Ecological Bulletins 54: 101–115, 2013

Litter-based invertebrate communities in forest floor and bromeliad microcosms along an elevational gradient in Puerto Rico

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Relationships between litter invertebrate communities, climate, and forest net primary productivity (NPP) were investigated in two microhabitats along an elevational gradient in the Luquillo Experimental Forest. In forest floor litter communities, using palm litter as a control for forest type, although overall NPP declined with increasing elevation and rainfall, animal abundance, biomass and species richness were remarkably similar along the gradient. In non-palm litter, all community parameters declined with increasing elevation, along with NPP and litter nutrient concentrations. Nutrient concentrations were higher in palm than non-palm litter, and did not decline significantly along the gradient, and palm litter provided a more stable physical environment than other litter types. Thus, adaptations of invertebrates to the secondary factors of resource base and habitat (i.e. forest type), as seen in palm litter, may be more important in determining community structure than the primary effects of changing climate along the gradient. In structurally more complex bromeliad microcosms, which contain both litter and aquatic detritivore communities, abundance and species richness were independent of each other. Animal abundance declined, along with NPP, with increasing elevation, but species richness and animal biomass peaked at mid-elevation, confirming the monotonic pattern reported in other tropical elevation studies. The mid-elevation palo colorado forest is more architecturally complex, and richer in epiphytes and ground species than the other forests, and its intermediate climatic conditions may be more favourable to invertebrate survival than other forests. Bromeliad community parameters reflect forest characteristics specifically, rather than NPP and climate. The aquatic component of the bromeliad fauna was habitat-specific, with many species being endemic to bromeliads and to Puerto Rico.

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Invertebrate communities are at the interface between forests and their underlying mineral soils. Knowledge of their diversity and dynamics is essential in understanding nutrient circulation in the wider ecosystem. Invertebrates unlock minerals from litterfall for re-cycling by fragmenting leaf and woody litter, enhancing microbial substrates, and by directly feeding on hyphae, spores, and fungal fruiting bodies growing on detritus (Seastedt 1984). Litter breakdown also maintains epiphytes, many of which are 'keystone species' contributing to forest structural complexity and animal diversity (Nadkarni 1994). In this chapter we ask how variations in plant productivity and physical factors along elevational gradients affect animal communities responsible for litter breakdown in the forest floor and in epiphytic bromeliads.

The biotic and abiotic changes resulting from seasonality and hurricanes can cause fluctuations in both animal and fungal communities, which in turn affect the rate of litter breakdown (Richardson et al. 2010). Rainfall is weakly seasonal in the Luquillo Experimental Forest (LEF), with a dry season, between December and March, which can cause drying out of litter on the forest floor in tabonuco forest, although this is less marked at higher elevations. Litterfall is also seasonal, with a main peak from March to June, and a secondary peak in September (Zalamea and González 2008); in addition there can be large pulses of litter deposited from hurricanes. Hurricane Hugo in 1989, for example, caused tree fall, defoliation and a fine litter deposition of 1.2–1.9 times normal annual litterfall (Lodge et al. 1991).

Forest floor litter communities

Litter was sampled down to the mineral soil surface, over three years 1999–2001, at three elevations in the LEF. These were in tabonuco forest (lower montane rain forest, with *Dacryodes excelsa* Vahl dominant, 330–500 m a.s.l.), palo colorado forest (subtropical wet forest, with *Cyrilla racemiflora* L. dominant, 750–780 m a.s.l.), and dwarf or cloud forest (*Tabebuia rigida* Urban dominant, 950–1000 m a.s.l.), with equal samples of palm (*Prestoea montana* (R. Grah.) Nichols.) and non-palm litter at each elevation. Invertebrates were extracted using Tullgren funnels (Richardson et al. 2005). The main components of the communities overall, numerically and in terms of distribution, were Acari, Formicidae, Collembola, Isoptera, Coleoptera adults and Hemiptera/Homoptera, in total comprising 80% of the fauna (Table 1 and Fig. 1). In terms of biomass, however, the large-bodied termites, millipedes, adult beetles, molluscs, spiders, an onychophoran (*Peripatus* sp.), ants, and isopods predominated, even though some, such as *Peripatus*, were rare (Table 1). In general, for most taxonomic groups, populations were higher in palm than non-palm litter at the same elevation.

Detritivores form the largest group, but it is not always known whether an organism feeds on detritus for its fungal and microbial content or decay products (panphytophagous), or consumes the detritus directly for its nutrients. Some oribatid mites are consumers of litter (detritivores) and have cellulases in their guts derived from fungal symbionts, and others are fungivores (microbiovores) with the enzyme trehalase for digesting trehalose, a sugar characteristic of fungal hyphae. Similarly, some prostigmatic mites are predators, others microbiovores. Numerically, mites usually comprise the most abundant taxon in forest litter (Petersen 1982) and this has been confirmed in Puerto Rican studies. Collections in tabonuco

Table 1. Abundance, biomass (mg dry wt), and % of totals, of major taxonomic groups in litter (total from 18 m^2) from non-palm and palm areas in each of three forest types over three years (Richardson et al. 2005).

Abundance			Biomass		
Taxonomic group	no.	%	Taxonomic group	mg dry wt	%
Acari	17624	33.9	Isoptera	2356	23.3
Formicidae	9452	18.2	Diplopoda	1476	14.6
Collembola	5132	9.9	Coleoptera (adults)	1085	10.7
Isoptera	4452	8.6	Mollusca	1002	9.9
Coleoptera (adults)	3244	6.2	Araneae	711	7.0
Hemiptera and Homoptera	2023	3.9	Onychophora	600	5.9
Diptera (adults)	1890	3.6	Formicidae	557	5.5
Diptera (immature)	1778	3.4	Isopoda	425	4.2
Isopoda	1416	2.7	Chilopoda	377	3.7
Coleoptera (immature)	1320	2.5	Hemiptera and Homoptera	357	3.5
Diplopoda	1206	2.3	Diptera (adults)	236	2.3
Pseudoscorpiones	914	1.8	Lepidoptera (adults)	176	1.7
Araneae	526	1.0	Blattodea	144	1.4
Chilopoda	148	0.3	Acari	116	1.1
Lepidoptera (adults)	131	0.3	Coleoptera (immature)	94	0.9
Lepidoptera (larvae)	104	0.2	Pseudoscorpiones	89	0.9
Opiliones	80	0.2	Diptera (immature)	82	0.8
Blattodea	65	0.1	Opiliones	52	0.5
Mollusca	20	<0.1	Lepidoptera (larvae)	47	0.5
Onychophora	2	<0.1	Collembola	16	0.2
All other taxa*	477	0.9	All other taxa*	136	1.3
Total	52004		Total	10132	

* 'All other taxa' includes those that, separately, occurred either more infrequently than those in the table, or comprised a relatively small biomass.

