Structure and functioning of oribatid mite communities along an elevational gradient of tropical mountain rainforests

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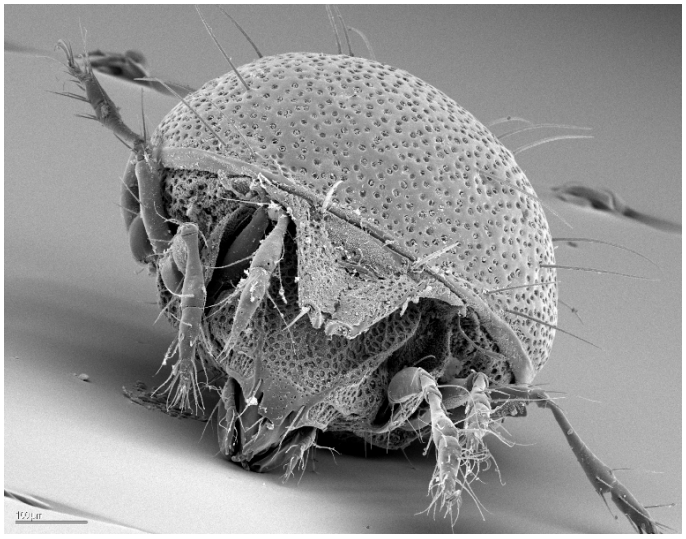

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Publications resulting from this Dissertation

CHAPTER 2.

Brehm G, Homeier J, Fiedler K, Kottke I, **Illig J,** Nöske NM, Werner F, Breckle S-W (2008). Are mountain rain forests in southern Ecuador a hotspot of biodiversity? Limited knowledge and diverging patterns. In: Beck E, Bendix J, Kottke I, Makeschin F, Mosandl R (eds). Gradients in a tropical montane ecosystem. *Ecological Studies*, 198, Springer Verlag, Berlin

CHAPTER 3.

Maraun M, **Illig J,** Sandmann D, Krashevskaya V, Norton RA, Scheu S (2008). Fauna: Composition and function: Soil fauna. In: Beck E, Bendix J, Kottke I, Makeschin F, Mosandl R (eds) Gradients in a tropical montane ecosystem. *Ecological Studies*, 198, Springer Verlag, Berlin, in press

CHAPTER 4.1.

Niedbala W, **Illig J** (2007a). New species and new records of ptyctimous mites (Acari, Oribatida) from Ecuador. *Tropical Zoology*, 20 (2), 107-122

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CHAPTER 4.2.

Illig J, Scheu S, Maraun M (in prep.). Density and community structure of soil and bark living microarthropods along an altitudinal gradient in a tropical montane rainforest.

CHAPTER 4.3.

Illig J, Schatz H, Maraun M (2008). Checklist of the Oribatid mites From the Reserva San Francisco, Ecuador. in: Liede-Schuhmann S, Breckle S-W (eds) Provisional Checklists of Flora and Fauna of the San Francisco valley and its surroundings (Estacion Cientifica San Francisco), Southern Ecuador. *Ecotropical Monographs*, in press

CHAPTER 5.1.

Illig J, Langel R, Norton RA, Scheu S, Maraun M (2005). Where are the decomposers? Uncovering the soil food web of a tropical montane rain forest in southern Ecuador using stable isotopes (^{15}N). *Journal of Tropical Ecology*, 21, 589-593

CHAPTER 5.2.

Illig J, Schatz H, Scheu S, Maraun M. (2008). Decomposition and colonization by microarthropods of litter (*Purdiaea nutans*, *Graffenrieda emarginata*) in a tropical mountain rain forest in southern Ecuador. *Journal of Tropical Ecology*, submitted

Contents

Zusammenfassung

Tropische Bergwälder gehören zu den artenreichsten Regionen der Welt. Das in dieser Arbeit untersuchte Gebiet in Südecuador, RBSF (Reserva Biológica San Francisco), gilt als “hotspot“ der Biodiversität. Neben dem Ziel diese herausragende Vielfalt zu erfassen, gilt es vor allem die komplexen Interaktionen zwischen den Organismen und das Zusammenwirken der biotischen und abiotischen Faktoren des Ökosystems tropischer Bergregenwäldern zu entschlüsseln. In der Region des RBSF sind außergewöhnlich diverse Gruppen, wie z.B. Vögel, Spanner, Orchideen und andere Epiphyten untersucht worden. Die Diversität vieler untersuchter Tier- und Pflanzengruppen ist wesentlich höher als in den gemäßigten Breiten, bei einigen Gruppen liegt die maximale Diversität aber vermutlich in tiefer gelegenen Regionen.

Die hohe Artenfülle der Hornmilben (Acari: Oribatida) und anderer Bodenbewohner gilt als eines der großen Rätsel in der Bodenökologie. Während in den gemäßigten Breiten deren Gemeinschaft gut untersucht ist, sind in den tropischen Regenwäldern und speziell in den Bergregionen nur wenige Arten taxonomisch erfasst. Ziel der vorliegenden Arbeit war es, die Gemeinschaft der Bodenmikroarthropoden qualitativ und quantitativ zu erfassen. Im Wald der RBSF wurde entlang eines Höhengradienten von 1850 bis 2270 m die Gemeinschaft der Mikroarthropoden in verschiedenen Bodenhorizonten (L, F/H, Ah) und auf Borke angrenzender Bäume untersucht. Die Dichte war bei den Hornmilben (Oribatida) am höchsten, gefolgt von Raubmilben (Gamasina) und Springschwänzen (Collembola). Die generell geringe Dichte der Mikroarthropoden nahm von 1850 nach 2200 m ab, stieg aber auf 2270 m wieder leicht an. Die Siedlungsdichte von Mikroarthropoden im Boden war wesentlich höher als auf Borke und nahm mit der Bodentiefe ab. Die geringere Dichte mit zunehmender Höhe ist vermutlich auf “strengere“ abiotische Faktoren, wie z.B. niedrigere Temperatur, stärkere Sonneneinstrahlung und Staunässe zurückzuführen. Die Gemeinschaft der Hornmilben unterschied sich zwischen den Höhenstufen. Geringere Streuqualität und mikrobielle Biomasse sind vermutlich die Hauptursache für die Abnahme der Dichte der Mikroarthropoden mit der Meereshöhe und auch für die unterschiedliche Struktur der Gemeinschaften.

Die zahl- und auch artenreichste Gruppe, die Hornmilben (Oribatida), wurden genauer untersucht. Insgesamt wurden 193 Arten aus 48 Familien nachgewiesen. Neun für die

Wissenschaft neue Hornmilbenarten aus der Gruppe der Ptyctima wurden beschrieben. Der geschätzte Anteil unbestimmter Arten liegt bei etwa 40 %. Die Diversität der Hornmilben ist hoch, jedoch nicht wesentlich höher als in temperierten Wäldern. Die Hornmilbengemeinschaft änderte sich entlang eines Höhengradienten von 1850 bis 2270 m. Entlang des Höhengradienten war die Untergruppe der Poronota die häufigste, gefolgt von Pycnonotic Apheredermata.

Um das Nahrungsnetz mit seinen trophischen Gilden in tropischen Bergregenwäldern besser zu verstehen, wurden die δ^{15} N und δ^{13} C Signaturen von 32 Bodenarthropoden und von einer basalen Resource, Laubstreu von *Graffenrieda emarginata*, ermittelt. Die untersuchten Arten lagen innerhalb von vier trophischen Ebenen. Ähnlich wie in den gemäßigten Breiten, bildeten sie einen Gradienten von Pflanzenfressern über Zersetzer bis zu Aasfressern und Räubern. Wider Erwarten zeigte sich, dass der überwiegende Teil der "Zersetzergemeinschaft" nicht direkt an totem organischen Material frisst, sondern sich vermutlich vor allem von Pilzen und Tieren ernährt.

In einem Freilandexperiment wurde die Bedeutung der Mikroarthropoden für die Zersetzungsprozesse der Laubstreu untersucht. In Streubeuteln wurden zwei Streutypen (*Graffenrieda emarginata* und *Purdiaea nutans*) und eine gleiche Mischung aus beiden auf 1850 und 2280 m ein Jahr lang ausgelegt. Generell war die Streuabbaurate gering. Nach einem Jahr war durchschnittlich noch 68 % der Trockenmasse der eingesetzten Streu in den Streubeuteln. Dies deutet darauf hin, dass in tropischen Bergregenwäldern andere Einflussgrößen von Bedeutung sind als in tropischen Tiefland-Regenwäldern, in denen die Streu schneller abgebaut wird. Die Streu wurde auf 1850 m schneller abgebaut als auf 2280 m, vermutlich auf Grund von höheren Temperaturen und erhöhter mikrobieller Biomasse. Nach 12 Monaten war die Zersetzung der Mischstreu weiter vorangeschritten als bei den beiden Einzelstreutypen ("nicht-additiver" Effekt). Der Einfluss der Bodenmikroarthropoden auf die Zersetzung der Streu war eher gering. Höhere Dichten von Mikroarthropoden und höhere mikrobielle Biomasse in den Streubeuteln auf 1850 m im Vergleich zu 2280 m unterstützen die Hypothese höherer biotischer Aktivität auf geringerer Meereshöhe. Die Zusammensetzung der Hornmilbengemeinschaft unterschied sich nicht wesentlich in den beiden Streutypen. Dies deutet auf eine wenig spezialisierte Lebensweise der Mikroarthropoden hin.

Summary

Tropical mountain rain forests are among the most species rich regions in the world. The RBSF (Reserva Biológica San Francisco) area in southern Ecuador is a hotspot of biodiversity. To characterise this exceptional high diversity it is essential to investigate the complex interactions between the organisms and their abiotic environment. A number of groups of organisms, including birds, moths, orchids and mosses, have been investigated, whereas knowledge on others, including soil invertebrates, is minute.

This study focuses on (1) the characterisation of the hidden diversity of soil animal species, in particular that of oribatid mites (Oribatida), (2) the composition and function of soil microarthropods including their trophic relationship, (3) decomposition processes including altitude (temperature, moisture), litter type (low and high quality) and microarthropods (small and large mesh of litterbags).

(1) At the study site 193 species of 48 families of oribatid mites were determined which is high but compared to temperate forest ecosystems not extraordinary divers. The proportion of not described species is assumed to be around 40 %. Nine new species of ptyctimous oribatid mites were described. Many species are restricted to tropical regions indicating specific community structures in the tropics. Furthermore, the oribatid mite community differed along the elevation gradient from 1850 to 2270 m indicating distinct oribatid mite communities at different altitudes.

(2) The high diversity of oribatid mites and decomposer soil animals in general, is one of the great riddles in soil ecology. Whereas in deciduous forests the soil microarthropods are well characterised, taxonomical knowledge in tropical rainforests and especially in mountain regions is low. One aim of this study was to investigate the microarthropod soil community. The density of microarthropods and oribatid mite communities at three horizons (L, F/H, Ah) and on the bark of adjacent trees along an elevation gradient (1850, 2020, 2200 and 2270 m) in the RBSF forest were studied. Oribatid mites were the most abundant group followed by Collembola and Gamasina. The compared to temperate forests generally low number of microarthropods declined with elevation in the order 1850 > 2020 > 2270 ~ 2200 m and with soil depth (L, F/H, Ah). Microarthropods on bark were less abundant than in soil. Declining numbers of soil microarthropods with altitude is concluded to be due to harsh abiotic conditions (e.g. lower temperatures, waterlogging, solar radiation). Low microbial biomass

and resource quality presumably also contribute to the low abundances of soil microarthropods.

The trophic structure of 32 species and potential basal food resources (litter of *Graffenrieda emarginata*) was investigated by analysing natural variations in stable isotope ratios ($^{15}N/^{14}N$; $^{13}C/^{12}C$). The results indicate that the soil food web is similar to that of temperate forests and spans about four trophic levels. Primary decomposers, i.e. litter feeding species, were rare, potentially reflecting low litter quality. A large number of 'decomposer' animals were in fact predatory or necrophagous, suggesting that various putative decomposer soil animal species (especially in oribatid mites) presumably feed on other soil invertebrates, in particular nematodes or animal carcasses.

(3) We studied leaf litter decomposition of two abundant tree species with higher and lower litter quality (*Graffenrieda emarginata*, *Purdiaea nutans*) and a mixture of both in a litterbag field experiment at two altitudes (1850 and 2280 m). Litter quality was measured as microbial biomass and N content. Decomposition rates at the studied tropical mountain rain forest were generally low (average of 32 % y^{-1}). The slow decomposition rates may have been due to low litter quality (e.g. high C-to-N ratios) but also due to low temperatures. Litter generally decomposed slower at higher elevation supporting our assumption that temperature is a major driving force for litter decomposition at our study sites and indicating that organic matter accumulates at high altitudes. *P. nutans* litter after 2 and 6 months of exposure decomposed slower than that of *G. emarginata*, but not at the end of the experiment, after twelve months. We suggest that litter chemistry affect decomposition mainly at early stages of decomposition. After 12 months the mixture of *G. emarginata* and *P. nutans* litter decomposed significantly faster than both single litter types indicating that combining the two litter types accelerates decomposition processes ('non-additive effect'). Soil microarthropods contributed little to decomposition processes. Microbial biomass and density of microarthropods in the litterbags were higher at 1850 than at 2280 m indicating higher biological activity at lower altitudes. Species composition was similar in both litter types supporting previous findings that the structure of soil decomposer microarthropod communities is little affected by litter type.

CHAPTER 1 GENERAL INTRODUCTION

1.1. Tropical mountain rainforests in Ecuador

Tropical mountain rainforests represent 10 % of the worldwide occurring rainforests. The majority of mountain rain forests in Ecuador are located along the Andean Cordillera which runs the length of the country. These forests have very high endemism of both fauna and flora. However, they are under severe pressure from the rapidly increasing population in the Interandean valleys due to agricultural encroachment, grazing, hunting and cutting for fuelwood. The enormous species richness in Ecuador is severely threatened by an alarming annual loss of 2.4 percent of total forest cover – the second highest rate in South America (Whitmore and Sayer 1992); primary mountain rainforests show an even higher deforestation rate than the lowland forests (Doumenge *et al.* 1995). In the humid tropics, montain rain forests are found between 500 and 3,500 m altitude. Within this zone vegetation gradients with increasing altitude occur: diminishing tree height, simplified stratification, smaller leaf size, more open understory and floristic changes with more epiphytes, mosses and lichens (Doumenge *et al.* 1995).

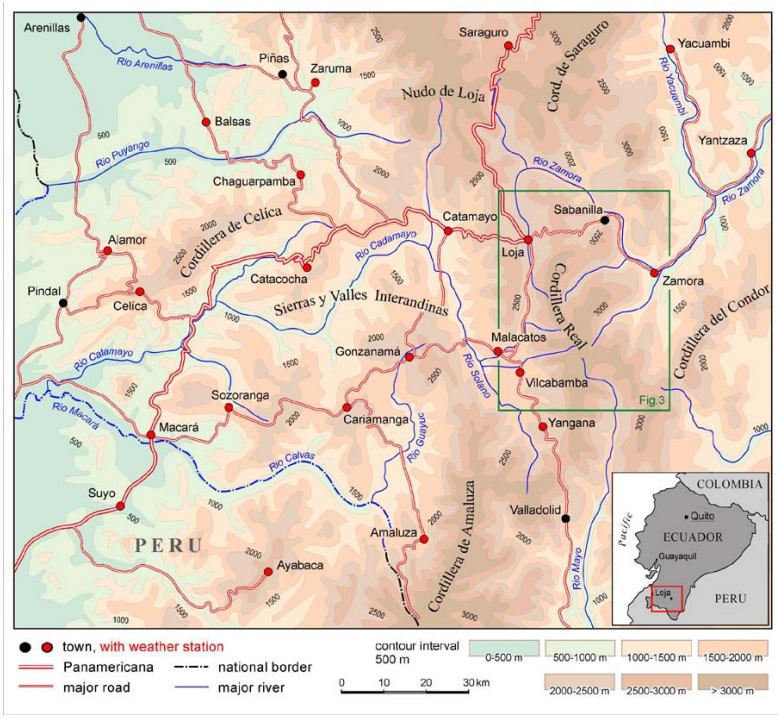

Fig. 1.1. Geographical map of Southern Ecuador; the marked area is shown in Fig. 1.2. (Beck *et al.* 2008).

Podocarpus National Park

The Podocarpus National Park established in 1982 is situated in the easternmost montane chain (Cordillera del Consuelo) in Southern Ecuador and covers 146,300 ha. The park has a very irregular topography covering altitudes from 950 m to 3700 m (90% above 1500 m), with large tracts of undisturbed forest, continuous from upper tropical to temperate zones. Most of the park is situated between 2,000 and 3,000 m, consisting of hillsides covered with moist cloud forest. This is the only large remaining tract of continuous Andean forest in Ecuador. The name of the park results from Podocarpus trees (e.g. *Podocarpus oleifolius*) which are the only conifers native to Ecuador. The park represents a hotspot of biodiversity par excellence, and still has large areas of diverse natural habitats (Brehm *et al.* 2007). Furthermore, the region has been identified as a center of endemism and diversity for a couple of organisms such as birds, geometrid moths and vascular plants (Rahbek *et al.* 1995, Brehm *et al.* 2005, Brummitt and Lughadha 2003, Werner *et al*. 2005). Over 40% of the parks 3,000-4,000 plant species are endemic. Heavy agricultural activity in the area, as well as infrastructure projects such as mining and road development, have impacted the biological diversity of the park. Cajanuma represents the north-western and Bombuscaro the eastern gate to the park. The primary forest at 3000 m a.s.l. of the ridge of Cajanuma (04°06’71’’ S, 79°10’58’’ W) is an elfin forest with small stunted trees, with diagonal stems, a high coverage of epiphytic mosses and vascular epiphytes and a high percentage of Cunoniaceae, Podocarpaceae, Cyrillaceae, Rubiaceae and Aquifoliaceae species (Moser *et al.* 2007, Paulsch *et al.* in press. 2008). The area Bombuscaro (04°06’54’’ S, 78°58’02’’ W) represents the lowest part of the national park around 1050 m a.s.l.; the tree families Sapotaceae, Moraceae and Mimosaceae are dominating. The organic layer atop of the mineral soil in the area ranges in thickness from about 48 mm at 1050 m to 430 mm at 3060 m (Moser *et al.* 2007).

Reserva Biológica San Francisco

The study area is part of the Reserva Biológica San Francisco (RBSF, 3°58′S, 79°04′W, and adjacent fractions of the Podocarpus National Park) in the province of Zamora- Chinchipe located in the Cordillera Real, an eastern range of the South Ecuadorian Andes, orientated towards the Amazon basin. It is covered with undisturbed or slightly disturbed montane rainforest (Madsen and Øllgaard, 1994). The vegetation of the study area is described by Bussmann (2001), Paulsch (2002) and Homeier (2004). *Graffenrieda emarginata* (Melastomataceae) is the dominant tree species on the mountain ridge in the RBSF forest within the altitude range of 1800 m to 2200 m. *Purdiaea nutans* (Cyrillaceae) the only species

of the genus in continental south America is the most frequent tree species at higher altitudes between 2200 m and 2400 m (Homeier *et al.* 2002).

The climate is semi-humid with up to 10 humid months. The annual dry season ranges from October to December (Beck 2001, Ohl and Bussmann 2004). The average annual precipitation at 2000 m a.s.l. is 2031 mm and increases with altitude (Emck 2005). The mean annual air temperature decreases with altitude from 19.4, to 15.7 to 8.9 °C at 1000, 2000 and 3000 m (Krashevska *et al.* 2007). Average soil temperature is 1.4 °C lower (Leuschner *et al.* 2007). The bedrock consists mainly of weakly metamorphosed Paleozoic schists and sandstones with some quartz veins. Dominating soil types are Eutric, Dystric and Humic Cambisols (Wilcke *et al.* 2001). The organic soil layer is thick and increases with elevation, the pH ranges between 3.0 and 5.5 (Wilcke *et al.* 2002) and is decreasing slightly with increasing altitude (Soethe *et al.* 2006). Even at small scale soils are highly heterogeneous because of the various substrates for soil formation, varying hydrological conditions, element redistribution on a landscape level as a consequence of the steep and variable morphology, and potentially due to the enormous diversity of plant species.

The research station "Estacion Científica San Francisco" (ECSF) situated at the bottom of the valley at 1850 m a.s.l. served as logistic centre (Fig. 1.2.).

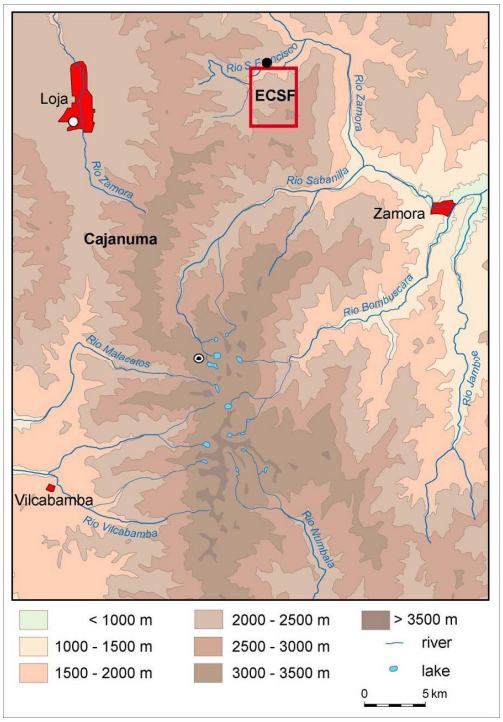

Fig. 1.2. "Estacion Científica San Francisco" (ECSF) situated between the provinceCapitals Loja and Zamora (Beck *et al.* 2008).

1.2. Oribatid mites

Oribatid mites (Oribatida, Acari) are among the most important soil living decomposer microarthropods in almost all ecosystems. Their distribution ranges from arid coniferous forests over floodplain forests to salt marshes (Weigmann 1971, Usher 1975, Mitchell 1978). In temperate to subtropical forests oribatid mites are often the most abundant arthropods (Walter and Proctor 1999) and reach highest densities in acidic forests, e.g. up to 200,000 ind. m^2 in boreal forests (Maraun and Scheu 2000). Oribatid mites live in very different microhabitats, e.g. in the litter layer, the humus layer, in dead wood, in moss and on the bark of trees, which may contribute to the high diversity of oribatid mites (Aoki 1967, Hammer 1972, Wunderle 1992, Hansen 2000).

Oribatid mites are a very old taxon; the first fossils of oribatid mites have been found in Devonian sediments (380 mya; Shear *et al.* 1984, Norton *et al.* 1988a, Kethley *et al.* 1989). With about 10,000 described species worldwide (Subias 2004) they are the third largest mite suborder, after Prostigmata and Mesostigmata. The total species number is estimated to be up to 100,000 (Schatz 2002). In general, about 50-120 species of oribatid mites are found in most forest ecosystems (Wunderle 1992). Oribatid mite diversity increases from boreal to tropical habitats (Maraun *et al.* 2007a). Investigations of oribatid mites from the Cordillera de Talamanca in Costa Rica and Panama included 165 species (Schatz 2006). Prior to my study, only 54 oribatid species were recorded from Ecuador (except Galapagos, see Schatz 1998). Phylogenetic relationship of oribatid mites are debated (Balogh and Balogh 1992, Woas 2002, Subias 2004, Weigmann 2006). According to Grandjean (1953, 1965, 1969) oribatid mites are divided into six series, (1) the basal Palaeosomata, (2) the species rich Enarthronota, (3) the small group Parhyposomata, (4) the "Mixonomata" including the box mites, (5) the "Desmonomata" and the diverse (6) Circumdehiscentiae (=Brachypylina). The cluster Circumdehiscentiae comprises a large number of families which are divided into five subdivisions: Opsiopheredermata, Eupheredermata, dorsodeficient Apheredermata, pycnonotic Apheredermata and Poronota. It is still unclear if oribatid mites are a monophyletic group. Some authors have proposed that Astigmata evolved within the oribatid mites, as a paedomorphic lineage (e.g. O´Connor 1984, Norton 1998). However, molecular studies do not support the origin of Astigmata within Oribatida (Maraun *et al.* 2004, Domes *et al.* 2007b). Oribatid mites comprise a large number of parthenogenetic taxa that may have radiated while being parthenogenetic (Palmer and Norton 1992, Schaefer *et al.* 2006, Heethoff *et al.* 2007) and furthermore re-evolved sexuality (Domes *et al.* 2007a).

Oribatid mites are generally characterized as K-strategists (Norton 1994) by low fecundity (1-12 eggs per clutch with 1-3 generations per year), low metabolic rates and long immature and adult lifespans (up to 3 years in Ptyctima; Travé *et al.* 1996).

Oribatid mites have six postembryonic instars: an inactive prelarva, and active larva, protonymph, deutonymph, tritonymph and adult. All active instars feed, and in the same species feeding habits may differ between immatures and adults (Siepel 1990). Along with direct feeding on dead plant material and the resulting comminution of it, oribatid mites contribute to decomposition processes and nutrient cycling in the soil system by feeding on microorganisms and by the dispersal of microbial propagules (Behan and Hill 1978, Seastedt 1984, Moore *et al.* 1988, Maraun *et al.* 1998b). Very little is known concerning the predators of this important group, other than several families of small beetles (Pselaphidae, Ptiliidae, Scydmaenidae) and ants of the genus *Myrmecina* and *Pheidole* (Masuko, 1994, Wilson 2005). Considering only predators, adult oribatid mites likely live in enemy-free space, due to the hardness of the cuticle, which are stiffened with calcium carbonate and calcium oxalate (Norton and Behan-Peletier, 1991); but this may not apply to soft-bodied immatures (Peschel *et al.* 2006).

1.3. Objectives

Biodiversity

Biodiversity received increasing interest during the past decades. Ecological experiments, observations, and theoretical developments show that ecosystem properties depend greatly on biodiversity in terms of the functional characteristics of organisms present in the ecosystem and the distribution and abundance of those organisms over space and time (Loreau *et al.* 2001, Hooper *et al*. 2005). It is evident that the tropical Andes are a hotspot of biodiversity (e.g. Rahbek *et al*. 1995, Myers *et al.* 2000, Brehm *et al.* 2005). Using data on vertebrates and vascular plants, Brummitt and Lughadha (2003) ranked the tropical Andes as the top global hotspot. Regarding many groups of organisms, the Neotropical region is more species-rich than any other region of the world. However, data from the Andes are scarce. Traditional descriptive disciplines such as taxonomy, systematics and natural history provide names, phylogenies and life history data as a service for other fields of science and their applications. However, these disciplines have suffered a great loss of capacity in the past decades (e.g. Breckle 2002, Gotelli 2004). In **Chapter 2,** mountain rain forests in southern Ecuador as a hotspot of biodiversity are discussed in general.

Composition and function of soil fauna

Compared to what is known about organisms that live above-ground there is little information on changes in microarthropod diversity in soil. The high α-diversity of decomposer animals in soil is one of the great enigmas of soil biology since their habitat seems to be rather uniform (Anderson 1975b, Maraun *et al.* 2003a, 2007a). One important component of the animal community, the soil fauna, has rarely been studied in tropical rain forests, especially in mountain regions. The reasons for this presumably is that (1) soil animals have to be extracted from a 3-dimensional medium by heat or other methodology, (2) there are few keys for determination and (3) a large number of species is still not described.

At the RBSF forest soil microarthropods primarily contribute to the microbial activity and decomposition processes of organic matter, since the density of soil macrofauna (e.g. earthworms, diplopods and termites) is low. Therefore I focused on the investigation of microarthropods, especially oribatid mites. We evaluated the composition and function of soil microarthropods in a tropical mountain rainforest in southern Ecuador **(Chapter 3)**. In addition, the density of oribatid mites along an elevational gradient (1000, 2000 and 3100 m) was investigated. By increasing the supply of resources to decomposer biota in the laboratory and in a field experiment we expected to be able to uncover the role of resource limitation in the studied decomposer system.

Oribatid mites

Oribatid mites are the most abundant and diverse microarthropods in soil and contribute to the decomposition processes and nutrient cycling by feeding on microorganisms and by the dispersal of microbial propagules (Behan and Hill 1978, Maraun *et al.* 1998). Due to little knowledge about the tropics (Holt 1985, Olson 1994), microarthropod communities in the soil and on the bark of trees were investigated along a smaller elevational gradient (1850, 2020, 2200 and 2270 m) in the RBSF forest **(Chapter 4.2.)**. Declines in invertebrate species richness and abundance at high elevations in the tropics have been documented (Janzen *et al.* 1976, Olson, 1994) and suggest that physical parameters that vary continuously with altitude are important determinants. We hypothesised that microarthropod densities (1) decline with increasing altitude due to harsher environmental conditions and lower soil quality and (2) differ with soil depths (0-5, 5-10 and 10-15 cm) and bark material. Furthermore, we expected that (3) oribatid mite communities differ between bark and soil as a result of distinct microhabitat conditions.

In comparison with other neotropical countries, taxonomical studies on oribatid mites in Ecuador are scarce. Prior to this study, only 54 oribatid mite species were recorded from continental Ecuador. New records and new species of ptyctimous oribatid mites were determined in **Chapter 4.1.** Since comprehensive taxonomical studies on oribatid mites in Ecuador are lacking and knowledge on lower taxa levels are needed for ecological research, a checklist of oribatid mites from the RBSF is shown in **Chapter 4.3.**

The soil food web

Trophic niche differentiation may lead to reduced competition between species and may therefore explain the high diversity of soil animal species (Anderson 1975a). Even small differences in food preferences of microarthropods may reduce competition between species. But concerning there edaphic life style knowledge on feeding biology of small soil invertebrates (e.g. oribatid mites) is poor. Soil animals tend to be food generalists (Giller 1996) due to their close spatial association with food materials (Scheu and Setälä 2002). In contrast, results of food choice experiments suggest that oribatid mites preferentially feed on certain fungal species (Schneider and Maraun 2005). Generally, there are difficulties in assigning oribatid mites to functional groups (Schneider *et al.* 2004), but stable isotope signatures ($\delta^{15}N$ $\delta^{13}C$) of animals have been shown to be a powerful tool in evaluating the trophic structure of animal communities (Minagawa and Wada 1984, Ponsard and Arditi 2000, Scheu and Falca 2000, Post 2002). Schneider *et al.* (2004) carried out a detailed study on the trophic position of oribatid mites from four different temperate forests. The data suggest that oribatid mites form at least four feeding guilds: (1) phycophages/fungivores, (2) primary decomposer, (3) secondary decomposer and (4) carnivores/scavengers/omnivores. Obviously, trophic niche differentiation in oribatid mites strongly contributes to the high diversity of this animal group in temperate regions. Differences in stable isotope signatures in oribatid mite species may be due to feeding on different mixtures of fungal species, detritus and animal prey. Overall, the term 'choosy generalists' well characterises the trophic strategy of oribatid mite species. It has been suggested that several species of putative litter-feeding oribatid mites are not primary decomposers but mainly feed on fungi or are predatory or necrophagous (Schneider *et al.* 2004), and similar results have been obtained for collembolans (Chahartaghi *et al.* 2005). This suggests that litter-feeding decomposer animals at least in temperate regions are less diverse than previously assumed. Although stable isotope analyses of tropical species are increasing (Blüthgen *et al.* 2003, Kupfer *et al.* 2006), until now, no studies in the tropical montane rainforest used this method to investigate the trophic structure

of the soil food web. Since nutrient poor systems – such as tropical forests – are species rich it was suggested that the large number of interactions between species results in more trophic levels (Vander Zanden *et al.* 1999). I investigated stable isotope ratios ($^{15}N/^{14}N$) of different soil microarthropods, mainly oribatid mites, to characterize the trophic relationship in a tropical montane rainforest **(Chapter 5.1.)** In addition, I measured the $^{13}C/^{12}C$ ratio to facilitate identification of primary and secondary decomposers (Schmidt *et al.* 2004; **Chapter.3.**).

Effects on decomposition

Especially in highly unproductive ecosystems most of the organic matter produced by plants (up to 99 %), is not consumed by herbivores but returned to the soil as litter. Differences in litter decomposition are determined by the qualitative and quantitative composition of the animal and microbial decomposer community, their physical environment (i.e. temperature, moisture, pH-value) and the quality of the resource itself. Separating these effects is essential for understanding decomposition effects on ecosystem functioning. In the field litterbag experiments are commonly the best method for the measurement of decomposition rates (Anderson 1975a, Wardle *et al.* 2003). Exclusion of invertebrates by using small mesh sizes enable to discover effects of invertebrates on litter decomposition.

We conducted a litterbag experiment considering major driving forces of decomposition processes including altitude (temperature, moisture), litter type (low and high quality as indicated by nitrogen concentrations) and microarthropods (small and large mesh of litterbags; **Chapter 5.2.)**. We hypothesized that decomposition rates in tropical montane rain forests are faster at lower altitudes since the temperature at lower altitudes is higher. We also expected that decomposition of low quality litter would be slower than of high quality litter and that mixed litter being intermediate. Furthermore, we expected the microarthropod fauna not to discriminate between the different litter types since most decomposer animals are generalists (e.g. Hättenschwiler *et al.* 2005). We expected the microarthropod fauna to differ between altitudes, since abiotic characteristics are more important than litter species for colonization by microarthropods.

