*Journal of Animal Ecology* 2005
**74**, 926–936

# Separating the effects of forest type and elevation on the diversity of litter invertebrate communities in a humid tropical forest in Puerto Rico

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**Summary**

**1.** The primary effects of climatic conditions on invertebrate litter communities, and the secondary effects of different forest types, were distinguished by using the sierra palm as a control in a natural experiment along an elevational gradient in the Luquillo Mountains. These mountains have three well-defined forest types along the gradient, with the palm occurring as stands within each forest.

**2.** Palm litter samples were richer in nutrients, particularly phosphorus, than nonpalm litter, significantly so at higher elevations where leaching would have been expected. In nonpalm litter, mineral concentrations were significantly lower at higher elevations.

**3.** Animal abundance mirrored the pattern of mineral amounts and declined significantly in mid- and high-altitude forests, but did not decline with increasing elevation in palm stands. A pulse of post-hurricane litterfall was reflected in the high abundance of Coleoptera and Isoptera the following year.

**4.** The species richness of communities (Margalef's index) declined with increasing elevation in nonpalm forest litter, but was remarkably similar in palm litter at all elevations.

**5.** Palm litter communities were more similar to each other (Sørensen's index) than nonpalm communities, which became less similar with increasing elevation.

**6.** The differences observed from the lower slopes to the summits, in animal abundance, species richness and the uniformity of communities, are better explained by the contribution of forest composition to the chemical and physical nature of litter and forest heterogeneity, rather than to direct effects of temperature and rainfall differences.

*Key-words*: biomass, microcosms, microhabitats, nutrients, species richness.

*Journal of Animal Ecology* (2005) **74**, 926–936
doi: 10.1111/j.1365-2656.2005.00990.x

## Introduction

Many attempts have been made to relate species richness and abundance to productivity along ecological gradients. Changing climatic conditions with increasing elevation affect plant productivity in a variety of ways, but chiefly increased rainfall, leaching and waterlogging of soils, lower temperatures and increased wind speeds, result in declining productivity towards the summits of mountains. The primary effect of climate may also affect animal communities, but it is difficult to distinguish between these primary influences and the secondary effects of different vegetation types along the gradient, which provide animals with a variety of habitats and nutrient resources. We aim to distinguish between these effects on the invertebrate communities of forest floor litter in Puerto Rico.

The decline in species richness with elevation is generally accepted, but the pattern of this decline and the understanding of its ecological correlates is still debatable. A review of 97 papers and analysis of the data (Rahbek 1995) supported the view that species richness declines with elevation, but not that the decline is necessarily monotonic. Patterns where the species richness curve is almost horizontal up to a certain elevation before declining, or is unimodal, seem more typical than a monotonic decline. Standardization of the data for sampling effort and area at different elevations is essential, as it was only when Terborgh (1977) corrected his



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data for tropical birds of the Peruvian Andes that a unimodal pattern was revealed.

There are numerous examples of a species richness peak at intermediate levels of productivity (Rosenzweig 1995), with bryophytes and pteridophytes peaking at mid-elevation on mountainsides in the tropics, as do some animal taxa (Janzen *et al*. 1976). Measurements of diversity are scale dependent and, in their review, Waide *et al*. (1999) found unimodal as well as positive and negative linear relationships with productivity. They demonstrated, however, that unimodal patterns prevail when the data span a number of different community types.

Different life forms in the same geographical zone may show different patterns. In the mountains of California and Oregon tree species diversity decreases linearly from low to high elevation, but herbs and shrubs have a mid-elevational peak (Whittaker 1960). This pattern is again seen in the tropical forests of Puerto Rico, where the number of tree species declines with increasing elevation (Waide, Zimmerman & Scatena 1998), but vascular epiphytes and vines attain maximum species richness in the intermediate palo colorado forest (Brown *et al*. 1983).

These differences are usually attributed to different plant responses to the direct effects of changing climatic conditions, i.e. the two opposing gradients of declining temperature and increasing precipitation. Somewhere along the elevational gradient will be the 'most favourable' combination of conditions (Brown & Lomolino 1998) for particular plant groups, e.g. different species of pine trees or epiphytes in tropical rain forest. Some groups, such as epiphytes, increase the structural complexity of the forest, providing more potential habitats for invertebrates, and more foraging opportunities for birds (Nadkarni & Matelson 1988; Nadkarni 1994) and other predators.

Studies of diversity along a complete elevational gradient are relatively few, and have been restricted to individual groups of plants or animals rather than whole communities and, because of the sampling difficulties involved, quantitative studies are rare. In this paper we demonstrate the usefulness of microcosms and microhabitats in censusing invertebrate communities along an elevational gradient. These habitats are manageable units whose resource base, sample size and animal communities can be quantified by a standardized methodology. As we have chosen detritivore invertebrate communities dependent on litter derived from the forest canopy, the standing litter of the forest floor and, previously, in epiphytic bromeliads (Richardson 1999, 2001; Richardson *et al*. 2000), they can be directly related to known measures of forest productivity at different elevations, such as annual litterfall.

Canopy leaves, twigs, fruits and seeds inevitably become litter, which either lodges in epiphytes, branches and tree holes, and mycelial webs in the understorey (Lodge 1996), or falls to the forest floor, to provide a habitat for mainly detritivore and fungivore invertebrate communities which aid its breakdown. The decomposition and mineralization of litter provides the major pathway for transferring nutrients from vegetation to soils. Knowledge of nutrient pools, the fluxes between them, and losses from the system, is essential for an understanding of nutrient recycling and forest productivity.

The low productivity of tropical montane forests is usually attributed to the low availability of mineral nutrients in their soils ( Vitousek 1984; Cuevas & Medina 1988). Phosphorus combines with aluminium and iron oxides to form insoluble complexes, and is also immobilized by the fungal and bacterial biomass. Lodge (1993), reviewing the role of saprotrophic fungi in nutrient cycling, reported that, at El Verde in Puerto Rico, the proportion of forest floor P in fungal biomass varied from 3 to 85%. Variation in fungal biomass and fungal P concentrations may regulate the availability and timing of nutrient mineralization from leaf litter in this forest. Litter invertebrates help unlock minerals by fragmenting leaf and woody litter, enhancing bacterial substrates, and by directly feeding on hyphae and fungal fruiting bodies (Pfieffer 1996).

Invertebrate communities are essential for the litter breakdown which maintains epiphytes. An understanding of their diversity, and of the communities at the interface between forests and the underlying mineral soils, is essential for teasing out factors important in whole-ecosystem function.

