrence of army ants (Ecitoninae) and distance to water bodies.

The number of degree-days over a time-lag of 1 month prior to trap survey appeared to be a more accurate variable to predict trap catches (and to some extent its composition) than air temperature. Several tropical studies reported that the influence of litter moisture on soil arthropods is greater than air temperature. Usually, arthropod abundance increases with rainfall and litter moisture (Lieberman and Dock, 1982; Levings and Windsor, 1984; Frith and Frith, 1990; Wiwatwitaya and Takeda, 2005). Further, arthropod abundance is usually greater in years with wetter than usual dry seasons, as observed in our study (Fig. 1 and Table 2; Levings and Windsor, 1985; Pearson and Derr, 1986). During the dry season, the San Lorenzo forest remains humid and experiences almost no loss of canopy cover (Condit et al., 2000). This suggests that environmental conditions within the forest litter during the dry season at San Lorenzo may not be as severe as in other studies. Our results emphasize the importance of air temperature when humidity is near saturation (see also Pearson and Derr, 1986). Rising air temperatures (or degree-days)

may increase arthropod activity and possibly trap catches (Adis, 1979) but this action may be offset by increasing evaporation rates and, consequently, decreasing litter moisture and arthropod abundance. This hypothesis is consistent with the action of wind speed, affecting negatively arthropod abundance (Table 4). Thus, arthropod abundance at San Lorenzo may depend on interactions between air temperature and litter moisture instead of rainfall, and may not necessarily be depressed during the dry season (Fig. 1).

Overall, since the seasonal availability of fresh litter and live fungi is expected to vary more than that of dead organic litter, we predict that (1) litter-dwelling arthropods may be more seasonal than soil microarthropods in tropical rainforests; and (2) tropical litter-dwelling arthropods may be more seasonal (and perhaps less likely to migrate in deeper soil layers: Sgardelis et al., 1993) than temperate counterparts, when respective populations are compared during the growing season.

## Conclusions

We observed important spatial and seasonal differences in abundance, species richness and composition of litter-dwelling arthropods in the San Lorenzo forest. Often these differences appeared weakly related to geographical coordinates, and reflected, to some extent, forest structure (basal area) and local plant composition, and less so, illumination patterns or seasonal changes in radiation. Seasonal variability was rather high and mostly appeared to be related to surrogate variables accounting for seasonal changes in litter moisture.

The implications of our results for conservation studies using pitfall traps in tropical rainforests are three-fold. First, changes in family or species composition, as opposed to mere changes in total abundance, appear crucial to understand the functional complexity of soil organisms. Second, spatial replication should address subtle changes in plant composition throughout the study area, and these effects should be factored out from those resulting from edge effects or forest fragmentation. Lastly, seasonal replicates should be commensurate with seasonal changes in litter moisture and litterfall.

## Acknowledgments

We thank Pro-Natura International, Océan Vert, the Blaise Pascal University (France), the University of Panama and the Smithsonian Tropical Research

Institute (STRI) for initiating and organizing the IBISCA-Panama project. A. Hernandez and O. Valdez helped with plant identification and S.J. Wright provided litter trap data. N. Winchester commented on an earlier draft of the manuscript. Core funding for IBISCA was provided by Solvin-Solvay, STRI, the United Nations Environment Programme, a Walcott endowment fund grant from the Smithsonian Institution, the European Science Foundation and the Global Canopy Programme. GCM was supported by a postdoctoral scholarship of the Dirección General de Asuntos del Personal Académico, Universidad Nacional Autónoma de México. Thanks to all IBISCA participants for help in the field and collegial activities.

## Appendix A. Supplementary materials

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.pedobi.2007.03.004](https://doi.org/10.1016/j.pedobi.2007.03.004).