forest in 1984–1985 (Pfeiffer 1996) yielded mite densities of 2000–3500 m^{-2}; in tabonuco litter we recorded slightly lower numbers (1000–2700 m^{-2}) in the same forest, and overall in the LEF they contributed 34% of abundance, but only 1.1% total animal biomass (Table 1). Franklin et al. (2004) working in Amazonian forest found that both mites and collembola (also highly abundant) had little direct effect on the decomposition and mass loss of leaves and that they may act principally as 'grazing arthropods' (Hanlon and Anderson 1979) on fungal hyphae. Larger

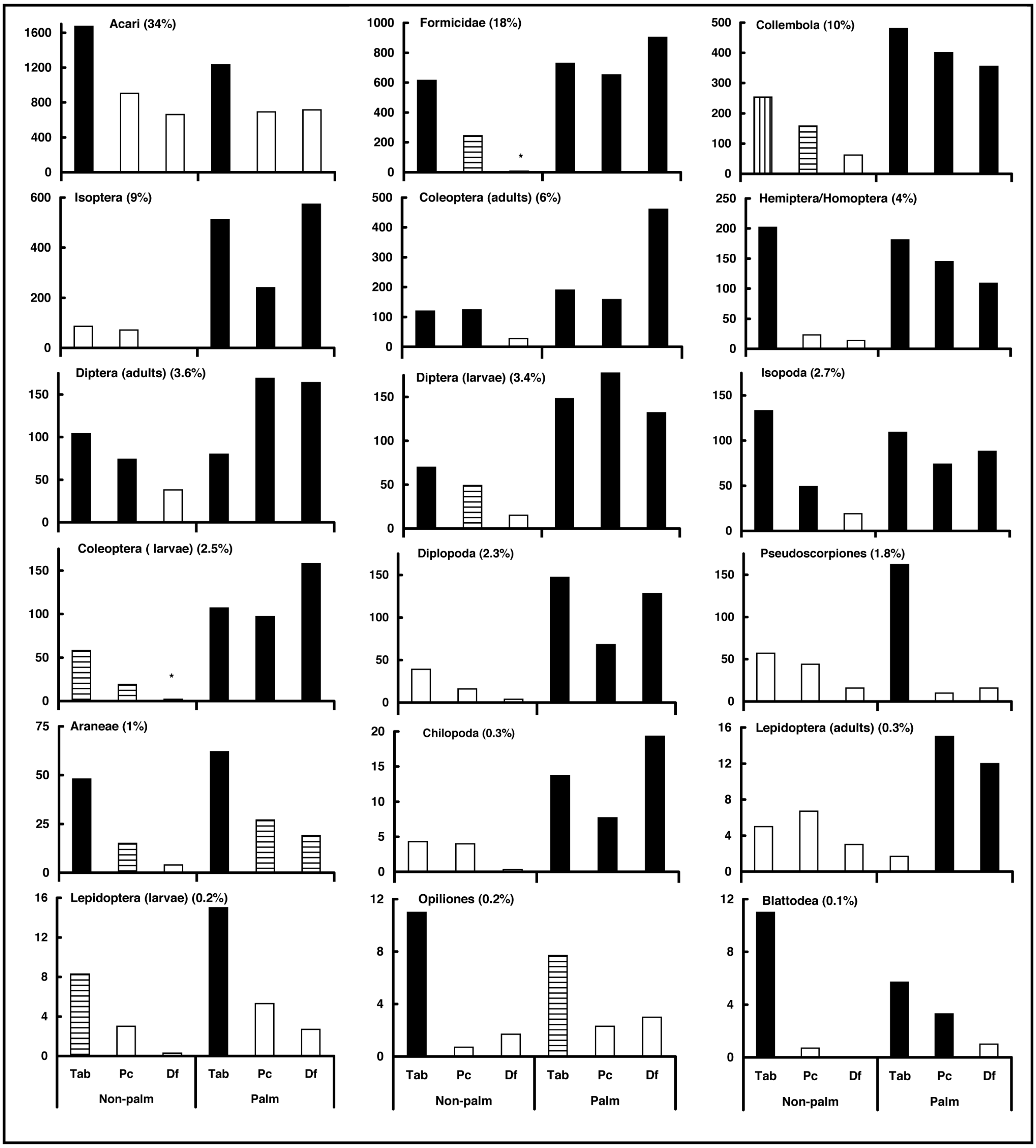

Figure 1. Mean abundance (no. m^{-2}) of animals of the main invertebrate groups in samples of litter from non-palm and palm areas from each of three forest types (Tab = Tabonuco; Pc = Palo Colorado; Df = dwarf forest) over three years. These groups represented over 99% of all animals collected. In this and subsequent figures, adjacent columns with different shading are significantly different (3-way ANOVA, LSD test, $p < 0.05$). Data from 4 × 0.25 m^{2} samples from non-palm and palm areas in each of three forest types in each of three years (Richardson et al. 2005).

invertebrates, such as millipedes, are likely to be more effective as shredders of litter. Mites and collembola may be more important in mobilizing nutrients than in direct litter breakdown. Although collembola are ecologically differentiated into many feeding guilds, those in tropical forest litters are characterized as specialist fungivores (hyphae and fungal spores), with only low densities of litter-shredding species (Rusek 1998). They were, therefore, all classified as microbiovores in our study and, although highly abundant (9.9% total fauna), only contributed 1.2% to invertebrate biomass. Both mites and collembola are the major prey of staphylinid beetles and arachnids, such as small spiders and pseudoscorpions, and are important in the food web of forest floor litter.

Larger detritivores are mainly the leaf shredding millipedes and isopods, and wood-feeding Coleoptera and termites. The commonest termite, *Nasutitermes costalis* (Holmgren), was at a density of 49 individuals m^{-2} in tabonuco forest, similar to previously recorded densities (Wiegert 1970, McMahan 1996). 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 for any significant period of time, even with the possibility of short-lived land-connections (GAARlandia) during the mid-Cenozoic period 33–35 Ma (Iturralde-Vinent and MacPhee 1999). Colonization is, therefore, dependent on chance dispersal. The 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 et al. 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. In Puerto Rico, termites were absent from dwarf forest litter, though highly abundant in palm forest litter at similar high elevations (Fig. 1).

Some uncommon taxa, such as adult microlepidopteran moths, had a very high diversity. There were at least 37 species among the 131 individuals recovered from the LEF litter, most cryptic and some mimicking broken leaf fragments, belonging to genera with species that are mainly night-flying. Litter provides a refuge from predators during the day, although some, with debris-feeding larvae, such as Tineidae, were laying eggs in the litter. Most genera recorded, however, have species with larvae that are leaf-feeders or leaf-miners in the shrub layer or canopy. Other small soft-bodied adult insects such as Diptera may also be using litter as a refuge, as well as laying eggs there because many of their larvae are detritus feeders.

Diversity in some abundant taxa, such as Coleoptera, was as expected high, but events such as storms and hurricanes also affect distribution, abundance and diversity, as they produce a pulse in litterfall, particularly woody litter. The palo colorado and dwarf forests were badly hit by Hurricane Georges in September 1998 and the effect of the litter pulse may be reflected in increased abundance within specialist families. In all forests, Coleoptera counts were at their highest in 1999, but particularly so in dwarf forest palm litter, due to high numbers of 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 Ptiliidae (minute feather wing beetles that feed on fungal spores). Staphylinidae, which includes both predators and detritivores, were also highly abundant. In the following year, coleopteran abundance dropped markedly before beginning to recover.