The results of all studies including a short outlook for future research are reviewed and discussed in **Chapter 6**.

CHAPTER 2

Mountain rain forests in southern Ecuador as a hotspot of biodiversity? Limited knowledge and diverging patterns

2.1. Introduction

Why do we need biodiversity inventories?

Highly complex ecosystems such as the tropical mountain rain forest in southern Ecuador probably harbour tens of thousands species that interact with each other. It is impossible to understand an ecosystem without knowing the composition of its community. Such knowledge cannot be achieved without the examination of all major groups of animals, fungi, plants, and bacteria. For example, insects such as leaf beetles, ants, or hymenopteran and dipteran parasitoids have a high impact on forest ecosystems (Moutinho *et al.* 2005, Soler *et al*. 2005), but have not been studied at the RBSF so far. The question of how many species there are on earth is still unresolved. Estimates range from 4 to 30 million species (e.g. Novotny *et al.* 2002). Ultimately, only counting and naming species can answer this question.

A hot debate about the methodological approaches, i.e. the usefulness and efficiency of 'traditional' taxonomy vs. DNA barcoding approaches is still going on (e.g. Meyer and Paulay 2005, Will *et al.* 2005). Barcoding techniques provide useful sets of new characters for species descriptions and phylogenies, especially in cryptic species or taxa otherwise poor in morphological characters (e.g. Hajibabaei *et al*. 2006). However, species definition based on DNA sequence data can be problematic. For example, ribosomal genes can show intraspecific variation in the multinucleate Glomeromycota. The sequence types obtained from the vegetative stage can rarely be related precisely to either morphological or biological species (Sanders 2004). In our opinion, the only strategic way forward can reside on a synthesis of 'classic' and 'modern' approaches with regard to sampling campaigns, application of up-to-date information technology (Godfray 2005) and thorough taxonomic and systematic work. This might include in vitro cultivation in case of fungi and bacteria.

Traditional descriptive disciplines such as taxonomy, systematics and natural history provide names, phylogenies and life history data as a service for other fields of science and their applications. However, these disciplines have suffered a great loss of capacity in the past decades (e.g. Breckle 2002, Gotelli 2004). Many species identifications from the RBSF are

not the primary result of research efforts in taxonomy and systematic. Rather, the recently published species checklists (Liede-Schumann and Breckle in press) are essentially a by-product of ecological and physiological research. This explains why many lists are still far from being complete (see below), and why only a few species have been newly described from the area thus far. Many (probably many thousands) of species in the RBSF alone are new to science and await description, but specialists are lacking for many taxa. Only some vertebrate groups are well known: All currently recorded bird and bat species are described (Paulsch in press, Matt 2001, Muchhala *et al*. 2005). In other groups, however, the proportion of described species drops from bryophytes (98%, Gradstein *et al.* in press), trees (>5 cm dbh, 90%), lichens (85%, Nöske *et al*. in press), to geometrid moths (63%, Brehm *et al*. 2005), oribatid mites (60%, Illig *et al.* 2007, Niedbala and Illig 2007a,b) to fungi (5%, Haug *et al.* 2004, Setaro *et al.* 2006, Suárez *et al.* 2006, Kottke *et al.* 2007).

2.2. Inventory coverage in the RBSF

After eight years of research in southern Ecuador, our knowledge about certain taxa is excellent. The area is one of the most thoroughly investigated neotropical mountain rain forests (see the contributions to this volume). Geometrid and pyraloid moths, oribatid mites or bush crickets (Tettigoniidae) have never been studied quantitatively in other Andean forests before (Braun in press, Brehm *et al.* 2005, Illig *et al.* 2007, Süßenbach 2003). None of the mycorrhizal fungi has previously been known from the northern Andean forests (Haug *et al.* 2004, 2005, Setaro *et al.* 2006, Suarez *et al.* 2006, Kottke *et al.* 2007). However, there is little reason to rest on the laurels. Our knowledge about species richness in the area remains biased and incomplete, and sampling is far away from reaching an asymptote (Fig. 2.1.).

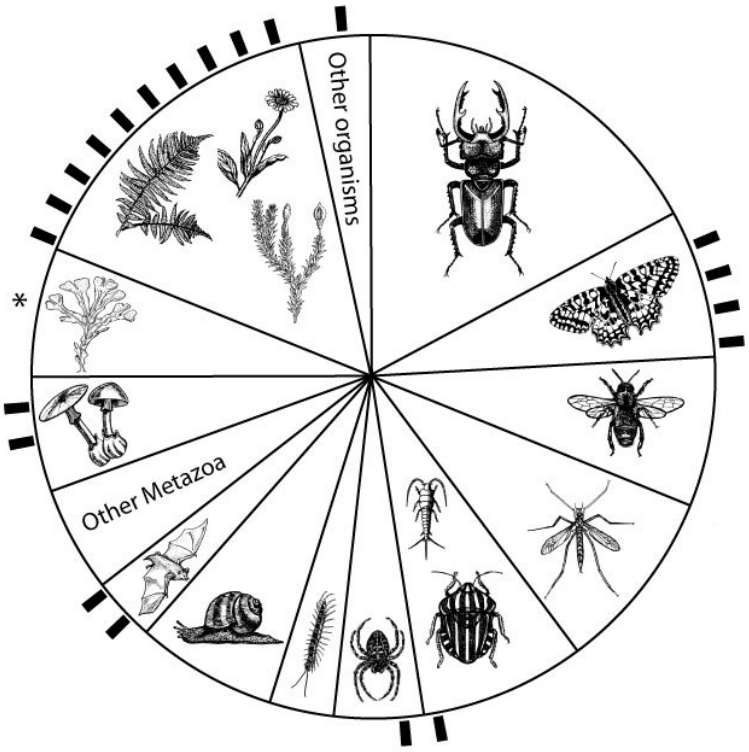

Figure 2.1. Proportions of described species of the major taxa at a global scale and coverage of inventories at RBSF (for details see Table 2.1.). Taxa (clockwise): Coleoptera, Lepidoptera, Hymenoptera, Diptera, other Insecta, Chelicerata, other Arthropoda, Mollusca, Vertebrata, other Metazoa, Fungi, Stramenopilata+Haptophyta, Embryophyta, other organisms. More than two thirds of all known species are animals, and more than half of all organisms are arthropods – likely more. The figure covers organisms from all habitats, including marine ecosytems. However, only the brown algae (marked with an asterisk) are not expected to be present at the RBSF whereas all other taxa are. Groups not sorted and identified at species level (e.g. Nematoda) are not included. Only a small proportion of the expected total richness has been covered so far. Illustration from G. Brehm.

Bacteria or Archaea have not been investigated in the study area. So far, the only group of single-cell organisms studied are the Testacea (Krashevska 2007; Table 1). Due to their dominant role in material and energy flows in ecosystems, plants have received relatively much attention, and groups such as vascular and non-vascular cryptogams have been investigated in detail (Homeier *et al.* 2007). However, botanical collections have focused on the existing trail system that is biased towards ridge sites. Bryophytes and ferns have been collected systematically across the whole altitudinal range (e.g. Kürschner and Parolly 2004; Table 2.1.).

Table 2.1. Taxa investigated in the RBSF and adjacent areas.

Taxon	**Observed species number**	**References**
Chiroptera	21 (RBSF)	Matt (2001)
(bats)	24 (1000-2900 m)	
Aves	227 (RBSF)	Paulsch (in press), Rasmussen *et al.*
(birds)	379 (1000-2800 m)	(1994): old road Zamora-Loja
Geometridae	1075 (RBSF)	Brehm *et al.* (2005), Fiedler *et al.* (in press)
(geometrid moths)	1266 (1040-2677 m)	
Arctiidae	287 (RBSF)	Hilt (2005), Fiedler *et al.* (in press)
(arctiid moths)	446 (1040-2677 m)	
Pyraloidea	748 (1040-2677 m)	Süßenbach (2003), Fiedler *et al.* (in press)
(pyraloid moths)		
Sphingidae	36	Fiedler *et al.* (in press)
(hawkmoths)		
Papilionoidea	243	Häuser *et al.* (in press)
(butterflies)		
Tettigoniidae	101 (1000-3100 m)	Braun (2002), Braun (in press)
(bush crickets)		
Oribatida	154 (RBSF)	Illig *et al.* (in press)
(mites)	193 (1000-3100 m)	
Testacea	78 (RBSF)	Krashevska (in press)
	110 (1000-3100 m)	
Lichenes	311 (RBSF)	Nöske *et al.* (in press)
(lichens)		
Glomeromycota	83 (RBSF)	Haug *et al.* 2004, Kottke *et al.* 2007
Ascomycota	4 (RBSF)	Haug *et al.* 2004
Basidiomycota	96 (RBSF)	Haug *et al.* 2005, Kottke *et al.* 2007,
(Homobasidiomycetes,		Suarez *et al.* (2006)
Heterobasidiomycetes)		
Bryophyta	515 (RBSF)	Gradstein *et al.* (in press), Kürschner and
(hornworts, liverworts		Parolly (in press)
and mosses)		
Spermatophyta	1178 (RBSF)	Homeier and Werner (in press)
(seed plants)		
Pteridophyta (ferns)	257 (RBSF)	Lehnert *et al.* (in press)

Lichens haven been sampled intensively at least in the lowermost parts (up to 2100 m) of the area (e.g. Nöske 2005). Moreover, life forms such as trees (Homeier 2004), climbers (S. Matezki, pers. comm.) and epiphytes (Werner *et al.* 2005) have been treated in extensive ecological studies, whereas terrestrial shrubs and, especially, herbs still remain poorly known. Concerning the large group of fungi, only mycorrhiza forming groups were investigated. The molecular diversity of Glomeromycota forming mycorrhizas with trees and two basal groups of Basidiomycota (Sebacinales and Tulasnellales) forming mycorrhizas with orchids, ericads and liverworts, respectively, were studied, but are far from being complete (Haug *et al.* 2004, 2005, Setaro e*t al.* 2006, Suarez *et al.* 2006, Kottke *et al.* 2007, Table 2.1.). Saprophytic and plant parasitic fungi remain to be investigated.

Table 2.1. provides an overview of available species lists. Inventories have been carried out on birds, bats, and parts of the arthropod clades Lepidoptera, Orthoptera and Arachnida. Although Fig. 2.1. gives global numbers of organisms and does not provide the (unavailable) proportions of taxa in an Andean forest, it roughly estimates a reasonable scenario. Thus far, the largest gaps are represented by three of the major insect orders: The Coleoptera (beetles), the Hymenoptera (ants, wasps, bees etc.), and the Diptera (flies). With the exception of few selected families of arthropods (see above), no other insect group was studied (e.g. dragonflies, homopterans). Molluscs (e.g., land snails) as well as aquatic communities as a whole have been ignored. Even prominent vertebrate groups such as amphibians or mammals (except for bats, Matt 2001, Matt *et al.* in press) have not been studied. A sample of studied and unexplored taxa is provided in Fig. 2.1.

Fig. 2.2. Text next page

Fig. 2.2. Examples of nine (mostly unidentified) species belonging to taxa that have not yet been investigated or inventoried in the RBSF (a-i), and nine taxa in which inventories have been carried out or started (j-r). a) beetle (Chrysomelidae), b) wasp (Pompilidae), c) fly (Tachinidae), d) *Olceclostera* sp. (Apatalodidae), e) stick insect (Phasmatodea), f) snail (Orthalicidae), g) *Gastrotheca* sp. (Hylidae), h) Dusky Lancehead *Bothriopsis pulchra* (Viperidae), i) Two-toed sloth *Choloepus hoffmanni* (Megalonichidae), j) *Pantherodes colubraria* (Geometridae), k) *Dolicheremaeus* sp. (Oribatida), l) *Itarissa* sp. (Tettigoniidae), m) Cinnamon Flycatcher *Pyrrhomyias cinnamomea* (Tyrannidae), n) *Sturnira ludovici* (Chiroptera), o) unknown Gomeromycota, p) *Frullanoides densifolia* (Marchantiophyta: Lejeuneaceae), q) *Purdiaea nutans* (Cyrillaceae), r) *Fernandezia subbiflora* (Orchidaceae). Images from G. Brehm (a-e, j, l, m), J. Homeier (f-h, n, q, r), J. Illig (i, k), A. Beck (o), and N. M. Nöske (p).

A complete inventory of tropical rain forests such as the RBSF can probably never be achieved since species-rich tropical communities must be sampled intensively and over very long periods of time. An example is provided by geometrid moths: So far, 35,238 individuals representing 1223 species have been sampled during quantitative assessments at elevations of 1040-2670 m between 1999 and 2003. However, richness estimators (Colwell 2006) indicate that despite a great sampling effort ca. 200 more species must be expected in the area (Brehm *et al.* 2005). The species checklists of less well sampled taxa therefore often provide observed minimum numbers that do not yet allow serious estimates of the actual richness. Particularly poorly sampled areas outside the RBSF such as the Rio Bombuscaro valley (the lowermost part of Podocarpus National Park, PNP) certainly harbour far more species than the currently available lists of species suggest (e.g. Matt *et al.* in press, Fiedler *et al.* 2007).

The use of "biodiversity indicators" in "rapid biodiversity assessments" appears to be a tempting shortcut. A good indicator group is supposed to reflect the 'complete' biodiversity. However, the use of indicators is highly problematic along altitudinal gradients because the composition of taxa changes non-linearly throughout the gradient, and patterns of alpha diversity are often discordant even between closely related groups of organisms (Brehm and Fiedler 2003, Fiedler *et al.* 2007, Fig. 3). Moreover, we have to expect diverging species richness patterns in different taxa along the gradient (Fiedler *et al.* 2007), and too little is still known about the diversity patterns of most groups to allow general conclusions.

2.3. The RBSF and Podocarpus National Park as biodiversity hotspots

It is evident that the tropical Andes are a hotspot of biodiversity (e.g. Rahbek *et al.* 1995, Myers *et al.* 2000, Brehm *et al.* 2005). Using data on vertebrates and vascular plants, Brummitt and Lughadha (2003) ranked the region as the top global biodiversity hotspot.

Regarding many groups of organisms, the Neotropical region is more speciose than any other region of the world. However, data from the Andes are still scarce. Two large-scale diversity patterns overlap in tropical mountains in general and in the Andes in particular: Species richness of most groups of organisms peaks around the equator and declines towards the poles (Gaston 2000).

There is a high species turnover along elevational gradients and usually a peak of richness not at lowest, but at medium elevations (Herzog *et al.* 2005, Krömer *et al.* 2005, Rahbek 2005). Many hypotheses have been formulated to explain these patterns. Some of the most frequently used explanations are (1) Evolution and biogeography (2) Climate history (3) Biotic and abiotic factors (4) Stochastic effects.

Each of the concepts is plausible to some extent, and it seems most probable that a combination is actually responsible for the observed richness patterns with all their group-specific variations (Brehm *et al.* 2007).

The diversity of the studied organisms in the tropics is usually much higher than in temperate regions, reflecting the latitudinal gradient of species richness. Some groups are exceptionally rich in the RBSF while others are not, probably because they peak at lower elevations (Fig. 2.3). Unfortunately, no hard data are available for the majority of taxa so far (see above).

Comparisons of inventories from the RBSF with other montane neotropical sites are hampered by (1) the scarcity or absence of such inventories, (2) differences in sampling schemes, and (3) differences in elevational range and area of the sites.

One of the most suitable approaches is therefore to compare the local (alpha) diversity. Vascular epiphytes in the RBSF are outstandingly speciose. Single trees hosted up to 98 species (Werner *et al.* 2005), among the highest species number recorded for single trees. Six trees held a total of 225 species (Werner *et al.* 2005), more than have been recorded for entire Andean sites in Venezuela or Bolivia (Ibisch 1996, Engwald 1999). The RBSF harbours more than 500 species of bryophytes, probably the highest number ever recorded from a relatively small area in the tropics (Gradstein *et al.* in press, Kürschner and Parolly in press). Within the spermatophytes, the orchids are the most speciose family of the RBSF with a total of ca. 340 registered species (many more are expected, Homeier and Werner in press). So far, this is the highest number recorded for a neotropical forest site. The genera Stelis (Orchidaceae), Piper (Piperaceae), and the family Lauraceae unexpectedly show high species numbers (Homeier *et al.* in press).

Other very speciose groups include the moth family Geometridae. Brehm *et al.* (2005) observed 1266 morphospecies between 1000 and 2700 m – a higher number than observed anywhere else in the world. Interestingly, the family did not show a pronounced peak of diversity but a very broad plateau with a high and regular species turnover (Fig. 2.3., Brehm *et al.* 2003a, 2003b, but see Brehm *et al.* 2007). On the contrary, pyraloid moth richness peaked around 1000 m (Bombuscaro) and declined with increasing elevation (Fiedler *et al.* 2008). Certain taxa of plants and animals are species-rich in tropical lowlands only. Among plants, many families such as Araceae, Arecaceae and Fabaceae show a high richness in Amazon lowland and Andean foothill forests that quickly drops as elevation increases (Jørgensen and León-Yánez 1999). Elevational richness patterns are far less well known in animals. Ants have not been investigated in the RBSF, but it is evident from qualitative observations that the area is not a hotspot for this group at all since only a few species occur (Brehm *et al.* 2005, G. Brehm, J. Illig, K. Fiedler, own observations). However, ants are obviously far more abundant and speciose at lower elevations such as in the Rio Bombuscaro valley at 1000 m. This corresponds to observations by van der Hammen and Ward (2005) and Mackay *et al.* (2002) in Colombia who found a pronounced decline in ant species richness along an altitudinal gradient (see also Bruehl *et al.* 1999 for a palaeotropical altitudinal gradient of ants). Ant richness might peak at rather low elevations at the foothills of the Andes similarly as observed below 500 m by J.T. Longino (pers. comm.) in Costa Rica. However, no appropriate data along a complete altitudinal gradient are available from the tropical Andes so far.

Birds are the best-known group of animals in Ecuador. The Eastern slope of the Andes is renowned for its outstanding bird diversity (Rahbek *et al.* 1995, Ridgely and Greenfield 2001). Paulsch (in press) observed a total of 227 bird species between 1999 and 2002 in the RBSF. The number increases considerably when lower and higher elevations are included. Rasmussen *et al.* (1994) recorded a total of 362 bird species along the (old) Loja-Zamora road (1000-2800 m) that passes the RBSF, 292 species from the Rio Bombuscaro area (950-1300 m) and 210 species from the Cajanuma area (2500-3700 m). Only the latter number represents a near-complete list whereas the other numbers are still underestimations (C. Rahbek pers. comm.). The species richness is at the high end for Ecuador, and only some areas in Peru and Bolivia have similar bird diversity (C. Rahbek, pers. comm.). The elevational pattern of local bird richness in southern Ecuador is not known, but is anticipated to resemble the pattern (a foothill peak and high-elevational plateau) recorded by Herzog *et al.* (2005) in Bolivia.

Hypothetical curves for three selected animal taxa (geometrid moths, ants and birds) are diverging, and qualitatively similar divergences of species-richness patterns are expected to occur across the whole range of organism diversity. The curves visualize that the RBSF cannot be regarded as a hotspot of biodiversity in general. The richness of many taxa is likely to peak at lower elevations (Fig. 2.3.). PNP covers a much broader elevation range (1000-3600 m) and certainly a far higher biodiversity than the narrow elevational belt of the RBSF alone. Hence, while there is little doubt that the Tropical Andeans and PNP can be called hotspots of biodiversity, the RBSF is 'only' a selective hotspot.

From a conservation point of view it would be highly desirable to include lower elevations in a system of protected areas because groups showing a peak of species richness below 1000 m currently do not receive legal protection in south-eastern Ecuador. Moreover, the protection of a complete altitudinal gradient similarly as e.g. in Manú National Park in Peru is undoubtedly the best conservation strategy with regard to the threats caused by global warming. Given the already dramatic decline of natural habitats in tropical Andean countries and mountain forests (Svenning 1998, Hofstede *et al.* in press, Mosandl *et al.* in press), biodiversity inventories must play an important role in selecting such areas for conservation.

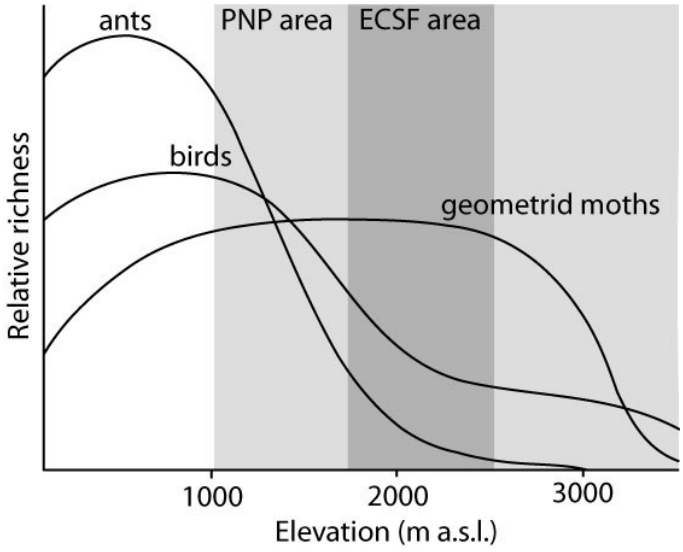

Fig. 2.3. Hypothetical curves of relative species richness of three animal taxa along an altitudinal gradient in the Eastern Andeans of southern Ecuador using available literature data (see text). Ant richness is expected to peak at low elevations and to decline strongly between 1000 and 2000 m. On the contrary, richness of geometrid moths and birds peaks at higher elevations and is expected to decline only at very high altitudes. Richness of all taxa at the lowest elevations is expected to be lower than at medium elevations. Illustration from G. Brehm.

2.4. Conclusion

Biodiversity inventories combined with systematic and taxonomic work ensure that trustworthy scientific names can be provided for organisms encountered during ecological or experimental work. An excellent knowledge has already been gathered in the RBSF in some groups, e.g., bats, birds, arctiid and geometrid moths, cryptogamic plants and trees. However, large gaps still remain to be filled, e.g., in groups such as beetles, ants, wasps, bees, dipterans, most other arthropods or molluscs. Large proportions of species are apparently new to science and particularly many arthropod species need to be described taxonomically. The RBSF is situated in the Eastern Andean hotspot of biodiversity but the species-richness of most taxa in the study area and its surroundings is still unknown. While some groups are extraordinarily diverse (e.g. geometrid moths, orchids), the richness of other taxa is low in the area and peaks far below 1800 m (the lower elevation limit of the reserve). A coordinated sampling and research approach is required to fill the most important gaps of knowledge about the biodiversity of the area in the future.

CHAPTER 3

Composition and function of soil fauna in a tropical mountain rain forest

3.1. Introduction

Tropical mountain rain forests are among the most species-rich ecosystems of the world (Küper *et al.* 2004, see Chapter 2.). In these biodiversity 'hot spots' the number of species of animal and plant taxa may exceed that of temperate forests by orders of magnitude; e.g. the number of tree species per hectare in tropical mountain rain forests may be as high as 100, whereas in temperate forests only a handful of taxa are present per hectare (Whitmore 1998, Oosterhoorn and Kappelle 2000, Kessler *et al.* 2005). Similarly, the diversity of animal taxa, such as Coleoptera (Lucky *et al.* 2002) and Lepidoptera (Brehm and Fiedler 2003), is exceptionally high. Only few taxa, such as parasitic Hymenoptera, appear not to conform to the general rule of increasing diversity from temperate to tropical regions (Gauld *et al.* 1992). However, one important component of the animal community, the soil fauna, has rarely been studied in tropical rain forests, especially in montane regions. The reasons for this presumably is that (1) soil animals have to be extracted from a 3-dimensional medium by heat or other methodology, (2) there are few keys for determination and (3) a large number of species is still not described.

3.2. Material and Methods

We investigated the density and diversity of the soil microarthropod community in a tropical mountain rain forest in southern Ecuador. We focused on microarthropods (mainly oribatid mites and collembolans), since at our study site the density of soil macrofauna, such as earthworms, diplopods and isopods, is low, which may be due to low pH and low resource (litter) quality. Due to the low density of large decomposer animals we expected soil microarthropods to significantly affect decomposition processes. Changes in density and community structure of the soil mesofauna were investigated along an altitudinal gradient spanning over 2000 m. For evaluating the trophic structure of the soil food web natural variations in stable isotope ratios ($^{15}N/^{14}N$; $^{13}C/^{12}C$) of dominant soil fauna taxa were studied. Knowledge of the trophic structure of the decomposer food web is necessary for

understanding the limiting factors of soil animal species and the role of decomposer species for decomposition processes. By manipulating carbon and nutrient availability we evaluated limiting factors for soil microorganisms and investigated the role of microorganisms as food resources for animal decomposers. Finally, by investigating the decomposition of leaf litter enclosed in litterbags of different mesh size we evaluated the role of decomposer animals for litter decomposition at different altitudes.

The studies were carried out at the RBSF (Beck *et al.* 2008). The region is covered with mostly undisturbed mountain rain forest. The climate is semihumid, the average annual precipitation at 1900 m altitude is about 2000 mm and the average annual temperature is 16 °C. The soil types are mainly Aquic and Oxaquic Dystropepts (Schrumpf *et al.* 2001) and the pH ranges between 4.0 and 4.5 (Wilcke *et al.* 2002). The study sites were located at 1000 m (Bombuscaro), 1850 m (Estacion Scientifica San Francisco, ECSF) and 3100 m (Cajanuma).

3.3. Results and Discussion

Soil microarthropod density, diversity and reproductive mode

The density of oribatid mites was about 34,400 ind m^{-2} at 1000 m (Fig. 3.1.). This density is similar to that of other tropical forests (rainforest in Australia; 43,000 ind/m^2; Plowman 1981) and to limestone forests of the temperate zone (35,000 ind m^{-2} at a base rich Danish beech forest; Luxton 1981), but much lower than that of acidic deciduous forests of the temperate zone where oribatid mite densities may reach 180,000 ind m^{-2} (Maraun and Scheu 2000) or more (Persson *et al.* 1980). This is rather surprising since the lower density of oribatid mites (and also that of other microarthropods) in base rich as compared to acidic temperate forests presumably is due to the activity of earthworms and other large decomposers which remove the litter layer (Migge 2001, Eisenhauer *et al.* 2007), but as stated above these large decomposers are rare at our study site.

Surprisingly, the density of oribatid mites further decreased with increasing altitude. At 2000 m the density of oribatid mites was only 20,000 ind m^{-2} and at 3100 m a.s.l. only 5400 ind m^{-2}. This decline was particularly unexpected since the thickness of the organic layers increases with altitude and in temperate forests the density of microarthropods increases with the thickness of the organic layers (Maraun and Scheu 2000).

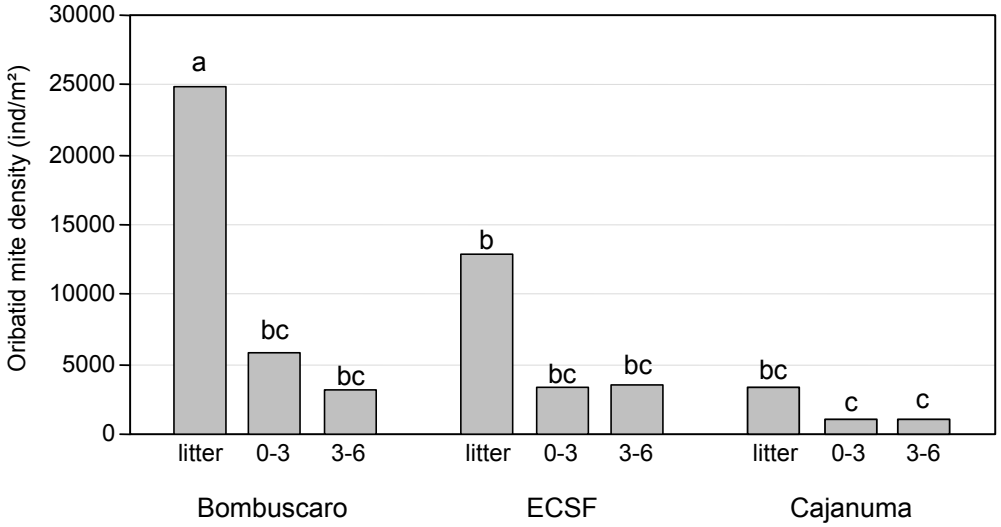

Figure 3.1. Oribatid mite densities at Bombuscaro (1000 m); ECSF (2000 m) and Cajanuma (3100 m) in the litter and upper soil layers (0-3 cm and 3-6 cm depth). Bars sharing the same letter are not significantly different (Tukey's HSD test; $P > 0.05$).

At the RBSF we found about 154 oribatid mite species including several new species (Chapter 4.1. and 4.3.). This is higher than in most temperate forests where species numbers usually range between 30 and 80 (Luxton 1975, Persson *et al.* 1980, M. Maraun, unpublished data). Possibly, high plant diversity and the associated high litter diversity is responsible for the high species number of soil microarthropods, but factors driving oribatid mite species diversity are generally little understood (Anderson 1975b, Maraun *et al.* 2003a). In temperate forest ecosystems it increases from open to forest habitats but is little affected by tree species diversity (Migge *et al.* 1998, Hansen 2000).

Compared with temperate forests, the number of parthenogenetic taxa of oribatid mites at the studied tropical mountain rain forest is small. In temperate forests about 60 % of the species and up to 90 % of the individuals of oribatid mites reproduce via parthenogenesis (Maraun *et al.* 2003b), whereas at the studied tropical forest (3100 m) only 23 % of the species and about 35 % of the individuals reproduce via parthenogenesis (V. Eissfeller and M. Maraun, unpublished data). These findings are consistent with the hypothesis that due to more pronounced biotic interactions, such as competition, the proportion of sexually reproducing taxa increases towards the tropics (Sanders 1968, Glesener and Tilman 1978). However, densities of oribatid mites at the studied tropical forests are low and therefore intra- and interspecific competition likely are of little importance.

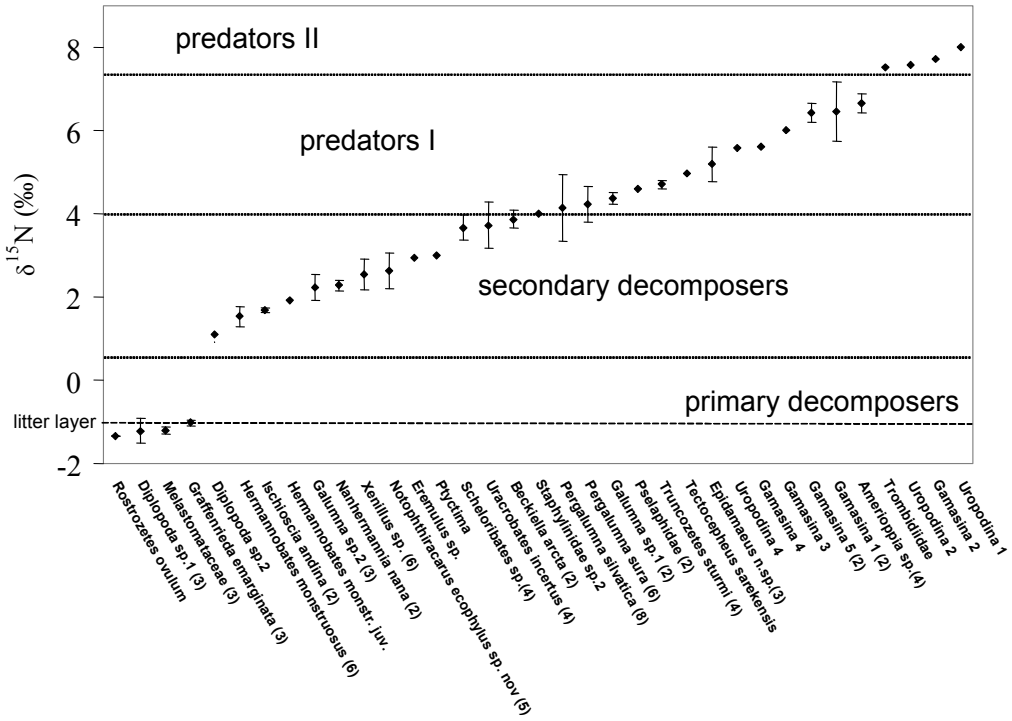

Fig. 3.2. Variation of $\delta^{15}N$ signatures of soil animals extracted from *Graffenrieda emarginata* leaf litter material from the ECSF site (1850 m a.s.l.). Single measurements and means of 2-8 replicate measures (numbers in brackets) with SD. If no standard deviation is shown only a single sample was analysed. Species were ordered by increasing $\delta^{15}N$ signatures.

The soil food web

The structure of food webs, i.e. the trophic relationships between animals, plants and microorganisms, has mainly been studied in temperate ecosystems. It has been suggested that compared to temperate forests the number of trophic levels in tropical forests is increased (Reagan *et al.* 1996). However, recent studies indicate that the number of trophic levels in tropical food webs in fact is similar to that in temperate systems (Kupfer *et al.* 2006).