The Luquillo Experimental Forest (LEF), in northeastern Puerto Rico, is a moist neotropical forest, with a well documented temperature, rainfall, and productivity gradient across three distinct forest types (Brown *et al*. 1983; Weaver & Murphy 1990; Waide *et al*. 1998). Previous studies of the diversity of detrital and aquatic communities of tank bromeliads and their ecological correlates across these three forest types (Richardson 1999; Richardson *et al*. 2000), demonstrated a unimodal pattern of species richness peaking in the intermediate palo colorado forest and a general decline in animal abundance towards the summits. Those studies could not, however, distinguish between the primary effects of climate and the secondary effects of changes in vegetation, with consequent differences in the quality and quantity of impounded litter and forest heterogeneity on invertebrate assemblages. To separate these factors a control for forest type was needed. This could be provided by the sierra palm, which occurs in stands at all elevations and its large leaves form piles of litter, containing only a few windblown leaves of other species. By sampling palm litter and forest-type litter in a 'natural experiment' at each of three elevations, we aimed to discriminate between the influences of elevation and forest type on forest floor litter faunal diversity.

The approach of using a particular plant species to test resource effects on animal communities has been tried across latitudinal gradients (Lawton, Lewinsohn & Compton 1993; Thompson & Townsend 2002), but there are few plant species distributed along whole elevational gradients, and only one other study is known (Lawton, MacGarvin & Heads 1987).

### STUDY AREA

The LEF is located in the windward portion of Puerto Rico. There are four forest types, three with different dominant tree species at different elevations. Tabonuco *Dacryodes excelsa* Vahl forest occupies areas below 600 m a.s.l., palo colorado *Cyrilla racemiflora* L. forest occurs in areas above the cloud condensation level from 600 to 900 m a.s.l., and the dwarf forest (dominant tree *Tabebuia rigida* Urban), with stunted vegetation and waterlogged anoxic soils, is located only on the highest peaks above 900 m a.s.l. The fourth type, palm forest (sierra palm *Prestoea montana* (R. Grah.) Nichols. syn. *P. acuminata* (Willd.) H. E. Moore *p.p.*), occurs at all elevations, principally on windward slopes and in wet gullies and stream valleys. In these palm brakes palm is dominant, with few other tree or herbaceous species (Wadsworth 1951; Brown *et al*. 1983; Weaver & Murphy 1990; Lugo, Bokkestijn & Scatena 1995).

Rainfall increases with elevation, with the tabonuco, palo colorado and dwarf forest zones having annual rainfall of approximately 3·5, 4·2 and 4·8 m, respectively (Garc'a-Martinó *et al*. 1996). The number of rainless days decreases with elevation, such that on average the tabonuco, palo colorado and dwarf forest have 97, 65 and 38 rainless days year$^{-1}$, respectively (Garc'a-Martinó *et al*. 1996). Total above-ground net primary productivity (NPP) is related to rainfall, and declines with elevation (10·5, 7·6, and 3·7 t ha$^{-1}$, respectively) in these three forests (Weaver & Murphy 1990).

A major climatological event before this work started was Hurricane Georges in September 1998, which provided a pulse of litter, particularly woody debris, reported by Ostertag, Scatena & Silver (2003) as 1·2–2·5 times pre-hurricane standing stocks in different parts of the LEF. The initial effects of this pulse, and its decline, as described by Ostertag *et al*. (2003), may have had an effect on the observations made over the sampling period.

## Methods

### SAMPLING

Samples of litter were collected from tabonuco forest (tab) (Quebrada Sonadora area, El Verde Field Station, 330–500 m a.s.l. 18·32°N, 65·82°W), palo colorado forest (Tradewinds Trail, 750–780 m a.s.l. 18·29°N, 65·81°W), and dwarf forest (Pico del Este, 950–1000 m a.s.l. 18·28°N, 65·76°W, and Pico del Oeste, 820–880 m a.s.l. 18·28°N, 65·77°W). In each forest type one set of samples was collected from under the typical forest canopy, away from palms, and another set of samples was collected from a palm brake. No suitable palm sites were present in the dwarf forest on Pico del Este, so samples were collected on the nearest and highest adjacent ridge, Pico del Oeste. Samples were collected from the three forest types over a 11–18-day period in each of 3 years during the periods January–March 1999–2001. All litter and dead organic material from each of four 0·25-m$^2$ plots (0·5 m × 0·5 m), in each sampling area, was collected into plastic sacks, to give a sampling scheme of years (3) × forest type (3) × nonpalm/palm (2) × replicates (4), a total of 72 samples. Within forest types, samples were collected from different localities in successive years and therefore independent. Individual samples were a sufficient distance apart to avoid pseudoreplication.

Animals were extracted from litter using Tullgren funnels. As soon as possible after collection samples were divided and placed on a coarse mesh (7–8 × 6–7·5 mm) in 21·5 cm diameter funnels, the number for each sample depending on its volume, usually two to five, and illuminated from above by a 60-W incandescent light bulb, and extracted for 3 days. Organisms moving downwards to escape light and heat were collected into ethanol from the bottom of the funnel. Collections from each sample were cleaned of debris and sorted into main taxonomic groups. Individuals, apart from mites, were identified to morphospecies, counted and measured. For mites only a total count was recorded as an indication of their prevalence in the litter. Although some distinctive morphospecies could be recognized, species identification was not considered practicable because of their high abundance and taxonomic difficulty. Mites therefore were included in number and weight considerations, but not in diversity calculations.

### ANIMAL BIOMASS ESTIMATION

In earlier work with the fauna of bromeliad phytotelmata (Richardson *et al*. 2000) length × dry weight relationships were established for different groups of invertebrates. Many of these relationships were used in the current study, and additional data to cover adult Diptera and Lepidoptera, Hemiptera, lumbricid worms, Isoptera and slugs were obtained and archived at http://luq.lternet.edu/data.