Generally predators occur at much lower abundances than prey species; here the arachnid predators such as spiders, opilionids and pseudoscorpions were in relatively low abundance in most samples (except tabonuco palm, Fig. 1), as were the small parasitoid wasps Myrmaridae, which parasitise the eggs of other insects.

Productivity along the gradient – separating the effects of forest type and elevation on the diversity of litter communities

Many attempts have been made to relate species richness and abundance to productivity along ecological gradients. Climatic conditions change with increasing elevation, and these changes affect plant productivity in various ways, chiefly through increased rainfall, leaching, water-logging of soils, higher wind speeds and lower temperatures, resulting in declining productivity towards the summits of mountains. The climatic differences result in different forest types, as only those tree species adapted to them can survive at particular elevations. Climate may also affect animal communities directly, and it is generally accepted that there is a decline in species richness with elevation, although the pattern of decline is not necessarily monotonic (Rahbek 1995). It is difficult, however, to distinguish between the primary influences of climate (temperature and rainfall), and the secondary (biotic) effects of different vegetation types along the gradient, which provide animals with various habitats and nutrient resources.

To separate the effects of these factors a control for forest type is needed at all elevations and this is why we sampled areas under sierra palm *Prestoea montana* (Graham) G. Nicholson, which occurs in stands at all elevations, and its large leaves form piles of litter containing only a few windblown leaves of other species (Richardson et al. 2005). By sampling palm litter and forest-type litter in a ‘natural experiment’ at three elevations, we aimed to discriminate between the influences of elevation and forest type on forest floor litter communities within areas characteristically known as tabonuco, palo colorado, and dwarf forest.

Dwarf forest non-palm standing litter amounts were significantly lower than in any other litter type (Table 2) and, therefore, showed much lower net primary productivity (NPP), when litterfall is used as a surrogate for productivity. Other forests overall had similar amounts of litter, and there was no significant difference between palm and non-palm, but there were significant differences among years, with palo colorado and dwarf forests having larger amounts in the first year of study, 6 months after Hurricane Georges (Richardson et al. 2005).

Palm litter at all elevations contained significantly less wood than non-palm litter, and palm litter was generally richer in nutrients than non-palm, significantly so at higher elevations where leaching might have been expected (Fig. 2). Phosphorus showed a significant decline in non-palm forests with increasing elevation, but not in palm litter, which had nine times more P than dwarf forest litter at a similar elevation, probably because of the large amount of palm fruits in the litter. Palm litter also had significantly higher amounts of N, K, Ca, and Mg than other litter types. Dwarf forest litter had significantly lower amounts of N, P, K and Ca per unit area than all other vegetation types. C/N ratios increased up the elevational gradient indicating lower decay rates in the increasingly wet conditions of palo colorado and dwarf forests.

Animal abundance declined significantly with increasing elevation in non-palm forests, but not in palm litter subject to the same environmental conditions (Fig. 3) and these trends in abundance can also be seen in many individual taxa (Fig. 1). Similarly animal biomass declined towards the summit and was significantly lower in dwarf forest, but was at its highest in palm litter at the same elevation (Fig. 3). Species richness (Margalef's index) was significantly higher in palm litter at all elevations (Fig. 4) than in type-forests (tabonuco, palo colorado and dwarf forest) and there was only a slight and non-significant decline with elevation. Species richness in dwarf forest non-palm litter was significantly lower than in all other forests with some taxa such as termites, ants, Coleoptera larvae and cockroaches absent (Fig. 1).

These observed patterns 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 non-palm 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 (Richardson et al. 2005). 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. It is tempting to attribute the constantly high species richness to the high concentration of nutrients, especially phosphorus, but physical attributes such as its layered decaying fronds, noticeably wet condition under the surface and stability, may in addition give greater protection to animal communities than small-leaved litter of other forest types which is easily wind-blown when dry.

The common factor in the palm areas is the constant chemical and physical nature of the resource base and a uniform forest structure. In the only other known study of insect communities associated with a single plant species (bracken fern *Pteridium aquilinum* (L.) Kuhn) along an elevational gradient, Lawton et al. (1987) also found that the total number of species did not decline with elevation. 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 and habitat may be a more important factor in determining community structure than the primary effects of climate, to which they appear tolerant, at least along the elevational ranges in these two examples.

The role of epiphytes in forest ecosystems

Epiphytes such as mosses and liverworts, ferns, orchids, and bromeliads, typically grow attached to branches of

Table 2. Mean total standing litter and proportion of wood from 4 × 0.25 m^2 samples from non-palm and palm areas in each of three forest types over three years (Richardson et al. 2005).

	Litter ($g\ m^{-2}$)						Wood (%)					
	Tabonuco		Palo colorado		Dwarf forest		Tabonuco		Palo colorado		Dwarf forest	
	Non-palm	Palm	Non-palm	Palm	Non-palm	Palm	Non-palm	Palm	Non-palm	Palm	Non-palm	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

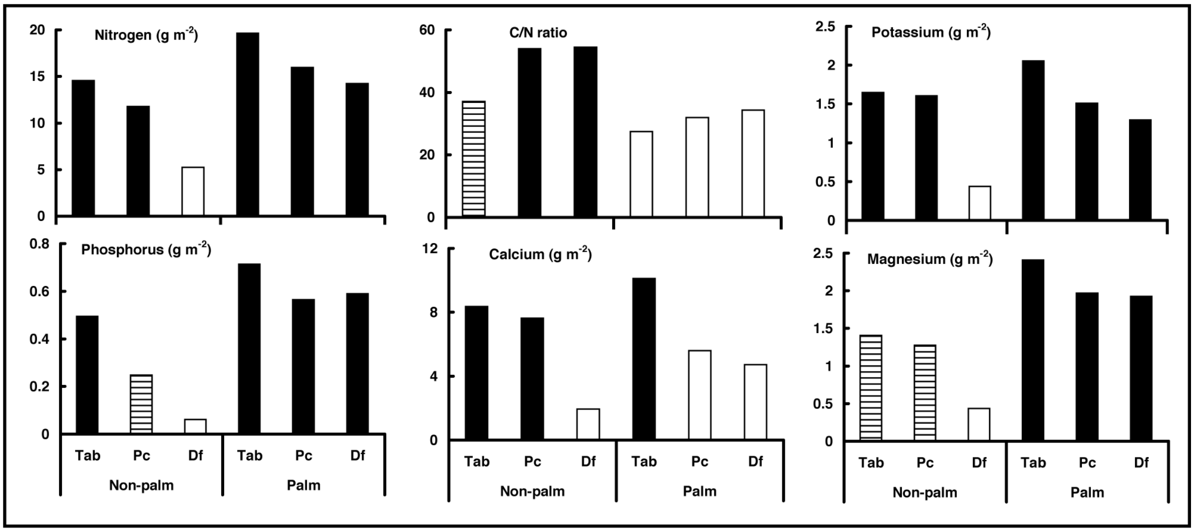

Figure 2. Mean mineral amounts in, and C/N ratio of, litter from samples in non-palm and palm areas from each of three forest types over three years.

trees and shrubs, though in permanently wet conditions, such as cloud forests, many species can also grow on the ground. Trees and shrubs simply provide a point of attachment and support, and epiphytes rely for nutrients on the minerals in throughfall water, and from decaying canopy litter that lodges on branches, or is trapped by the epiphytes themselves. They contain little woody material and, therefore, have a high proportion of nutrients, and Nadkarni (1984) found that in a Costa Rican cloud forest, although epiphytic biomass was < 2% of total forest dry weight, their mineral capital constituted up to 45% of that held in the foliage of the same forest. They thus increase the labile mineral capital of the above-ground portion of the forest and, on death or dislodgement, fall to the forest floor and are incorporated into the decay processes of the litter. Epiphytic litterfall was equivalent to 5–10% of total fine litter biomass, and nutrient transfer via epiphytic litterfall was up to 8% of annual nutrient transfer in total fine litterfall (Nadkarni and Matelson 1992) in the same Costa Rican forest.