We investigated the trophic structure of the soil food web of the studied mountain rain forest at 1850 m by analysing natural variations in stable isotope ratios ($^{15}N/^{14}N$; $^{13}C/^{12}C$). The results indicate that the soil food web of the studied tropical rain forest spans about four trophic levels (Fig. 3.2.) which is similar to that in temperate forests (Scheu and Falca 2000). In the studied food web primary decomposers, i.e. litter feeding species, were rare potentially reflecting low litter quality (Chapter 5.1.). A large number of 'decomposer' animals were in fact predatory or necrophagous, suggesting that various putative decomposer soil animal species (especially in Oribatida) feed on other soil invertebrates, in particular nematodes or on animal carcasses (Schneider *et al.* 2004).

Another interesting pattern was that parthenogenetic oribatid mite species had lower ^{15}N values than sexually reproducing species. This suggests that parthenogenetic reproduction prevails in primary decomposers but not in predators. Potentially, predominance of parthenogenetic reproduction in primary decomposers reflects that these species do not co-evolve with their resources, i.e. dead organic material, and therefore sexuality can be abandoned more easily (Hamilton 2001). In contrast, species at higher trophic levels may be confronted with co-evolutionary arms races with their prey and need to reproduce sexually for not going extinct (Red Queen hypothesis; Hamilton, 1980).

In addition to the $^{15}N/^{14}N$ ratios in a number of soil animal species we also measured the $^{13}C/^{12}C$ ratio. The data support the conclusion that primary decomposers indeed are rare in the studied forest. As suggested earlier (Scheu and Falca 2000) decomposer animals constitute of two trophic guilds, differing significantly in ^{15}N signatures, i.e. primary and secondary decomposers. Schmidt *et al.* (2004) proposed that the combined analysis of the ratios of $^{15}N/^{14}N$ and $^{13}C/^{12}C$ facilitates identification of primary and secondary decomposers since the latter not only are more enriched in ^{15}N but also less depleted in ^{13}C. In fact, in our study $\delta^{13}C$ signatures (cf. Lajtha and Michener 1994) of most decomposer taxa were less depleted by about 1.5-2.5 δ units compared to leaf litter of *Graffenrieda emarginata* (Fig. 3.3.). Surprisingly, we did not find any mesofauna taxon classified as primary decomposer by $\delta^{15}N$ and $\delta^{13}C$ signatures. The only primary decomposer species we identified was Diplopoda sp. 1 and this species was rare. Signatures of $\delta^{15}N$ and $\delta^{13}C$ of Diplopoda sp. 1 were very similar to that of leaf litter of *G. emarginata*. This is surprising since consumers generally are enriched in ^{15}N by average 3.4 δ units (Post 2002). Similar $\delta^{15}N$ signatures of primary decomposers and their food resources have been found previously. It has been suggested that ^{15}N fractionation in decomposer animals generally is low compared to herbivores and predators (Vanderklift and Ponsard 2003).

Signatures of $\delta^{13}C$ of predators also spanned over a range of more than two units. In some predators, such as Staphylinidae sp., Pselaphidae sp. and *Amerioppia* sp., the $\delta^{13}C$ signatures were close to those of primary decomposers. In other predators, such as Uropodina sp. and Gamasina sp. 1 and 2, they were close to those of secondary decomposers. This suggests that at our study site, and potentially in soil food webs in general, there are two predator guilds, one predominantly feeding on primary decomposers, the other predominantly on secondary decomposers. Generally, the secondary decomposer channel appears to be more diverse supporting the view that predators in soil predominantly feed on secondary decomposers rather than on primary decomposers (Scheu and Falca 2000).

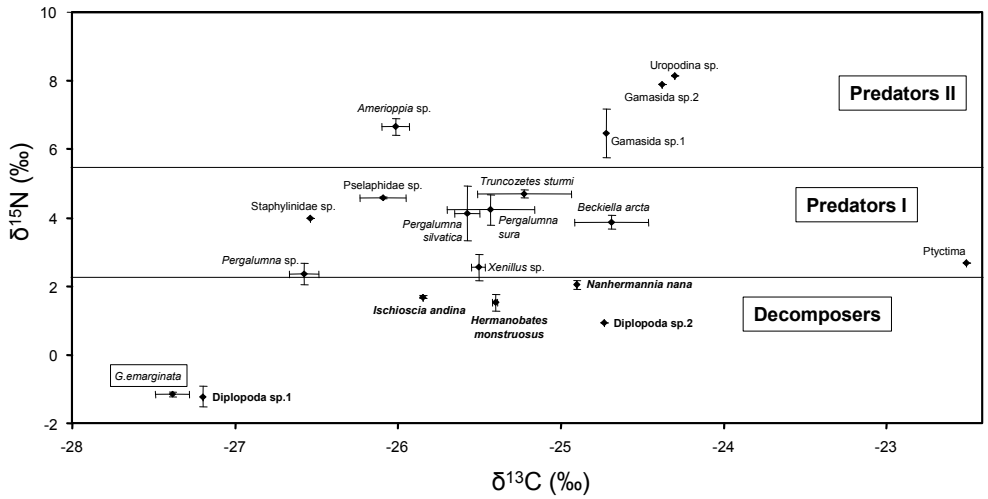

Fig. 3.3. Variation of $\delta^{13}C$ and $\delta^{15}N$ signatures of soil animals extracted from *Graffenrieda emarginata* leaf litter material from the ECSF site (1850 m). If no standard deviation is shown only a single sample was analysed.

Decomposition and microarthropod colonization of litter

Litter decomposition in tropical mountain rain forests is slower than in lowland tropical rain forests (Heneghan *et al.* 1999) which may be due to lower temperatures in mountain rain forests or due to low litter quality. We studied the leaf litter decomposition of two abundant tree species (*G. emarginata*, *P. nutans*) at the studied tropical mountain rain forest (Chapter 5.2.). In addition, we studied the role of the soil mesofauna for the decomposition of these two litter types. To exclude mesofauna the litter was enclosed in litterbags of 48 µm mesh; litter accessible to mesofauna was enclosed in 1 mm mesh. Litter mass loss, content of C and N, basal respiration, microbial biomass and the colonisation of the litterbags by microarthropods were analyzed after exposure in the field for 2, 6 and 12 months at 1850 and 2270 m. Both litter types decomposed slowly (average of 68.5 % of initial dry weight remaining after 12 months), and generally, *P. nutans* litter decomposed slower than *G. emarginata* and mixed litter (Fig. 3.4.). The decomposition rates were similar to those of oak-pine litter in a forest stand in Japan (Kaneko and Salamanca 1999), to sweet chestnut and beech litter in two deciduous woodland forests in England (Anderson 1973) and to *Quercus coccifera* litter in Northern Greece (Argyropoulou *et al.* 1993). However, compared to tropical lowland forests decomposition rates were low; in these systems only about 30 % of the initial dry weight remained after one year (Paoletti *et al.* 1991, Heneghan *et al.* 1999, Franklin *et al.* 2004).

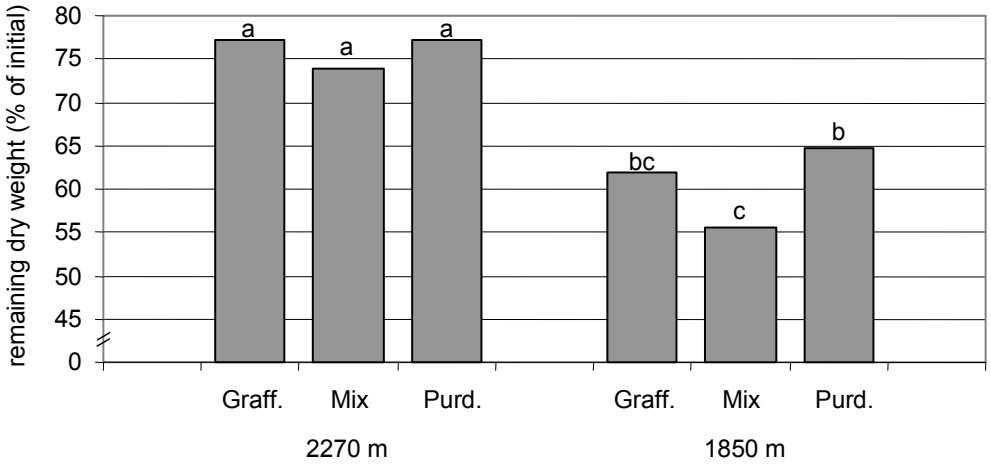

Fig. 3.4. Decomposition (measured as remaining dry weight) of leaf litter of *Graffenrieda emarginata* (Graff.), *Purdiaea nutans* (Purd.), and a mixture of both (mix) exposed in the field for 12 month at two different altitudes. Bars sharing the same letter are not significantly different (Tukey's HSD test; $P > 0.05$).

One of the reasons for the slow decomposition may be low litter quality, i.e. low nutrient concentrations, in particular that of nitrogen (Enriques *et al.* 1993). Indeed, nitrogen concentrations of the leaf litter (F material) of *P. nutans* and *G. emarginata* were lower (C –to- N ratio of 73.6 and 41.9, respectively; Chapter 5.2.) than those of F material of European beech (C –to- N ratio of 21; Maraun and Scheu 1996). Each of the litter materials (*G. emarginata, P. nutans* and mixed litter) decomposed faster at 1850 m than at 2270 m (average of 60 % and 76 % of the initial litter mass remaining after 12 months, respectively). Lower decomposition rates at higher altitudes likely were due to lower temperatures.

At 1850 m altitude the mixture of *G. emarginata* and *P. nutans* litter decomposed significantly faster than both single litter types (Fig. 3.4.) indicating that combining the two litter types accelerates decomposition processes ('non-additive effect'). The reason for this non-additive litter decomposition may be the higher humidity in mixed litter (Wardle *et al.* 2003) or the mixing of litter of different resource quality which may stimulate the decomposition of low quality litter, i.e. litter low in nitrogen (Smith and Bradford 2003; Quested *et al.* 2005).

The most abundant microarthropods in the litterbags were oribatid mites followed by Collembola, Gamasina, Uropodina, Prostigmata + Astigmata. Each of these taxa were more abundant at 1850 m than at 2270 m. Oribatid mites in the litter bags constituted of 37 species and were dominated by *Scheloribates* spp., *Pergalumna sura* and *Truncozetes sturmi*. Species composition was similar in both litter types supporting previous findings that the structure of soil decomposer microarthropod communities is little affected by litter type (Walter 1985;

Migge *et al.* 1998; Hansen 2000). Soil microarthropods generally did not significantly affect litter decomposition (F=0.04; P=0.84). This is consistent with results of our food web analysis suggesting that litter feeding soil meso- and macrofauna are scarce. However, higher density and diversity of secondary decomposers as compared to primary decomposers suggest that soil animals may affect decomposition processes at later stages of decay. Therefore, exposure of litter for 12 month, as done in the present study, may not have been long enough to evaluate the role of decomposers for litter decomposition in the studied tropical mountain rain forest. Long-term studies are needed to prove if this in fact is the case. Furthermore, soil microfauna should also be investigated in these studies since microfauna groups, such as Nematoda and Testacea, are abundant at the studied mountain rain forest and their role for decomposition processes may well exceed that of meso- and macrofauna.

Bottom-up forces in the soil food web

Animal, plant and microbial communities are structured by bottom-up (i.e resources) and top-down forces (i.e. predators), but the relative importance of both is debated (Hairston *et al*. 1960, McQueen *et al*. 1989, Hunter and Price 1992, Moran and Scheidler 2002). For soil systems Hairston *et al.* (1960) suggested that especially saprophagous animals and microbial decomposers, such as bacteria and fungi, are regulated by the availability of resources, i.e. the input of dead organic matter. Scheu and Schaefer (1998) confirmed the importance of resource limitation for earthworms in a temperate deciduous forest. However, decomposer animals are not only regulated by bottom-up forces; indirect effects, such as bioturbation by earthworms, may override bottom-up effects, especially in soil microarthropods (Maraun *et al.* 2001; Salamon *et al.* 2006). Though the latter presumably are of little importance in the studied mountain rain forest since large decomposer animals are virtually lacking.

By increasing the supply of resources to decomposer biota we expected to be able to uncover the role of resource limitation in the studied decomposer system. First, in a short-term laboratory experiment we studied the role of nutrients (N, P) and carbon (C, glucose) added as C, CN, CP and CNP for the growth of soil microorganisms. The study evaluated if microbial growth in the litter layer is limited by nutrient availability. Second, by adding nutrients (N, P) and carbon (C, glucose) in all combinations (control, C, N, P, CN, CP, NP, CNP) repeatedly to the soil of the studied rain forest for one year we investigated nutrient and carbon limitation of microorganisms and soil animals under natural conditions in the field.

In the short-term laboratory experiment microbial growth (measured as the slope of the respiration curve after resource addition) was measured (Scheu and Parkinson 1995). We

hypothesized (1) that carbon addition will not stimulate microbial growth since nitrogen and phosphorous limit microbial growth (Enriques *et al*. 1993) and (2) that nitrogen addition (together with carbon) stimulates microbial growth in the studied rain forest since nitrogen has been assumed to be more important than phosphorous for plants and microorganisms whereas in lowland rain forests the opposite may be true (Tanner *et al.* 1998). In agreement with our first hypothesis, carbon addition stimulated microbial growth little in particular at higher altitude (Fig. 3.5.) indicating that nutrient limitation increases with altitude. However, in contrast to our second hypothesis, the addition of carbon together with nitrogen also only little affected microbial growth indicating that nitrogen is not limiting microbial growth. Unexpectedly, the addition of phosphorous (together with C or CN) generally strongly increased microbial growth, and this effect increased with altitude indicating that phosphorus limitation increases with altitude. Overall, the results indicate that microbial growth is mainly limited by the availability of phosphorous, and that the availability of nutrients (especially that of phosphorous) declines with altitude.

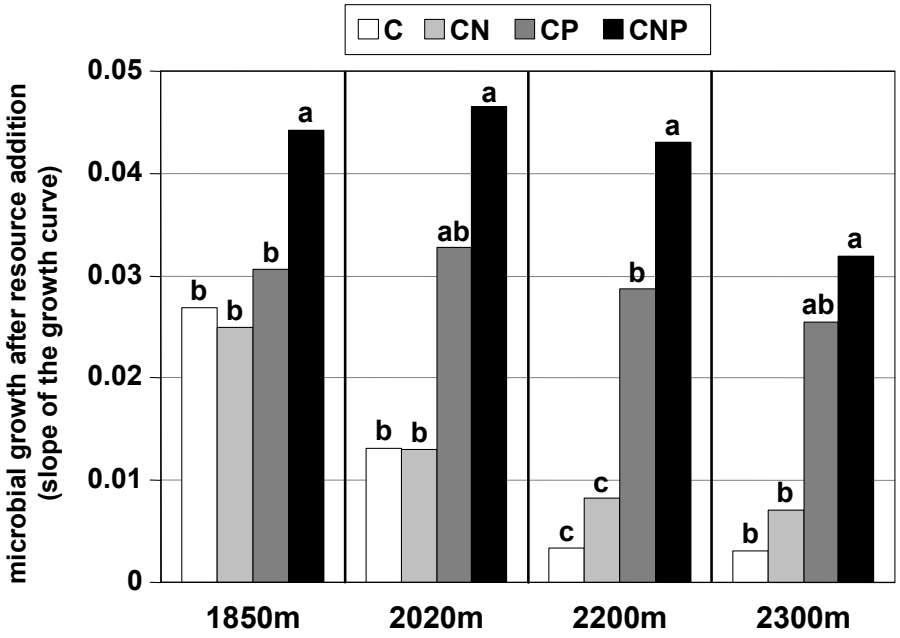

Fig. 3.5. Microbial growth in F litter material from the ECSF site at different altitude after the addition of carbon (C), carbon + nitrogen (CN), carbon + phsophorous (CP) and carbon + nitrogen + phosphorous (CNP) (see text for details). Bars sharing the same letter are not significantly different (Tukey's HSD test; $P > 0.05$).

In the long-term field experiment the amount of resources added was equivalent to about five times the annual input of C, N and P with aboveground plant litter. We hypothesised that the additional resource supply will predominantly affect lower trophic levels, i.e.

microorganisms and decomposer animals, and propagate to higher trophic levels but with decreasing intensity due to the dampening of bottom-up forces at higher trophic levels in soil systems (Salamon *et al.* 2006). Indeed, fungal biomass (measured as erogosterol content) and density of Astigmata strongly increased after addition of carbon (Fig. 3.6.). Density of Entomobryidae, Onychiuridae, Ptyctima, Desmonomata and juvenile Oribatida and also predatory taxa (Uropodina, Gamasina) increased after N and C application, although the response was not uniform, and some taxa remained unaffected (e.g. Arachnida, Prostigmata, Formicidae and some subgroups of oribatid mites). Predatory taxa generally responded little to resource additions. Overall, the results support the hypotheses (1) that additional resources mainly affect lower trophic levels and (2) that carbon and less pronounced also nitrogen and phosphorous are important limiting factors for basal trophic taxa, in particular fungi and decomposer soil mesofauna, and (3) that resource addition effects propagate only little to higher trophic levels, i.e. to predatory taxa.

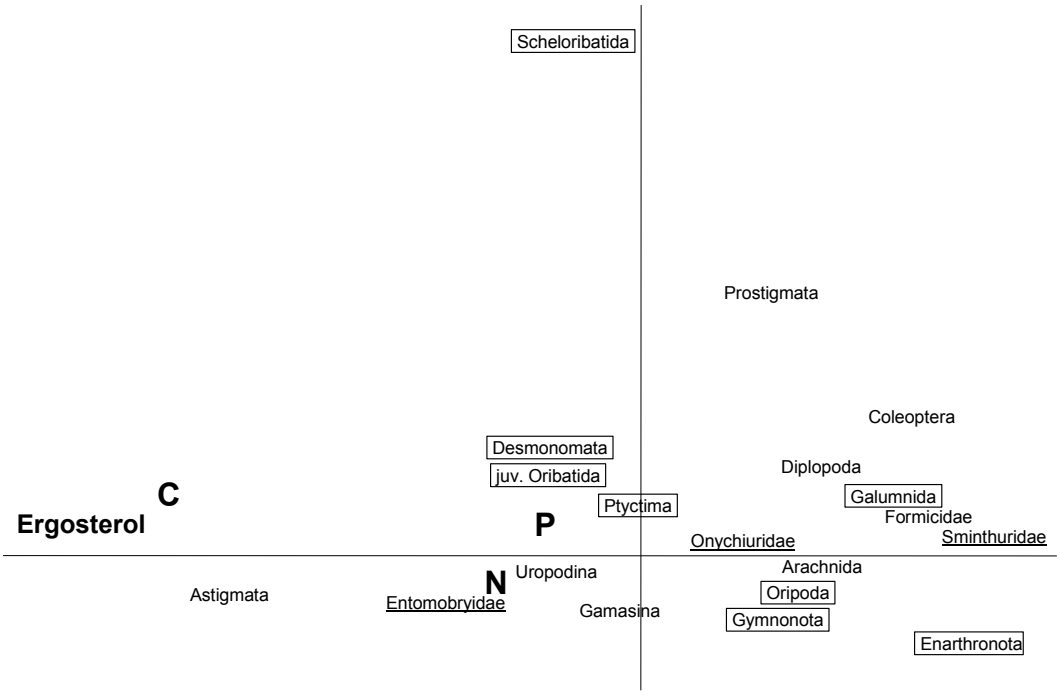

Fig. 3.6. Canonical correspondence analysis (CCA) plot of fungi (indicated by ergosterol) and soil animal taxa after one year addition of carbon (C), nitrogen (N) and phosphorous (P) separately and in combintaion (CN, CP, NP, CNP). Collembola are underlined; oribatid mites are enclosed in boxes (eigenvalue of axis 1 = 0.28; eigenvalue of axis 2 = 0.12).

3.4. Summary and prospect for future studies

In the studied mountain rain forest densities of soil macrofauna and soil microarthropods (oribatid mites, collembolans) were low. As in temperate forests, low densities of decomposer soil macrofauna may be caused by low soil pH. However, the low densities of soil microarthropods are surprising since in temperate and boreal forests resembling the studied mountain rain forest in respect to low pH and thickness of organic layers, the density of soil microarthropods is high. In contrast to density, the diversity of soil microarthropods in the studied tropical mountain rain forest was high compared to temperate and boreal forests. High diversity might be due to the presence of a high number of microhabitats (e.g. litter types), but results of the present study and from temperate forest ecosystems suggest that the diversity of decomposer animals is only little affected by the diversity of leaf litter types.

The natural variation in the stable isotope signatures (^{15}N, ^{13}C) in soil animals indicates that the number of trophic levels and the structure of the soil food web in the studied tropical mountain rain forest resembles that of temperate forest ecosystems, however, there appear to be less species functioning as primary decomposers. As reported from temperate forests secondary decomposer animals were more enriched in ^{13}C than primary decomposers, and this may allow to separate consumer chains based on primary and secondary decomposers.

Litter decomposition in the studied tropical mountain rain forest was generally slow and decreased with altitude. High moisture and low litter quality may limit the decomposition process but more detailed studies including the nutrient content of the litter material at different stages of decomposition are needed. Acceleration of litter decomposition in mixed litter material, as observed for litter of *P. nutans* and *G. emarginata*, suggests that non-additive effects significantly contribute to decomposition processes. This might be particularly important in tropical forest ecosystems with high tree species diversity as in the studied tropical mountain forest.

Short-term addition of carbon (glucose) and nutrients (N, P) to litter material (F layer) indicated that phosphorous is limiting microbial growth in the studied tropical mountain rain forest and that the nutrient deficiency increases with altitude. Long-term (one year) addition of carbon (sugarcane) and nutrients (N, P) indicated that in particular carbon is limiting soil fungi and Astigmata whereas densities of decomposer taxa (Entomobryidae, Onychiuridae, Ptyctima, Desmonomata, juvenile Oribatida) and some predatory taxa (Uropodina, Gamasina) increased after combined application of C and N. Most predatory taxa did not respond to the addition of resources indicating that bottom-up forces are dampened at higher trophic levels. The results suggest that carbon and less pronounced nitrogen are limiting elements for basal

trophic taxa in the long-term. However, longer lasting experiments at larger scales are needed to evaluate the limiting elements for microorganisms, plants and animals in tropical mountain rain forests.

CHAPTER 4

4.1. New species and new records of ptyctimous mites (Acari, Oribatida) in an altitudinal gradient from the Ecuador rainforest

4.1.1. Abstract

Thirty one species of ptyctimous mites have been found in the Reserva Biológia San Francisco (~2000 m), in Bombuscaro (~1000 m) and Cajanuma (~3000 m). The ptyctimous mite fauna has been shown to differ strongly between Bombuscaro and Cajanuma but to overlap slightly with the RBSF.

This chapter comprises the description of nine new species (*Oribotritia paraalajuela* sp. nov., *Acrotritia parabrasiliana* sp. nov., *Acrotritia rhopalota* sp. nov., *Austrophthiracarus elconsulei* sp. nov., *Protophthitracarus paraminisetosus* sp. nov., *P. quasiminisetosus* sp. nov., *Notophthiracarus ecphylus* sp. nov., *Euphthiracarus bombuscaroensis* sp. nov. and *Austrophthiracarus cajanumaensis* sp. nov.) and presentation of eight additional species which are new for continental Ecuador.

The specimens of two species: *Protophthiracarus quasiminisetosus* sp. nov. and *Notophthiracarus aculeatus* Niedbała, 1988 found in Ecuador have some morphological characters different from their analogues in the type specimens.

4.1.2. Introduction

Classification of ptyctimous mites is still discussed (Weigmann 2006). According to Subías (2004) ptyctimous mites (Euptyctima) include three subgroups: Mesoplophoroidea, Euphthiracaroidea and Phthiracaroidea.

Ptyctimous mites are a cosmopolitan group and their taxonomic diversity is high (Niedbala 1992). In well examined temperate regions like Germany approximately 40 species of ptyctimous mites exist (Weigmann 2006). The greatest number of neotropical species occur in the equatorial zone; about 80 species are known from Andean regions (Niedbala 2003, 2004). The fauna of ptyctimous mites of the Neotropical Region is characterised by a large number of endemites and is much richer than the faunas of the other regions of the world. The

similarity of the ptyctimous mite fauna of the Neotropical Region with those of the Nearctic, Ethiopian and Australian Regions is slight (Niedbala 2004). They are inhabitants of organic litter. Juvenile instars live and feed inside leaf and needle litter material (Hayes, 1966). The ptychoid habitus as a defensive adaptation protect them against predation (Norton 1994, Sanders and Norton 2004). Adult members of this group were ascribed to the secondary decomposers indicating food generalism (Chapter 5.1.).

4.1.2. Material and methods

Samples were collected in an Andean Mountain Rainforest in south Ecuador at three study sites. The first study site is part of the Reserva Biológia San Francisco (RBSF), located in Zamora-Chinchipe province, near the city of Loja in southern Ecuador at 1850 m (3^{o}58'S, 79^{o}5'W). The region on the border to the Podocarpus Nationalpark is covered with mostly undisturbed rainforest. *Graffenrieda emarginata* (Melastomataceae) are the most abundant plants in this region (Homeier *et al.* 2002). The organic soil layer is thick and the pH ranges between 4 and 4.5 (Wilcke *et al.* 2002). The decomposition rate is lower than in the tropical lowland forests (Chapter 5.2.).

In February 2004 and March 2005 L/F litter material from *Graffenrieda emarginata* (Melastomatacea) were sampled. Additionally, no specific litter fermentation layers samples were taken within the Podocarpus Nationalpark in Bombuscaro (4°06.87' S, 78°08.31' W) at 1040 m in November 2005 and in Cajanuma (04°06'711'' S, 79°10'581'' W) at 3060 m in December 2005.

Oribatid mites were selected by using a modified high gradient heat extractor (Kempson *et al.* 1963) and then transferred to 70% ethanol. Drawings were made of the specimens, which were cleaned in lactic acid and examined under a phase-contrast microscope. Terminology is based on that of Niedbała (2004). Descriptions of gnathosoma and legs are given in papers of Mahunka (1990) and Niedbala (1992). Measurements are given in micrometres. Types are deposited in Department of Animal Taxonomy and Ecology, Poznań.

Identified species

Reserva Biológia San Francisco (RBSF)

Mesoplophora (*Mesoplophora*) *cubana* Călugăr and Vasiliu, 1977 (10 specimens) *Oribotritia paraalajuela* sp. nov. (1 specimen), *Mesotritia curviseta* (Hammer 1961) (1 specimen), *Acrotritia clavata* (Märkel 1964) (7 specimens) *Acrotritia dikra* (Niedbała and Schatz 1996) (1 specimen), *Acrotritia monodactyla* (Niedbała 2002) (3 specimens), *Acrotritia parabrasiliana* sp. nov. (3 specimens), *Acrotritia rhopalota* sp. nov. (1 specimen), *Phthiracarus anonymus* Grandjean 1933 (4 specimens), *Austrophthiracarus elconsulei* sp. nov. (4 specimens), *Protophthitracarus paraminisetosus* sp. nov. (5 specimens), *P. quasiminisetosus* sp. nov. (7 specimens), *Notophthiracarus ecphylus* sp. nov. (6 specimens).

Bombuscaro

Mesoplophora (Mesoplophora) cubana Călugăr and Vasiliu 1977 (1 specimen), *Mesoplophora (Mesoplophora) hauseri* Mahunka 1982 (2 specimens), *Microtritia tropica* Märkel, 1964 (3 specimens), *Euphthiracarus bombuscaroensis* sp. nov. (3 specimens), *Atropacarus (Hoplophorella) cucullatus* (Ewing, 1909) (3 specimens), *A. (H.) vitrinus* (Berlese, 1913) (1 specimen).

Cajanuma

Austrophthiracarus diazae Ojeda 1985 (1 specimen), *Protophthiracarus quasiminisetosus* sp. nov. (2 specimens), *P. paraminisetosus* sp. nov. (12 specimens), *Austrophthiracarus cajanumaensis* sp.nov. (4 specimens), *Notophthiracarus aculeatus* Niedbała 1988 (8 specimens), *Notophthiracarus pedanos* Niedbała 2003 (1 specimen).

4.1.3. Determination and Description of species

***Mesoplophora (Mesoplophora) cubana* Calugar and Vasiliu, 1977**

(Fig. 4.1. A-B)

Measurements of one specimen

Prodorsum: length 212, height 85.8, sensillus 139, setae: interlamellar 109, lamellar 96.1, rostral 65.8, exobothridial 27.8; notogaster: length 303, height 182, c_1 seta 58.2; genitoaggenital plate 88.5 x 15.2, anoadanal plate 93.6 x 16.6.

Taxonomical notes. The dimensions of all specimens are larger than Cuban specimens. Sensilli with 5 small spines, notogastral setae smooth.

Material examined

Southern Ecuadorian Andes, Cordillera El Consuelo, Zamorra-Chinchipe province, Biological Reserve "Estación Cientifica San Francisco" (03°59´S,79°04´W), at 1850 m altitude, bark, organic litter and the upper soil layer, especially from *Graffenrieda emarginata* litter, leg. J. Illig; February 2004: 3 specimens; March 2005: 7 specimens.

Distribution

The first locality outside of Cuba.

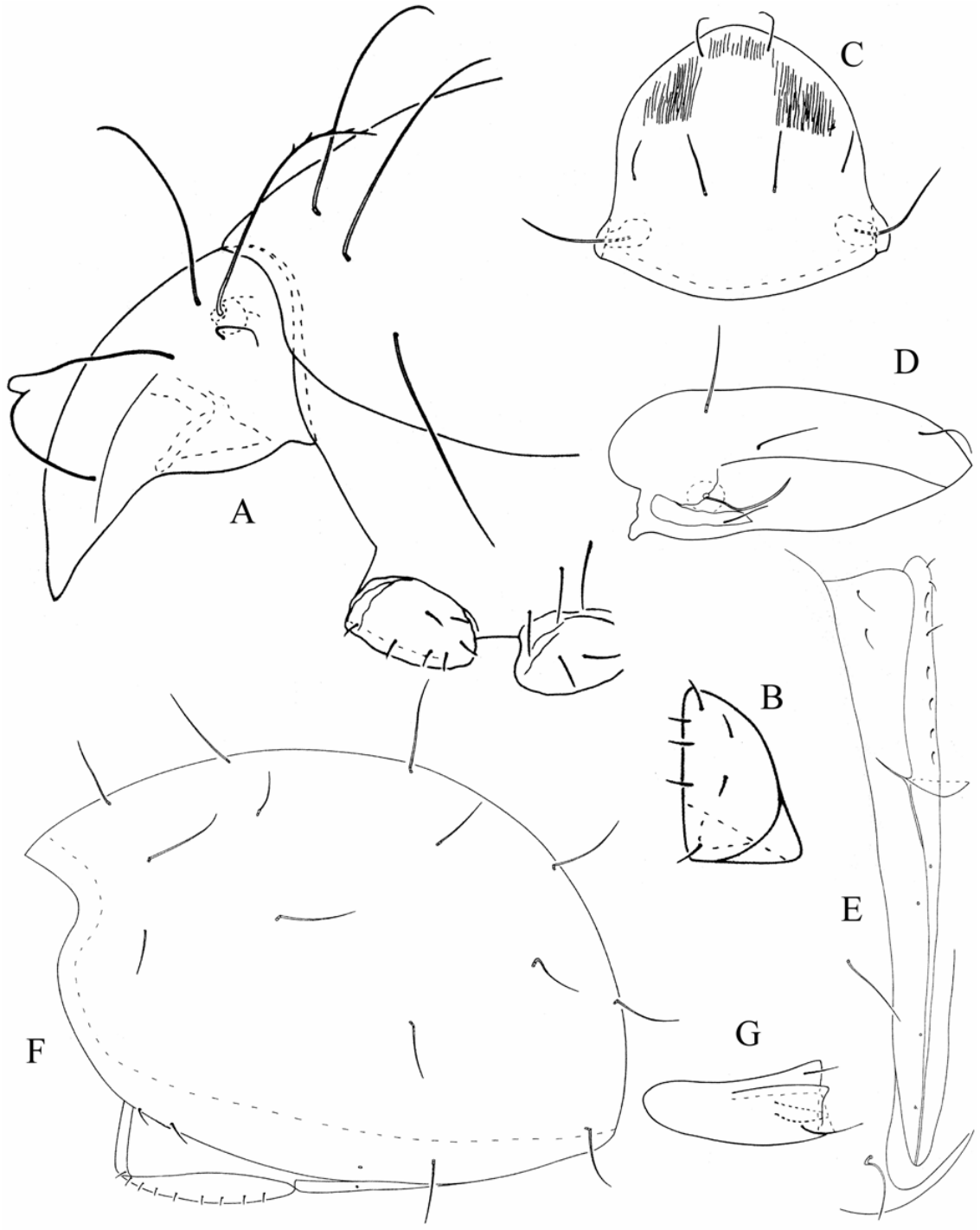

Fig. 4.1. A, B. – *Mesoplophora* (*M.*) *cubana* Calugar and Vasiliu, 1977. A – anterior part of body, lateral view, B – genital plate; C-G. – *Oribotritia paraajaluela* sp. nov. C – prodorsum, dorsal view, D – prodorsum, lateral view, E – right genital, aggenital, anal and adanal plates, F – opisthosoma, lateral view, G – femur of leg I.