### LITTER AND CHEMICAL ANALYSIS

The dried litter sample obtained, after extraction of animals from each plot, was separated into wood and nonwood components, and weighed. They were analysed at the International Institute of Tropical Forestry, Rio Piedras, Puerto Rico, using standard methods that have been used to determine the nutrient content of other vegetation in the LEF (Scatena *et al*. 1993). Samples of each component were oven dried at 105 °C for at least 24 h and ground with a Wiley mill. The ground material was analysed for P, K, Ca and Mg using a Beckman plasma emission spectrometer (Spectra Span V) after a digestion using concentrated $HNO_3$ and 30% $H_2O_2$ (Luh Huang & Schulte 1985). Nitrogen, carbon and sulphur were analysed using a LECO CNS-2000 and the dry combustion method (Tabatabai & Bremmer 1991). Precision for all analyses was assured by running samples of known chemical composition every 40 samples. Amounts of nutrients per unit area were calculated

**Table 1.** Mean total standing litter and proportion of wood from 4 × 0·25-m$^2$ samples from nonpalm and palm areas in each of three forest types over 3 years

| | Litter (g m$^{-2}$) | | | | | | Wood (%) | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Tabonuco | | Palo colorado | | Dwarf forest | | Tabonuco | | Palo colorado | | Dwarf forest | |
| | Nonpalm | Palm | Nonpalm | Palm | Nonpalm | Palm | Nonpalm | Palm | Nonpalm | Palm | Nonpalm | Palm |
| 1999 | 1142 | 1195 | 2511 | 1877 | 687 | 1316 | 24·3 | 15·6 | 37·6 | 11·3 | 47·3 | 14·2 |
| 2000 | 1390 | 1139 | 796 | 802 | 368 | 817 | 53·2 | 18·8 | 48·1 | 9·4 | 47·1 | 22·1 |
| 2001 | 1003 | 1004 | 1021 | 659 | 610 | 510 | 28·8 | 14·2 | 54·8 | 7·0 | 67·7 | 5·5 |
| **Mean** | **1178** | **1113** | **1443** | **1113** | **555** | **881** | **37** | **16** | **44** | **10** | **55** | **15** |

**Table 2.** Significance of main effects and interactions (three-way ANOVA, LSD test) for litter and nutrient parameters. Bold type highlights significant values ($P < 0·05$). Data from 4 × 0·25-m$^2$ samples from nonpalm and palm areas in each of three forest types over 3 years

| | Main effects | | | Two-way interactions | | | Three-way interaction |
|---|---|---|---|---|---|---|---|
| | Forest type | Palm/nonpalm | Year | F × P | F × Y | P × Y | F × P × Y |
| Litter (g dry wt m$^{-2}$) | **0·022** | 0·889 | **0·004** | 0·277 | **0·043** | 0·851 | 0·758 |
| Wood (%) | 0·504 | **0·000** | 0·190 | 0·120 | 0·763 | 0·274 | 0·603 |
| Nitrogen (g m$^{-2}$) | **0·002** | **0·000** | **0·001** | 0·451 | 0·140 | 0·066 | 0·915 |
| C/N ratio | **0·000** | **0·000** | 0·057 | 0·056 | 0·156 | 0·794 | 0·502 |
| Potassium (g m$^{-2}$) | **0·001** | 0·054 | **0·001** | 0·153 | 0·091 | 0·105 | 0·936 |
| Phosphorus (g m$^{-2}$) | **0·005** | **0·000** | **0·004** | 0·175 | 0·322 | **0·049** | 0·577 |
| Calcium (g m$^{-2}$) | **0·000** | 0·356 | 0·364 | 0·079 | 0·071 | 0·269 | 0·662 |
| Magnesium (g m$^{-2}$) | **0·020** | **0·000** | **0·001** | 0·329 | 0·168 | 0·154 | 0·911 |

**Table 3.** Significance of differences (three-way ANOVA, LSD test) for comparisons of litter and nutrient parameters. Bold type highlights significant values ($P < 0·05$). Data from 4 × 0·25-m$^2$ samples from nonpalm and palm areas in each of three forest types over 3 years

| | Between palm and nonpalm | | | Between tab and pc | | Between tab and df | | Between pc and df | |
|---|---|---|---|---|---|---|---|---|---|
| | tab | pc | df | Palm | Nonpalm | Palm | Nonpalm | Palm | Nonpalm |
| Litter (g dry wt m$^{-2}$) | 0·820 | 0·257 | 0·263 | 1·000 | 0·363 | 0·425 | **0·035** | 0·425 | **0·003** |
| Wood (%) | **0·022** | **0·000** | **0·001** | 0·436 | 0·096 | 0·621 | **0·035** | 0·775 | 0·643 |
| Nitrogen (g m$^{-2}$) | 0·079 | 0·145 | **0·003** | 0·202 | 0·333 | 0·063 | 0·619 | 0·545 | **0·025** |
| C/N ratio | **0·015** | **0·000** | **0·000** | 0·244 | **0·000** | 0·084 | **0·000** | 0·561 | 0·896 |
| Potassium (g m$^{-2}$) | 0·242 | 0·778 | **0·015** | 0·118 | 0·905 | **0·031** | **0·001** | 0·531 | **0·001** |
| Phosphorus (g m$^{-2}$) | 0·069 | **0·010** | **0·000** | 0·214 | **0·041** | 0·301 | **0·001** | 0·831 | **0·005** |
| Calcium (g m$^{-2}$) | 0·267 | 0·197 | 0·078 | **0·005** | 0·633 | **0·001** | **0·000** | 0·574 | **0·001** |
| Magnesium (g m$^{-2}$) | **0·010** | 0·072 | **0·000** | 0·250 | 0·735 | 0·204 | **0·013** | 0·904 | **0·030** |

tab, tabonuco forest; pc, palo colorado forest; df, dwarf forest.

using weighted mean concentrations of minerals, taking account of the proportions and analyses of the wood and nonwood components, and the amount of litter per plot. Raw data are archived at http://luq.lternet.edu/data.

## Results

### LITTER QUANTITY AND QUALITY

Dwarf forest nonpalm standing litter amounts were significantly lower than in any other litter type (Tables 1–3). Other forests overall had similar amounts of litter, but there were significant year differences, with palo colorado and dwarf forests having larger amounts in the first year of study, 6 months after Hurricane Georges. Palm litter at all elevations contained significantly less wood than nonpalm litter, and some palm forest samples had almost no wood (Tables 1–3).