Epiphytes are regarded as a 'keystone resource' by Nadkarni (1994) because, although a relatively minor component of the forest ecosystem, they are able to gain access to nutrients from allochthonous atmospheric sources (e.g. bryophytes can sequester inorganic nitrogen and bromeliads impound throughfall water) and pass these resources to other members of the ecosystem. They thus enhance the nutrient reserve as a whole through their own growth, and also increase the structural complexity of the forest, providing habitat, food, shelter, and breeding sites for many species, particularly arthropods, which in turn are prey for many canopy vertebrates, such as tree frogs, lizards, and

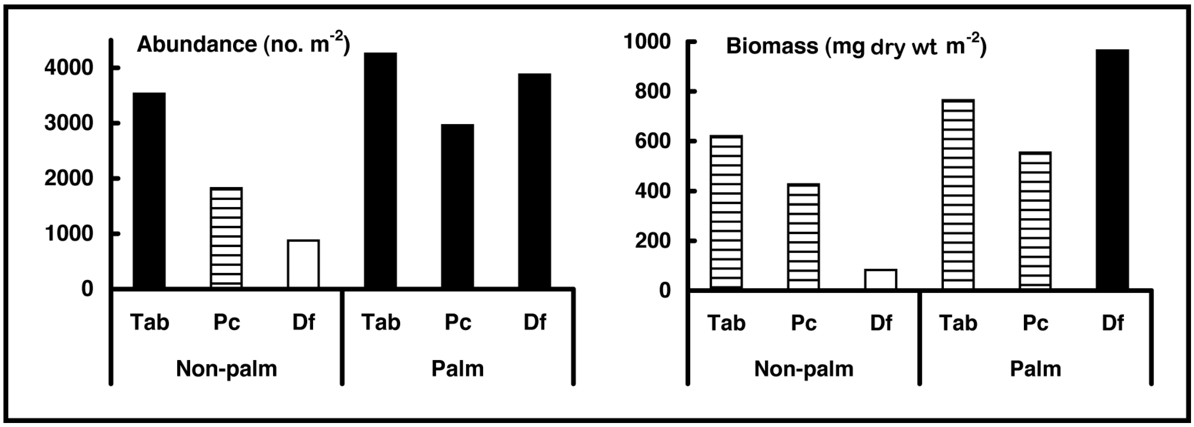

Figure 3. Mean invertebrate abundance and biomass in samples of litter from non-palm and palm areas from each of three forest types over three years.

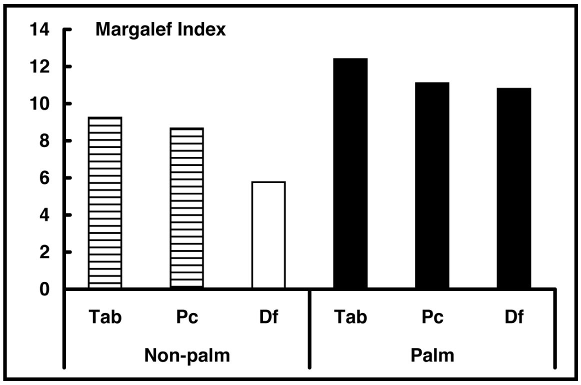

Figure 4. Mean Margalef indices of species richness in samples of litter from non-palm and palm areas from each of three forest types over three years.

birds. High diversity in the canopy may be largely explained by this pool of species supported by epiphytes.

Bromeliads often dominate neotropical epiphyte communities, with many species being highly specialized morphologically for the interception and utilization of non-soil nutrients, and their animal inhabitants have attracted the attention of many biologists (Picado 1913, Laessle 1961, Frank 1983). They have been classified as anemophilous types, found in the high canopy and reliant on wind blown inorganic nutrients, and dendrophilous types, with rosettes of tightly overlapping leaves which intercept canopy litter and throughfall water containing leachates from foliage (Frank 1983). The latter types are most abundant in the lower canopy and on the forest floor and are usually known as tank bromeliads (Fig. 5).

Nutrients, released from decomposing litter in the water-filled tanks (phytotelmata), enter the plant via absorptive foliar trichomes (Benzing 1980, 1990), and Nadkarni and Primack (1989) have demonstrated that foliage, rather than roots, appears to be the primary site of nutrient acquisition. Invertebrates are major contributors to litter breakdown at all stages, from coarse litter collected by the rosette of leaves to the fine particulate organic matter (FPOM), and faeces, which are washed into the base of the phytotelm, providing food for collector gatherers and filter feeders. Thus, there is transfer of nutrients from lit-

Figure 5. Tank bromeliads from the LEF: (top left) Epiphytic bromeliads on the Quebrada Sonadora in the tabonuco forest; (top right) dwarf forest habitat on Pico del Este; (bottom) dwarf forest bromeliads on Pico del Este.

ter to animal populations, many of which are aquatic and terrestrial larvae that, as adults, pass into the wider forest ecosystem. Tanks do not usually dry out completely even after a series of rainless days, so bromeliads provide a stable environment and a refuge in the dry season.

Elevational changes in bromeliad communities in the LEF, and their contribution to forest nutrient dynamics

Tank bromeliads are discrete microcosms with physical and chemical parameters that can be measured accurately, along with their complete detrital and aquatic communities and, as they receive nutrient input from the canopy, they function in parallel with the general forest ecosystem along the gradient. They can, therefore, be used to answer fundamental ecological questions, which can be difficult to answer in a more diffuse and complex forest ecosystem, and they have been studied over many years in the Luquillo Forest (Richardson 1999, Richardson et al. 2000a, b)

In the LEF, tank bromeliads occur at all elevations, with the commonest species on lower tree trunks and on the ground being *Guzmania lingulata* (L.) Mez and *G. berteroniana* (Schult. f.) Mez in the tabonuco and palo colorado forests and *Vriesia sintenisii* (Baker) L.B.Sm. & Pittend. dominant in the dwarf forest. These species have very precise light and humidity requirements and their density increased markedly with increasing elevation (Richardson 1999). The closed canopy with large leaves shades them out in the tabonuco forest and they are only found alongside river-courses and occasional tree-gaps, with a rapid decrease in density into the forest edge, but in palo colorado and dwarf forests, with decreasing tree height, smaller sclerophyllous leaves, and greater light penetration, density increased up the gradient to an estimated 32 000 plants ha^{-1} in the dwarf forest (Table 3).