Oribotritia paraajaluela sp. nov.
(Fig. 4.1. C-G)

Measurements of holotype
Prodorsum: length 475, width 333, height 167, sensillus 134, setae: interlamellar 106, lamellar 53.1, rostral 68.3, exobothridial 43.0; notogaster: length 798, width 566, height 576, setae: c_1 95.9, h_1 and ps_1 101; genital and aggenital plates 217 x 136, anal and adanal plates 379 x 70.7.
Colour deep brown. Surface of body dotted.
Prodorsum with sensilli rigid, thick, bent. Interlamellar setae thick, erect, rough, similar to notogastral setae. Lamellar, rostral and exobothridial setae shorter, filiform.
Notogaster with short, rigid, rough setae. Setae of row *c* remote from anterior border, setae c_3 shorter than other.
Ventral region. Setae *h* of mentum considerably longer than distance between them. Nine pairs of genital and two pairs of aggenital setae present. Right anal plate with one seta remote from anterior end. Left plate without seta. Adanal plates with three pairs of setae, distance between setae ad_1 and ad_2 shorter then between ad_2 and ad_3.
Chaetome of legs (without tarsi) as in *Oribotritia geminata* Niedbała 2004, namely: I: 1-4-5(2)-5(1), II: 1-4-4(1)-5(1), III: 3-2-3(1)-3(1), IV: 3-2-2(1)-3(1). Femora I with dorsal crista.
Holotype. Southern Ecuadorian Andes, Cordillera El Consuelo, Zamorra-Chinchipe province, Biological Reserve "Estación Cientifica San Francisco" (03°59´S, 79°04´W), at 1850 m altitude, bark, organic litter and the upper soil layer, especially from *Graffenrieda emarginata* litter, February 2004, leg. J. Illig.

Etymology
The prefix *para* is Latin meaning "near" and refers to the similarity of the new species with *Oribotritia alajuela* Niedbała 2003.

Comparison
The new species is similar to *O. alajuela* Niedbała 2003 which has always two pairs of anal setae.

Mesotritia curviseta (Hammer 1961)

Material examined
Southern Ecuadorian Andes, Cordillera El Consuelo, Zamorra-Chinchipe province, Biological Reserve "Estación Cientifica San Francisco" (03°59´S, 79°04´W), at 1850 m altitude, bark, organic litter and the upper soil layer, especially from *Graffenrieda emarginata* litter, March 2005, leg. J. Illig: 1 specimen.

Distribution
The first locality from Ecuador; neotropical, disjunctive distribution.

Acrotritia clavata (Märkel 1964)

Material examined
Southern Ecuadorian Andes, Cordillera El Consuelo, Zamorra-Chinchipe province, Biological Reserve "Estación Cientifica San Francisco" (03°59´S,79°04´W), at 1850 m altitude bark,

organic litter and the upper soil layer, especially from *Graffenrieda emarginata* litter, leg. J. Illig, February 2004: 6 specimens; March 2005: 1 specimen.

Distribution
The first locality from continental Ecuador; widely distributed Neotropical species.

Acrotritia dikra (Niedbała and Schatz 1996)

Material examined
Southern Ecuadorian Andes, Cordillera El Consuelo, Zamorra-Chinchipe province, Biological Reserve "Estación Cientifica San Francisco" (03°59´S, 79°04´W), at 1850 m altitude, bark, organic litter and the upper soil layer, especially from *Graffenrieda emarginata* litter, March 2005, leg. J. Illig – 1 specimen.

Distribution
The first locality from Ecuador. Neotropical, northern part.

Acrotritia monodactyla (Niedbała 2002)

Material examined
Southern Ecuadorian Andes, Cordillera El Consuelo, Zamorra-Chinchipe province, Biological Reserve "Estación Cientifica San Francisco" (03°59´S, 79°04´W), at 1850 m altitude, bark, organic litter and the upper soil layer, especially from *Graffenrieda emarginata* litter, March 2005, leg. J. Illig – 3 specimens.

Distribution
The first locality from Ecuador. Neotropical, disjunctive distribution.

Acrotritia parabrasiliana sp. nov.
(Fig. 4.2. A-C)

Description
Measurements of holotype: prodorsum: length 257, width 192, height 111, sensillus 98.7, setae: interlamellar 114, lamellar 70.8, rostral 60.7; notogaster: length 515, width 328, height 348, setae: c_1 70.8, h_1 and ps_1 75.9; length of genitoaggenital plate 177, length of anoadanal plate 232.
Colour light yellow. Surface of body dotted.
Prodorsum with distinct lateral carinae, forked distally. Sensilli with narrow stalk and fusiform head covered with small spines at distal end. Setae typical for genus, exobothridial setae vestigial.
Notogaster with short setae covered with cilia in distal half.
Ventral region. Setae *h* of gnathosomal mentum longer than distance between them. Genitoaggenital plates with nine pairs of genital and two pairs of aggenital setae present.
Chaetome of legs I (without tarsi): I: 1-3-5(2)-5(1); II: 1-3-3(1)-4(1); III: 2-2-2(1)-3(1); IV: 2-1-3-2(1). Tarsi are monodactylous.
Holotype and 2 paratypes. Southern Ecuadorian Andes, Cordillera El Consuelo, Zamorra-Chinchipe province, Biological Reserve "Estación Cientifica San Francisco" (03°59´S,

79°04´W), at 1850 m altitude, bark, organic litter and the upper soil layer, especially from *Graffenrieda emarginata* litter, February 2004, leg. J. Illig; March 2005: 3 specimens.

Etymology
The prefix *para* is Latin meaning "near" and refers to the similarity the new species with *Acrotritia brasiliana* Mahunka 1983.

Comparison
Only two species from Neotropical region has monodactylous tarsi: *Acrotritia brasiliana* Mahunka 1983 and *Acrotritia dixa* Niedbała and Schatz 1996, but both have another shape of sensilli.

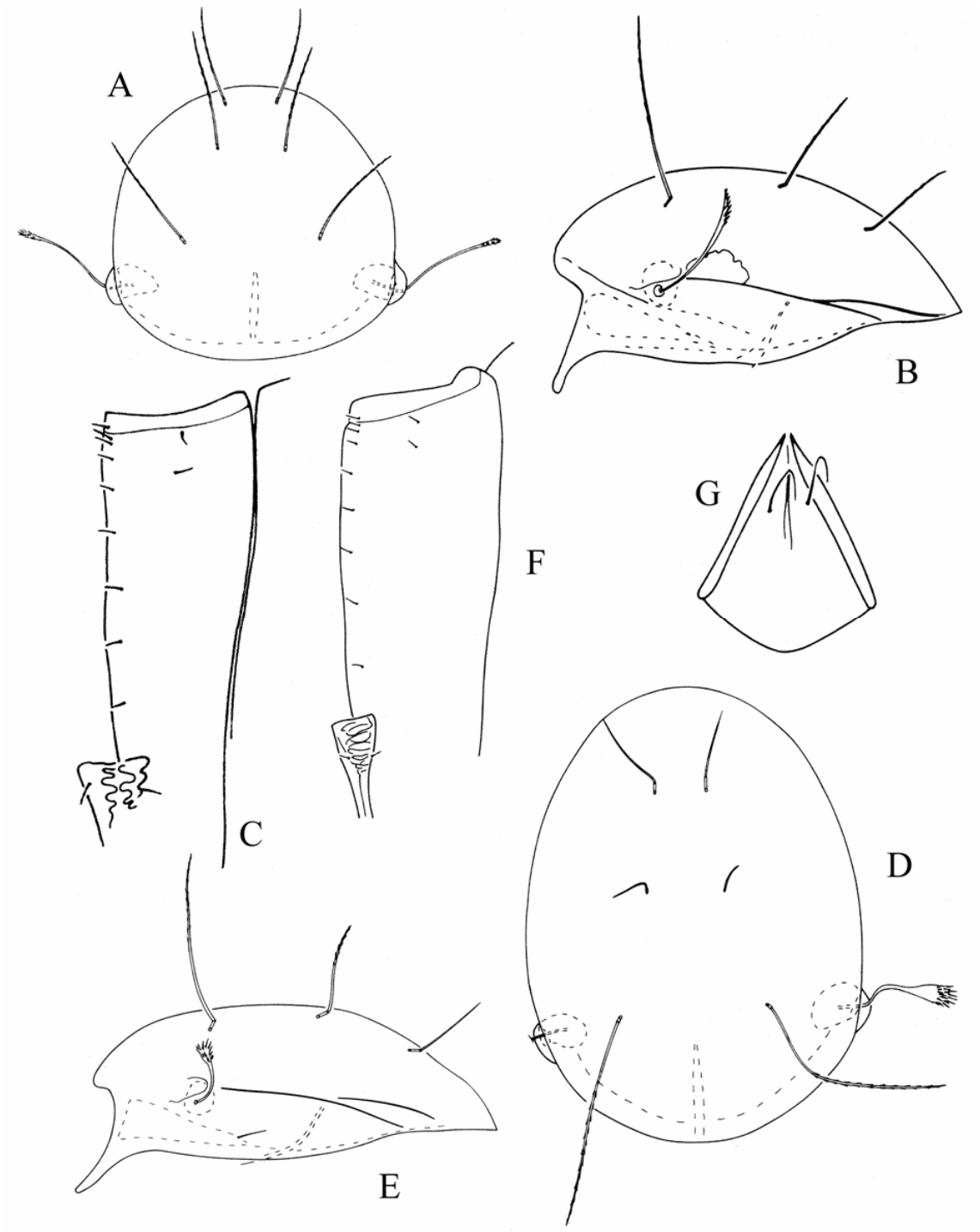

Fig. 4.2. A-C. – *Acrotritia parabrasiliana* sp. nov. A – prodorsum, dorsal view, B – prodorsum, lateral view, C – left genitoaggenital plate; D-G. – *Acrotritia rhopalota* sp. nov. D – prodorsum, dorsal view, E – prodorsum, lateral view, F – left genitoaggenital plate, G – mentum of infracapitulum.

Acrotritia rhopalota sp. nov.
(Fig. 4.2. D-G)

Description
Measurements of holotype: prodorsum: length 281, width 202, height 106, sensillus 60.7, setae: interlamellar 132, lamellar 68.3, rostral 63.2, exobothridial 20.2; notogaster: length 566, width 384, height 409, setae: c_1 70.8, h_1 and ps_1 75.9; length of genitoaggenital plate 169, length of anoadanal plate 252.
Colour light, yellow. Surface of body dotted.
Prodorsum with distinct lateral carinae forked distally but shorter branch slightly separated from principal trunk. Sensilli with narrow pedicel and club-like head covered with spines. Interlamellar and lamellar setae covered with small spines, rostral setae rough, lamellar setae obtuse distally.
Notogaster with short setae covered with cilia in distal half.
Ventral region. Setae *h* of gnathosomal mentum longer than distance between them. Genitoaggenital plates with 9 pairs of genital and 2 pairs of aggenital setae present.
Chaetome of legs (without tarsi) as in *Acrotritia parabrasiliana*, namely: I: 1-3-5(2)-5(1); II: 1-3-3(1)-4(1); III: 2-2-2(1)-3(1); IV: 2-1-3-2(1). Tarsi of legs I heterobidactylous, tarsi II-IV heterotridactylous.
Holotype. Southern Ecuadorian Andes, Cordillera El Consuelo, Zamorra-Chinchipe province, Biological Reserve "Estación Cientifica San Francisco" (03°59´S,79°04´W), at 1850 m altitude, bark, organic litter and the upper soil layer, especially from *Graffenrieda emarginata* litter, February 2004, leg. J. Illig.

Etymology
The specific name *rhopalotos* is Greek for "shaped like a club" and alludes to club-like shape of sensilli.

Comparison
The new species is easy distinguishable from congeners by the shape of lateral carinae with separated branch, club-like head of sensilli with distinct spines and obtuse distally lamellar setae. Similar species *Acrotritia dikra* Niedbała and Schatz 1996 has different shape of sensilli and *Acrotritia dixa* Niedbała and Schatz 1996 has tarsi of legs monodactylous.

Phthiracarus anonymus Grandjean 1933

Material examined
Southern Ecuadorian Andes, Cordillera El Consuelo, Zamorra-Chinchipe province, Biological Reserve "Estación Cientifica San Francisco" (03°59´S, 79°04´W), at 1850 m altitude, bark, organic litter and the upper soil layer, especially from *Graffenrieda emarginata* litter, February 2004, leg. J. Illig: 2 specimens; March 2005: 2 specimens.

Distribution
The first locality from continental Ecuador, semicosmopolitan distribution.

Austrophthiracarus elconsulei sp. nov.
(Fig. 4.3. A-F)

Description
Measurements of holotype: prodorsum: length 303, width 227, height 101, sensillus 152, setae: interlamellar and lamellar 40.5, rostral 126, exobothridial 27.8; notogaster: length 581, width 414, height 409, setae: c_1 215, c_1/c_1-d_1 = 1.55, h_1 204, h_3 93.6, ps_1 260; genitoaggenital plate 121 x 111, anoadanal plate 242 x 121.
Colour light brown. Surface of body finely dotted.
Prodorsum without lateral carinae. Lateral sides covered with irregular striation. Sigillar fields weakly visible. Sensilli very long, rigid, obtuse distally, rough. Interlamellar and lamellar setae short, conical, rough. Rostral setae very long, rigid, rough similar to sensilli.
Notogaster with 21 pairs of long, stout, obtuse distally setae covered sparsely with small spines. Dorsal setae longer than ventral setae. Additional setae in rows *h* and *ps*. Setae c_1 located at anterior border, setae c_2 and c_3 slightly remote from border. Vestigial setae f_1 posteriorly of h_1 setae. Two pairs of lyrifissures *ia*, *im* present.
Ventral region. Setae *h* of mentum longer than distance between them. Formula of genital setae: 4+5: 0. Anoadanal plates with six pairs of rough setae. Two pairs of posterior adanal setae the longest, two pairs of anterior adanal setae the shortest. Anal setae of intermediate length.
Chaetome of legs of "complete type", setae *d* of femora I remote from anterior end of the article.
Types. Holotype and 3 paratypes. Southern Ecuadorian Andes, Cordillera El Consuelo, Zamorra-Chinchipe province, Biological Reserve "Estación Cientifica San Francisco" (03°59´S, 79°04´W), at 1850 m altitude, bark, organic litter and the upper soil layer, especially from *Graffenrieda emarginata* litter, March 2005, leg. J. Illig.

Etymology
This species is named after Cordillera El Consuelo.

Comparison
The new species is distinguishable by the presence of long rostral setae and sensilli and short interlamellar and lamellar setae, long and stout notogastral setae and formula of genital setae 4+5: 3. The most similar *Austrophthiracarus hirtus* (Balogh 1984) has longer interlamellar and lamellar setae, shorter rostral setae and short, rounded sensilli.

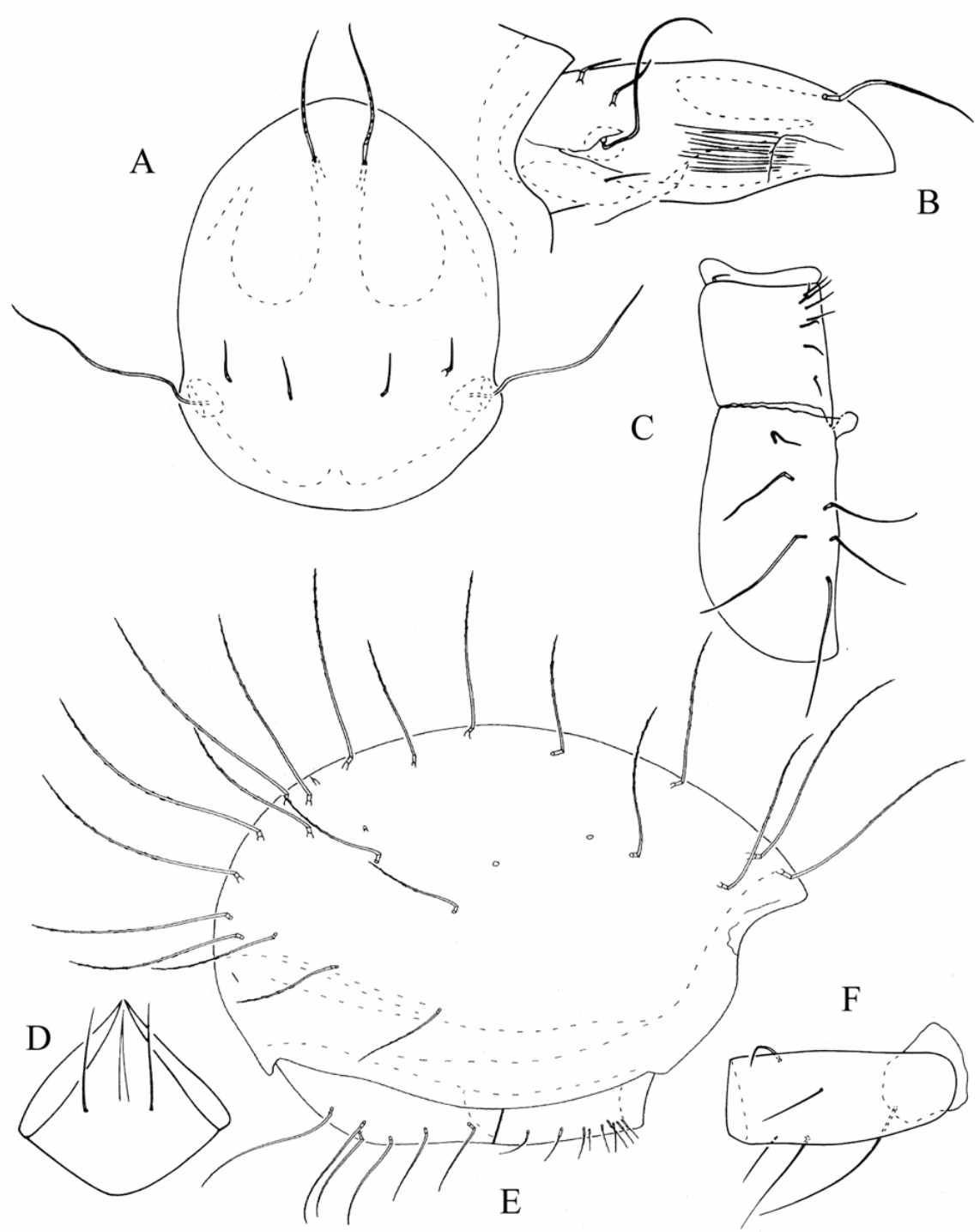

Fig. 4.3. A-F. – *Austrophthiracarus elconsulei* sp. nov. A – prodorsum, dorsal view, B – prodorsum, lateral view, C – right genitoaggenital and anoadanal plates, D – mentum of infracapitulum, E – opisthosoma, lateral view, F – trochanter and femur of leg I.

Protophthiracarus paraminisetosus sp. nov.
(Fig. 4.4. A-F)

Description
Measurements of holotype: prodorsum: length 242, width 177, height 101, sensillus 35.4, setae: interlamellar and rostral 22.8, lamellar 17.7; notogaster: length 449, width 308, height 283, setae: c_1, h_1 and ps_1 20.2-22.8; genitoaggenital plate 126 x 85.8, anoadanal plate 177 x 101.
Colour light, brown. Surface of body dotted.
Prodorsum with long, narrow sigillar fields, laterals longer than median. Lateral carinae absent. Sensilli short, with rather long pedicel and short, rounded, smooth head. Setae simple, minute, smooth, except vestigial exobothridial setae. Lamellar setae situated anteriorly of interlamellar setae.
Notogaster with 20 pairs of minute setae. Additional setae in rows *h* and *ps*. Setae c_1 and c_3 remote from anterior border, setae c_2 far from border. Vestigial setae f_1 posteriorly of setae h_1. Two pairs of lyrifissures *ia* and *im* present.
Ventral region. Setae *h* of mentum considerably longer than distance between them. Arrangement of genital setae: 4+5: 0. Anoadanal plates with neotrichy of adanal (five pairs) setae. All setae minute.
Chaetome of legs of "complete type", setae *d* of femora I rigid and remote from distal end of article.
Holotype and 5 paratypes. Southern Ecuadorian Andes, Cordillera El Consuelo, Zamorra-Chinchipe province, Biological Reserve "Estación Cientifica San Francisco" (03°59´S, 79°04´W), at 1850 m altitude, bark, organic litter and the upper soil layer, especially from *Graffenrieda emarginata* litter, February 2004, leg. J. Illig; March 2005: 4 specimens.

Etymology
The prefix *para* is Latin meaning "near" and refers to the similarity of the new species with *Austrophthiracarus minisetosus* Niedbała 2004.

Comparison
The new species is similar to *Austrophthiracarus minisetosus* Niedbała 2004 but differs by the arrangemet of interlamellar and lamellar setae, the presence of three pairs setae in anal position and the arrangement of genital setae: 4+5: 0.

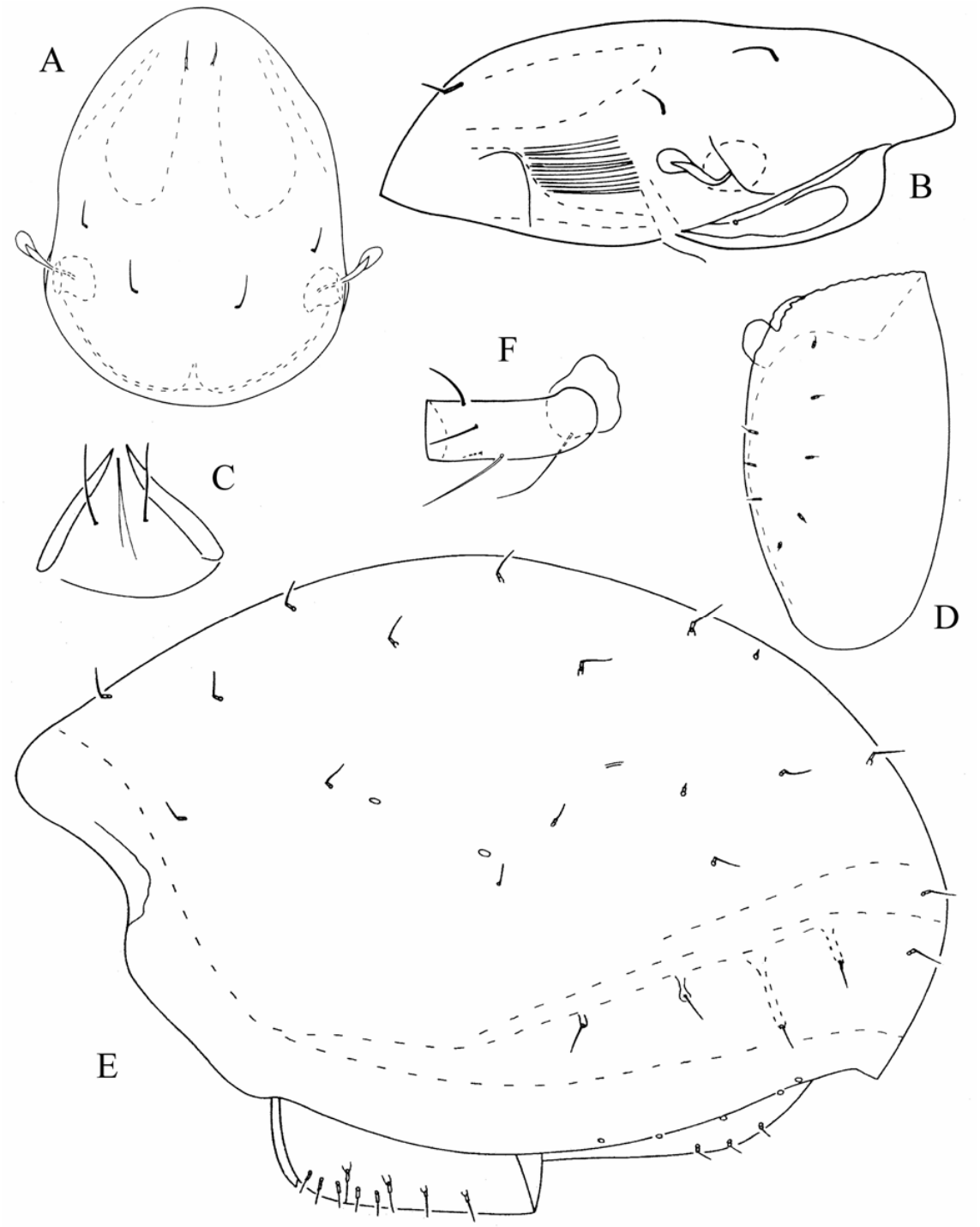

Fig. 4.4. A-F. – *Protophthiracarus paraminisetosus* sp. nov. A – prodorsum, dorsal view, B – prodorsum, lateral view, C – mentum of infracapitulum, D – left anoadanal plate, E – opisthosoma, lateral view, F – trochanter and femur of leg I.

Protophthiracarus quasiminisetosus sp. nov.
(Fig. 4.5. A-G)

Description
Measurements of holotype: prodorsum: length 429, width 328, height 187, sensillus 30.4, setae: interlamellar 15.2, lamellar 28.2, rostral 40.5, exobothridial 23.0; notogaster: length 828, width 687, height 636, setae: c_1, h_1 and ps_1 12.6; genitoaggenital plate 202 x 162, anoadanal plate 313 x 177.
Colour light, brown. Microsculpture of integument finely dotted. Neotrichy of notogastral and adanal setae present.
Prodorsum with narrow sigillar fields, median longer than laterals. Sensilli minute, fusiform. Setae short, spiniform, rough. Notogaster with 21 pairs of minute, needle-shaped setae. Setae of row *ps* longer than other. Additional setae in rows *h* and *ps*. Setae c_1 and c_3 remote from anterior border, setae c_2 far from border. Three pairs of lyrifissures *ia*, *im* and *ip* present. Vestigial setae f_1 posteriorly of h_1.
Ventral region. Setae *h* of mentum considerably longer than distance between them. Arrangement of genital setae: 4+5: 0. Anoadanal plates with rough, rather short setae, three pairs of anal and five pairs of adanal setae.
Chaetome of legs of "complete type". Setae *d* of femora I rigid and remote from distal end of article.
Holotype and one paratype. Southern Ecuadorian Andes, Cordillera El Consuelo, Zamorra-Chinchipe province, Biological Reserve "Estación Cientifica San Francisco" (03°59´S, 79°04´W), at 1850 m altitude, bark, organic litter and the upper soil layer, especially from *Graffenrieda emarginata* litter, February 2004, leg. J. Illig; March 2005: 3 specimens.

Etymology
The prefix *quasi* is Latin meaning "near" and refers to the similarity of the new species with *Austrophthiracarus minisetosus* Niedbała 2004.

Comparison
The new species is similar to *A. minisetosus* Niedbała 2004 but is distinguishable by the presence of three pairs of setae in anal position in anoadanal plates, the different shape of sensilli, the longer setae of row *ps* and the different arrangement of genital setae. *Protophthiracarus paraminisetosus* n. sp. is different from the new species by the different shape of sensilli, different placement of interlamellar and lamellar setae, the shorter *ps* setae and adanal setae.

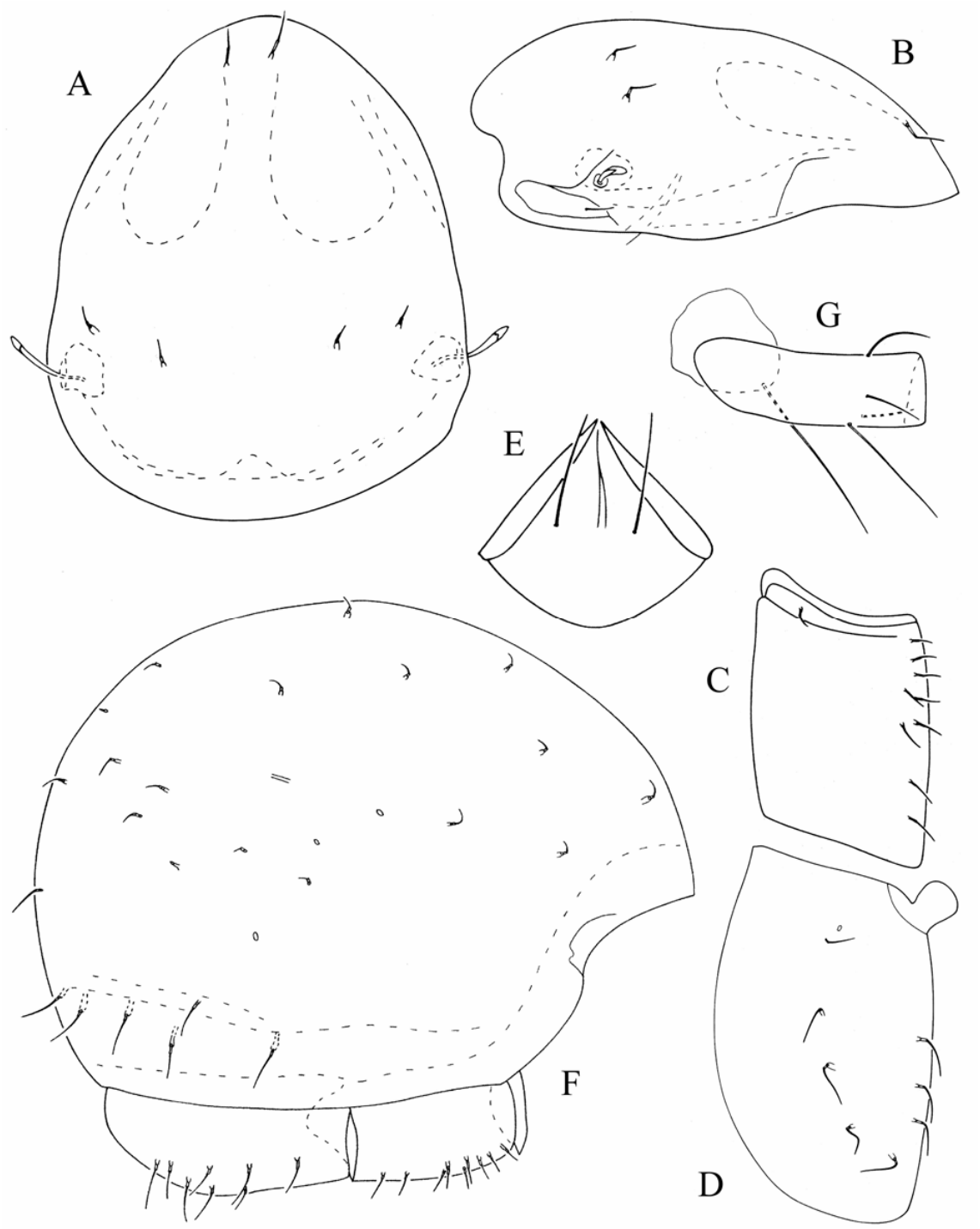

Fig. 4.5. A-G. *Protophthiracarus quasiminisetosus* sp. nov. A – prodorsum, dorsal view, B – prodorsum, lateral view, C – right genitoaggenital plate, D - right anoadanal plate, E –mentum of infracapitulum, F – opisthosoma, lateral view, G – trochanter and femur of leg I.

Notophthiracarus ecphylus sp. nov.
(Fig. 4.6. A-H)

Measurements of holotype
Prodorsum: length 384, width 257, height 146, sensillus 30.4, setae: interlamellar 70.8, lamellar 58.2, rostral 30.4, exobothridial 10.1; notogaster: length 717, width 465, height 505, setae: c_1 58.2, h_1 101, ps_1 86.0; genitoaggenital plate 202 x 121, anoadanal plate 212 x 95.9.
Colour deeply brown. Surface of body covered by sparse concavities.
Prodorsum with humped median carina. Posterior furrows distinct. Median sigillar field pear-shaped, longer than narrow lateral fields. Sensilli short with club-like, smooth head. Rostral setae short, needle-shaped, rough. Interlamellar and lamellar setae short, dilated, covered with small spines similar to notogastral setae. Exobothridial setae minute.
Notogaster with fiveteen pairs of short, dilated setae, covered with small spines. Setae c_1 remote from anterior border, setae c_3 inserted near border, setae c_2 far from border. Two pairs of lyrifissures *ia* and *im* present. Vestigial setae f_1 posteriorly of h_1.
Ventral region. Setae *h* of mentum considerably longer than distance between them. Formula of genital setae: 6: 3 but arrangement of these setae is unusual. Setae $g_{1\text{-}3}$ in progenital position but setae g_1 distanced from setae $g_{1,2}$, setae $g_{4,5}$ inserted near each other but setae $g_{6\text{-}9}$ in normal position of plates. Anal setae rigid, long, rough, adanal setae minuscule.
Chaetome of legs of "complete type", setae *d* of femora I small but robust, strongly remote from distal end of article.
Holotype and 4 paratypes. Southern Ecuadorian Andes, Cordillera El Consuelo, Zamorra-Chinchipe province, Biological Reserve "Estación Cientifica San Francisco" (03°59´S, 79°04´W), at 1850 m altitude, bark, organic litter and the upper soil layer, especially from *Graffenrieda emarginata* litter, February 2004, leg. J. Illig; February 2004; March 2005 – 1 specimen.