Palm litter was generally richer in nutrients than nonpalm, significantly so at higher elevations where leaching might have been expected (Fig. 1, Tables 2 and 3). Phosphorus showed a significant decline in

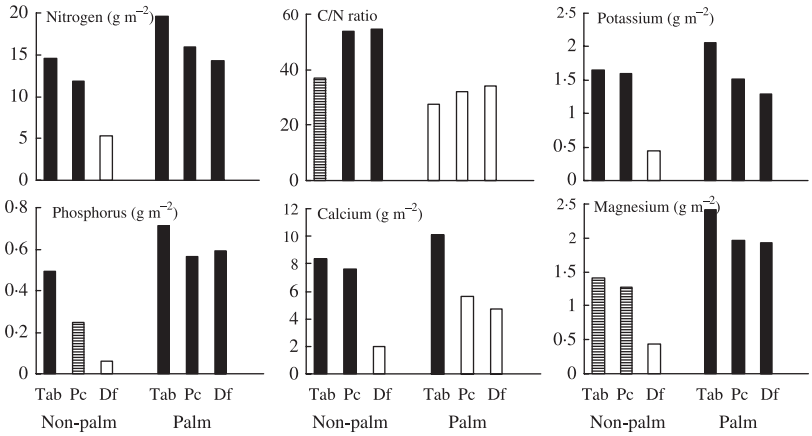


**Fig. 1.** Mean of litter nutrient amounts in, and C/N ratio of, litter from $4 \times 0{\cdot}25\text{-m}^2$ samples from nonpalm and palm areas from each of three forest types over 3 years. In this, and subsequent figures, adjacent orthogonal values with different shading are significantly different (three-way ANOVA, LSD test, $P < 0{\cdot}05$). Data from $4 \times 0{\cdot}25\text{-m}^2$ samples from nonpalm and palm areas in each of three forest types over 3 years.

**Table 4.** Significance of differences (three-way ANOVA, LSD test) for comparisons of species richness and Margalef's index. Bold type highlights significant values ($P < 0{\cdot}05$). Data from $4 \times 0{\cdot}25\text{-m}^2$ samples from nonpalm and palm areas in each of three forest types over 3 years

| | Between palm and nonpalm | | | Between tab and pc | | Between tab and df | | Between pc and df | |
|---|---|---|---|---|---|---|---|---|---|
| | tab | pc | df | Palm | Nonpalm | Palm | Nonpalm | Palm | Nonpalm |
| No. of spp./sample | **0·000** | **0·000** | **0·000** | 0·098 | 0·132 | 0·095 | **0·000** | 0·990 | **0·001** |
| Margalef's index | **0·000** | **0·006** | **0·000** | 0·127 | 0·516 | 0·074 | **0·000** | 0·786 | **0·001** |

tab, tabonuco forest; pc, palo colorado forest; df, dwarf forest.

nonpalm forests with increasing elevation, but not in palm litter, which had nine times more P than dwarf forest litter at a similar elevation. Palm litter also had significantly higher amounts of N, K, Ca, Mg (Fig. 1, Tables 2 and 3), S and Mn (data not shown) than other litter types and lower, but not significantly lower, Fe and Al concentrations (data not shown). Dwarf forest litter had significantly lower amounts of N, P, K and Ca than all other vegetation types (Fig. 1, Tables 2 and 3). C/N ratios increased up the elevational gradient (Fig. 1, Tables 2 and 3), indicating lower decay rates in the palo colorado and dwarf forests.

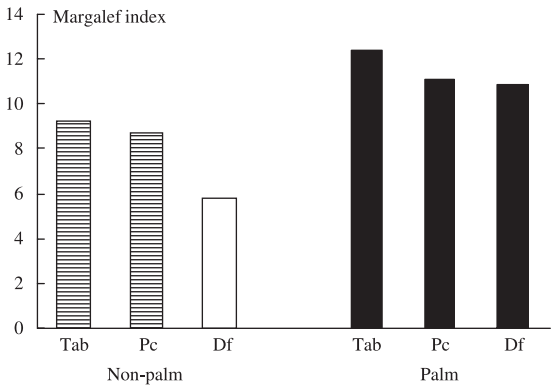


**Fig. 2.** Mean Margalef indices of species richness in $4 \times 0{\cdot}25\text{-m}^2$ samples of litter from nonpalm and palm areas from each of three forest types over 3 years.

## INVERTEBRATE SPECIES RICHNESS, ABUNDANCE AND BIOMASS

There were highly significant differences ($P < 0{\cdot}001$) in species richness (Margalef's index, Magurran 2003) among forest types, and between palm and nonpalm litter. Species richness was significantly greater in palm forest stands than in type-forests (i.e. tabonuco, palo colorado or dwarf forest) at the same or similar (dwarf forest) elevation, and there was only a very slight, and nonsignificant, decline in species richness with increasing elevation in palm forests (Fig. 2, Table 4). There were no significant year differences or year interactions. Species richness in dwarf forest nonpalm litter was significantly lower than in all other forests. The indices represent means of 65–85 species in the $4 \times 0{\cdot}25\text{-m}^{-2}$ samples of palm litter, from the three elevations over the 3 years, whereas there were 50–60 species in the tabonuco, 37–60 in the palo colorado litter, and only 20–30 in dwarf forest litter (Fig. 2). The mid-elevational peak of species richness seen in bromeliad microcosms (Richardson *et al*. 2000) in the palo colorado forest was not apparent.

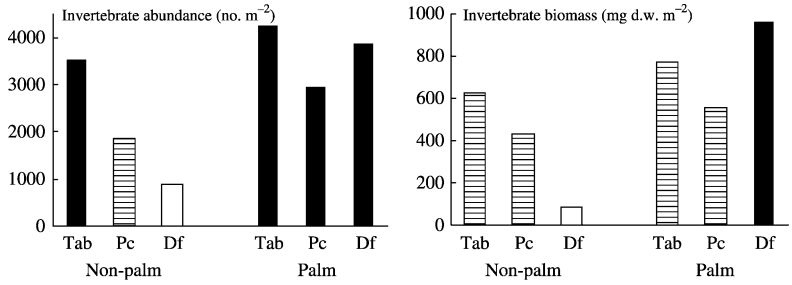


**Fig. 3.** Mean invertebrate abundance and biomass in $4 \times 0{\cdot}25$-m$^2$ samples of litter from nonpalm and palm areas from each of three forest types over 3 years.