Plants differed significantly in size at different elevations, with the largest plants found at mid-elevation in the palo colorado forest and the smallest in the dwarf forest, and this has implications for their individual storage capacity. The amount of litter impounded reflects plant size and forest decay rates, with tabonuco and palo colorado plants holding most litter, which was approximately equal to the dry weight of the bromeliad biomass. This is consistent with values reported for interception by epiphytic flowering plants in Costa Rica (Ingram and Nadkarni 1993). In the dwarf forest, debris was only 26% of bromeliad biomass, reflecting lower tree litterfall and catchment area per plant (Table 3). Because of their different densities they are, however, increasingly important at higher elevations where tree litterfall is least, but a greater proportion of it is held by bromeliads than in other forests (Table 4). Forest NPP declines markedly with increasing elevation, from 10.5 t ha^{-1} yr^{-1} in the tabonuco to 3.7 t ha^{-1} yr^{-1} in the dwarf forest. Bromeliad productivity, calculated from growth rates and density in each forest type, was found to be < 1% of total forest NPP per year in the tabonuco and palo colorado forests, but in the dwarf forest was 12.8% of forest NPP, which could make a significant contribution in this nutrient-poor and highly leached environment, as bromeliad leaves and impounded debris reach the forest floor and their nutrients are released (Table 4). The total bromeliad biomass in the LEF (with a maximum of 0.55 t ha^{-1} in the dwarf forest) is low compared with that reported for total epiphytes, including bryophytes and ferns, in other forests, e.g. Colombia, Costa Rica, Jamaica (mean = 10.7 t ha^{-1}, Hofstede et al. 1993).

Table 3. Physical parameters and biomass of bromeliads (means of three sampling periods, 1993–1996) in each of three forest types in Luquillo Experimental Forest (after Richardson 2000a).

	Forest type [1]		
	Tabonuco	Palo colorado	Dwarf forest
Mean area/plant (m^2)	0.49^a	0.57^b	0.08^c
Mean no. of green leaves/plant	36^a	29^b	22^c
Mean no. of dead leaves/plant	8^a	6^b	19^c
Water (ml/plant)	168^a	134^a	103^b
Water (t ha^{-1})	0.007	0.41	3.3
Plant density (ha^{-1})	45	3100	32000
Bromeliad mean dry wt/plant (g)	27.1^a	35.5^b	17.2^c
Total litter (g dry wt/plant)	28.1^a	39.3^b	4.6^c
Bromeliad plant dry wt (kg ha^{-1})	1.2	111	550
Total plant and debris dry wt (kg ha^{-1})	2.5	233	696

[1] Values in any row with a different superscripted letter significantly different (Fisher's LSD test, $p < 0.05$).

Table 4. Forest productivity and litterfall, and the relative importance of bromeliads as impounders of litter in three forest types in the Luquillo Experimental Forest (after Richardson 2000a).

	Forest type		
	Tabonuco	Palo colorado	Dwarf forest
Total aboveground NPP (t ha^{-1} yr^{-1})[a]	10.5	7.6	3.7
Tree litterfall (t ha^{-1} yr^{-1})[a]	8.6	6.8	3.1
Total bromeliad litter/yearly tree litterfall (%)	0.015	1.79	4.71
Forest floor standing litter (t ha^{-1})[b]	6.0	8.76	4.34
Bromeliad debris (g m^{-2} bromeliad)[c]	57.6	68.9	57.5
% of litter stock held by bromeliads	0.02	1.4	3.4
Bromeliad productivity (kg ha^{-1} yr^{-1})	0.42	38.8	474.1
% forest NPP[a]	0.004	0.51	12.8

[a] From Weaver and Murphy (1990).
[b] From Weaver (1994).
[c] Projected area of bromeliads derived from plant diameter measurements.

Concentrations of phosphorus, potassium, and calcium in canopy-derived debris, and nitrogen and phosphorus in phytotelm water, declined with increasing elevation. Tabonuco debris contained significantly higher concentrations of P, K, and Ca than palo colorado debris, and palo colorado debris had more P and Ca than dwarf forest, but not significantly so. Compared to rainfall and throughfall in the tabonuco forest, bromeliad water had higher concentrations of all nutrients. The high concentrations of DOC and NH_4 and low concentrations of NO_3 suggest a tendency towards anoxia in phytotelmata, decreasing from tabonuco to dwarf forest (Richardson et al. 2000a).

The relative importance of bromeliads as storage compartments (plant material, debris, water, animals) increases as bromeliad density increases with elevation (Table 5). Thus, in the dwarf forest, at least, bromeliads provide a buffering system, allowing the slow release of nutrients from canopy debris and impounded water, in an environment subject to leaching from rainfall which is over 4 m yr^{-1}. Similarly, although the amount of water in individual bromeliads decreases with increasing elevation, the estimated amount on a forest basis is 3.3 t ha^{-1} in the dwarf forest (Table 3), a considerable amount in a landscape without permanent standing ground water, and which provides a breeding habitat which has been likened to a 'fragmented lake', for insects with aquatic stages in their life cycle.

This study of bromeliad microcosms conveniently comprises a natural experiment in which forest productivity declines with elevation, but bromeliad density, and hence the total area available for animal colonisation, increases markedly in these forests with increases in elevation. It was, therefore, possible to test the alternative hypotheses that 1) animal diversity declines with decreases in NPP towards higher elevations or 2) that diversity increases with the increase in total available habitat area at high elevations.

Animal community composition

Bromeliads sampled were facultative epiphytes of similar morphological type (*Guzmania* and *Vriesea* spp.) growing on trunks and lower branches within hands-reach, and on exposed rocks and roots. No attempt was made to collect plants from the canopy and no very young plants were sampled which would have been unlikely to have a well-developed animal community. Plants were not usually collected from palms, as matched palm sites with plentiful bromeliads could not be found, because of intense shading. Physical measurements such as size, and height above the ground, were taken in the field, the contained water poured into containers for later measurement and for obtaining aquatic larvae, and the plant and corresponding container put into a sealed plastic bag. Plants were dissected and leaves washed out in the laboratory, where size fractions of detritus were removed for later weighing and analysis, and invertebrates sorted on white trays under water, before being preserved in 80% alcohol for sizing, counting and identification. Using these methods we were reasonably certain that resident populations were measured comprehensively and accurately (Richardson 1999).

Communities were made up of terrestrial organisms, e.g. spiders, cockroaches, isopods, some of which were also characteristic of forest floor litter communities; semi-aquatic organisms with a preference for a film of water, but not usually submerged, such as *Scirtes* sp. (beetle larvae) and adult *Omicrus ingens* M. Hansen & B.A. Richardson (hydrophilid beetles); and truly aquatic organisms, typically dipteran larvae, in the plant pools. Community struc-

Table 5. Nutrient storage in bromeliads by compartment and forest type in the Luquillo Experimental Forest, as mass-weighted concentrations of selected nutrients in the bromeliad microcosm. Values in the table are calculated from the nutrient analyses for each component, and take account of the plant population in each forest type. Debris values are weighted according to the relative proportion of coarse, medium and fine debris in each forest type. Note change in units between component and total values (Richardson et al. 2000a).