Etymology
The specific name *ekphylus* is latinized Greek for "strange, alien" and alludes to the unusual arrangement of genital setae.

Comparison
This species is easy distinguishable by the unusual arrangement of genital setae and also by the curious shape of body setae.

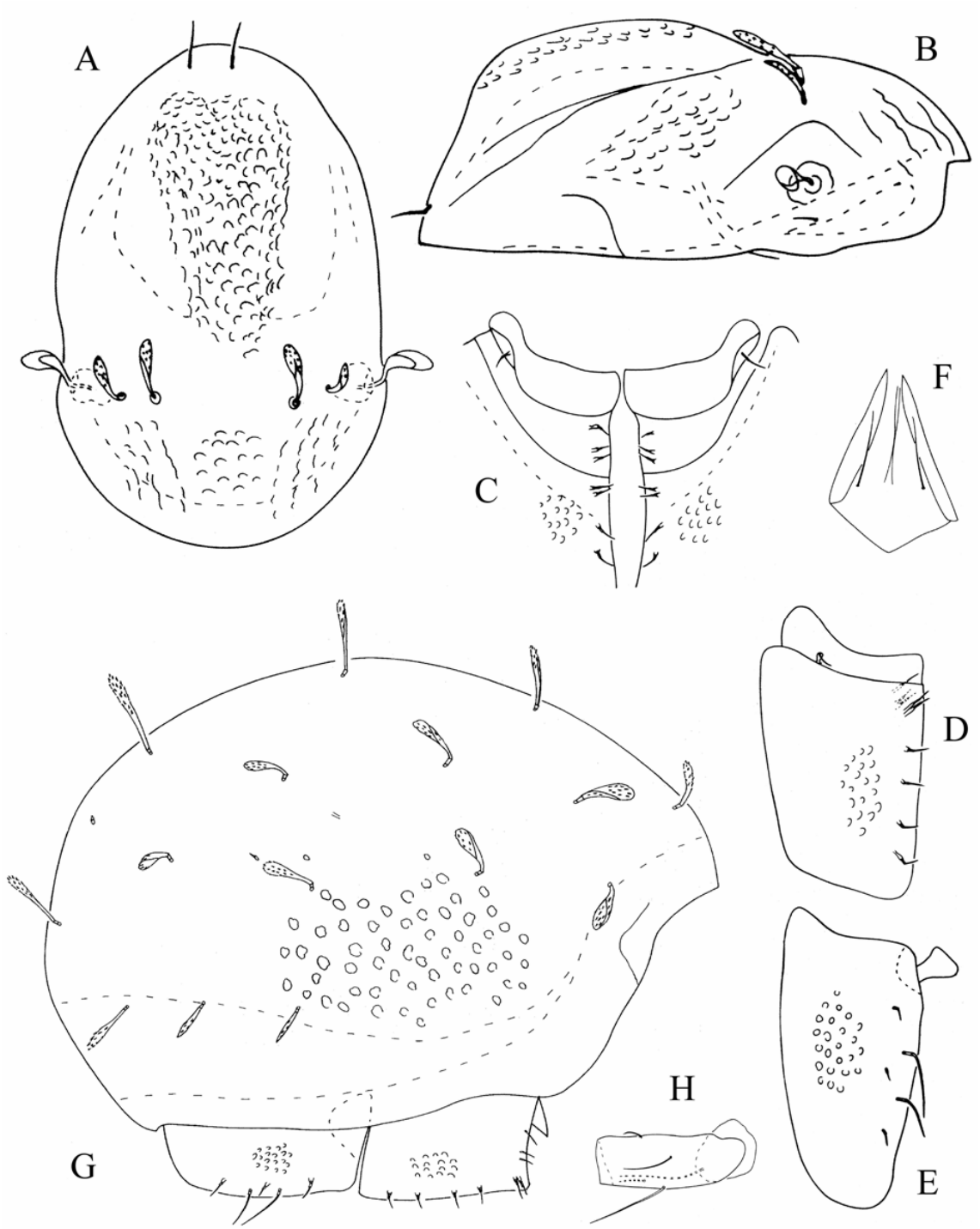

Fig. 4.6. A-H. *Notophthiracarus ecphylus* sp. nov. A – prodorsum, dorsal view, B – prodporsum, lateral view, C – anterior part of genitoaggenital plates, D – right genitoaggenital plate, E – right anoadanal plate, F – mentum of infracapitulum, G – opisthosoma, lateral view, H – trochanter and femur of leg I.

Euphthiracarus bombuscaroensis sp. nov.
(Fig. 4.7. A-C)

Material examined
Holotype and two paratypes: Ecuador, Podocarpus Nationalpark, Bombuscaro, 4° 06.87' S, 78° 08.31' W, 1040 m, soil litter fermentation horizon, November 2005, leg. J. Illig.

Measurements of holotype
Prodorsum: length 215, width 147, height 96.1, sensillus 91.1, setae: interlamellar 96.1, lamellar 75.9, rostral 88.5, exobothridial 15.2; notogaster: length 374, width 257, height 252, setae: c_1 81.0, h_1 75.9, ps_1 50.6, c_3 27.8, ps_3 32.9; genitoaggenital plate 119 x 50.6, anoadanal plate 182 x 37.9.

Description
Colour yellow. Integument densely dotted.
Prodorsum with a pair of long lateral carinae. Sensilli long, baciliform, curved, covered with seven to nine cilia in distal half. Setae long, flagellate distally (especially rostral setae), interlamellar and lamellar setae erect, covered with small spines, rostral setae bent towards the end of rostrum, rough, exobothridial setae the smallest, *in* > *ro* > *le* > *ex*. Distance between rostral setae shorter than between lamellar and interlamellar setae. Mutual distance between rostral setae slightly longer than between lamellar setae.
Notogaster with rather short setae ($c_1 < c_1$-d_1), covered with small spines in distal half, dorsal setae longer than other setae. Setae c_1 and c_2 remote from anterior border more than c_3 setae. Nine pairs of genital setae present, two pairs in progenital position. Two pairs of aggenital setae present, setae ag_2 longer than ag_1. Three pairs of anal and three pairs of considerably longer adanal setae present. Anal setae an_1 considerably longer than an_2 and an_3 setae. Adanal setae ad_1 and ad_2 also considerably longer than ad_3 setae.
Tarsi of legs monodactylous.

Etymology
The specific name *bombuscaroensis* refers to the locality Podocarpus Nationalpark, Bombuscaro.

Comparison
The new species is distinguishable by the following character states: presence of two pairs of lateral carinae of prodorsum, long and baciliform sensilli, flagellate rostral setae, aggenital setae ag_2 longer than ag_1 setae and setae ad_1, ad_2, an_1 longer than setae an_2, ad_3, an_3.

Protophthiracarus quasiminisetosus sp. nov.
(Figure 4.7. D, E)

Measurements of one specimen from Podocarpus Nationalpark, Cajanuma.
Prodorsum: length 404, height 136; notogaster: length 828, height 535, c_1 53.1, c_1/c_1-d_1 = 0.26, h_1 63.2, ps_1 55.7.

Remark
Morphological characters of prodorsum and genitoaggenital plates are similar to those of the type species. Morphological differences concern the considerably longer notogastral and anal

setae, greater number (24 pairs) of notogastral setae (21 pairs in holotype) and different arrangement of *ps* row setae.

Notophthiracarus aculeatus Niedbała, 1988
(Fig. 7. F-H)
Measurements of one specimen from Podocarpus Nationalpark, Cajanuma
Prodorsum: length 228, height 88.5, sensillus 27.8, interlamellar setae 68.3, lamellar setae 15.2; notogaster: length 409, height 257, c_1 106, c_1/c_1-d_1 = 1.3.

Remark
All morphological characters are similar to those in the type species except for the presence of longer interlamellar and dorsal notogastral setae; also the surface of the notogaster is not covered with concavities but by a kind of mosaic.

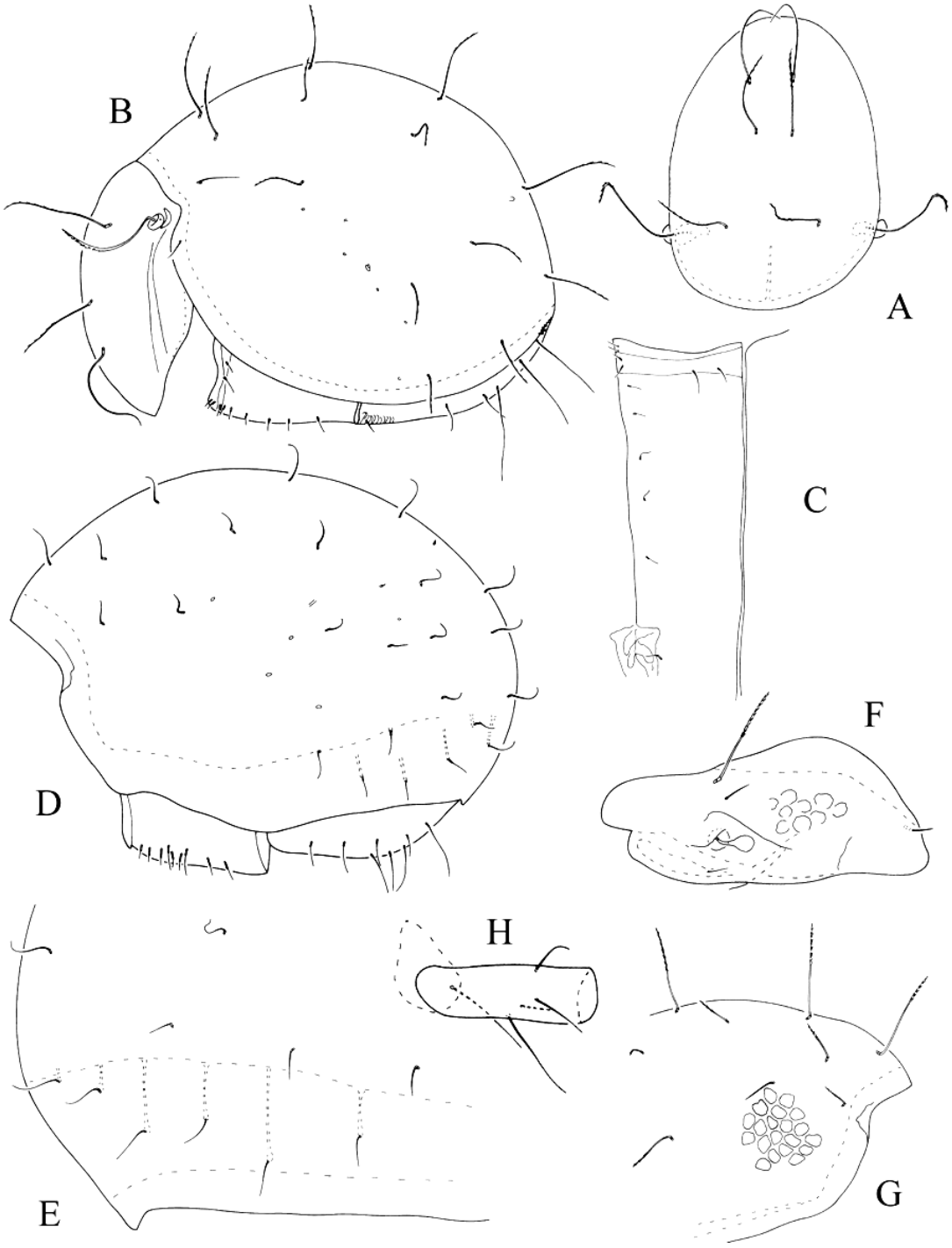

Fig. 4.7. A-C *Euphthiracarus bombuscaroensis* sp. nov., holotype. A – prodorsum, dorsal – view, B – lateral view of body, C – genitoaggenital plate; D, E. *Protophthiracarus quasiminisetosus* Niedbała et Illig, 2006, specimen from Cajanuma. D – opisthosoma, lateral view, E – posterior and lower part of opisthosoma; F-H. *Notophthiracarus aculeatus* Niedbała, 1988, specimen from Cajanuma. F – prodorsum, lateral view, G – anterior part of opisthosoma, H – trochanter and femur of leg I.

Austrophthiracarus cajanumaensis sp. nov.
(Figure 4.8. A-G)

Material examined
Holotype and three paratypes: Ecuador, Podocarpus Nationalpark, Cajanuma, 04°06'711'' S, 79°10'581'' W, soil, litter fermentation horizon, December 2005, leg. J. Illig.

Measurements of holotype
Prodorsum: length 379, width 212, height 116, sensillus 35.4, setae: interlamellar 37.9, lamellar 40.5, rostral 43.0, exobothridial 22.8; notogaster: length 616, width 454, height 429, c_1 227, c_1/c_1-d_1 = 1.61, h_1 222, ps_1 263, ps_4 60.6; genitoaggenital plate 151 x 95.9, anoadanal plate 263 x 111.

Description
Colour brown. Surface of body dotted.
Prodorsum without posterior furrows and lateral carinae, sigillar fields well discernible. Sensilli short, with narrow pedicel and club-like head, smooth. Setae short, spiniform. Notogaster with 21 pairs of rather long setae ($c_1 > c_1$-d_1), flagellate, covered with small cilia at distal half. Setae c_1 and c_3 situated near anterior margin, setae c_2 far from margin. Vestigial setae f_1 posteriorly of h_1 setae. Two pairs of lyrifissures *ia* and *im* present.
Setae *h* of mentum slightly longer than distance between them. Genitoaggenital plates with nine pairs of genital setae with arrangement: 4+4: 1. Anoadanal plates each with seven pairs of flagellate setae, two anal and five adanal setae; anterior adanal setae shorter than others. Legs. Formulae of setae and solenidia of "complete type". Setae *d* of femora I remote from distal end of article.

Etymology
The specific name *cajanumaensis* refers to the locality Podocarpus Nationalpark, Cajanama.

Comparison
The new species is similar to *Austrophthiracrus hirtus* (Balogh, 1984) from Colombia but the latter species has longer prodorsal setae, fewer pairs (18) of notogastral setae and four pairs of adanal setae.

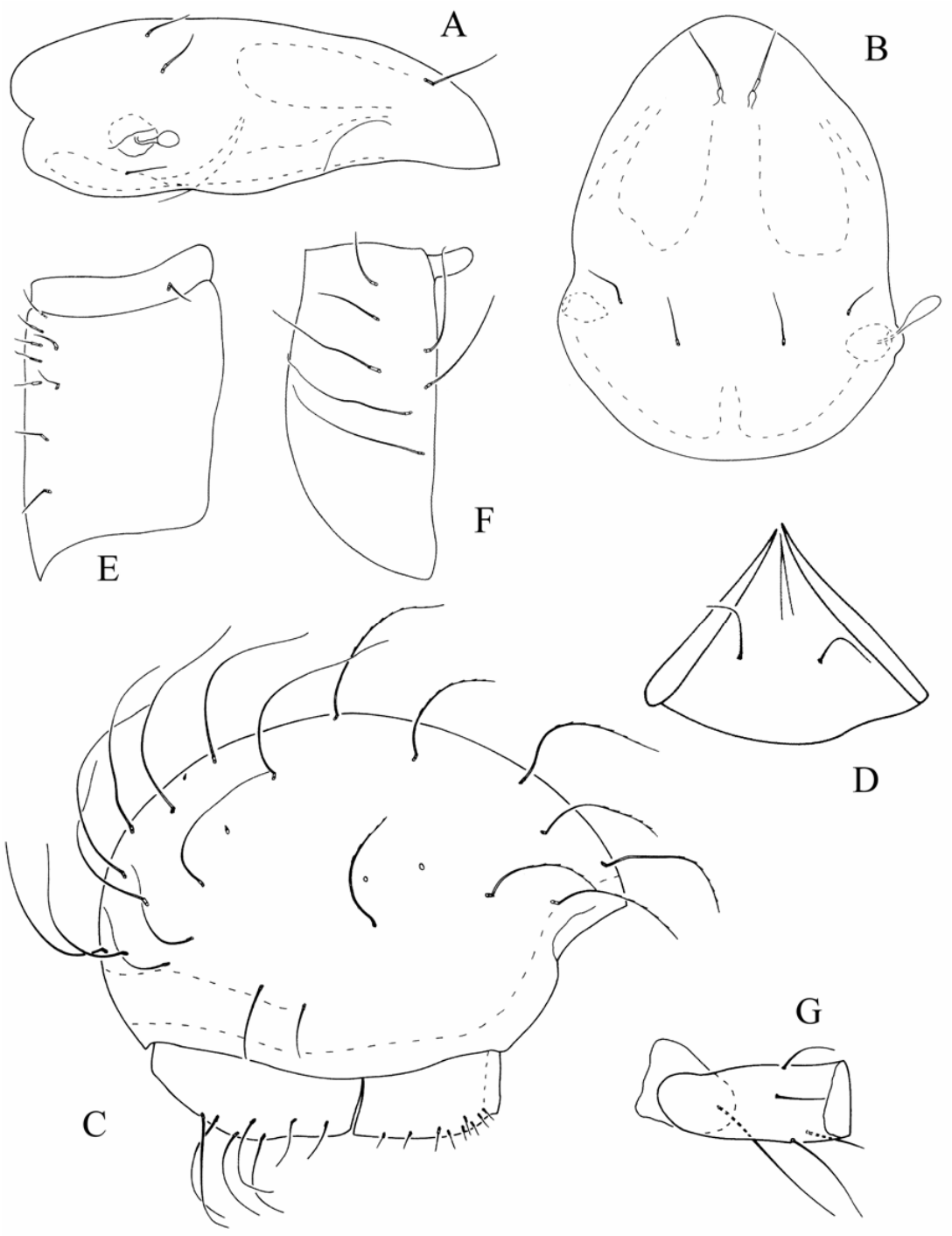

Fig. 4.8. *Austrophthiracarus cajanumaensis* sp. nov., holotype. A – prodorsum, lateral view, B – prodorsum, dorsal view, C – opisthosoma, lateral view, D – mentum of infracapitulum, E – genitoaggenital plate, F – anoadanal plate, G – trochanter and femur of leg I.

4.1.4. Discussion

During a survey conducted in three localities in southern Ecuador: Bombuscaro, RBSF and Cajanuma, 23 species of ptyctimous mites have been found. Ten were new for science and nine new for Ecuador indicating a very high number of not described taxa at the study sites (Chapter 2.). In general most oribatid mite species are restricted to one zoogeographical region (Schatz 2005). Indeed, high numbers of oribatid mite species in the study sites were described from Neotropical regions, only few were cosmopolitan (Chapter 4.3.). However, the majority of oribatid mites is still not determined. Species composition of ptyctimous mites between Bombuscaro and Cajanuma was entirely different, probably because of the difference in altitude. Around 44 ptyctimous mites are described from Germany and adjacent regions. (Weigmann 2006). In comparison Schatz and Niedbala (in prep.) compiled 126 ptyctimous mite species from the Central American landbridge. Schatz (2006) examined different elevational occurrence of ptyctimous mites from the Cordillera de Talamanca in Costa Rica and Panama, but for 80% of all oribatid mite species an altitudinal limit can be observed at the 2800 m contour line, probably caused by lower temperatures at higher altitudes.

Protophthiracarus quasiminisetosus sp. nov. and *Protophthitracarus paraminisetosus* sp. nov. were present in the RBSF and in Cajanuma; *Mesoplophora cubana* reside in the RBSF and in Bombuscaro. Sympatrical occurrence of *Protophthiracarus quasiminisetosus* sp. nov. and *Protophthitracarus paraminisetosus* sp. nov. in the RBSF and in Cajanuma suggest high niche breadth (e.g. higher tolerance to lower temperatures) in these taxa. Knowledge about the geographical distribution of *Mesoplophora cubana* is scarce. Further specimens were only found in Cuba. Norton (1980) observed phoresy by *Mesoplophora* spp. allowing rapid colonization of new resources. However, phoresy in oribatid mites is scarce and occurs occasionally.

The ptychoid habitus of the adults as a defensive adaptation protect ptyctimous mites against predation (Sanders and Norton 2004). Considering only predators, Peschel *et al.* (2006) postulated well-sclerotized oribatid mite groups live in nearly enemy-free space. However, featherwing beetles (Coleoptera: Ptiliidae) also frequent at the study sites are able to predate on ptyctimous mites (Riha 1951). In addition, oribatid mites are preyed upon by amphibians and reptiles (e.g. Norton and MacNamara 1976). Less sclerotizised immatures of ptyctimous mites living harboured within conifer needless indicating successional change on a small scale (Hayes, 1966). Adaptative radiation with evolutionary rather old vascular plants such as gymnosperms suggests that ptyctimous mites are an ancient taxon. Indeed, ptyctimous

mites existed in the jurassic period or earlier (Niedbala 1992). Co-evolution, the mutual adaptation of two or more species by complementary evolution, can influence species abundance and distribution. Since conifers are rare at the study side and in tropical rainforests in general, ptyctimous instars may also develop within angiosperm leaves.

Preferences and feeding habits may change dependent on the state of decomposition of the substrate. Ptyctimous mites do not reproduce via parthenogenesis specifying them as K-strategists (Norton 1994). Also the long life span of ptyctimous mites of up to 3 years (Travé *et al.* 1996) suggests high resistence against environmental changes. However, mainly abiotical factors, like temperature, differing at the three study sites may explain distinct ptyctimous mite communities allowing high γ-diversity in the heterogeneous tropical mountain rainforest.

The specimens of two species known from Ecuador: *Protophthiracarus quasiminisetosus* and *Notophthiracarus aculeatus* have been found to have some morphological characters different from the analogous ones in the type specimens. This may be due to evolutional adaptation concerning differing environmental factors on a local scale.

4.2. Density and community structure of soil and bark living microarthropods along an altitudinal gradient in a tropical mountain rain forest

4.2.1. Abstract

Microarthropod communities in the soil and on the bark of trees were investigated along an elevation gradient (1850, 2020, 2200, 2270 m) in a tropical mountain rain forest in southern Ecuador. We hypothesised that the densities of microarthropods decline with horizon (L>F/H>Ah) and with increasing altitude due to lower amounts of resources and harsher environmental conditions, respectively. In addition, we expected bark and soil communities to differ strongly since the bark of trees is more exposed to abiotic factors. Microarthropod densities (Oribatida, Gamasina, Uropodina and Collembola) were generally low and decreased with altitude. Also, the density of each of the groups decreased with soil depth. Densities of microarthropods on tree bark were lower than in soil. Overall, 43 species of oribatid mites were found. The most abundant oribatid mite taxa were Poronota, Pycnonotic Apheredermata, Mixonomata and Eupheredermata. Most oribatid mite species (81 %) occurred exclusively in soil. The number of oribatid mite species declined with altitude (24, 23, 17 and 13 species at 1850, 2020, 2200 and 2270 m, respectively). Abundances of Pycnonotic Apheredermata and Poronota were highest at 1850 m. The oribatid mite community on bark did not differ significantly from that in soil. Results of this study indicate (1) that microarthropods are limited by resources at high altitudes and at deeper soil layers, and (2) that the bark of trees and the soil are similar habitats for oribatid mites with only few species being 'endemic' on bark. The latter finding is in contrast to temperate forests where oribatid mite communities between bark and soil differ strongly.

4.2.2. Introduction

Until today there is only very limited knowledge about patterns of microarthropod density, diversity and community structure in tropical mountain rain forests. Among soil microarthropods oribatid mites are the dominant group in temperate and tropical forest soils. They contribute to decomposition processes and nutrient cycling by feeding on microorganisms and by dispersal of microbial propagules (Behan and Hill 1978, Maraun *et al.* 1998). Generally, the litter and soil fauna of temperate forests is richer in individuals than that of tropical forests but there are slightly more species in tropical forest soils than in temperate forests (Beck 1971, Plowman 1981, Maraun *et al.* 2007a).

Abiotic conditions such as temperature, precipitation and humidity change profoundly with increasing altitude (Tanner 1977). Hence, density and diversity of below- and above-ground animals change with altitude (Walter 1985, Olson 1994, Brehm *et al.* 2005). Diversity of above-ground arthropods along altitudinal gradients in tropical regions has been investigated (Janzen 1976, Brühl *et al.* 1999, Brehm and Fiedler 2004, 2005). The results suggest that species richness and abundances is at a maximum at intermediate elevations (Janzen 1976, Olson 1994). However, studies on soil microarthropod communities along tropical elevation gradients are rare (Holt 1985).

Studies of forest soils have generally considered the litter and soil together but communities of oribatid mites in soil may differ between soil horizons (Mitchell 1978, Plowman 1981). Generally, microarthropod densities decrease with increasing soil depth due to reduced microhabitat complexity and resource quality (Usher 1970, Pande and Berthet, 1975).

Oribatid mites are also an important component of the arboreal arthropod community (Travé 1963, Behan-Pelletier and Winchester 1998, Proctor *et al.* 2002). The diversity and abundance of arboreal oribatid mite communities is affected by microclimate, bark structure and dispersal patterns of individual species (Prinzing and Woas 2003, Lindo and Winchester 2006). Tropical mountain rain forests are characterized by large numbers of epiphytes, including mosses, ferns, lichens, orchids and ericoids providing microhabitats for microarthropods. Prinzing and Woas (2003) concluded that the stratification of microarthropods in a tropical rain forest resembles a sandwich; with microarthropod

communities in suspended soils being more similar to the fauna in the soil than to the fauna on the tree bark.

There is little information on vertical movement of oribatid mites from the soil to the canopy and vice versa (Mitchell 1978, Norton 1994, Ojala and Huhta 2001). Behan-Pelletier and Winchester (1998) hypothesised that oribatid mites use random movement to colonize canopy habitats from low vegetation. Oribatid mite communities on trees in temperate regions function as a distinct spatial microhabitat (Aoki 1973, Lindo and Winchester 2006, Erdmann *et al.* 2006). Proctor *et al.* (2002) concluded that tree trunks serve as habitats rather than "highways" for oribatid mites. However, Lindo and Winchester (2007) found that tree trunks in temperate rain forests do not function as corridor for ground species to colonize tree crowns. They assumed that corticolous oribatid mite assemblages are likely dispersal-limited residents.

In the present study microarthropod density and oribatid mite communities of organic layers (L, F/H and Ah) and on the bark of adjacent trees along an elevation gradient (1850, 2020, 2200 and 2270 m) in a tropical mountain rain forest in southern Ecuador were investigated. We hypothesised, that microarthropod density declines with altitude due to harsher environmental conditions and with horizon (L>F/H >Ah) due to limitation of resource quantity and quality. Furthermore, we expected that oribatid mite communities from bark and soil differ as a result of different microhabitats.

4.2.3. Materials and Methods

Study side and sampling

This study was conducted at the RBSF (Reserva Biológica San Francisco) forest (3°58′S, 79°5′W) in southern Ecuador on the eastern slopes of the Andes. The mean annual temperature at 1950 m is 16.2 °C (Wilcke *et al.* 2002). The forest has a stem density of 1000 stems ha^{-1} with a medium diameter at breast height (DBH) of ~ 0.1 m and of 6000 stems ha^{-1} with a DBH of ~ 0.05 m. The vegetation of the gentle lower slopes is dominated by Euphorbiaceae, Solanaceae, Cecropiaceae and Lauraceae; the steeper higher slopes by Melastomataceae, Lauraceae, Euphorbiaceae and Rubiaceae. The most abundant tree species at 1800 to 2200 m is *Graffenrieda emarginata* (Melastomataceae). The ground flora is dominated by large ferns, e.g. Dryopteridaceae, and some large herbs (mainly Lobeliaceae).

The thickness of the organic soil layer ranges from 5 to 16 cm (Wilcke *et al.* 2002), and increases with altitude resulting in Histosols (mainly Folic Histosols) above 2100 m, whereas Cambisols (mainly Dystric and Humic Cambisols) dominate below 2100 m (Wilcke *et al.* 2002).

In January 2004 samples were taken at 1850, 2020, 2200 and 2270 m. Three replicate litter and soil samples (Ø 5 cm) were taken from each altitude to a depth of 15 cm and divided in three horizons (L, F/H and Ah). Additionally, next to the soil cores bark material with associated corticolous cover at about 1.5 m height of the tree of randomly chosen living tree trunks were sampled at each altitude to a depth of 2-5 mm with the same method. Samples were transferred to the laboratory and microarthropods were extracted by heat using a modified high gradient extractor (Kempson *et al.* 1963). Microarthropods were quantified and determined to group level (Oribatida, Gamasina, Uropodina, Collembola); adult oribatid mites to species level if possible and classified according to Grandjean (1953, 1965, 1969).

Statistical analysis

The density of the microarthropod taxa (Oribatida, Uropodina, Gamasina, and Collembola) as affected by altitude (1850, 2020, 2200 and 2270 m) and habitat (L, F/H, Ah and bark) was analyzed by analysis of variance (ANOVA). Post-hoc comparisons were carried out by Tukey´s HSD test. STATISTICA 7.1 (Statsoft, Tulsa, USA) and SAS 9.13 (SAS Institute Inc., Cary, USA) software packages were used for statistical analyses. To analyze the response of oribatid mite taxa multidimensional scaling (MDS) and discriminant function analysis (DFA) was performed.

4.2.4. Results

Density of microarthropods

Density of microarthropods declined in the order 1850, 2020, 2270 and 2200 m with 98,070, 47,180, 30,540 and 16,290 ind./m^2, respectively. Density of microarthropod groups (Oribatida, Gamasina, Uropodina, Collembola) differed between 1850, 2020, 2200 and 2270 m, and also between the three horizons and the bark (Table 4.2.1., Fig. 4.2.1.). Oribatid mites were most abundant followed by Collembola, Gamasina and Uropodina. Similar to microarthropods in total the density of oribatid mites in soil generally declined with altitude

from 49,700 ind./m^2 at 1850 m to 19,680 ind./m^2 at 2020 m and to 8,310 and 12,560 ind./m^2 at 2200 and 2280 m, respectively (Fig 4.2.1.a). Respective densities of Collembola were 12,560, 8,140, 1,700 and 3,400 ind./m^2 (Fig 4.2.1.d), those of gamasid mites 11,030, 9,840, 1,020 and 1,020 ind./m^2 (Fig 4.2.1.b) and those of uropodid mites 5,430, 1,190, 680 and 170 ind./m^2 (Fig 4.2.1.c). Generally, the density of each of the microarthropod groups declined with soil depth (Fig. 4.2.1.). Further, compared to the soil the densities of Oribatida, Collembola, Gamasina and Uropodina were lower on tree bark (7,550, 980, 2,550, 340 ind./m^2, respectively) (Fig. 4.2.1; Table 4.2.1.).

Abundances of each of the mesofauna taxa declined strongly from the litter to deeper soil layers at 1850 m; this decline was less pronounced at the other altitudes (significant Altitude x Habitat interaction; Table 4.2.1., Fig. 4.2.1).

Table 4.2.1. MANOVA table of *F*-values on the effect of altitude (1850, 2020, 2200, 2270 m) and habitat (L, F/H, Ah horizons and bark) on microarthropod groups.

Taxa		Oribatida		Gamasina		Uropodina		Collembola	
	df	*F*		*F*		*F*		*F*	
Altitude	3,32	4,43	*	3.35	*	3.80	*	4.79	**
Habitat	3,32	6.90	**	2.72		5.20	**	11.77	***
Altitude x Habitat	9,32	3.74	**	2.41	*	2.98	*	3.73	**

***P<0.001;**P<0.01;*P<0.05

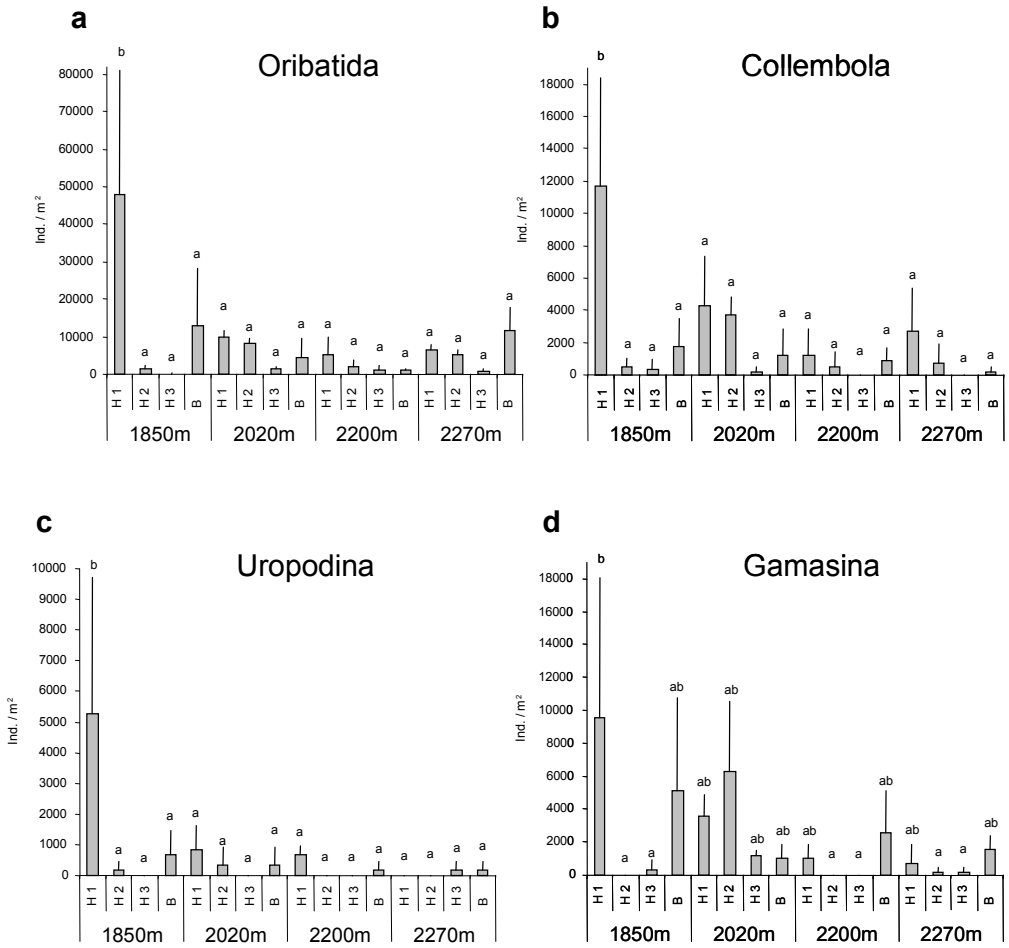

Fig. 4.2.1. Abundances of Oribatida (a), Collembola (b), Uropodina (c) and Gamasina (d) at different horizons (H1: L-horizon, H2: F/H-horizon, H3: Ah-horizon) and on the bark of trees at different altitudes (1850, 2020, 2200, 2270 m); means ± SD. Different letters indicate significant differences between means at $p<0.05$ (Tukey´s HSD test).