**Table 5.** Significance of main effects and interactions (three-way ANOVA, LSD test) for abundance of organisms ($\log_N n + 1$) of the main taxonomic groups, all animals and total biomass. Bold type highlights significant values ($P < 0{\cdot}05$). Data from $4 \times 0{\cdot}25$-m$^2$ samples from nonpalm and palm areas in each of three forest types over 3 years

| | Main effects | | | Two-way interactions | | | Three-way interaction |
|---|---|---|---|---|---|---|---|
| | Forest type | Palm/nonpalm | Year | F × P | F × Y | P × Y | F × P × Y |
| Acari | **0·006** | 0·270 | 0·730 | 0·760 | 0·064 | 0·291 | 0·145 |
| Formicidae | **0·000** | **0·000** | 0·324 | **0·000** | 0·944 | 0·342 | 0·999 |
| Collembola | **0·000** | **0·000** | **0·002** | **0·042** | 0·701 | **0·018** | 0·062 |
| Isoptera | 0·261 | **0·001** | 0·927 | 0·859 | **0·050** | 0·890 | 0·544 |
| Coleoptera adult | 0·290 | **0·000** | **0·000** | **0·001** | 0·541 | 0·092 | 0·882 |
| Hemiptera & Homoptera | **0·000** | **0·000** | 0·599 | **0·046** | 0·497 | 0·814 | 0·391 |
| Diptera adult | **0·024** | **0·002** | **0·000** | **0·021** | 0·415 | 0·950 | 0·052 |
| Diptera immature | **0·017** | **0·000** | **0·007** | 0·057 | 0·898 | 0·491 | 0·464 |
| Isopoda | **0·018** | **0·002** | 0·543 | 0·051 | 0·675 | 0·986 | 0·171 |
| Coleoptera immature | 0·080 | **0·000** | 0·876 | **0·003** | 0·576 | 0·954 | 0·976 |
| Diplopoda | **0·039** | **0·000** | 0·307 | 0·104 | 0·062 | 0·553 | 0·807 |
| Pseudoscorpiones | **0·000** | 0·414 | **0·002** | **0·003** | 0·949 | 0·406 | 0·974 |
| Araneae | **0·000** | **0·010** | 0·084 | 0·213 | 0·368 | 0·557 | 0·081 |
| Chilopoda | 0·449 | **0·000** | 0·830 | **0·021** | **0·014** | 0·583 | **0·008** |
| Lepidoptera immature | **0·000** | **0·016** | 0·538 | 0·872 | **0·006** | 0·144 | 0·183 |
| Lepidoptera adult | **0·000** | **0·004** | **0·000** | **0·001** | 0·755 | 0·882 | 0·385 |
| Opiliones | **0·000** | 0·401 | 0·525 | 0·664 | 0·225 | 0·092 | 0·286 |
| Blattodea | **0·000** | 0·491 | **0·034** | 0·221 | 0·290 | 0·802 | 0·575 |
| Animal abundance (no. m$^{-2}$) | **0·000** | **0·000** | 0·993 | **0·001** | 0·806 | 0·137 | 0·413 |
| Animal biomass (g dry wt m$^{-2}$) | 0·425 | **0·006** | 0·500 | **0·040** | 0·478 | 0·625 | 0·725 |

Total animal abundance mirrored the pattern of litter nutrient amounts, with higher abundance in palm than nonpalm litter, significantly so in palo colorado and dwarf forests. Overall animal abundance declined significantly with increasing elevation in tabonuco, palo colorado and dwarf forests (Fig. 3, Tables 5 and 6) but there was no corresponding decline in the palm litter fauna along the gradient. The same pattern can be seen repeatedly in a variety of taxonomic groups, e.g. Coleoptera, Formicidae, Diplopoda and Diptera (Fig. 4). An exception was in the Arachnida (spiders, opilionids and pseudoscorpions), predators that declined considerably in both palm and nonpalm litter with increasing elevation.

Total animal biomass (Fig. 3, Tables 5 and 6) followed the patterns of abundance and nutrient concentrations, higher in palm than in nonpalm litter, and without any significant change along the elevational gradient in palm forest. The highest animal biomass, in palm litter at the highest elevation, can be explained by the high numbers of bark, fungivore and wood-boring beetles recorded in the first year of the study, immediately after Hurricane Georges. The significantly lowest animal biomass was in nonpalm dwarf forest litter.

In all forests and all years the main components of the communities, numerically and in terms of distribution, were Acari, Formicidae, Collembola, Isoptera, Coleoptera adults and Hemiptera/Homoptera, in total comprising 80% of the fauna (Tables 5–7). In terms of biomass (Table 7), however, the large-bodied termites, millipedes, adult beetles, molluscs, spiders, an onchyophoran (*Peripatus*), ants and isopods predominated, even though some, such as *Peripatus*, were rare.

Communities were compared pairwise using Sørensen's index of similarity (Magurran 2003) (Table 8). Nonpalm litter communities showed a decreasing similarity with

**Table 6.** Significance of differences (three-way ANOVA, LSD test) for comparisons of abundance of organisms ($\log_N n + 1$) of the main taxonomic groups, all animals and total biomass. Bold type highlights significant values ($P < 0{\cdot}05$). Data from $4 \times 0{\cdot}25\text{-m}^2$ samples from nonpalm and palm areas in each of three forest types over 3 years

| | Between palm and nonpalm | | | Between tab and pc | | Between tab and df | | Between pc and df | |
|---|---|---|---|---|---|---|---|---|---|
| | tab | pc | df | Palm | Nonpalm | Palm | Nonpalm | Palm | Nonpalm |
| Acari | 0·446 | 0·278 | 0·946 | 0·058 | 0·114 | 0·065 | **0·013** | 0·961 | 0·301 |
| Formicidae | 0·756 | **0·001** | **0·000** | 0·702 | **0·001** | 0·617 | **0·000** | 0·907 | **0·003** |
| Collembola | **0·007** | **0·000** | **0·000** | 0·157 | **0·021** | 0·132 | **0·000** | 0·927 | **0·009** |
| Isoptera | 0·060 | 0·119 | **0·022** | 0·295 | 0·474 | 0·379 | 0·187 | 0·866 | 0·545 |
| Coleoptera adult | 0·192 | 0·587 | **0·000** | 0·679 | 0·238 | **0·046** | **0·012** | 0·110 | **0·000** |
| Hemiptera & Homoptera | 0·509 | **0·000** | **0·002** | 0·356 | **0·000** | **0·037** | **0·000** | 0·233 | 0·657 |
| Diptera adult | 0·653 | **0·005** | **0·002** | **0·001** | 0·997 | 0·086 | 0·061 | 0·108 | 0·062 |
| Diptera immature | 0·106 | **0·004** | **0·000** | 0·852 | 0·258 | 0·778 | **0·000** | 0·640 | **0·012** |
| Isopoda | 0·460 | 0·299 | **0·000** | 0·215 | 0·125 | 0·677 | **0·001** | 0·407 | **0·043** |
| Coleoptera immature | 0·053 | **0·002** | **0·000** | 0·943 | 0·197 | 0·429 | **0·000** | 0·389 | **0·009** |
| Diplopoda | **0·000** | **0·003** | **0·000** | 0·070 | 0·327 | 0·494 | **0·007** | 0·251 | 0·073 |
| Pseudoscorpiones | **0·001** | 0·187 | 0·528 | **0·000** | 0·552 | **0·000** | 0·344 | 0·730 | 0·723 |
| Araneae | 0·692 | 0·197 | **0·006** | **0·004** | **0·000** | **0·002** | **0·000** | 0·814 | 0·074 |
| Chilopoda | **0·010** | 0·200 | **0·000** | 0·133 | 0·873 | 0·536 | **0·047** | **0·036** | 0·067 |
| Lepidoptera immature | 0·109 | 0·318 | 0·101 | **0·013** | 0·058 | **0·001** | **0·001** | 0·371 | 0·124 |
| Lepidoptera adult | 0·138 | **0·003** | **0·001** | **0·000** | 0·495 | **0·000** | 0·325 | 0·222 | 0·099 |
| Opiliones | 0·807 | 0·349 | 0·447 | **0·006** | **0·000** | **0·001** | **0·001** | 0·812 | 0·678 |
| Blattodea | 0·338 | 0·146 | 0·491 | 0·185 | **0·000** | **0·010** | **0·000** | 0·193 | 0·594 |
| Animal abundance (no. $m^{-2}$) | 0·385 | **0·013** | **0·000** | 0·151 | **0·003** | 0·392 | **0·000** | 0·554 | **0·003** |
| Animal biomass (g dry wt $m^{-2}$) | 0·535 | 0·589 | **0·000** | 0·368 | 0·411 | 0·398 | **0·025** | 0·084 | 0·144 |