	C	N	P	K	Ca	Mg	S
Tabonuco							
Animals (g ha^{-1})	1.68	0.41	0.05	0.1	0.13	0.01	0.02
Debris (g ha^{-1})	609	22.9	0.57	1.86	11.2	2.03	7.18
Plant (g ha^{-1})	568	8.76	0.59	31.1	2.3	2.64	2.98
Total in plant (kg ha^{-1})	1.18	0.032	0.0012	0.033	0.014	0.0047	0.010
Water (g ha^{-1})	430	22.3	3.21	120	28.0	11.9	6.57
Total (kg ha^{-1})	1.61	0.05	0.004	0.15	0.04	0.02	0.02
Palo colorado							
Animals (g ha^{-1})	175	42.2	4.83	10.1	14.0	1.43	2.22
Debris (g ha^{-1})	58130	1742	30.3	115	632	132	542
Plant (g ha^{-1})	51430	829	39.0	2999	199	266	291
Total in plant (kg ha^{-1})	110	2.61	0.074	3.12	0.845	0.399	0.834
Water (g ha^{-1})	8100	341	74.8	2910	1446	847	444
Total (kg ha^{-1})	118	2.95	0.15	6.03	2.29	1.15	1.28
Dwarf forest							
Animals (g ha^{-1})	240	57.8	6.62	13.8	19.2	1.96	3.05
Debris (g ha^{-1})	75658	2103	27.9	146	623	236	650
Plant (g ha^{-1})	277363	4145	102	8563	393	553	1211
Total in plant (kg ha^{-1})	353	6.31	0.137	8.72	1.04	0.79	1.86
Water (g ha^{-1})	27027	2044	98.9	9888	1879	2175	2472
Total (kg ha^{-1})	380	8.35	0.24	18.6	2.91	2.97	4.34

ture in terms of relative abundance of species was broadly consistent among years for each forest type and communities could be distinguished among forests (Fig. 6).

The species shown make up about 90% of the whole community, and species with high abundance occurred at high frequency in at least one forest type and, therefore, characterized the major components of the fauna. Scirtid beetle larvae, the most abundant species in the two lower forests, were absent from the dwarf forest, as were the hydrophilid beetles *Omicrus ingens.* Many detritivores present in all three forests (e.g. *Trentepohlia dominicana* Alexander (Tipulidae) and *Culex antillummagnorum* Dyar (Culicidae) larvae, and isopod crustaceans) showed a markedly lower abundance in the dwarf forest with the exception of the larvae of a cased chironomid midge, *Tanytarsus bromelicola* Cranston, which was the most abundant organism in bromeliads in the dwarf forest. In general, organisms with a patchy distribution showed low abundance and appear toward the tail of the rank abundance graphs. Many rare species or singletons are not shown. This pattern of abundance and distribution is general and widespread, and is found in many groups of plants, fungi, insects, and vertebrates. It is thought to be related to niche width and is discussed in detail by Brown (1984, 1995).

Effects of forest NPP and other elevational changes on community parameters

Animal abundance declined as elevation increased. Dwarf forest plants had significantly fewer animals and significantly lower animal biomass than all other forests. Animal biomass was significantly higher in palo colorado plants. Animal size followed the same pattern as plant size, with

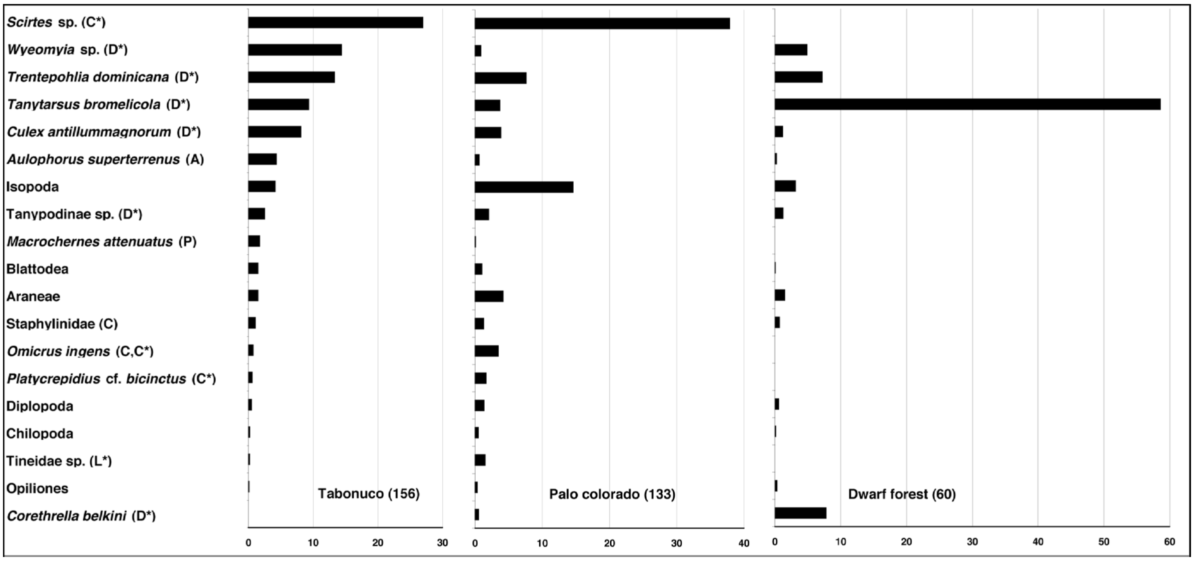

Figure 6. Relative abundance of different organisms in three forests at different elevations in the LEF. Data from 80, 70 and 60 bromeliads from the three forest types (tabonuco, palo colorado and dwarf forest, resp.), collected 1993–1997 and 10 each in 2010. Values are the mean relative percentage abundance of each taxon in the respective forest. Values in parentheses at each forest type label are the mean total no. of organisms per plant. (C = Coleoptera; D = Diptera; A = Annelida; P = Pseudoscorpiones; L = Lepidoptera; * = larval forms, with occasional pupae.) The taxa included represent 87–91% of the total fauna recorded from each forest type.

the largest animals occurring in the palo colorado, and the smallest in the dwarf forest (Table 6).

Within forests, larger bromeliads contained more detritus resources, and both animal abundance and species richness were positively correlated with plant size (Fig. 7). The species–area relationship is one of the best-documented relationships in nature (Brown and Lomolino 1998) and, regardless of the taxonomic group or type of ecosystem being considered, species number tends to increase with increasing area. This was used as part of MacArthur and Wilson's (1967) explanation of island biogeography and, indeed, tank bromeliads may be considered as islands in a 'sea' of forest, but they differ from biological islands, as defined by Rosenzweig (1995), in that they are not entirely self-contained regions. Many animal species live only part of their lifecycles in bromeliads and, as adults, come under the influence of the wider forest ecosystem. As cohorts of larvae hatch they may be replaced in the microhabitat by the same or other species. Bromeliad 'islands' are, therefore, more dynamic, with more immigration events than other islands, and the pool of organisms available and adapted to colonize them, depends on the features of the particular surrounding forest ecosystem and its diversity.