Oribatid mite community structure

Overall, 22 families and 43 species of oribatid mites were found; 22.5 % were juveniles and 8.8 % were damaged and/or could not be determined. On average 81 % of total were restricted to the soil. The ratio of juveniles to adults did not differ between bark and soil. The number of oribatid mite species declined with increasing altitude with 24, 23, 17 and 13 at 1850, 2020, 2200 and 2270 m, respectively. The most abundant oribatid mite groups were Poronota (31.4%), followed by Pycnonotic Apheredermata (23.4%), Mixonomata (8.5%), Eupheredermata (3.5%) and Desmonomata (1.1%). Enarthronota, Opsiopheredermata and Dorsodeficient Apheredermata occurred only sporadically. Abundance of Ptyctima

(Mixonomata) in the upper horizon (L) significantly exceeded that in horizon Ah and on the bark of trees; abundances in horizon F/H were intermediate (Table 4.2.2.). Desmonomata (*Nanhermannia elegantissima* and *Malaconthrus* cf *angulatus*) only occurred at 2020 and 2280 m in the upper layer of the soil and at 2280 m on the tree bark. Abundances of Pycnonotic Apheredermata (Carabodidae, Dampfiellidae, Oppiidae, Rhynchoribatidae, Sternoppiidae and Suctobelbidae) and Poronota (Scheloribatidae, Galumnidae, Haplozetidae, Tectocepheidae) were higher in horizon L compared with the other horizons and the bark; this difference was most pronounced at 1850 m.

Table 4.2.2. MANOVA table of *F*-values on the effect of altitude (1850 m, 2020 m, 2200 m and 2270 m) and habitat (L, F/H, Ah and bark) on oribatid mite subgroups (Ptyc Ptyctima, Des Desmonomata, Opsio Opsiopheredermata, Euph Eupheredermata, Pyc Aph Pycnonotic Apheredermata and Poro Poronota)

Subgroups		Ptyc		Des		Opsio	Euph	Pyc Aph		Poro	
	df	*F*		*F*		*F*	*F*	*F*		*F*	
Altitude	3,32	1.19		8.25	***	0.67	0.70	5.00	**	3.77	*
Horizon	3,32	4.55	**	4.25	*	0.67	1.19	9.23	***	6.88	**
Altitude x Horizon	9,32	1.47		2.92	*	1.11	0.66	6.22	***	4.11	**

***P<0.001;**P<0.01;*P<0.05

With 18 species oribatid mite diversity was highest in horizon L at 1850 m. Fourteen species were confined to the soil and six only occurred on bark. Discriminant function analysis (DFA) separated oribatid mite soil communities from different altitudes (Wilks' Lambda = 0.006; $F_{9,14}$ = 11.90; $p < 0.001$; Table 4.2.3., Fig. 4.2.2.) but did not separate soil horizons from each other or from the bark (Wilks' Lambda = 0.45; $F_{26,42}$ = 0.79; p = 0.74).

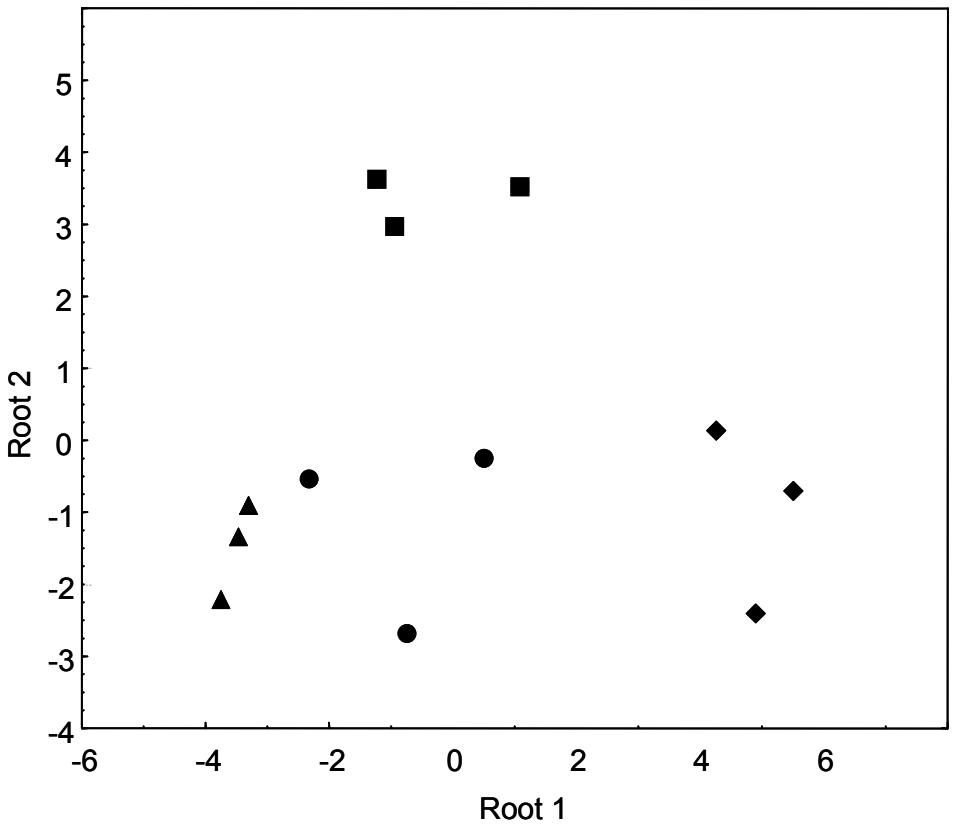

Fig. 4.2.2. Discriminant function analysis (DFA) of soil oribatid mite communities at different altitudes in soil: 1850 m (circle), 2020 m (square), 2200 m (diamond) and 2270 m (triangle).

Table 4.2.3. Squared Mahalanobis distances between group centroids and reliability of the discrimination between different altitudes (1850, 2020, 2200, 2270 m) for the soil community structure of oribatid mite species.

	2020 m	2200 m	2270 m
1850 m	22.71 *	29.33 **	22.81 *
2020 m		28.25 **	18.60 *
2200 m			54.88 **

**P<0.01;*P<0.05

4.2.5. Discussion

Densities of microarthropods

In general, oribatid mites were the most abundant microarthropods in the soil and on the bark of the studied tropical mountain rain forest, confirming the hypothesis that oribatid mites are usually the most abundant microarthropods in forest ecosystems (Petersen and Luxton 1982, Wallwork 1983). Paoletti *et al.* (1991) also found that oribatid mites dominate the microarthropod fauna in tropical Venezuelan rain forests in soil and on trees. The highest density of oribatid mites at the study site (~ 50,000 ind./m² at 1850 m) is comparable to other rain forests (Plowman 1979, Holt 1985, Olson 1994) but also to base rich European forests (Luxton 1981, Maraun and Scheu 2000). Since larger predators of microarthropods at the RBSF forest are rare, we assume that soil microarthropods are not top-down controlled. Microarthropod densities in temperate regions are usually lower in the presence of endogeic earthworms, probably through mechanical disturbances and resource competition (Eisenhauer *et al.* 2007). However, the density of macrodecomposers (e.g. earthworms, millipedes and termites) at the study site is low. Rather, the low density of microarthropods at the study site is more likely to be controlled by bottom-up forces, i.e. the quality and quantity of resources. Indeed, the quantity and quality of plant litter is known to strongly affect the populations of soil biota (Coleman and Crossley 1996, Salamon *et al.* 2006).

Altitude

Generally, the density of microarthropods at our study site declined in the order 1850, 2020, 2270 and 2200 m. At the wider altitudinal gradient at our study site oribatid mite densities also declined from 1000 to 3100 m (Chapter 3.1.3.). Similarly, in our litterbag field experiment densities of microarthropods were at a maximum at lower altitude (1850 m; Chapter 5.2.). Further, declining numbers of litter invertebrates along a Neotropical altitudinal gradient were also found in other studies (Olson 1994, Richardson *et al.* 2005). Factors detrimentally affecting the density of microarthropods at higher altitudes include (1) high soil acidity, (2) harsh abiotic conditions (low temperatures, high precipitation, waterlogging) and (3) low quantity and quality of resources. At the study site soil pH indeed decreases from 4.4 to 3.9 at 1870 and 2250 m, respectively (M. Oesker, pers. comm.). However, since oribatid mite densities generally increase with soil acidity (Maraun and Scheu 2000) – reaching

maximum densities in acidic boreal forests of 400,000 ind./m^2 – microarthropod densities at the study site very likely are not affected by soil acidity. Low temperatures also are unlikely to be responsible for low density of microarthropods at higher altitudes since temperatures in boreal forests, where densities of microarthropods are high, are lower. Similarly, high humidity also is unlikely to be responsible for low density of microarthropods at higher altitudes since the water content of boreal forest soils also is high. At high altitudes of our study site organic material is accumulating (Wilcke *et al.* 2002) indicating that the amount of resources does not limit soil microarthropods. Therefore, the most important factor for the low densities of soil microarthropods at high altitudes probably is the quality of the available resources. Indeed, the C-to-N ratio of the organic material is at a maximum at higher altitudes indicating low resource quality. The low resource quality also results in low decomposition rates at high altitudes (Leuschner *et al.*, 2007; see also Chapter 3.2.).

Oribatid mite density at the same study site at 2000 m sampled in march 2005 (Chapter 3.1.3.) with 20,000 ind./m^2 were similar to this study at 2020 m indicating low temporal variability of oribatid mite abundances in this ecosystem.

Soil depth

Densities of Oribatida, Collembola, Gamasina and Uropodina declined with soil depth which is typically the case in forest and also arable soils (Adis *et al.* 1987, Hijii 1987, Migge *et al.* 1998). In a rain forest in Queensland 92 % of all arthropods sampled to a soil depth of 16 cm were located in the upper 8 cm (Holt 1985). Fragmentation and mineralisation processes during decomposition of litter material result in homogenisation of soil organic matter with soil depth. Hence, low numbers of soil microarthropods in deeper soil horizons may be due to reduced habitat complexity. Further, lower densities of microarthropods in deeper soil layers presumably are due to reduced availability of resources caused by longer exposure of litter materials to microbial attack. Indeed, microbial biomass at the study site decreases with soil depth indicating reduced availability of resources (J. Illig; unpubl. data).

Despite the density of microarthropods generally decreases with soil depth, there are taxa which follow a contrasting pattern. For example, Enarthronota preferentially colonize deeper soil layers and may reach high densities (Maraun and Scheu 2000). However, their density at the study site was low and this may contribute to the low density of microarthropods in deeper horizons.

Bark of trees

Generally, the number of soil microarthropods on bark was lower than in soil. Karasawa and Hijii (2007) and Proctor *et al.* (2002) also found lower densities of oribatid mites on the bark of trees than in forest litter in subtropical forests. Low microarthropod abundances on the bark may be due to harsh microclimatic conditions, including variations in temperature, stronger wind, more frequent wet/dry cycles, reduced habitat complexity (Delamare-Debouteville 1951, Vareschi 1980, Prinzing and Woas 2003), low quantity of resources, or defence mechanisms of resources on the bark (e.g. secondary compounds of lichens). Presumably, a combination of these factors is responsible for the low microarthropod densities of oribatid mites on the bark of trees.

Oribatid mite densities on bark at 1850 and 2270 m were higher than at intermediate altitudes, whereas densities of collembolans on bark were lowest at 2270 m. Since oribatid mites and collembolans compete for resources (Anderson 1975a, Seastedt 1984) oribatid mites may be more efficient than collembolans in exploiting resources at 2270 m. However, the differential response of oribatids and collembolans may also be due to changing environmental conditions. Surprisingly, gamasid mites were more abundant on bark than their putative prey (oribatid mites and collembolans). Gamasid mites preferentially feed on collembolans (Koehler 1999) but may also attack oribatid mites (Peschel *et al.* 2006). However, strongly sclerotised adult oribatid mites presumably live in enemy free space (Norton 1994, Peschel *et al.* 2006). Therefore, gamasid mites on the bark of trees presumably preferentially feed on less protected animals, such as collembolans and nematodes, whereas oribatid mites more likely are controlled by the availability of resources, i.e. by bottom-up forces.

Oribatid mite community structure

Derived groups of oribatid mites, such as Poronota and Pycnonotic Apheredermata, dominated the oribatid mite community indicating that they are either strong competitors or well adapted to abiotic conditions in tropical mountain rain forests (or both). Interestingly, species of these taxa are often predators, scavengers or fungal feeders and reproduce sexually. If these characters indeed contribute to their success in tropical forests needs further investigations.

The number of oribatid mite species declined with altitude with 24, 23, 17 and 13 at 1850, 2020, 2200 and 2270 m, respectively. Walter (1985) also found declining oribatid mite diversity with elevation in a forest in Oregon. A review of Rahbek (1995) supported the view that species richness usually declines with elevation. Presumably, low resource quality at higher altitudes not only is responsible for low density of microarthropods but also for the low number of oribatid mite species (see Chapter 5.2.).

At our study sites the oribatid mite community on bark did not differ significantly from that in soil which is in contrast to temperate forests. The similar community structure of oribatid mites in soil and on the bark of trees at our study sites likely is due to less pronounced microhabitat differences between soil and bark in tropical as compared to temperate forests (Aoki 1973, Proctor *et al.* 2002, Lindo and Winchester 2006, Erdmann *et al.* 2006). Beaulieu *et al.* (2006) also found microhabitat structure to vary little on the bark of trees in subtropical rain forests. Erdmann *et al.* (2007) suggested that most oribatid mites on bark are generalists and occupy similar trophic niches as soil living oribatid mites. However, Lindo and Winchester (2007) found species richness, community structure and abundance of oribatid mites on the bark of trees at about 4 and 6 m above the ground to differ significantly from that in soil. These contrasting results may be due to the fact that we sampled at lower tree height but also by the fact that very different forests have been studied (tropical forest in this study and temperate forest in the study of Lindo and Winchester (2007).

Species list of oribatid mites at three altitudes (1850 m, 2020 m, 2200 m and 2270 m) and substrate (H1: L horizon, H2: F/H horizon and H3: Ah horizon) and on bark (B).

Altitude	1850 m														2020 m												2200 m												2270 m											
Substrate	H1			H2			H3			B			H1			H2			H3			B			H1			H2			H3			B			H1			H2			H3			B		
Replicate	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Acaroceras sp. nov.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Amerioppia sp.	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Beckiella recta	-	-	27	-	-	-	-	-	-	-	-	-	1	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Brachyoppiella cf *periculosa*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Carabodes granulatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cultroribula zicsii	1	-	3	-	-	-	-	-	-	-	-	1	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dolicherimaeus cf *bolivianus*	-	-	3	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dyobelba sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Epidamaeus sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Eremulus cf *berlesei*	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Euphthiracaridae sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Eutegaeus sp. nov.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Galumnidae sp. 1	-	-	11	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-
Galumnidae sp. 2	15	7	5	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hermanobates sp.	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Malaconthrus cf *angulatus*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	-	-	-	-	-	-	-
Nanhermannia elegantissima	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-
Neoamerioppia sturmi	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Notophthiracarus ecphylus	1	16	5	1	-	-	-	-	-	-	-	-	1	2	3	4	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	6	4	-	1	-	-	1	-	-
Notophthiracarus sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	1
Oppiella nova	-	-	-	-	-	-	-	-	-	-	-	-	3	4	-	-	-	1	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Oppia sp.1	12	19	13	2	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Oppiidae sp.2	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	1	1	5	5	1	3	-	-	1	1	-
Pergalumna silvatica	-	-	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pergalumna sura	5	1	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Plateremaeus berlesei	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Protophthiracarus paraminisetosus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rhynchoribates cf *ecuadoriensis*	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rostrozetes ovulum	-	-	2	-	-	1	-	-	1	-	1	1	2	2	6	2	3	3	1	-	1	1	-	-	-	2	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-
Rostrozetes sp.	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rugozetes cf sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Scheloribates cf *elegans*	17	-	8	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Scheloribates cf *praeincisus*	-	1	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hemileius cf *microclava*	-	-	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9	1	2
Scheloribatidae sp.	-	-	8	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	3	1	-	2	1	-	-	1	-	-	-
Sellnickochthonius tropicus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sternoppia incisa	-	-	-	-	-	-	-	-	-	-	-	-	-	4	1	1	-	1	-	-	-	-	-	-	-	1	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Fenestrobelba cf *subcomplexa*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Suctobelbella sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Suctoribates cf sp. nov.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tectocepheus sp.	-	-	-	-	-	-	-	-	-	-	-	4	1	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11	-	-	-	-	-	1	1	-
Tectoppia *cf* nigricans	3	2	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Xenillus sp. nov.	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

4.3. Checklist of the Oribatid mites From the Reserva San Francisco

4.3.1. Introduction

Oribatid mites (Oribatida, Acari) are mainly soil dwelling microarthropods. They are a very old taxon; the first fossils of oribatid mites have been found in Devonian sediments (380 mya; Shear *et al.* 1984, Norton *et al.* 1988). Data on species diversity are recognized as fundamental for the understanding of natural and disturbed ecosystems, yet these data are meagre for Acari in the Neotropics, and limited by poor taxonomy (Behan-Pelletier *et al.* 1993). Oribatida are the dominant microarthropod group in tropical soils.

Approximately 9 900 currently valid, described species are systematically recorded (Subias 2004), but up to 100 000 in fact may exist (Schatz 2002). In total about 1850 known species are known from the Neotropical region (Schatz 2005).

Species diversity can be measured as local (α-) and regional (γ-) diversity (MacArthur 1965, Whittaker 1972). The difference in species from one habitat to the next, β-diversity, characterises species turnover. In forest soils α-diversity of oribatid mites is high (average of 50 – 70 species per site; Luxton 1975, Persson *et al.* 1980) is high. The high α-diversity of decomposer animals in soil is one of the great enigmas of soil biology since their habitat seems to be rather uniform (Anderson 1975b, Maraun *et al.* 2003a, 2007a).

In tropical mountain rainforests the density of soil macrofauna such as earthworms, diplopods and isopods is low (Maraun *et al.* 2007b). Therefore, soil microarthropods likely function as main drivers of decomposition processes. They affect decomposition processes largely by comminution, channeling and mixing of litter and soil. Oribatid mites are the most abundant and highly diverse soil microarthropods in tropical forests (Plowman 1979, Heneghan *et al.* 1999, Franklin *et al.* 2004). However, compared to densities in temperate forest soils (Maraun and Scheu 2000) the density of oribatid mites at the mountain rain forest of the Reserva San Francisco is rather low at about 1850 m (ca. 49 700 ind./m²) and even decreased with increasing altitude (ca. 12 560 ind/m² at 2270 m; Chapter 4.2.1.).

In comparison with other neotropical countries, taxonomical studies on oribatid mites in Ecuador are scarce. Prior to this study, only 54 oribatid mite species were recorded from Ecuador (except Galapagos, see Schatz 1998), most of them described by Balogh (1988, 1989) and Niedbala (2004). On the other hand, 245 species are recorded from Peru (Schatz unpubl.) and almost 500 from Brazil (Oliveira 2004). In a faunistic investigation of the

highlands of the Central American Cordillera de Talamanca (Costa Rica, Panamá) above 1900 m asl 165 oribatid were encountered (Schatz 2006).

At our study sites in the mountain rain forests of Ecuador 48 Families and 193 species or morphospecies of oribatid mites were recorded; some of them new to science (Niedbala and Illig 2007a,b). Poronotic oribatid mites are the most abundant subgroup followed by Gymnonota, Enarthronota and Desmonomata.

4.3.2. Methods for Sampling and Classification

Soil and bark materials were transported to the laboratory, where oribatid mites were extracted using a modified high-gradient extractor (Kempson *et al.* 1963), then transferred to 70% ethanol and identified to species level. Voucher specimens are deposited at the University of Darmstadt, Department of Zoology and in Department of Animal Taxonomy and Ecology, Poznań. Classification of taxa followed Subías (2004).

Taxonomic References

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4.3.3. New described species

Euphthiracaridae:
Acrotritia parabrasiliana Niedbala & Illig, 2007a
Acrotritia rhopalota Niedbala & Illig, 2007a
Euphthiracarus bombuscaroensis Niedbala & Illig, 2007b
Oribotritia paraajaluela Niedbala & Illig, 2007a

Phthiracaridae:
Austrophthiracarus cajanumaensis Niedbala & Illig, 2007b
Austrophthiracarus elconsulei Niedbala & Illig, 2007a
Notophthiracarus ecphylus Niedbala & Illig, 2007a
Protophthiracarus paraminisetosus Niedbala & Illig, 2007a
Protophthiracarus quasiminisetosus Niedbala & Illig, 2007a

4.3.4. Checklist of the Oribatid mites

Name	Locality	Frequency	Chorotype	Degree of Novelty
Brachychthoniidae				
Brachychthonius cf sp.	A			
Brachychthonius sp.	C			
Brachychthonius cf sp.	C			
Liochthonius mollis Hammer, 1958	A		Am-S	
Liochthonius cf *rigidisetosus* Hammer, 1962	A		Am-S	
Liochthonius sp.	C			
Sellnickochthonius cf *elsosneadensis* (Hammer, 1958)	A		Subcos	
Sellnickochthonius cf *muara* Mahunka, 1995	A		Pantrop	
Sellnickochthonius tropicus (Hammer, 1958)	A		Am-S	
Hypochthoniidae				
Eohypochthonius gracilis (Jacot, 1936)	C	++	Pantrop, Subcos	
Malacoangelia remigera Berlese, 1913	C		Pantrop	
Epilohmanniidae				
Epilohmannia cf *maurii* Fernandez, 1978	C		Am-S	

Mesoplophoridae				
Mesoplophora cubana Calugar & Vasiliu, 1977	A,C	++	Am-C	nE
Mesoplophora hauseri Mahunka, 1982	C		Neotrop	nE
Euphthiracaridae				
Acrotritia clavata (Märkel, 1964)	A		Neotrop	nE
Acrotritia dikra (Niedbala & Schatz, 1996)	A		Neotrop	nE
Acrotritia monodactyla (Niedbala, 2002)	A		Neotrop	nE
Acrotritia parabrasiliana Niedbala & Illig, 2007a	A		Am-S	nS
Acrotritia peruensis (Hammer, 1961)	A	++	Pantrop	nE
Acrotritia rhopalota Niedbala & Illig, 2007a	A		Am-S	nS
Euphthiracarus bombuscaroensis Niedbala & Illig, 2007b	C		Am-S	nS
Euphthiracaridae sp.	B			
Mesotritia curviseta (Hammer, 1961)	A		Neotrop	nE
Microtritia tropica Märkel, 1964	C		Pantrop	
Oribotritia paraajaluela Niedbala & Illig, 2007a	A		Am-S	nS
Rhysotritia sp. 1	A		Neotrop	
Phthiracaridae				
Austrophthiracarus cajanumaensis Niedbala & Illig, 2007b	D			nS
Austrohthiracarus dilucidus (Niedbala, 1988)	A		Am-S	
Austrophthiracarus elconsulei Niedbala & Illig, 2007a	A,D	++	Am-S	nS
Hoplophthiracarus sp.	A		Am-S	
Hoplophorella cucullata (Ewing, 1909)	C		Subcos	nE
Hoplophorella vitrina (Berlese, 1913)	C		Subcos	
Notophthiracarus aculeatus Niedbala, 1988	D		Neotrop	
Notophthiracarus ecphylus Niedbala & Illig, 2007a	A	++	Am-S	nS
Notophthiracarus sp.	B		Am-S	
Notophthiracarus pedanos Niedbala, 2003	D		Am-C	nE
Phthiracarus anonymus Grandjean, 1933	A		Subcos	nE
Phthiracarus diazae (Ojeda, 1985)	A,D		Am-S	
Phthiracarus pygmaeus Balogh, 1958	A		Pantrop	
Phthiracaridae sp. 1	A			
Phthiracaridae sp. 2	A			

Protophthiracarus paraminisetosus Niedbala & Illig, 2007a	A,D	++	Am-S	nS
Protophthiracarus quasiminisetosus Niedbala & Illig, 2007a	A,D	++	Am-S	nS
Trypochthoniidae				
Allonothrus neotropicus Balogh & Mahunka 1969	D		Neotrop	
Malaconothridae				
Fossonothrus sp. n.	A		Am-S	nS
Malaconothrus cf *angulatus* Hammer, 1958	A		Am-S	
Malaconothrus sp.	C			
Nothridae				
Nothrus sp. n.	A			nS
Camisiidae				
Heminothrus biangulatus (Hammer, 1962)	D			
Heminothrus castanaeus (Hammer, 1961)	A		Am-S	
Platynothrus sp.	A			
Crotoniidae				
Crotonia sp. n.	A		Am-S	nS
Crotoniidae sp. n.	B		Am-S	nS
Nanhermanniidae				
Nanhermannia elegantissima Hammer, 1958	A,B	++	Neotrop	
Nanhermannia nana (Nicolet, 1855)	A,D	++	Cosmopolit	
Hermanniellidae				
Hermannobates monstruosus Hammer, 1961	A		Neotrop	
Hermannobates cf sp.	A			
Hermannobates sp. 1	A			
Hermannobates sp. 2	A			
Neoliodidae				
Neoliodes sp.	B			
Neoliodidae sp. 1	B			
Neoliodidae sp. 2	B			
Neoliodidae sp. 3	A			
Platyliodes sp.	A			

Plasmobatidae				
Solenozetes flagellatus Balogh & Mahunka, 1969	A		Am-S	
Solenozetes cf sp.	A			
Plateremaeidae				
Pheroliodes cf *intermedius* (Hammer, 1961)	A		Am-S	
Pheroliodes sp. 1	B			
Pheroliodes sp. 2	B			
Pheroliodes sp. 3	A			
Plateremaeus berlesei Balogh & Mahunka, 1978	B		Neotrop	
Damaeidae				
Dyobelba sp.	A			
Epidamaeus cf *flagelloides* Norton, 1979	A		Am-S	
Epidamaeus sp.	A			
Epidamaeus cf sp.	A			
Cepheidae				
Eupterotegaeus sp.	D			
Eutegaeidae				
Eutegaeus sp. n.	A		Am-S	nS
Nodocepheidae				
Nodocepheus dentatus Hammer, 1958	D		Am-S	
Microtegeidae				
Microtegeus similis Balogh & Mahunka, 1980	A,C		Am-C	
Microzetidae				
Acaroceras sp. n.	A		Am-S	nS
Acaroceras sp.	B			
Berlesezetes peruensis (Hammer, 1961)	C		Am-S	
Cosmozetes vermiculatus (Balogh & Mahunka, 1980)	A		Am-C	
Licnozetes granulatus (Balogh & Mahunka, 1969)	C		Neotrop	
Plumozetes sp. n.	A		Am-S	nS
Rugozetes cf sp.	A			
Microzetidae sp.	A			
Astegistidae				
Cultroribula argentiniensis Balogh & Csiszar, 1963	A		Am-S	
Cultroribula zicsii Balogh et Mahunka, 1981	A	++	Am-S	

Liacaridae				
Xenillus brasilianus Balogh & Mahunka, 1969	A		Am-S	
Xenillus sp. n.	A,B		Am-S	nS
Eremulidae				
Eremulus cf *berlesei* Mahunka, 1977	A	++	Pantrop	
Eremulus rigidisetus Balogh & Mahunka, 1969	C		Neotrop	
Eremulus sp. 1	A			
Eremulus sp. 2	A			
Eremulus cf sp. 3	A			
Damaeolidae				
Fosseremus laciniatus Berlese, 1905	A		Cosmopolit	
Eremobelbidae				
Eremobelba sp. n.	C		Am-S	nS
Arceremaeidae				
Arceremaeus cf *incaensis* Hammer, 1961	A		Am-S	
Oppiidae				
Amerioppia sp.	B			
Austroppia petrohuensis Hammer, 1962	A		Am-S	
Brachioppia cf sp.	A			
Brachioppia sp.	C			
Brachioppiella cf *periculosa* Hammer, 1962	D	++	Am-S	
Brachioppiella sp. n.	D		Am-S	nS
Mahunkella cf *transitoria* (Balogh & Mahunka, 1978)	C		Am-S	
Neoamerioppia sturmi (Balogh, 1984)	A		Am-S	
Oppia cf *concolor*.Koch, 1839	A		Subcos	
Oppia sp. 1	A			nS
Oppia sp. 2	A			
Oppiella nova (Oudemanns, 1902)	A		Cosmopolit	
Oppiidae sp.	A			
Oxyoppia cf sp.	A			
Oxyoppia cf *pilosa* Balogh & Mahunka, 1981	A		Am-S	
Oxyoppia sp.	A			
Ramusella sp.	C		-	
Tectoppia cf *nigricans* Wallwork, 1961	A	++	Pantrop	

Teratoppiidae				
Teratoppia pluripectinata Balogh & Mahunka, 1978	C	++	Am-S	
Sternoppiidae				
Sternoppia incisa Balogh & Mahunka, 1977	A	++	Neotrop	
Sternoppia cf *quadriseta* (Balogh & Mahunka, 1969)	A		Am-S	
Sternoppia sp. 1	A			
Sternoppia sp. 2	A			
Sternoppia striata Mahunka, 1983	A	++	Am-C	
Synoppia cf sp.	A			
Suctobelbidae				
Fenestrobelba cf *subcomplexa* (Balogh & Mahunka, 1968)	A	++	Pantrop	
Neosuctobelba transitoria Balogh & Mahunka, 1969	C		Am-S	
Suctobelba sp.	C			
Suctobelbella cf *macrodentata*	A		Am-S	
Suctobelbella peracuta (Balogh & Mahunka, 1980)	A		Am-C	
Suctobelbella cf *penicillata* (Balogh & Mahunka, 1980)	A			
Suctobelbella cf *pseudornata* (Woas, 1986)	A		Am-C	
Suctobelbella sp. n.	A		Am-S	nS
Suctobelbella sp.	A			
Suctobelbila squamosa (Hammer, 1961)	A	++	Pantrop	
Rhynchoribatidae				
Rhynchoribates cf *ecuadoriensis* Balogh, 1988	A		Am-S	
Rhynchoribates sp. 1	A			
Rhynchoribates sp. 2	A			
Rhynchoribates sp. 3	A			
Suctoribates cf sp.	A			
Dampfiellidae				
Beckiella recta Balogh & Mahunka, 1978	A,D	++	Am-C	
Beckiella sp.	D			
Dolicherimaeus cf *bolivianus* Balogh & Mahunka, 1969	A		Am-S	
Carabodidae				
Carabodes ecuadoriensis Balogh, 1989	A		Am-S	
Carabodes granulatus Banks, 1896	B			

Carabodes sp.	A		
Tectocepheidae			
Tectocepheus sp.	D		
Tectocepheus velatus sarekensis Trägardh, 1910	A		Cosmopolit
Cymbaeremaeidae			
Scapheremaeus cf sp.	A		
Phenopelopidae			
Eupelops cf *apicalis* (Hammer, 1962)	D		Am-S
Oribatellidae			
Oribatella cf sp.	A		
Epactozetidae			
Truncozetes sturmi Balogh, 1984	A	++	Neotrop
Ceratozetidae			
Zetomimus polpaicoensis (Hammer, 1962)	A		Am-S
Mochlozetidae			
Unguizetes incertus (Balogh & Mahunka, 1969)	A	++	Am-S
Oribatulidae			
Oribatula cf sp.	A		
Libstadiidae			
Totobates discifer (Hammer, 1961)	A		Neotrop
Scheloribatidae			
Hemileius cf *initialis* (Berlese, 1908)	A		Subcos
Hemileius cf *microclava* (Hammer, 1961)	B		Am-S
Ischeloribates cf sp.	A		
Perscheloribates cf *fissuratus* (Hammer, 1961)	A		Am-S
Scheloribates elegans Hammer, 1958	A	++	Pantrop
Scheloribates praeincisus (Berlese, 1910)	A	++	Subcos
Scheloribates cf *artigasi* Perez-Inigo & Baggio, 1980	C		Am-S
Scheloribates cf *laticlava* Hammer, 1961	A		Pantrop
Scheloribates cf *polygonatus* Balogh & Mahunka, 1974	A		Am-C
Scheloribates sp. 1	A		
Scheloribates sp. 2	B		
Scheloribatidae cf sp.	A		

Oripodidae				
Benoibates cf *chacoensis* Mahunka, 1984	A		Am-S	
Benoibates cf *minimus* Mahunka, 1985	A		Am-C	
Oripoda cf *australis* Berlese, 1916	B		Am-S	
Oripoda sp. n.	A		Am-S	nS
Haplozetidae				
Haplozetes cf *nudus* (Hammer, 1958)	A		Am-S	
Haplozetes sp.	C			
*Peloribates antillensis (*Mahunka, 1985)	C		Am-C	
Peloribates sp. n.	A		Am-S	nS
Protoribates cf *capucinus* Berlese, 1908	C	++	Cosmopolit	
Rostrozetes cf *foveolatus nebulosus* (Beck, 1965)	D		Am-S	
Rostrozetes ovulum Berlese, 1908	A	++	Cosmopolit	
Galumnidae				
Galumna sp.	B			
Galumnidae sp. 1	A			
Galumnidae sp. 2	A			
Galumnidae sp. 3	A			
Galumnidae sp. 4	A			
Galumnidae sp. 5	A			
Galumnidae sp. 6	A			
Galumnopsis cf sp.	A			
Galumnopsis sp.	A			nS
Pergalumna cf *nasica* Perez-Inigo & Baggio, 1986	A		Am-S	
Pergalumna parva Perez-Inigo & Baggio, 1981	A		Am-S	
Pergalumna silvatica Hammer, 1961	A	++	Am-S	
Pergalumna sura Balogh, 1987	A	++	Am-C	
Pergalumna sp. 1	A			
Pergalumna sp. 2	B			

Abbreviations

A: Area of the Reserva San Francisco 1850 m – 2280 m (litter/soil)
B: Area of the Reserva San Francisco 1850 m – 2280 m (bark)
C: Podocarpus National Park, entrance Rio Bombuscaro, ca. 1050 m
D: Podocarpus National Park, entrance Cajanuma, ca. 3000 m
cf: confer, compare
sp.: species
nS = New species
nE = New to Ecuador
Am-C = Central American (incl. Caribbean)
Am-S = South American
Cosmopolit
Neotrop
Pantrop = pantropical
Subcos = subcosmoplitan
++ regular

CHAPTER 5

5.1. Where are the decomposers? Uncovering the soil food web of a tropical mountain rain forest in southern Ecuador using stable isotopes (^{15}N)

5.1.1. Introduction

Trophic relationships among animals, plants and microflora are the basis for the construction of terrestrial and aquatic food webs, but both the structure and dynamics of food webs remain contentious. Examples of issues include how the overall nutrient status of a system affects the number of trophic levels, whether trophic-level omnivory and intraguild predation are rare or important, if different animal species can be aggregated into functional groups according to their taxonomic affiliation, how large numbers of decomposer animal species can coexist and why there are so many parthenogenetic taxa in soil.