tab, tabonuco forest; pc, palo colorado forest; df, dwarf forest.

**Table 7.** Total abundance, biomass (mean dry wt), and percentage of totals, of major taxonomic groups in litter from nonpalm and palm areas in the LEF over 3 years (total area sampled $72 \times 0{\cdot}25\text{-m}^2$ plots)

| | Abundance | | | Biomass | |
|---|---|---|---|---|---|
| | | % | | mg $m^{-2}$ | % |
| Acari | 17 624 | 33·9 | Isoptera | 130·9 | 23·3 |
| Formicidae | 9 452 | 18·2 | Diplopoda | 82·0 | 14·6 |
| Collembola | 5 132 | 9·9 | Coleoptera (adults) | 60·3 | 10·7 |
| Isoptera | 4 452 | 8·6 | Mollusca | 55·7 | 9·9 |
| Coleoptera (adults) | 3 244 | 6·2 | Araneae | 39·5 | 7·0 |
| Hemiptera & Homoptera | 2 023 | 3·9 | Onchyophora | 33·3 | 5·9 |
| Diptera (adults) | 1 890 | 3·6 | Formicidae | 30·9 | 5·5 |
| Diptera (immature) | 1 778 | 3·4 | Isopoda | 23·6 | 4·2 |
| Isopoda | 1 416 | 2·7 | Chilopoda | 20·9 | 3·7 |
| Coleoptera (immature) | 1 320 | 2·5 | Hemiptera & Homoptera | 19·8 | 3·5 |
| Diplopoda | 1 206 | 2·3 | Diptera (adults) | 13·1 | 2·3 |
| Pseudoscorpiones | 914 | 1·8 | Lepidoptera (adults) | 9·8 | 1·7 |
| Araneae | 526 | 1·0 | Blattodea | 8·0 | 1·4 |
| All other taxa* | 477 | 0·9 | All other taxa* | 7·6 | 1·3 |
| | | | Collembola | 6·9 | 1·2 |
| Chilopoda | 148 | 0·3 | Acari | 6·4 | 1·1 |
| Lepidoptera (adults) | 131 | 0·3 | Coleoptera (immature) | 5·2 | 0·9 |
| Lepidoptera (larvae) | 104 | 0·2 | Pseudoscorpiones | 4·9 | 0·9 |
| Opiliones | 80 | 0·2 | Diptera (immature) | 4·6 | 0·8 |
| Blattodea | 65 | 0·1 | Opiliones | 2·9 | 0·5 |
| Mollusca | 20 | < 0·1 | Lepidoptera (larvae) | 2·6 | 0·5 |
| Onchyophora | 2 | < 0·1 | | | |
| Total | 52 004 | | Total | 562·9 | |

*'All other taxa' includes those which occurred either more infrequently than those in the table, or those which comprised only a very small biomass, and so were not considered of major importance in the community.

increasing elevational separation, particularly between the widely separated tabonuco and dwarf forests. Palm litter communities were more uniform along the elevational gradient and would appear to be independent of climate. Between litter types, palm litter and nonpalm litter communities were similar in all years of the study in the tabonuco forest, but became increasingly dissimilar in the palo colorado and dwarf forests (Table 9).