## References

- Adis, J., 1979. Problems of interpreting arthropod sampling with pitfall traps. *Zool. Anz.* 202, 177–184.
- André, H., Ducarme, X., Lebrum, P., 2002. Soil biodiversity: myth, reality or conning? *Oikos* 96, 3–24.
- Arnold, C.Y., 1960. Maximum and minimum temperatures as a basis for computing heat units. *Proc. Am. Soc. Hortic. Sci.* 74, 430–445.
- Atkin, L., Proctor, J., 1988. Invertebrates in the litter and soil on Volcan Barva, Costa Rica. *J. Trop. Ecol.* 4, 307–310.
- Basset, Y., Mavoungou, J.F., Mikissa, J.B., Missa, O., Miller, S.E., Kitching, R.L., Alonso, A., 2004. Discriminatory power of different arthropod data sets for the biological monitoring of anthropogenic disturbance in tropical forests. *Biodivers. Conserv.* 13, 709–732.
- Basset, Y., Samuelson, G.A., Miller, S.E., 1996. Similarities and contrasts in the local insect faunas associated with ten forest tree species of New Guinea. *Pacif. Sci.* 50, 157–183.
- Beck, L., 1971. Bodenzoologische Gliederung und Charakterisierung des amazonischen Regenwaldes. *Amazonia* 3, 69–132.
- Borcard, D., Legendre, P., 2002. All-scale analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecol. Model.* 153, 51–68.
- Borcard, D., Legendre, P., 2004. SpaceMaker2 – User's guide. Département de sciences biologiques, Université de Montréal. Published at <http://www.fas.umontreal.ca/biol/legendre/>.
- Borcard, D., Legendre, P., Avois-Jacquet, C., Tuomisto, H., 2004. Dissecting the spatial structure of ecological data at multiple scales. *Ecology* 85, 1826–1832.
- Brussaard, L., Behan-Pelletier, V.M., Bignell, D.E., Brown, V.K., Didden, W., Folgarait, P., Fragoso, C., Wall Freckman, D., Gupta, V.V.S.R., Hattori, T., Hawsksworth, D.L., Klopatek, C., Lavelle, P., Malloch, D.W., Rusek, J., Soderstrom, B., Tiedje, J.M., Virginia, R.A., 1997. Biodiversity and ecosystem functioning in soil. *Ambio* 26, 563–570.
- Burgess, N.D., Ponder, K.L., Goddard, J., 1999. Surface and leaf-litter arthropods in the coastal forests of Tanzania. *Afr. J. Ecol.* 37, 355–365.
- Burghouts, T., Ernsting, G., Korthals, G., de Vries, T., 1992. Litterfall, leaf litter decomposition and litter invertebrates in primary and selectively logged dipterocarp forest in Sabah, Malaysia. *Philos. Trans. R. Soc. London B* 335, 407–416.
- Castaño-Meneses, G., Palacios-Vargas, J.G., Cutz-Pool, L.Q., 2004. Feeding habits of Collembola and their ecological niche. *Ana. Inst. Biol. Univ. Nac. Autón. México, Ser. Zool.* 75, 135–142.
- Chave, J., Condit, R., Aguilar, S., Hernandez, A., Lao, S., Perez, R., 2004. Error propagation and scaling for tropical forest biomass estimates. *Philos. Trans. R. Soc. London B* 359, 409–420.
- 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. *J. Veg. Sci.* 11, 649–658.
- Condit, R., Aguilar, S., Hernández, A., Pérez, R., Lao, S., Angher, G., Hubbell, S.P., Foster, R.B., 2004. Tropical forest dynamics across a rainfall gradient and the impact of an El Niño dry season. *J. Trop. Ecol.* 20, 51–72.
- Didham, R.K., Fagan, L.L., 2003. Project IBISCA – investigating the biodiversity of soil and canopy arthropods. *The Weta* 26, 1–6.
- Feener, D.H.J., Schupp, E.W., 1998. Effect of treefall gaps on the patchiness and species richness of neotropical ant assemblages. *Oecologia* 116, 191–201.
- Frith, D., Frith, C., 1990. Seasonality of litter invertebrate populations in an Australian upland tropical rain forest. *Biotropica* 22, 181–190.
- Goehring, D.M., Daily, G.C., Şekrçioğlu, C.H., 2002. Distribution of ground-dwelling arthropods in tropical countryside habitats. *J. Ins. Conserv.* 6, 83–91.
- 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.
- Hansen, R.A., 2000. Effects of habitat complexity and composition on a diverse litter microarthropod assemblage. *Ecology* 81, 1120–1132.
- Hardy, O., 2005. 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/bioancel/ohardy/index.html>.
- Joose, E.N.G., 1965. Pitfall trapping as a method for studying surface dwelling Collembola. *Z. Morph. Ökol. Tiere* 55, 587–596.