The relationship between ecosystem characteristics and the number of trophic levels has been the subject of controversy. It has been proposed that the number of trophic levels increases with productivity and resource availability by increasing population density at higher trophic levels (Persson *et al.* 1992). On the other hand, theoretical considerations suggest that since nutrient-poor systems (such as tropical forests) are species rich, the large number of interactions between species results in more trophic levels (Vander Zanden *et al.* 1999). Indeed, Reagan *et al.* (1996) found evidence for about five trophic levels in a tropical rain forest in Puerto Rico whereas Ponsard and Arditi (2000) and Scheu and Falca (2000) identified only two and three to four trophic levels, respectively, in soil food webs of temperate forests.

The aim of this study was to contribute to our understanding of the soil food web of a tropical mountain rain forest and to estimate the number of trophic levels in that system by analysing natural variations in stable isotope ratios ($^{15}N/^{14}N$). Stable isotope signatures of animals have been shown to be a powerful tool in evaluating the trophic structure of animal communities (Minagawa and Wada 1984, Ponsard and Arditi 2000, Post 2002, Scheu and

Falca 2000, Schneider *et al.* 2004, Vanderklift and Ponsard 2003, Vander Zanden *et al.* 1999, Wada *et al.* 1991). Empirical evidence indicates that animal tissues are more enriched in 15N than their food source (DeNiro and Epstein 1981) by a constant 3.4 δ units per trophic level (Post 2002).

In soil a large number of saprophagous animal taxa co-exist despite the homogeneity of the habitat, and despite the lack of direct co-evolutionary interactions between decomposers and their resource (Anderson 1975b, Maraun *et al.* 2003a). It has been suggested recently that several species of putative litter-feeding oribatid mites are not primary decomposers but mainly feed on fungi or are predatory or necrophagous (Schneider *et al.* 2004), and similar results have been obtained for collembolans (Chahartaghi *et al.* 2005). This suggests that litter-feeding decomposer animals are less diverse than previously assumed. To prove this hypothesis we investigated the affiliation of tropical soil animal taxa with the principal trophic groups, i.e. phycophages, saprophages, mycophages and predators.

5.1.2. Material and Methods

The study site is part of the Reserva Biológia San Francisco (3°58´S, 79°5´W), located in Zamora-Chinchipe province, near the city of Loja in southern Ecuador. The reserve is situated in the easternmost montane chain (Cordillera del Consuelo) of the Southern Ecuadorian Andes at the northern border of the Podocarpus National Park at 1850 m a.s.l.. The region is covered with mostly undisturbed mountain rain forest. Melastomataceae are the most abundant plants in this region (Homeier *et al.* 2002). The climate is semihumid with 8-10 humid months, the average annual precipitation is 2031 mm and the average annual temperature is 15.7 °C (P. Emck, unpubl. data). The soil types are mainly Aquic and Oxaquic Dystropepts (Schrumpf *et al.* 2001), the organic soil layer is thick and the pH ranges between 4 and 4.5 (Wilcke *et al.* 2002).

In March 2003 ten replicates of L/F litter material (*Graffenrieda emarginata* (Ruiz and Pav.), Melastomataceae) from about 1 m² each were sampled. In addition, three replicates of a mixture of L/F litter material of different species of Melastomataceae were sampled. Both litter materials were transferred to the laboratory, where animals were extracted from the *Graffenrieda emarginata* litter material using a modified high-gradient extractor (Kempson *et al.* 1963), then transferred to 70% ethanol and identified to different taxonomic levels. Voucher specimen are deposited at the University of Darmstadt, Department of Zoology. Storage in ethanol does not significantly affect the $^{15}N/^{14}N$ signature of arthropods (Fabian

1998). For analysis of $^{15}N/^{14}N$ ratios animals were placed into tin capsules and dried at 70°C. After 48 h the samples were weighed and stored in a desiccator until analysed. Replicates of species or higher taxa were analysed if possible. Each sample consisted of pooled individuals (1-150 individuals) to obtain sufficient material for ^{15}N analysis. In addition, litter material from the Melastomataceae mixture and from the *Graffenrieda emarginata* litter (three replicates) was analysed. Samples were dried (70°C), milled, weighed in tin capsules and stored in a desiccator until analysed.

The $^{15}N/^{14}N$ ratios of animals and litter material were determined by a coupled system of an elemental analyser (NA 1500, Carlo Erba, Milan) and a mass spectrometer (MAT 251, Finnigan). The system is computer controlled allowing on-line measurement of ^{15}N. Stable isotope abundance is expressed using the δ notation with $\delta^{15}N$ (‰) = $(R_{sample}-R_{standard})/R_{standard}$ x 1000. R_{sample} and $R_{standard}$ represent the $^{15}N/^{14}N$ ratios of the sample and standard, respectively. For ^{15}N, atmospheric N_2 served as the primary standard and acetanilide (C_8H_9NO, Merck, Darmstadt) for internal calibration. The mean standard deviation of samples of 10-200 µg N, the range of the samples measured, is 0.2‰ (Reineking *et al.* 1993).

To allow a grouping of the animals in different trophic levels we set the baseline similar to the study of Schneider *et al.* (2004). From that and other studies (Vanderklift and Ponsard 2003) it appears that primary decomposer animals, feeding on litter material, are not enriched in ^{15}N by 3.4 delta units per trophic level as are other consumers. Therefore, the signatures of the primary decomposers were assumed to vary around those of their resource (±1.7 ‰).

5.1.3. Results

The $\delta^{15}N$ signature of the litter material (L/F layer) of the mixture of different Melastomataceae trees was -1.23 (SD = 0.16). The $\delta^{15}N$ signature of pure *G. emarginata* litter material was very similar (-1.15; SD = 0.13). We used the *G. emarginata* litter as the baseline for the food web because all animals used for ^{15}N-analysis were extracted from that litter material.

$\delta^{15}N$ signatures of the animals ranged between -1.33 and 8.16 (Figure 5.1.) forming a gradient of about 9.5 δ units. The taxa were ascribed to four trophic groups spanning over 3.4 δ units each. Only two species had low $\delta^{15}N$ signatures similar to those of *G. emarginata*, *Rostrozetes ovulum* Sellnick (Oribatida) and Diplopoda sp. 1; they were ascribed to the primary decomposer group, i.e. species that feed mainly on litter material that is little colonized by micro-organisms. The $\delta^{15}N$ signatures of the secondary decomposers (animals

that feed mainly on fungi but may also ingest litter material), which include a number of oribatid mites and one isopod (*Ischioscia andina* Vandel) ranged between 1.53 (Diplopoda sp. 2) and 4 (*Beckiella arct*a Perez-Inigo and Baggio, Oribatida). $\delta^{15}N$ signatures of adults and juveniles of the oribatid mite *Hermannobates monstruosus* Hammer (Oribatida) were similar (1.53 and 1.80, respectively). The $\delta^{15}N$ signatures of the first group of predators ranged between 4.00 and 6.66 and comprised staphylinid and pselaphid beetles, some oribatid mites and Mesostigmata (Gamasina and Uropodina). A second group of predators includes four taxa with $\delta^{15}N$ signatures >7.5, mainly Mesostigmata (Gamasina and Uropodina) but also Trombidiidae (Prostigmata).

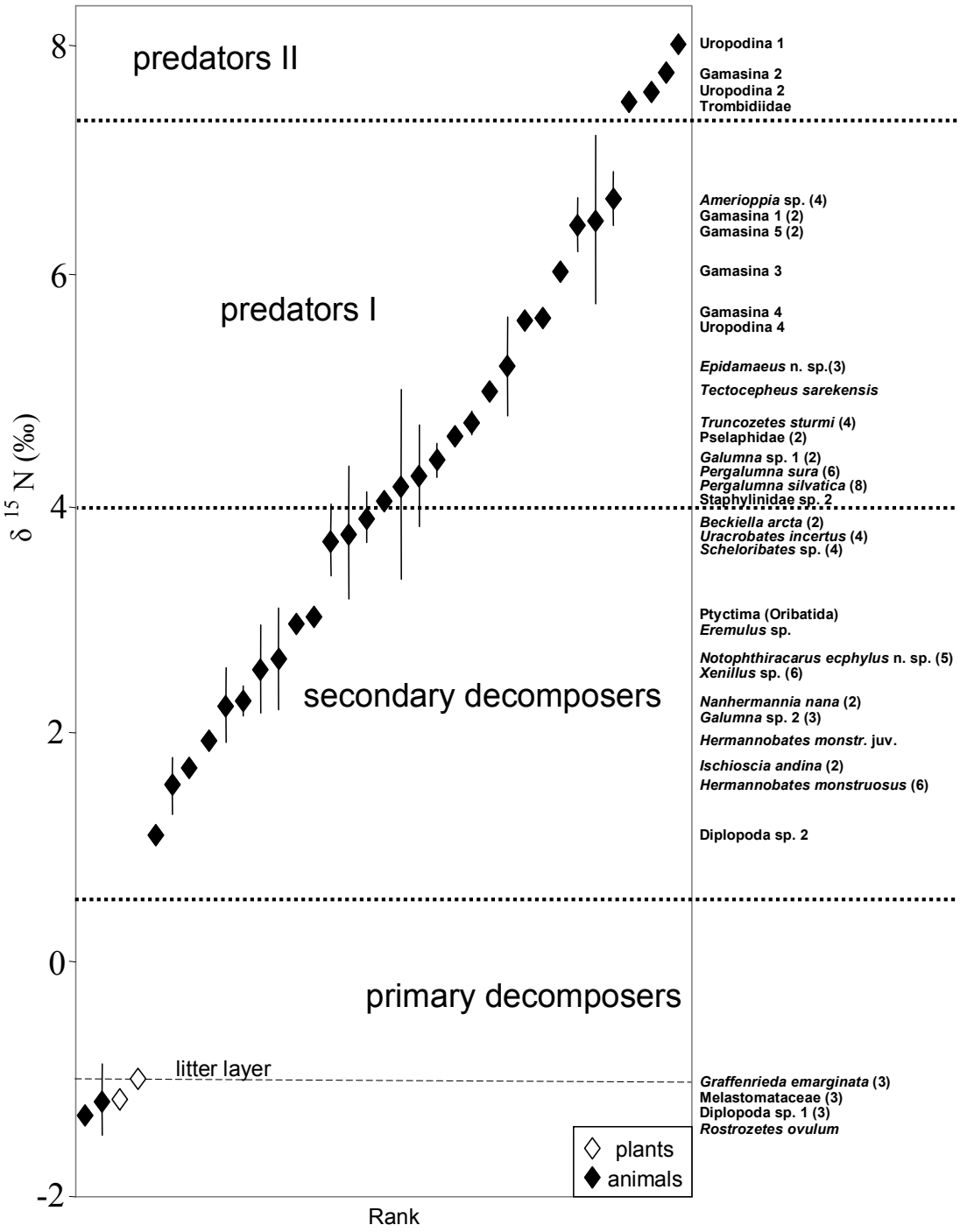

Fig. 5.1. Variation of $\delta^{15}N$ signatures of soil animals from *Graffenrieda emarginata* leaf litter from a tropical mountain rain forest in southern Ecuador. Single measurements (without SD) and means of 2-8 (numbers shown in brackets) replicates with SD. Species were ordered according to increasing $\delta^{15}N$ values. Plant names are underlined. All species identified to genus or species level are oribatid mites except *Ischioscia andina* (Isopoda).

5.1.4. Discussion

This is the first investigation of the soil food web of a tropical mountain rain forest using stable isotopes (^{15}N). The results suggest that the number of trophic levels exceeds neither that in temperate soil systems (Ponsard and Arditi 2000, Scheu and Falca 2000) nor that in aquatic or terrestrial tropical lowland systems.

The number of trophic levels in terrestrial and aquatic food webs is subject of intense discussion. It has been speculated that the number of trophic levels in food webs is correlated with either productivity or habitat complexity (Persson *et al.* 1992), with low-productivity systems having fewer trophic levels (Havens 1991). However, the number of trophic levels ascribed to terrestrial food webs may not reflect the actual situation due to the low resolution of trophic species (Martinez 1991). Using stable isotopes (^{15}N) the number of trophic levels in terrestrial food webs in tropical and temperate systems has been shown to be rather similar, usually 3-4 levels (Ponsard and Arditi 2000, Scheu and Falca 2000). This suggests that productivity and energy flow do not significantly affect the number of trophic levels. Presumably, the number of trophic levels is limited due to the low energy-use efficiency of consumers in detrital systems rather than by productivity.

A surprising result of this study was that the number of primary decomposers (=animals that feed mainly on litter) appears to be low. Only one oribatid mite (*Rostrozetes ovulum*) and one diplopod had ^{15}N signatures close to that of litter suggesting that they function as primary decomposers. Empirical evidence from other studies also suggests that primary decomposers are not or only slightly enriched in ^{15}N compared with the resource they feed on (Scheu and Falca 2000, Vanderklift and Ponsard 2003). The reason for this low enrichment is unknown but may be due to the fact that primary decomposers are limited by the availability of nitrogen (Yoneyama *et al.* 1997). Considering that the organic layer of the study site is thick (mean of 16 cm, Wilcke *et al.* 2002) low numbers of primary decomposer species are puzzling. Possibly, the quality of the litter is low (Cornejo *et al.* 1994). Low litter quality is also indicated by low microbial biomass and strong nutrient limitation of the soil microflora at the study site (Chapter 5.2.). Also, low pH at the study site may be responsible for the low number of primary decomposers. However, this does not apply to decomposer mesofauna (especially oribatid mites) since they are not sensitive to low pH (Maraun and Scheu 2000).

A number of oribatid mite species, one diplopod and one isopod species (*Ischioscia andina*) were ascribed to secondary decomposers, i.e. animals that mainly feed on fungi and bacteria but also consume litter to access the micro-organisms. Especially the grouping of

Ptyctima, *Hermannobates monstruosus* and *Xenillus* sp. is consistent with earlier observations that their juveniles feed inside decomposing litter material with fungi being probably their main food (Hansen 1999).

A surprising high number of oribatid mite species (seven) was ascribed to predators/necrophages. Oribatid mites generally have been assumed to be primary or secondary decomposers, however, the study of Schneider *et al*. (2004) documented that oribatid mites cannot be aggregated in one or two trophic groups but rather occupy four. This is supported by the present study with similar taxa being grouped to similar trophic groups as in the study of Schneider *et al.* (2004), e.g. Oppiidae and Galumnidae were grouped to predators/necrophages in both studies. The food of these mites is unknown, but most likely they feed at least in part on nematodes. The density and size of nematodes at the study site is high (L. Ruess, unpubl. data) and certain oribatid mite species have been shown to feed on nematodes (Muraoka and Ishibashi 1976, Rockett 1980). This first group of predators also includes some of the typical predators of forest ecosystems such as staphylinid and pselaphid beetles and mesostigmate mites (Uropodina, Gamasina). Pselaphid beetles feed on oribatid mites but also use other arthropods as prey (Park 1947), whereas the prey of most Mesostigmata is mainly nematodes and collembolans (Walter and Proctor 1999).

Four taxa (two uropodid mites, one gamasid mite and one prostigmate mite species) were ascribed to second-level predators. Their high ^{15}N signatures indicate that they feed on other predators, i.e. for gamasid mites it is known that they feed on other predatory mites and some Prostigmata are known to feed on eggs of soil invertebrates (Walter 1988). Interestingly, no evidence for phycophagous species was found in this study. Phycophagous species are characterized by very low ^{15}N signatures (cf. Schneider *et al.* 2004). This is surprising since epiphyllous algae and lichens are probably an abundant food on the surface of the litter.

The grouping of the animals into functional groups has to be considered with care. There is no objective way to adjust the lines that separate trophic groups. We used the knowledge on the ecology of the species, data on ^{15}N signatures of oribatid mites from temperate forests and evidence from other studies to group the animals into different feeding guilds. There is evidence that litter and fungal feeders do not have $\delta^{15}N$ signatures that are uniformly 3.4 δ units higher than their food (Kohzu *et al*. 1999, Scheu and Folger 2004). However, it seems likely that the trophic position and the number of trophic levels are properly reflected by the ^{15}N signatures as has been shown in a number of studies (Post 2002, Schmidt *et al.* 2003, Vanderklift and Ponsard 2003).

Results of this study suggest that oribatid mite species occupy distinct trophic niches as has been shown for temperate forests (Schneider *et al.* 2004). $\delta^{15}N$ signatures of oribatid mites ranged over 9 δ units indicating that they feed on very different resources. The different trophic niches of oribatid mite species help in explaining the high diversity of decomposer invertebrates in forest ecosystems. However, the enigma of soil animal species diversity (Anderson 1975b, Maraun *et al.* 2003a) is misleading in part since it applies to the high diversity of primary decomposers which are confronted with rather uniform dead resources. Results of the present study and other recent studies (Chahartaghi *et al.* 2005, Schneider *et al.* 2004) suggest that species-rich decomposer taxa, such as oribatid mites and collembolans, do not consist mainly of species which primarily feed on dead organic matter, rather most species appear to feed on fungi and other prey, including other invertebrates, i.e. in fact they are predators.

5.2. Decomposition and colonization by microarthropods of two litter types in a tropical mountain rain forest in southern Ecuador

5.2.1. Abstract

The decomposition of litter of two tree species *Graffenrieda emarginata* (Melastomataceae), Purdiaea nutans (Cyrillaceae) and the mixture of both was investigated in a tropical mountain rain forest in southern Ecuador at two different altitudes (1850 m and 2280 m). *G. emarginata* is the dominating tree species within the altitude range of 1800 m to 2200 m, *P. nutans* represents the most frequent tree species between 2200 m and 2400 m. The two litter types differed strongly in nitrogen concentrations, suggesting that *G. emarginata* (1.21 % N) is decomposing faster than P. nutans (0.73 % N). To study the effect of soil microarthropods on the decomposition process, litterbags with mesh-size of 48 µm, excluding soil microarthropods, and 1 mm, allowing colonization by soil microarthropods, were used. Litter mass loss was measured after 2, 6 and 12 months exposure in the field; further, microbial biomass and microarthropod colonisation of the litter were investigated after 2 and 12 months. Generally, litter decomposed faster at 1850 m than at 2280 m; *G. emarginata* and mixed litter decomposed faster than *P. nutans* litter. After 12 months mixed litter decomposed faster than both individual litter species indicating that non-additive effects contributed to litter decomposition. Microbial biomass increased during the experiment and was higher at 1850 m than at 2280 m. The most abundant microarthropods in both litter types were oribatid mites followed by Collembola, Gamasina, Uropodina and Prostigmata + Astigmata. Microarthropods were generally more abundant at 1850 m suggesting higher biotic activity at lower altitudes. Soil microarthropods contributed little to decomposition processes indicating that litter decomposition is mainly due to microorganisms.

5.2.2. Introduction

Litter decomposition is a key process for terrestrial ecosystems; up to 99% of the aboveground net primary production enters the decomposer subsystem as plant litter (McNaughton *et al.* 1989). Litter quality, macro- and microclimatic conditions and the structure of the decomposer community influence the rate of litter decomposition (Swift *et al.* 1979). Generally, decomposition processes in the humid tropics are faster than in temperate regions (Heneghan *et al.* 1999). Most of the litter in moist and wet tropical lowland forests decays within a year (Sampaio *et al.* 1993). However, little is known on decomposition processes in tropical mountain rain forests (Tanner 1981, Weerakkody and Parkinson 2006). Decomposition of leaf litter of fifteen tree species in Jamaican mountain rain forests at 1550 m ranged between 27 and 96 % in one year (Tanner 1981). Litter turnover rates in tropical mountain forests therefore are similar to those in temperate forests (Anderson and Swift 1983).

Differences in litter decomposition are due to differences in density and composition of the animal and microbial decomposer communities, the physical environment, e.g. temperature, moisture and pH, and the quality of the litter itself. Separating the influence of these factors is essential for understanding decomposition processes. In a mountain rain forest in southern Ecuador Wilcke *et al.* (2002) assumed that waterlogging as well as lower temperatures inhibit the decomposition of organic matter, in particular at higher altitudes. Vitousek *et al.* (1994) found a strong relationship between decomposition rates and elevation (and hence mean annual temperature) on the slopes of Mauna Loa volcano (Hawaii).

The influence of external and internal factors on decomposition processes has been intensively studied (Taylor *et al.* 1989, Maraun and Scheu 1996, Heneghan *et al.* 1999). Recent studies investigated to what extent litter decomposition is affected by interactions between litter of different plant species (Hansen and Coleman 1998, Albers *et al.* 2004, Wardle *et al.* 2006). Mixture effects can be synergistic, additive or antagonistic; often decomposition rates are accelerated by mixing of different plant species. A number of factors may contribute to mixture effects including higher humidity in mixed litter (Wardle *et al.* 2003) and the translocation of nutrients from high quality litter to low quality litter (Smith and Bradford 2003). Further, Schädler and Brandl (2005) concluded that non-additive effects may also be due to the activity of soil fauna. Virtually all information on litter mixture effects come from temperate and boreal sites, little is known on the effect of mixing of litter on decomposition rates in tropical rain forests (Gartner and Cardon 2004, Montagnini *et al.* 1993).

By consuming plant residues, decomposer animals mobilize nutrients and enhance soil fertility and plant performance (Swift *et al.* 1979, Wardle 2002). The soil microbial community is strongly structured and influenced by soil invertebrates which are extraordinary numerous and exceptionally diverse (Anderson 1975b, Bardgett 2002). Microarthropods affect the biomass, activity and diversity of bacteria and fungi directly by feeding, or indirectly by comminution of plant debris, dissemination of microbial propagules and changes in nutrient availability (Cragg and Bardgett 2001, Scheu *et al.* 2005).

In a tropical mountain rain forest in southern Ecuador we investigated (1) the decomposition of litter materials from dominating tree species at different altitudes, (2) the effect of litter mixing on decomposition processes and (3) the colonization of different litter materials by microarthropods and their effect on decomposition rates. To investigate changes with time, we followed the decomposition process over one year. We hypothesized that due to higher temperature and lower precipitation (waterlogging) decomposition rates in tropical mountain rain forests are faster at lower altitudes.

Graffenrieda emarginata (TRIANA) (Melastomataceae) and *Purdiaea nutans* (PLANSCH.) (Cyrillaceae) represent the most frequent tree species at the study area (Homeier *et al.* 2002). *Purdiaea nutans* flourishes at higher elevation (>2200 m) whereas *G. emarginata* is most abundant at intermediate altitude (<2200 m). Compared to *G. emarginata, P. nutans* produces foliage with a higher degree of sclerophylly. Since litter quality strongly influences decomposition processes (Loranger *et al.* 2002) we expected the decomposition of *P. nutans* to be slower than that of *G. emarginata* with decomposition rates of mixed litter being intermediate.

It is generally agreed that the biomass of soil macro-invertebrates in temperate deciduous forests exceeds that in tropical rain forests (Anderson and Swift 1983, Petersen and Luxton 1982). Indeed, at our study site in southern Ecuador the density of soil macrofauna such as earthworms, diplopods and isopods is low (Maraun *et al.* 2007b). Therefore, we expected soil microarthropods to be the main drivers of decomposition processes. They affect decomposition processes largely by comminution and stimulating microbial actions. Oribatid mites are the most abundant and diverse soil microarthropods in tropical forests (Franklin *et al.* 2004, Heneghan *et al.* 1999). Wardle *et al.* (2002) found no consistent effect of litter diversity on diversity and abundance of invertebrates. Walter (1985) detected no evidence of oribatid mite specificity among three coniferous litter species. Therefore, the oribatid mite community in tropical mountain rain forests may also not discriminate between different litter species.

Declines in invertebrate species richness and abundance at high elevations in the tropics have been documented (Janzen *et al.* 1976, Olson, 1994) suggesting that physical parameters that vary

continuously with altitude are important determinants. We expected the microarthropod fauna to differ between altitudes, since abiotic characteristics are more important for colonization of microarthropods than litter species.

5.2.3. Material and Methods

Study sites

The study area is located in southern Ecuador within the Eastern Cordillera of the Andes in the province of Zamora-Chinchipe. The experiment was conducted in the area of the Reserva Biológica San Francisco (RBSF) (3°58´S, 79°5W) at the border of the Podocarpus National Park. The study site is a biological reserve, covering about 1000 ha, on the steeply sloping (30°–50°) north facing flank of the valley of the Rio San Francisco which drains in the Amazon basin. The altitude ranges from 1800 m to 3200 m a.s.l. and the climate is semi-humid with 8 to 10 humid months. The average annual precipitation at 2000 m a.s.l. is 2031 mm and the average annual temperature is 15.7°C (Emck 2005). The bedrock consists mainly of weakly metamorphosed Paleozoic schists and sandstones with some quartz veins. Dominating soil types are Eutric, Dystric and Humic Cambisols (Wilcke *et al.* 2001). The organic soil layer is thick and increases with elevation, the pH ranges between 3.0 and 5.5 (Wilcke *et al.* 2002) and is decreasing with altitude (Soethe *et al.* 2006). The site is covered with mostly undisturbed mountain rain forest (Homeier *et al.* 2002).

Experimental design

Litter from *G. emarginata* and *P. nutans* was sampled in February 2004 at 1850 m and 2280 m, respectively. After drying at 65°C for 72 h, 10 g dry weight of the litter was filled in litterbags (20 x 20 cm) of different mesh-size (48 µm and 1 mm); the finer mesh-size prevents immigrating of soil microarthropods. A total of 144 litterbags with litter from *G. emarginata*, *P. nutans* and the mixture of both were exposed in the field at 1850 m (S 03˚58´38´´, W 79˚04´66´´) and 2280 m (S 03˚58´96´´, W 79˚04´41´´). Litterbags were fixed with tent pegs to ensure contact to the soil.

Microarthropods, microbial and chemical parameters

After 2, 6 and 12 months, 4 replicate litterbags were removed and transferred to the laboratory. Mesofauna from half of the wide-meshed litterbag material was extracted with a modified heat-extractor (Kempson *et al.* 1963) and microarthropods were determined (after 2 and 12 month only).

The remaining material was used for measuring microbial biomass (after 2 and 12 month only) using the substrate-induced respiration method (Anderson and Domsch 1978, Joergensen and Scheu 1999, Scheu 1992). The temperature coefficient (Q_{10}) for the two altitudes (a:1850 m and b:2280 m) was calculated using the exponential function $(Q_{10}) = (k_b/k_a)^{10(Tb-Ta)}$, where ka and kb are the reaction rates (=remaining dry weights) at temperatures T_a and T_b. Yearly decomposition rates, k (yr^{-1}), were calculated by fitting the amount of remaining litter to the simple exponential decay model, $x(t)/x(o) = e^{-k(t)}$ (Olson 1963). The samples collected after 12 months and also the initial litter materials, were analyzed for C and N concentration. The material was dried (65°C, 72 h) and milled, and concentrations of C and N were determined by dry combustion with a C-N analyzer (Carlo Erba EA 1108, Milano, Italy).

Statistical analysis

The remaining litter dry weight, microbial biomass, C and N content, C-to-N ratio and the response of the microarthropod groups (Oribatida, Uropodina, Gamasina, Astigmata–Prostigmata and Collembola) to altitude, litter type and time of exposure was analyzed by analysis of variance (ANOVA, GLM). Means were compared by Tukey´s honestly significant difference test (HSD). STATISTICA 6.0 (Statsoft, Tulsa, USA) and SAS 9.13 (Statistical Analysis System, SAS Institute Inc., Cary, USA) software packages were used for statistical analyses. To analyse the response of subgroups of oribatid mites to litter decomposition principal components analysis (PCA) was carried out. Time of exposure (2 and 12 month) was coded as a supplementary variable and included in the PCA using the passive analysis procedure (i.e. the variables do not contribute to the ordination; Jongmann *et al.* 1995) in CANOCO 5.0 (Microcomputer Power, Ithaca, USA). Taxa which occurred less than five times were not considered.

5.2.4. Results

Mass loss, C and N concentration

Overall, 90, 78 and 68 % of the initial dry mass of the litter remained after 2, 6 and 12 month, respectively (Table 1). Litter at 1850 m decomposed faster (decay constant k = 0.48) than at 2280 m (k = 0.27). Further, litter of *P. nutans* decomposed slower than that of *G. emarginata* and mixed litter (k = 0.27, 0.38 and 0.40, respectively). After 2 and 6 months *G. emarginata* litter had decomposed faster than the other two litter types but after 12 months the mixed litter had

decomposed faster than both single litter species (Time x Litter interaction; Table 5.2.1., Fig. 5.2.2.). Generally, litter decomposition was faster at the beginning of the exposure and slowed down at later stages. This decline in decomposition rates was more pronounced at 2280 m than at 1850 m (Time x Altitude interaction; Table 5.2.1., Fig.5.2.1.). At 1850 m litter in fine mesh-bags decomposed slightly faster than that in coarse mesh-bags (72.9 and 74.7 % dry mass remaining, respectively), whereas at 2280 m the opposite was true (84.9 vs. 82.7 %; Altitude x Mesofauna interaction; Table 5.2.1.).