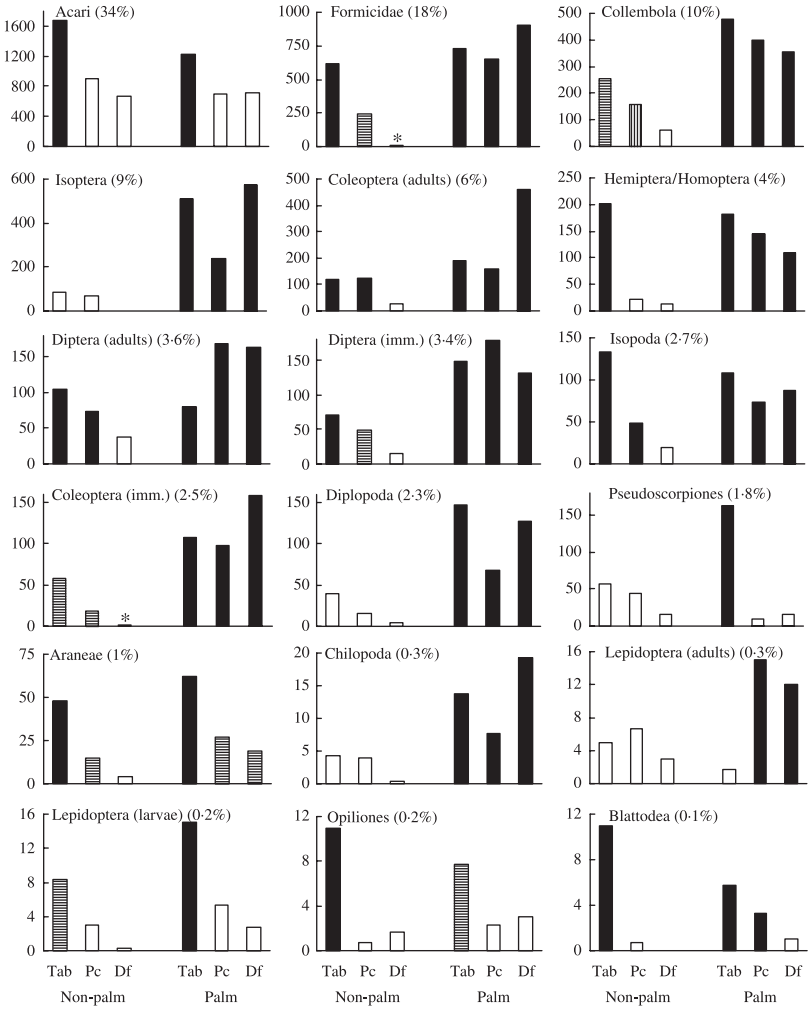


**Fig. 4.** Mean abundance (no. $m^{-2}$) of animals of the main invertebrate groups in $4 \times 0{\cdot}25\text{-}m^2$ samples of litter from nonpalm and palm areas from each of three forest types over 3 years. These groups represented over 99% of all animals collected. *Present, but values too small to register when plotted.

**Table 8.** Pairwise comparisons among forests (Sørensen's index of similarity – $C_s$)

| | tab/pc | pc/df | tab/df |
|---|---|---|---|
| 1999 Nonpalm | 0·366 | 0·330 | 0·292 |
| 2000 Nonpalm | 0·408 | 0·299 | 0·235 |
| 2001 Nonpalm | 0·426 | 0·400 | 0·277 |
| 1999 Palm | 0·453 | 0·518 | 0·514 |
| 2000 Palm | 0·599 | 0·635 | 0·543 |
| 2001 Palm | 0·471 | 0·558 | 0·518 |

$C_s = 2j/(a + b)$, where: J = no. of species common to both sites, and a, b = no. of species in site A or B, respectively. $C_s = 1$ indicates complete similarity. Differences between values for individual years of *c.* 0·07 are significant ($P = 0{\cdot}05$). tab, tabonuco forest; pc, palo colorado forest; df, dwarf forest.

**Table 9.** Similarity of invertebrate communities in nonpalm and palm litter (Sørensen's index of similarity – $C_s$) in three forest types

| | tab | pc | df |
|---|---|---|---|
| 1999 | 0·552 | 0·487 | 0·271 |
| 2000 | 0·595 | 0·482 | 0·286 |
| 2001 | 0·590 | 0·455 | 0·353 |

tab, tabonuco forest; pc, palo colorado forest; df, dwarf forest.

## Discussion

### COMMUNITIES

There are few studies with which the above litter communities can be compared, as most have included cores of mineral soil as well as above-ground litter and living plant tissue. In Puerto Rico, Pfieffer (1996) collected litter by D-Vac suctioning and Wiegert (1970) hand-collected litter. Both extracted animals by modifications of the Tullgren method, and both collected only in the tabonuco forest.

Numerically, mites usually comprise the most abundant taxon in forest litter (Petersen 1982) and this was confirmed in all the Puerto Rican studies. Collections during 1984–85 (Pfieffer 1996) yielded mite densities of 2000–3500 $m^{-2}$ and in this study we recorded slightly lower densities of 1000–2700 $m^{-2}$ in tabonuco forest, numerically 47% of all taxa in nonpalm litter, but only

1·8% of total biomass. Densities of Collembola in the tabonuco forest in the present study are slightly lower than Wiegert's (1970) figures, but similar in proportion of total taxa (7% and 5%). Collembola in tabonuco (present study) were, however, only 1·3% of total biomass, as many were juveniles. The higher abundance of Collembola in palm litter may be explained by their need to avoid dehydration and predators. The dominant family was the Emtomobryidae, as in the earlier studies. The commonest termite, *Nasutitermes costalis* (Hölmgren), at a density of 49 individuals $m^{-2}$ in tabonuco forest was also similar to previously recorded densities (Wiegert 1970; McMahan 1996).

Distribution of organisms was patchy, even in some numerically abundant groups such as termites, which were never found in dwarf forest litter, though abundant in palm litter within the dwarf forest. Termites were also infrequent or absent in the nonpalm litter of tabonuco or palo colorado forests. This may be due to presence or absence of suitable food resources, but such relatively large and soft-bodied animals are sought by predators, and the dense palm litter provides more shelter. Patchy distribution of some groups may also depend on previous land use history and Thompson *et al*. (2002) have shown that land-use history may be still reflected 50 years later in plant communities. Hurricane disturbance further increases the mosaic of plant communities. The degree of hurricane damage has been shown to be related to bacterial functional diversity in soils up to 5 years afterwards (Willig *et al*. 1996), and may also affect litter animal communities. The absence of a unimodal pattern of species richness in the litter over the elevational gradient, as found in the earlier bromeliad study in the same forest (Richardson *et al*. 2000), may be real, or may be a consequence of this patchy distribution and the small proportion of forest sampled.

Abundance is not necessarily a guide to diversity in a taxonomic group. Although highly abundant, there are only four species of termites in Puerto Rico, of which we commonly found one, *Nasutitermes costalis*, and another, *N. nigriceps* (Haldeman), only infrequently. Termites in the LEF are all xylophagous, feeding on sound dead wood or wood altered by fungal attack, and there are no soil feeders or fungus growers (McMahan 1996). Puerto Rico is largely volcanic in origin, and has never been connected to a continental landmass. Colonization is therefore dependent on chance dispersal. This low diversity of the Puerto Rican fauna is likely to be an island effect. Diversity is higher in other tropical forests, e.g. Sumatra (Gathorne-Hardy, Syaukani & Eggleton 2001), where 102 termite species were found, and even a change of 100-m elevation was suggested as being sufficient to affect their abundance and diversity.

Diversity in some abundant taxa such as Coleoptera was high, as would be expected, but some uncommon taxa, such as adult microlepidopteran moths, also had a very high diversity. There were at least 37 species in the 131 individuals recovered from the LEF litter, most cryptic and some mimicking broken leaf fragments, belonging to genera that are mainly night-flying. Litter provides a refuge from predators during the day, although some, with debris-feeding larvae, such as Tineidae, may have been laying eggs in the litter. Most genera recorded, however, have larvae which are leaf feeders or leaf miners in the shrub layer or canopy, which is a more spatially diverse habitat than the litter. Other small soft-bodied adult insects such as Diptera may also be using litter as a refuge.