Table 6. Estimates of mean animal abundance, size and biomass in bromeliads, relative to debris quantities, for three sampling periods (1993–1996) in each of three forest types in Luquillo Experimental Forest (after Richardson 2000a).

	Forest type[1]		
	Tabonuco	Palo colorado	Dwarf forest
Mean no. of organisms/plant	166^{a}	141^{a}	58^{b}
Mean animal biomass dry wt/plant (mg)	75^{a}	113^{b}	15^{c}
Total bromeliad debris dry wt/plant (g)	28.1^{a}	39.3^{b}	4.6^{c}
Mean animal biomass dry wt (g ha^{-1})	3.4	350	480
Total bromeliad debris (kg ha^{-1})	1.3	122	146
Animal biomass as % of bromeliad debris	0.26	0.29	0.33
Animal size (mean individual dry wt (mg))	0.45	0.80	0.26

[1] Values in any row with a different superscripted letter significantly different (Fisher's LSD test, $p < 0.05$).

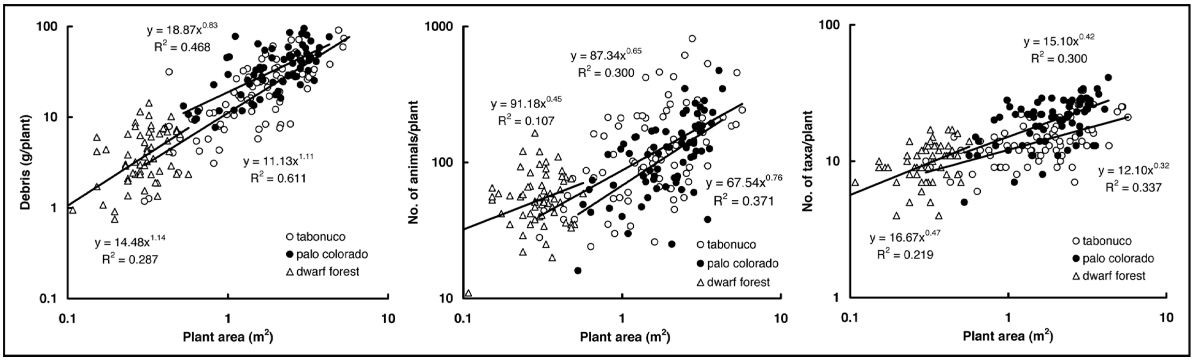

Figure 7. Relationship between bromeliad plant area and amount of retained debris, the number of animals and taxa in each rosette. Data from a total of 210 bromeliads from the LEF collected in 1993–1997. Plant area = πr^2 , where r = the mean of two orthogonal radii. The value serves as an indication of the size of the rosette available to collect and retain canopy litter (Richardson 1999).

Comparing forests, and using tabonuco values as a baseline, the decline in animal abundance with increasing elevation was associated with a decline in nutrient concentrations in the canopy debris collected by the rosettes, and known decreases in forest NPP (Fig. 8). Animal diversity and total animal biomass per plant, however, showed a unimodal pattern peaking at mid-elevation in the palo colorado forest, and with dwarf forest having the lowest values (Fig. 8). The total numbers of species collected over three years were 167, 198, and 97 for tabonuco, palo colorado, and dwarf forest respectively, and Margalef's indices of species richness in the three forests were 11.3, 14.6 and 7.5 respectively. The values of Simpson's index, which takes relative abundance into account and is, therefore, essentially a dominance index, were 7.1, 5.0 and 2.8 respectively.

It is evident from Fig. 8 that abundance and species richness are independent variables, and also that forest-wide species richness is unrelated to the total area of habitat available for colonization, as the dwarf forest, with the highest number of bromeliads per unit area, but smallest plant size, has the lowest species richness. The large patches of bromeliads do not operate functionally as large islands, but individual bromeliads do act as islands. Hypothesis 2, that diversity increases with the increase in total habitat area available at high elevations, is rejected, and hypothesis 1, that diversity declines with forest NPP, is only partially true. The dwarf forest, with the smallest plants (i.e. smaller islands) and lowest forest NPP, has the lowest species richness, but the intermediate palo colorado forest with a lower NPP than tabonuco forest has a higher species pool diversity.

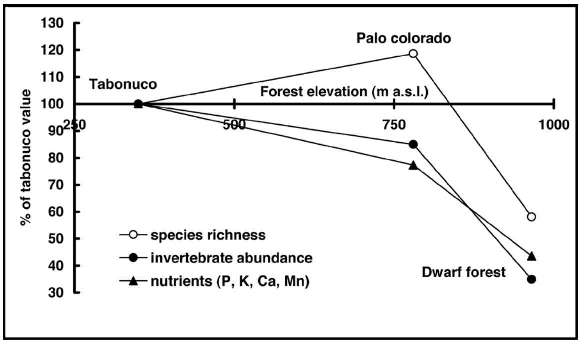

Figure 8. Levels of invertebrate abundance and species richness, and bromeliad litter nutrient concentrations (P, K, Ca and Mn) in three forest types in the Luquillo Experimental Forest at different elevations, compared with tabonuco levels = 100%. Elevational ranges: tabonuco <600 m; palo colorado 600–900 m; dwarf forest 900–1050 m.

Rosenzweig (1995) has reviewed a large body of evidence showing this mid-elevation 'diversity bulge' from tropical mountainsides in bryophytes, ferns, arthropods and birds when species richness is plotted against forest productivity and this trend is supported here. It has been suggested that the higher diversity at mid-elevations may be due to a mix of higher and lower elevation species, and if this were so, a lower proportion of unique species would be expected. In fact, the palo colorado forest had a slightly higher proportion (47%) of unique species than the tabonuco forest (44%), and the dwarf forest (33%). Species richness is also not related to nutrients in the forest ecosystem per se, and is highest in the palo colorado where major cation concentrations are significantly lower than in the tabonuco forest.

Explanations may lie in the nature of the different forest ecosystems. Many of the organisms sampled in the bromeliads do not live their whole lives in that habitat. Many of the litter invertebrates can move freely between bromeliad and forest floor and aquatic larvae emerge as adults, which have to survive in the general forest ecosystem. Greater habitat structural complexity is known to result in increased species diversity (MacArthur and MacArthur 1961, Safriel and Ben Eliahu 1991, Uetz 1991). Insects, because of their small body size, can exploit plant heterogeneity to a greater extent than other organisms (Lawton 1986). The palo colorado forest is the most heterogeneous of the three forests sampled, with the highest density of vines and epiphytes, soils are covered by a thick network of roots covered with bryophytes, and herbaceous ground cover is higher than in the tabonuco forest (Weaver 1994). This intermediate habitat may be the most favourable habitat for insect survival and, therefore, have fewer extinctions of species with low abundance. It has lower wind velocities than the dwarf forest, and intermediate rainfall levels with fewer rainless days, so that vegetation is less likely to dry out than in tabonuco forest. In the dwarf forest, selection favours small bromeliads because supporting branches are smaller, litter production is lower, and consequently bromeliads have a low nutrient base with greater competition for nutrients between its animal populations. This is reflected in the higher dominance of fewer species than in the other two forests, as shown by Simpson's diversity index.