- Kaspari, M., 1996. Litter ant patchiness at the 1-m<sup>2</sup> scale: disturbance dynamics in three Neotropical forests. *Oecologia* 107, 265–273.
- Klein, B.C., 1989. Effects of forest fragmentation on dung and carrion beetle communities in Central Amazonia. *Ecology* 70, 1715–1725.
- Legendre, P., Borcard, D., Peres-Neto, P., 2005. Analyzing beta-diversity: partitioning the spatial variance of community composition data. *Ecol. Monogr.* 75, 435–450.
- Levings, S.C., 1983. Seasonal, annual and among site variation in the ground ant community of a deciduous tropical forest: some causes of patchy species distributions. *Ecol. Monogr.* 53, 435–455.
- Levings, S.C., Windsor, D.M., 1982. Seasonal and annual variation in litter arthropod populations. In: Leigh, Jr., E.G., Rand, A.S., Windsor, D.M. (Eds.), *The Ecology of a Tropical Forest Seasonal Rhythms and Long-term Changes*. Smithsonian Institution Press, Washington, DC, pp. 355–388.
- Levings, S.C., Windsor, D.M., 1984. Litter moisture content as a determinant of litter arthropod distribution and abundance during the dry season on Barro Colorado Island, Panama. *Biotropica* 16, 125–131.
- Levings, S.C., Windsor, D.M., 1985. Litter arthropod populations in a tropical deciduous forest: relationships between years and arthropod groups. *J. Anim. Ecol.* 54, 61–70.
- Lieberman, S., Dock, C.F., 1982. Analysis of the leaf litter arthropod fauna of a lowland tropical evergreen forest site (La Selva, Costa Rica). *Rev. Biol. Trop.* 30, 27–34.
- Mattoni, R., Longcore, T., Novotny, V., 2000. Arthropod monitoring for fine-scale habitat analysis: a case study of the El Segundo sand dunes. *Environ. Manage.* 25, 445–452.
- McGroddy, M.E., Daufresne, T., Hedin, L.O., 2004. Scaling of C:N:P stoichiometry in forests worldwide: implications of terrestrial Redfield-type ratios. *Ecology* 85, 2390–2401.
- Moran, V.C., Southwood, T.R.E., 1982. The guild composition of arthropod communities in trees. *J. Anim. Ecol.* 51, 289–306.
- Noti, M.-I., André, H.M., Ducarme, X., Lebrun, P., 2003. Diversity of soil oribatid mites (Acari: Oribatida) from High Katanga (Democratic Republic of Congo): a multiscale and multifactor approach. *Biodiv. Conserv.* 12, 767–785.
- Novotny, V., Drozd, P., Miller, S.E., Kulfan, M., Janda, M., Basset, Y., Weiblen, G.D., 2006. Why are there so many species of herbivorous insects in tropical rainforests? *Science* 313, 1115–1118.
- Olson, D.M., 1994. The distribution of leaf litter invertebrates along a Neotropical altitudinal gradient. *J. Trop. Ecol.* 10, 129–150.
- Pearson, D.L., Derr, J.A., 1986. Seasonal patterns of lowland forest floor arthropod abundance in South-eastern Perú. *Biotropica* 18, 244–256.
- Pyke, C.R., Condit, R., Aguilar, S., Lao, S., 2001. Floristic composition across a climatic gradient in a neotropical lowland forest. *J. Veg. Sci.* 12, 553–566.
- Quintero, I., Roslin, T., 2005. Rapid recovery of dung beetle communities following habitat fragmentation in central Amazonia. *Ecology* 86, 3303–3311.
- R Development Core Team, 2006. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria Published at <<http://www.R-project.org>>.
- Şekerçioğ, C.H., Ehrlich, P.R., Daily, G.C., Aygen, D., Goehring, D., Sandi, R.F., 2002. Disappearance of insectivorous birds from tropical forest fragments. *Proc. Natl. Acad. Sci.* 99, 263–267.
- Sgardelis, S.P., Sarkar, S., Asikidis, M.D., Cancela Da Fonseca, J.P., Stamou, G.P., 1993. Phenological patterns of soil microarthropods from three climate regions. *Eur. J. Soil Biol.* 29, 49–57.
- Simpson, G.L., 2005. Cocorresp: Co-correspondence Analysis Ordination Methods for Community Ecology. R Foundation for Statistical Computing, Vienna, Austria Published at <<http://www.R-project.org>>.
- Stevens, G.C., 1989. The latitudinal gradient in geographical range: how so many species coexist in the tropics. *Am. Nat.* 133, 240–256.
- Stork, N.E., 1987. Guild structure of arthropods from Bornean rain forest trees. *Ecol. Entomol.* 12, 69–80.
- Takeda, H., Abe, T., 2001. Templates of food-habitat resources for the organization of soil animals in temperate and tropical forests. *Ecol. Res.* 16, 961–973.
- ter Braak, C.J.F., Smilauer, P., 1998. *CANOCO Reference Manual and user's Guide to Canoco for Windows: Software for Canonical Community Ordination (Version 4)*. Mirocomputer Power, Ithaca, NY.
- ter Braak, C.J.F., Schaffers, A.P., 2004. Co-correspondence analysis: a new ordination method to relate two community compositions. *Ecology* 85, 834–846.
- Thaiutsa, B., Granger, O., 1979. Climate and the decomposition rate of tropical forest litter. *Unasylva* 126, 28–38.
- Thomas, L., Proctor, J., 1997. Invertebrates in the litter and soil on the ultramafic Mount Giting-Giting, Philippines. *J. Trop. Ecol.* 13, 125–131.
- 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.
- Willett, T.R., 2001. Spiders and other arthropods as indicators in old-growth versus logged redwood stands. *Restor. Ecol.* 9, 410–420.
- Willis, E.O., 1976. Seasonal changes in the invertebrate litter on Barro Colorado Island, Panama. *Rev. Brasil. Biol.* 36, 643–657.

- Wiwatwitaya, D., Takeda, H., 2005. Seasonal changes in soil arthropod abundance in the dry evergreen forest of north-east Thailand, with special reference to collembolan communities. *Ecol. Res.* 20, 59–70.
- Wolters, V., 2001. Biodiversity of soil animal and its function. *Eur. J. Soil Biol.* 37, 221–227.
- Wood, S.L., 1982. The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae) a taxonomic monograph. *Great Basin Nat. Mem.* 6, 1–1359.
- Wright, S.J., Calderón, O., Hernández, A., Paton, S., 2004. Are lianas increasing in importance in tropical forests? A 17-year record from Panama. *Ecology* 85, 484–489.