Events such as storms and hurricanes also affect distribution, abundance and diversity in samples, as they produce a pulse in litterfall, particularly woody litter, after the event. The palo colorado and dwarf forests were badly hit by Hurricane Georges in September 1998 and the pulse may be reflected in some animal groups. In all forests, Coleoptera counts were at their highest in 1999, but particularly so in dwarf forest palm, due to the families Cossonidae (broad-nosed bark beetles that feed under the bark of dead wood and in litter), Scolytidae and Platypodidae (which attack dying wood) and the Ptilidae (minute feather wing beetles that feed on fungal spores). Staphylinidae, which includes both predators and detritus feeders, were also highly abundant. In the following year coleopteran abundance dropped markedly and began to recover in 2001.

### INFLUENCE OF PRIMARY AND SECONDARY FACTORS ON ANIMAL COMMUNITIES

Patterns observed among forests in animal abundance, species assemblages, and species richness are better explained by differences in forest composition, rather than the direct elevational effects of temperature and rainfall. Community parameters in nonpalm litter show increasing dissimilarity with increasing elevation with the dwarf forest having the lowest animal abundance and species richness, and the greatest dissimilarity in community assemblages compared with the low elevation tabonuco forest. These decreases correspond to the known decline in forest NPP with increasing elevation. In contrast community parameters are remarkably similar in palm litter invertebrates along the gradient. The common factor in the palm areas is the chemical and physical nature of the resource base and a uniform forest structure. In a study of insect communities feeding on a single plant species (bracken fern *Pteridium aquilinum*) along an elevational gradient, Lawton *et al*. (1987) also found that the total number of species did not decline with altitude. Only one species had a distribution that was clearly and consistently linked with altitude and as altitude increased it occurred at fewer sites and became less abundant at occupied sites. The adaptations of insects to a particular resource base may be a more important factor in determining community structure than climatic conditions, to which they appear tolerant, at least along the elevational ranges in these two examples. Although the elevational range at Lawton's study site in the UK is less than that

in the Puerto Rico experiment, the severity of annual climatic variation is greater.

The sierra palm is a subdominant species in the LEF, occurring within the three forest types, in forest flood plains, on steep slopes, and in areas of impeded drainage. The highest levels of productivity in the LEF have been found in palm-dominated flood plain in the palo colorado at 750 m. This has apparently been explained by specific adaptations of palms, including a high level of phosphorus translocation by leaves (Frangi & Lugo 1985). In their study area the mean phosphorus concentration in live palm leaves was almost twice that of the mean phosphorus concentration in dicotyledonous leaves (1·18 vs. 0·66 mg $g^{-1}$). Dead palm leaves still attached to the palm on senescence had less than half the phosphorus concentration of live leaves (0·65 mg $g^{-1}$) and this reduced to 28% of that of live leaves when palm leaves fell to the ground. Phosphorus concentrations then decreased to 10% that of live leaves and remained constant for at least 100 days. Our measurements of phosphorus concentrations (0·63, 0·49 and 0·62 mg $g^{-1}$ at the three elevations) in fallen palm litter are higher, but include fruits as well as leaves, because we only separated litter into the wood component and 'all other litter'. Palm fruits have high phosphorus concentrations (0·96 mg $g^{-1}$) (Frangi & Lugo 1985) and would therefore have contributed to higher readings. Fruits provide food for weevils, other Coleoptera, and Hemiptera.

There is a substantial body of evidence that P correlates with insect growth rate through RNA production (Sterner & Elser 2002). It is tempting to conclude that the significantly higher animal abundance in palm vs. nonpalm litter in all three forests is due to its higher nutrient base of P and other minerals. Palm litter is, however, physically very different from other litter types. The heavy flat fronds, as they decay, form layers like wet blotting paper and, although we did not carry out any weight loss measurements, it was noticeable that samples took longer to dry in Tullgren funnels. Small dicotyledonous leaves can be blown around by the wind and, although they can be bound together by fungal hyphae (Lodge 1993), it is noticeable that leaves in nonpalm areas can be piled up by the wind in dry conditions. The explanation for higher animal abundance in palm litter may in part be due to its greater stability and humidity, enabling animals to survive better in periods of drought, and to be better protected from predators by its density.

Palm stands were not sampled in the previous study of bromeliad communities (Richardson 1999), as these shaded areas contained few bromeliads. Comparisons of bromeliad and forest floor litter communities in the type-forests, however, showed striking similarities. Animal abundance and biomass in bromeliads declined with increasing elevation, along with a decline in nutrient concentrations of impounded litter and water, and a decline in forest NPP (Richardson 1999; Richardson *et al*. 2000). These results are consistent with those reported for other forests and a variety of animal and plant groups and have usually been interpreted as due to the primary effect of climatic change with elevation. Temperature, humidity, and periods of desiccation may affect growth and developmental rates of invertebrate populations and are usually species specific (Begon, Harper & Townsend 1996; Stewart & Woolbright 1996; Alvarez 1997). The data from palm forest litter would suggest, however, that the contribution of litter type is an important factor in determining the composition of these detritivore-based communities in forests.

Forest floor litter is part of a general continuum along the forest elevational gradient, unlike bromeliad microcosms, which are discrete units containing highly specialized aquatic and terrestrial communities. Nevertheless it can, by sampling methodically, also be used to compare invertebrate communities in different vegetation types, and allow the effects of some of the parameters involved to be identified. Its use has demonstrated conclusively that the composition of these invertebrate communities is determined by litter type or other habitat factors, rather than the direct effects of changing climatic conditions along the elevational gradient.

## Acknowledgements

This research was performed under grant DEB-0218039 from the National Science Foundation to the Institute for Tropical Ecosystems Studies, University of Puerto Rico, and the International Institute of Tropical Forestry, as part of the Long-Term Ecological Research programme in the LEF, and USDA IITF Grant 01-1G11120101-001. Felipe N. Soto-Adames worked under NSF grant DEB-0075548. Additional support was given by the plant analysis laboratory of the International Institute of Tropical Forestry, and the staff of the El Verde Field Station of the University of Puerto Rico. Drs Robert Edwards, Jon Gelhaus and Keith Bland provided detailed taxonomic help with the identification of spiders, Tipulidae, and Lepidoptera, respectively. Drs Nicholas Brokaw, Diane Srivastava and Jess Zimmerman helpfully reviewed an earlier draft, and Dr Robert Elton advised on the statistical treatment.

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*Received 23 October 2004; accepted 15 March 2005*