Bromeliad specialists and endemic species

Bromeliad specificity and niche separation were demonstrated in the tabonuco forest in a comparative study of bromeliad and heliconia phytotelmata (Richardson et al. 2000b), where only a few species, such as the naidid worm *Aulophorus superterrenus* Michaelsen and *Culex antillum-magnorum* were found in both. Two species of syrphid larvae were highly abundant in *Heliconia* but were absent from bromeliads, although syrphids are known to occur in bromeliads in other geographical areas such a Central and South America (Rotheray et al. 2007). Larvae of *Forcipomyia dominicana* Meillon & Wirth (Ceratopogonidae), that were the dominant organisms in heliconia bracts (and previously known only from the island of Dominica), were also absent from bromeliads. The tipulid larvae abundant in bromeliads, *Trentopohlia dominicana*, were never found in *Heliconia*, where they were replaced functionally by other tipulid species. Plant architecture in the two systems was similar in the size of the fluid-holding compartments, and both held detrital material, but the detritus in heliconia bracts is derived from decaying flower parts. Another essential difference between these two phytotelmata that could explain their different faunas is that heliconia bracts are seasonal and short-lived, lasting only months, so do not provide a suitable niche for animals with relatively longer-lived immature stages.

Bromeliads provide discrete habitats containing distinct aquatic communities that are usually detritus-based, although some in open sunny areas (Laessle 1961) and anemophilous types in the canopy (Frank 1983) have been reported to contain algae that are the basis for their food webs. In environments that have few alternative breeding sites, many insects and some other arthropods have become specialists in utilizing bromeliads. These groups have recently been reviewed by Frank and Lounibos (2009) and, as expected, most are insect taxa with aquatic stages in their life history, but there are also many typically terrestrial organisms, such as spiders, pseudoscorpions, and predatory beetles which are obligate bromeliad-dwellers. There are even some cockroaches that are amphibious, and dive into the water when disturbed.

In Puerto Rico a highly adapted pseudoscorpion, *Machrochernes attenuatus* Muchmore (Fig. 9), specific to bromeliads in the tabonuco forest, is found deep in the plant, but above the waterline, and its dorsoventrally flattened body allows for easy movement between the closely overlapping leaves, and long pedipalps enable its search for prey. All juvenile stages are present in the plant, it has

Figure 9. Two specialist and endemic members of the bromeliad fauna in Puerto Rico. *Omicrus ingens* (left); *Macrochernes attenuatus* (right), (scale bars = 1 mm).

never been found in forest floor litter, and is endemic to Puerto Rico. The predatory larvae of an elaterid beetle, *Platycrepidius* cf. *bicinctus* (Candèze) are similarly adapted for moving among compartments of bromeliad rosettes. Other bromeliad specialists living in the same part of the plant are larvae of scirtid beetles and adult *Omicrus ingens* (Hydrophilidae) (Fig. 9), the latter endemic to Puerto Rico, whose predatory larvae also occur in the plants (Hansen and Richardson 1998). Both species move over wet leaf surfaces feeding on fine organic particles, and the scirtids are the most abundant species in tabonuco and palo colorado forests. Although several species of spider were common in bromeliads, none were specialists and were also found in forest floor litter or lower canopy.

Most of the aquatic Diptera larvae in the tanks are from known phytotelm specialist groups such as the filter-feeding *Wyeomyia* and *Culex* (Culicidae) and the predatory Corethrellidae larvae. Adult mosquitoes are ectoparasites of a wide variety of invertebrate and vertebrate species, but *Corethrella* females are all species-specific specialists feeding on the blood of frogs of one species, or a group of closely related frog species (Borkent 2008), which they locate from the calls of males. This may explain their distribution pattern in the LEF, with highest abundance of *Corethrella belkini* Borkent (also an endemic species) in the dwarf forest and its absence from lower elevations (Fig. 6), as tree frog species distribution in the forest changes with elevation, and co-evolution with frogs may also explain their high rate of speciation in different geographical locations. High speciation rates appear to be a characteristic of bromeliad-dependent taxa and there are at least five species of *Wyeomyia* in Puerto Rico that have not yet been described (Zavortink pers. comm.), and different species are found on different Caribbean islands. The psychodid *Alepia zavortinki* Wagner has been newly described from Puerto Rico (Wagner et al. 2008), a new species *Alepia albomarginata* Wagner from the island of Saba (Wagner et al. 2010), and another new psychodid, *Neurosystasis bromeliphila* Wagner, from Florida (Wagner and Hribar 2010).

Puerto Rico has high numbers of endemic species, particularly tree frogs, lizards, and birds and the Luquillo Mountain summits are essentially an island, separated from the Central Cordillera by a wide valley, with the dominant tree *Tabebuia rigida* and many shrub species endemic to these mountains. Many insects in bromeliads have not yet been identified to species level, but preliminary surveys indicate that species composition may be different in summit forests to the west of the LEF (Richardson unpubl.), and there are known differences in species composition on the island of Dominica where epigeic earthworms dominate the litter fauna in these plants (Richardson et al. 2006).

The bromeliad habitat provides stable long-term conditions in which many successive generations of invertebrates can breed and leave as adults to pass into the general forest ecosystem, and their contribution to palo colorado and dwarf forest food webs could be considerable. Even species that only spend their larval stage in water are largely restricted to bromeliads, as bodies of still water are not available in the steep montane forest, and other phytotelmata (e.g. fallen leaves, palm floral bracts) are too ephemeral to support the same species. They also are a refuge for terrestrial invertebrates in dry conditions, essential for the survival of many endemic species, and a unique habitat contributing to forest diversity in different geographical areas.

In summary the two detailed quantitative studies presented here, of two detritivore communities in microhabitats along an elevation gradient in the LEF, show that simple explanations of the direct effects of climate, such as decreasing temperature, are insufficient to explain changes in community structure and composition with increasing elevation. Community changes are related to the secondary effects of changing forest composition, structure, and dynamics, particularly the quality and quantity of the nutrient base. In the spatially restricted habitat of small bromeliads, and low litter quality and quantity reaching the forest floor in the dwarf forest, animal abundance and diversity are lowest. The intermediate palo colorado forest appears to be the 'goldilocks' forest, with higher habitat heterogeneity and intermediate rainfall and, therefore, more amenable for species growth and survival.

Acknowledgements – This research was performed under grant DEB-0218039 from the National Science Foundation to the Inst. for Tropical Ecosystems Studies, Univ. of Puerto Rico, and the International Inst. of Tropical Forestry, as part of the Luquillo Long-Term Ecological Research programme in the Luquillo Experimental Forest, and USDA IITF Grant 01-1G11120101-001.

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