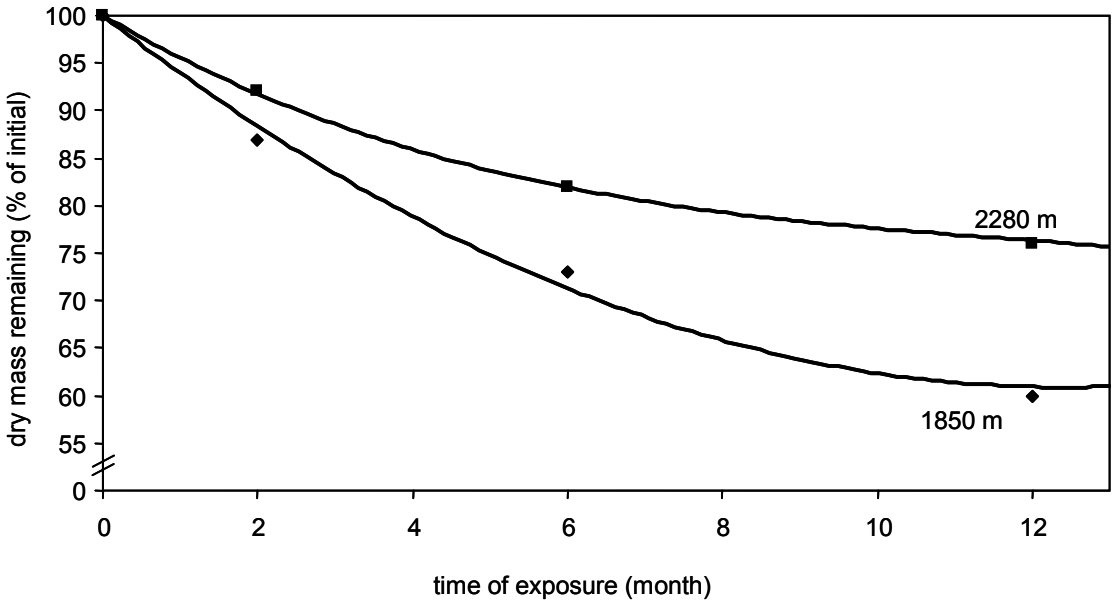

Fig. 5.2.1. Mass remaining (% of initial) of litter materials in litterbags exposed for 12 months at 1850 and 2280 m.

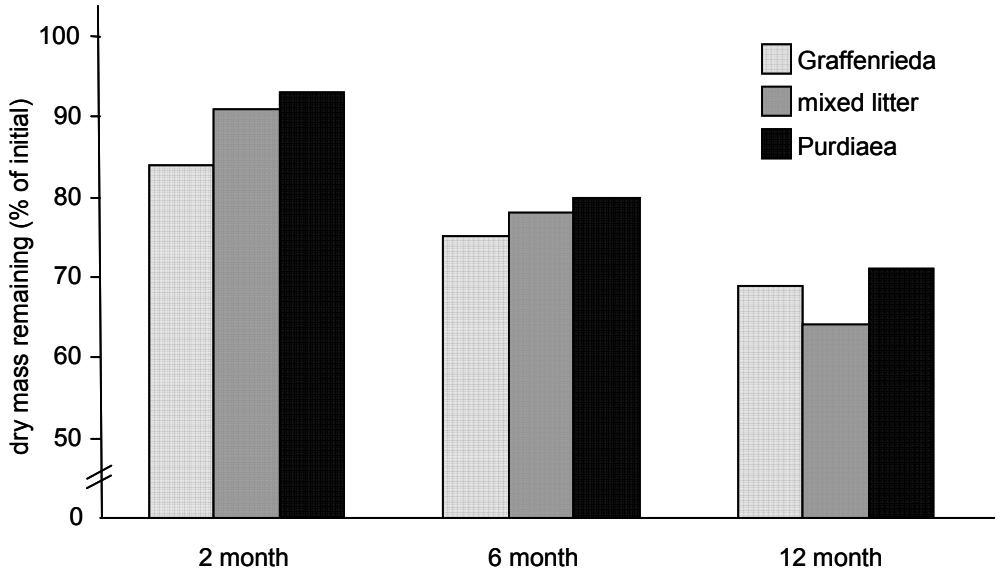

Fig. 5.2.2. Mass remaining (% of initial) of litter materials exposed in litterbags with different litter types (*Graffenrieda emarginata*, mixed litter and *Purdiaea nutans*) after 2, 6 and 12 months.

Table 5.2.1. Four factor ANOVA table of F-values on the effect time of exposure, litter type (*Graffenrieda emarginata*, *Purdiaea nutans* and mix), altitude (1850m and 2270m)and mesh size (1 mm and 48 μm) on mass loss and microbial biomass (C_{mic}) (mg C_{mic}*g dw^{-1}).

	mass loss		C_{mic}	
	df	*F value*	df	*F value*
time	2,108	224.6 ***	1,72	50.2 ***
litter	2,108	15.6 ***	2,72	12.9 ***
altitude	1,108	147.5 ***	1,72	230.8 ***
mesofauna	1,108	< 0.1	1,72	< 0.1
time x litter	4,108	5.9 ***	2,72	17.8 ***
time x altitude	2,108	12.1 ***	1,72	8.7 ***
time x mesh size	2,108	1.2	1,72	1.6
litter x altitude	2,108	2.6	2,72	8.8 ***
litter x mesh size	2,108	1.2	2,72	1.5
altitude x mesh size	2 108	5.9 *	1,72	0.1
time x litter x altitude	4,108	1.3	2,72	6.2 **
time x litter x mesh size	4,108	0.4	2,72	5.5 **
time x altitude x mesh size	2,108	2.2	1,72	6.2 **
litter x altitude x mesh size	2,108	1.4	2,72	0.8
time x litter x altitude x mesh size	4,108	1.6	2,72	2.5

***P<0.001;**P<0.01;*P<0.05

Carbon and nitrogen concentrations of the initial litter materials differed significantly (1.2, 1.0 and 0.7 % nitrogen and 50.5, 52.1 and 53.7 % carbon for *G. emarginata*, mixed and *P. nutans* litter material, respectively; Table 5.2.2.). N concentrations increased until the end of the experiment for *G. emarginata* from 1.2 to 2.3 %, mixed from 1.0 to 2.0 % and *P. nutans* litter from 0.7 to 1.6 % (Table 5.2.2.). Since the carbon concentration of the litter materials changed little, C-to-N ratios followed the changes in N concentrations. The increase in the N concentrations with time was strongest in *P. nutans* litter resulting in a stronger decrease in the C-to-N ratio compared to the other two litter materials (Time x Litter interaction; Table 5.2.2., Fig. 5.2.3.).

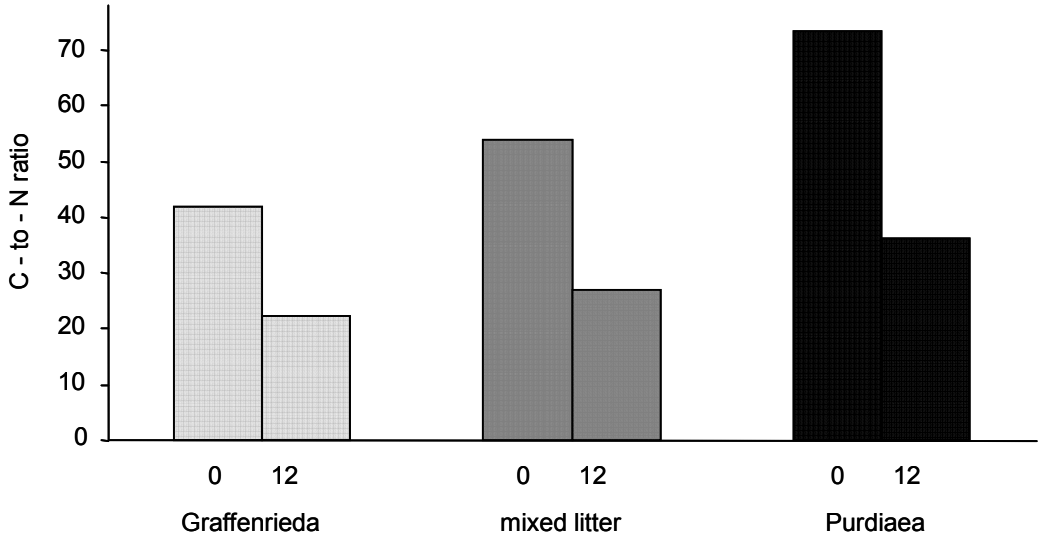

Fig. 5.2.3. C to N ratio of litter of *Graffenrieda emarginata*, mixed litter and litter of *Purdiaea nutans* prior to exposure and after 12 months of exposure in litterbags.

Overall, carbon concentrations in the litter materials after 12 months were higher at 2280 m compared to 1850 m (53.0 vs. 51.1 %), nitrogen concentrations were higher at 1850 m compared to 2280 m (2.3 vs. 1.6 %), resulting in higher C-to-N ratios at 2280 m (33.9) compared to 1850 m (23.2; Table 5.2.3.). Carbon concentrations of litter enclosed in coarse mesh-bags were lower than those of litter material enclosed in fine mesh-bags but only at 1850 m (Mesh-size x Altitude interaction; Table 5.2.3., Fig. 5.2.4.).

Table 5.2.2. Two factor GLM table of F-values on the effect of time of exposure (0 and 12 month) and litter type (*Graffenrieda emarginata*, *Purdiaea nutans* and mix), on C-content (%), N-content (%) and C-to-N ratio in the litterbags.

		F value		
	df	C (%)	N (%)	C:N
time	1,54	0.03	78.9 ***	195.2 ***
litter	2,54	18.3 ***	10.1 ***	44.8 ***
time x litter	2,54	0.5	0.6	6.6 **

***P<0.001;**P<0.01

Table 5.2.3. Three factor ANOVA table of F-values on the effect litter type (*Graffenrieda emarginata*, *Purdiaea nutans* and mix), altitude (1850m and 2280m) and mesh size (1 mm and 48 μm) on C-content (%), N-content (%) and C-to-N ratio after 12 month of exposure.

		F value		
	df	C (%)	N (%)	C:N
litter	2,36	97.6 ***	79.0 ***	81.0 ***
altitude	1,36	55.6 ***	177.8 ***	138.7 ***
mesh size	1,36	2.5	2.3	3.8
litter x altitude	2,36	4.1	1.1	3.2
litter x mesh size	2,36	0.7	0.9	1.8
altitude x mesh size	1,36	9.6 **	0.6	0.1
litter x altitude x mesh size	2,36	1.0	1.7	0.9

***P<0.001;**P<0.01

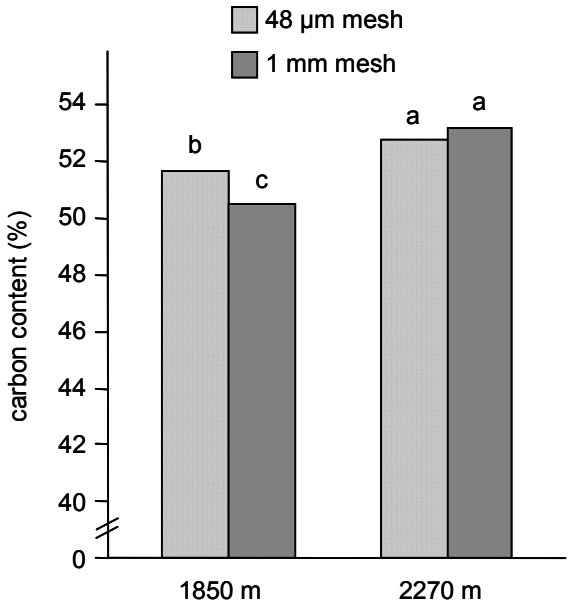

Fig. 5.2.4. Effect of mesh-size (48 µm and 1 mm) on carbon concentration (%) of litter materials in the litter bags at 1850 m and 2280 m altitude after 12 months of exposure. Different letters indicate significant differences between means at $p<0.05$ (Tukey's HSD).

Microbial biomass

Microbial biomass increased from 2 months of exposure to the end of the experiment from an average of 7.5 to 9.5 mg C_{mic} g^{-1} dry weight. Microbial biomass was significantly higher at 1850 m than at 2280 m (10.6 vs. 6.3 mg C_{mic} g^{-1} dry weight; Table 5.2.1.) with the difference being more pronounced after 12 than after 2 months of exposure (Time x Altitude interaction; Table 5.2.1.). Microbial biomass in *G. emarginata* and mixed litter significantly exceeded that in *P. nutans* litter after 2 months of exposure (9.2, 7.3 and 5.9 mg C_{mic} g^{-1} dry weight in *G. emarginata*, mixed and *P. nutans* litter, respectively), whereas microbial biomass was highest in mixed litter material at the end of the experiment (10.6 compared to 8.9 and 9.0 mg C_{mic} g^{-1} dry weight in mixed, *G. emarginata* and *P. nutans* litter, respectively; Time x Litter interaction; Table 5.2.1.). Microbial biomass in mixed and *P. nutans* litter was higher at the second sampling date but only at 1850 m; at 2280 m microbial biomass in each of the litter materials was similar at both sampling dates (Time x Litter x Altitude interaction; Table 5.2.1., Fig. 5.2.5a.). Microbial biomass in *G. emarginata* litter enclosed in coarse mesh-bags was lower than that in fine mesh-bags, whereas microbial biomass in mixed litter enclosed in coarse mesh-bags exceeded that in fine mesh-bags, but only after 2 months of exposure (Time x Litter x Mesh-size interaction; Table 5.2.1., Fig. 5.2.5b.).

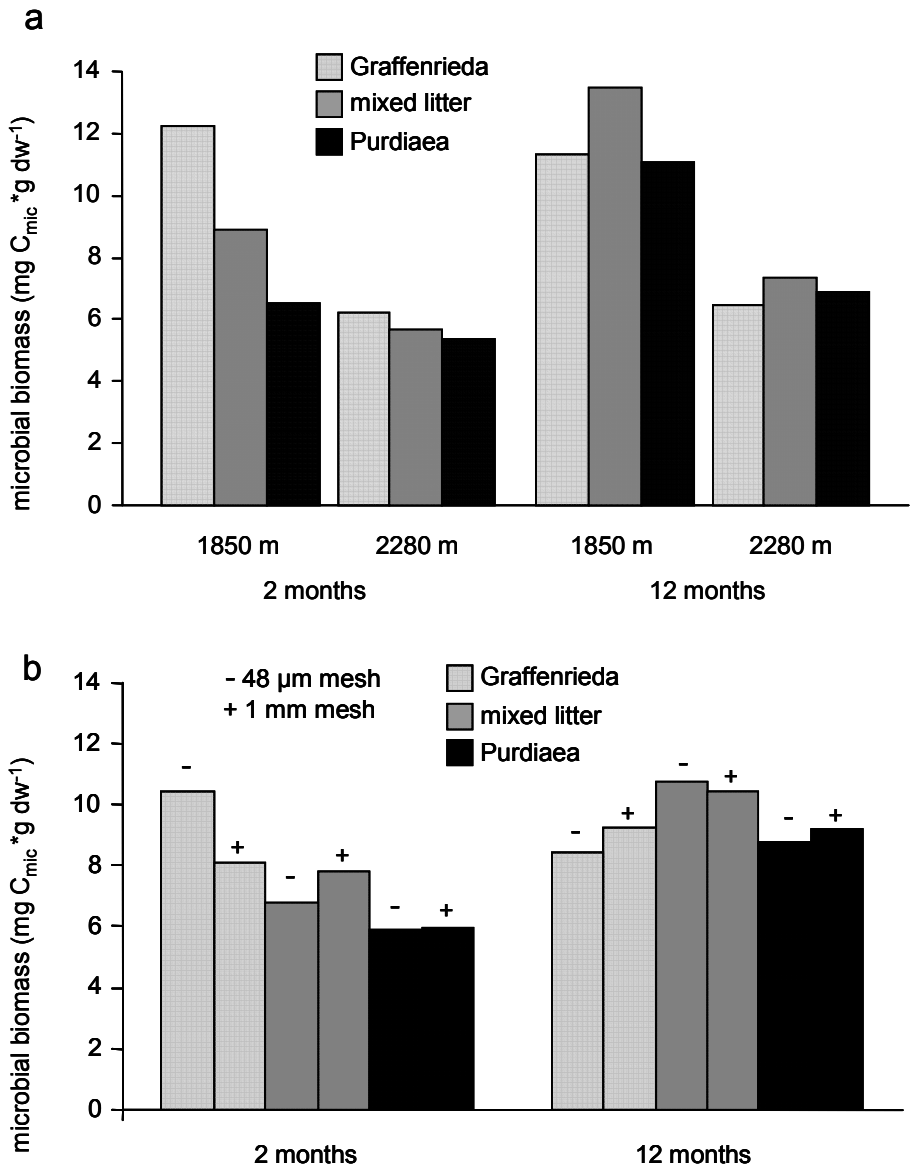

Fig. 5.2.5. Effects of altitude (1850 and 2280 m) and time of exposure (2 and 12 months) on microbial biomass in litter of *Graffenrieda emarginata*, mixed litter and litter of *Purdiaea nutans* (a) and effects of mesh-size (48 µm and 1 mm) and time of exposure (2 and 12 months) on microbial biomass in litter of *G. emarginata*, mixed litter and litter of *P. nutans* (b).

Colonization of litterbags by microarthropods

Numbers of microarthropods from half of the wide-meshed litterbag material were analysed. Microarthropods were more abundant at 1850 m than at 2280 m; Oribatida: (49.5 ± 17.9) vs. (10.6 ± 6.3), Gamasina: (15.0 ± 7.7) vs. (2.5 ± 2.2), Uropodina: (7.5 ± 6.4) vs. (0.5 ± 1.6), Prostigmata + Astigmata: (3.1 ± 3.0) vs. (1.2 ± 1.1), Collembola: (14.4 ± 9.0) vs. (4.5 ± 3.7). The number of Gamasina and Collembola declined from the first sampling date (2 month) to the end of the

exposure (12 month) with (10.7 ± 9.9) and (11.2 ± 10.3) vs. (6.8 ± 6.2) and (7.7 ± 5.8) individuals, respectively (Table 5.2.4.). Uropodina colonized *G. emarginata* litter with higher densities than P. nutans or mixed litter (6.8 ± 7.8, 2.3 ± 4.3 and 2.9 ± 3.6 individuals, respectively); Collembola were more abundant in litter of *G. emarginata* and mixed than in litter of *P. nutans* (11.6 ± 8.3, 11.5 ± 10.5 and 5.3 ± 3.9 individuals, respectively). Density of Collembola was higher at 1850 m at the first sampling date (19.1 ± 9.1 individuals) than at the second sampling date (9.7 ± 6.2 individuals), but at 2280 m density of Collembola was higher at the second sampling date (5.8 ± 4.8 individuals) compared to the first sampling date (3.3 ± 1.7 individuals), (Time x Altitude interaction; Table 5.2.4.). Density of Collembola at 1850 m was highest in mixed, intermediate in *G. emarginata* and lowest in *P. nutans* litter; at 2280 m density of Collembola was generally lower than at 1850 m, and their density was highest in *G. emarginata*, intermediate in mixed and lowest in *P. nutans* litter. At 1850 m densities of Uropodina and Prostigmata + Astigmata were higher in *G. emarginata* litter, intermediate in mixed litter and lowest in *P. nutans* litter whereas at 2280 m density of these taxa was similar in each of the litter materials (Litter x Altitude interaction; Table 5.2.4., Fig. 5.2.6.).

Table 5.2.4. Three factor ANOVA table of F-values on the effect of time of exposure (2 and 12 months), litter type (*Graffenrieda emarginata*, *Purdiaea nutans* and mix) and altitude (1850m and 2280m) on densities of Oribatida, Collembola, Gamasina, Pro- & Astigmata and Uropodina.

		F value				
	df	Oribatida	Collembola	Gamasina	Pro-Astigm.	Uropodina
time	1,36	2.7	6.2 *	6.2 *	1.5	1.6
litter	2,36	2.3	8.7 ***	0.4	3.3	6.4 **
altitude	1,36	112.6 ***	48.7 ***	65.0 ***	10.5 **	37.7 ***
time x litter	2,36	0.2	2.1	1.0	0.2	1.8
time x altitude	1,36	0.6	17.6 ***	2.3	0.3	0.6
litter x altitude	2,36	1.8	3.2 *	0.2	6.9 **	3.5 *
time x litter x altitude	2,36	1.7	1.8	0.3	0.4	2.3

***P<0.001;**P<0.01;*P<0.05

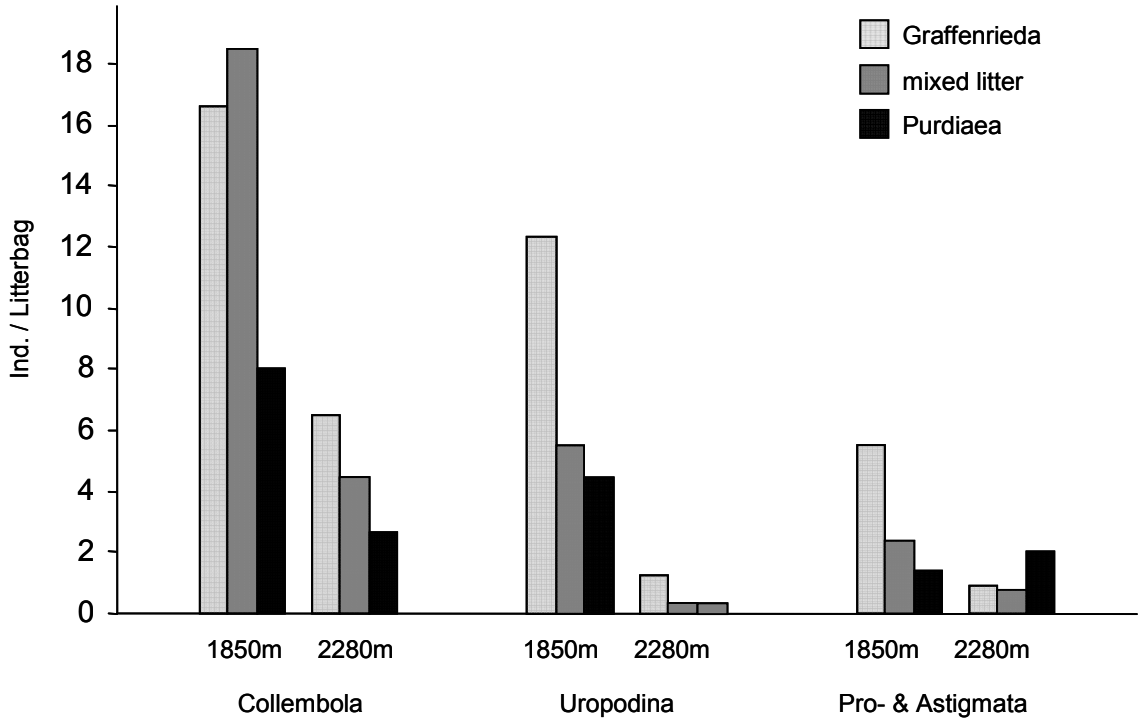

Fig. 5.2.6. Effects of litter of *Graffenrieda emarginata*, mixed litter and litter of *Purdiaea nutans* at 1850 m and 2280 m on abundance of Collembola, Uropodina and Pro- + Astigmata in litterbags.

In total 37 species of oribatid mites were found. Among the adults Poronota were most abundant followed by Gymnonota, Enarthronota, Mixonomata and Desmonomata with (13.3 ± 12.5), (6.7 ± 9.4), (1.8 ± 2.8), (1.1 ± 2.0) and (0.5 ± 1.1) individuals, respectively. The oribatid mite community was dominated by Scheloribates spp., Pergalumna sura, Scheloribates elegans and Truncozetes sturmi (16.8 %, 6.7 %, 6.3 % and 6.0 % of total, respectively). Seventeen taxa only occurred at 1850 m. In general, the density of oribatid mite subgroups did not varry between litter materials, with the exception of Enarthronota (Brachychthonioidea spp., Mesoplophora cubana) which preferentially colonized mixed litter ($F_{2,36}=12.57$, $P<0.0001$). In litterbags exposed 2 months in the field only few oribatid mite species occurred, whereas in more decomposed litter materials most oribatid mite taxa were found (Fig. 5.2.7.). Juvenile oribatid mites represented 22 % of total and were more abundant after twelve months ($F_{1,36}=19.26$, $P<0.0001$).

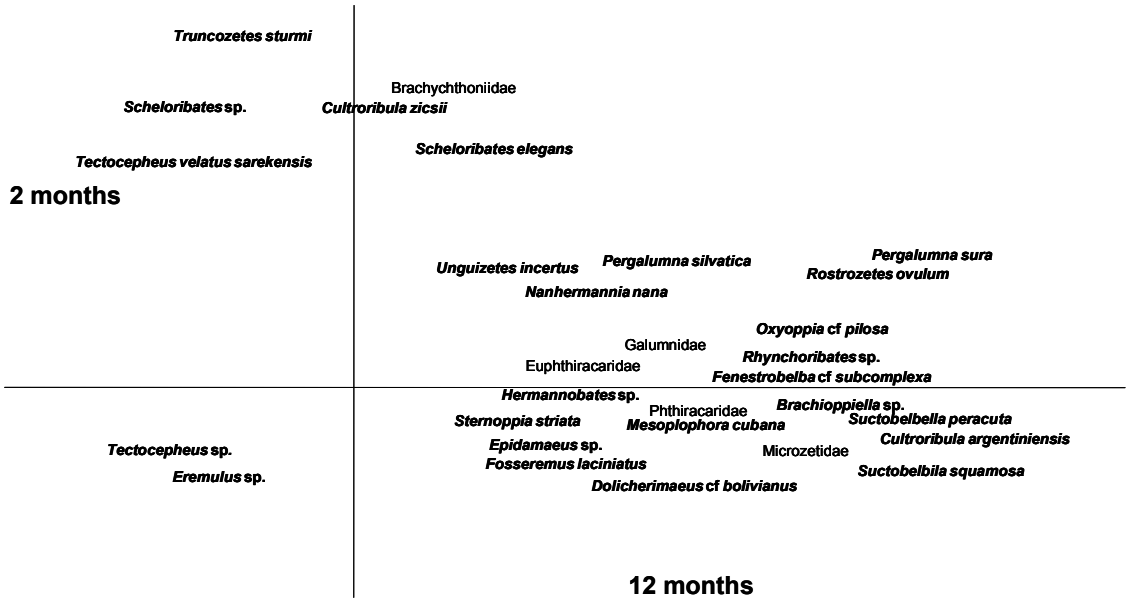

Fig. 5.2.7. Oribatid mite community structure analysed by principal components analysis (PCA) in the litterbags after 2 and 12 month of exposure. Eigenvalues of Axis 1 and Axis 2 of 0.281and 0.255, respectively.

5.2.5. Discussion

Litter decomposition

Decomposition rates at the studied tropical moutain rain forest were generally low (average of 32 % y-1) and resembles those observed by Tanner (1981). Decomposition rates at tropical lowland sites are usually higher (Anderson *et al.* 1983, Heneghan *et al.* 1999). Most of the litter in tropical lowland forests decays within one year (Sampaio *et al.* 1993) resulting in rapid nutrient cycling. The slow decomposition rates in the studied tropical mountain rain forest may be due to low litter quality (e.g. high C-to-N ratios) but also due to low temperatures. The slow litter decomposition rate at the study site is similar to beech litter decomposition in temperate forests (Albers *et al.* 2004, Anderson and Swift 1983) which is around 30 % per year (Albers *et al.* 2004, Wise and Schaefer 1994). However, temperatures in tropical mountain rain forests in southern Ecuador (16.2°C and 13.7°C at 1850 and at 2280 m, respectively) and temperate forests (7.7°C at the Göttinger forest in Germany) differ. Presumably, similar low decomposition rates are rather caused by functionally similar decomposer communities developing on lower quality litters of varying chemical composition. We did not collect data relevant to this assumption, but our results are consistent with the importance of nitrogen (see below).

Variations with altitude

Litter generally decomposed slower at higher elevation supporting our assumption that temperature is a major driving force for litter decomposition at our study sites and indicating that organic matter accumulates at high altitudes. The importance of the temperature can be derived from the temperature coefficient (Q_{10}) according to the difference in temperature between the sites at 1850 m and 2280 m which is low (1.67) compared to other litter materials (Vitousek *et al.* 1994). High humidity at high altitudes may also have contributed to slow down decomposition processes. Decomposition rates of leaves in Hawaiian mountain forests also declined with increasing precipitation (Schuur 2001). Wilcke *et al.* (2002) also assumed that an increased precipitation and waterlogging together with lower temperatures are responsible for the formation of thick organic layers at higher altitudes at our study site.

Variations with litter type

Decomposition of *P. nutans* litter was generally slower than that of litter of *G. emarginata*. Presumably, this was due to the low nitrogen content of *P. nutans* litter. Litter with low N concentration generally decomposes slower than litter with higher N concentration (Taylor *et al.* 1989). C-to-N ratios of *P. nutans* and *G. emarginata* litter at the beginning of the experiment were rather high (73.6 and 41.9, respectively) suggesting that both may decompose slowly (Swift *et al.* 1979). Since *G. emarginata* litter decomposed faster (significantly after 2 und 6 months) litter quality is an important factor for litter decomposition. In tropical rain forests where moisture is unlikely to limit decomposition processes (rather the opposite; see above) the quality of decomposing resources is likely to be more important for decomposition processes than in regions with at least temporarily arid conditions (Loranger *et al.* 2002).

After 12 months the mixture of *G. emarginata* and *P. nutans* had decomposed faster than the monospecific litter of *G. emarginata* or *P. nutans* indicating a non-additive effect of the two litter types. Non-additive effects have been observed in 67 % of litter mixture experiments (Gartner and Cardon 2004; but see Anderson *et al.* 1983). However, rather than predictable, effects of litter mixing on decomposition processes appear to be idiosyncratic (Wardle *et al.* 1997). Faster decomposition of the mixed litter likely was due to mixing of litter species differing in nutrient concentrations. It is known that litter low in nitrogen may decompose faster when litter with high nitrogen content is in close vicinity allowing fungi to translocate nitrogen from high to low N litter (Smith and Bradford 2003, Schimel and Hättenschwiler 2007).

Variations with mesh-size

Variations in decomposition with mesh-size of litter bags were generally low. This suggests that microarthropods only marginally affected decomposition rates. Unexpectedly, the data suggest that microarthropods reduced litter decomposition at 1850 m where their densities were higher than at 2280 m. Potentially, microarthropods at 1850 m reduced fungal biomass thereby slowing down litter decomposition. However, microbial biomass varied little with mesh-size (see below).

Microarthropods reduced microbial biomass in *G. emarginata* litter and increased it in mixed litter at the beginning of the experiment but not at the end. Since collembolan densities were highest at the beginning of the experiment they likely were responsible for reducing microbial biomass. In contrast to *G. emarginata* litter, microarthropods appeared to have increased microbial biomass in mixed litter, potentially by distribution of microbial propagules (Renker *et al.* 2005). Overall, however, effects of microarthropods on litter decomposition were limited which is similar to a tropical forest in Puerto Rico (González *et al.* 2001). Low effects presumably are related to overall low densities of microarthopods in tropical forests as compared to temperate and in particular boreal forests (Maraun *et al.* 2007a; see below).

Colonization by biota

Microorganisms

Microbial biomass in each of the litter types was higher at lower altitudes indicating that conditions for microbial growth declined with altitude. Presumably, this is related to lower temperatures and the dominance of low quality litter at higher altitudes. After two month of exposure microbial biomass in *G. emarginta* litter exceeded that in mixed and *P. nutans* litter, whereas after 12 month microbial biomass was highest in mixed litter. Higher microbial biomass in mixed litter may explain why it had decomposed faster than the monospecific litter by the end of the experiment.

C-to-N ratios were generally high in all litter types at the beginning of the experiment and decreased with time. Since the carbon concentrations remained rather constant during decomposition this indicates that nitrogen had been transferred from the soil into the litter (Frey *et al*. 2000). This probably was due to fungal colonization and associated nitrogen transfer into the litter necessary for the exploitation of complex carbon resources but also for the production of fruiting bodies (Berg and Staaf 1981). Interestingly, the C-to-N ratio of *P. nutans* litter decreased faster than that of *G. emarginat*a and mixed litter indicating that the relocation of nitrogen into the nitrogen-poor litter of *P. nutans* was faster than into *G. emarginata* litter. In general, the C-to-N

ratios of litter materials increase with altitude (Leuschner *et al*. 2007). However, it is not known if the low nitrogen content at high altitudes is a consequence of the adaptation of the trees to high altitude (high level of nitrogen withdrawel into the tree before litter fall) or if it is a consequence of the plant life style (presence of thick and sclerophyllic leaves at high altitudes).

Microarthropods

Compared to temperate forest litter the densities of microarthropod taxa in the litterbags in our study were low indicating that the amount and/or quality of resources for microarthropods in tropical mountain rain forests are low. Microarthropods in the litterbags were more abundant at 1850 m than at 2280 m which probably was influenced by low temperatures and/or higher temperature fluctuations at higher altitude. Previous studies also found low densities of invertebrates in tropical forests at higher elevations (Janzen *et al.* 1976, Olson 1994, Richardson *et al.* 2005). The differences in microarthropod densities may also be explained by the contribution of the chemical and physical nature of litter and habitat heterogeneity in the forest (Richardson *et al*. 2005).

The densitiy of Collembola and predatory Gamasida declined during the decomposition indicating that both preferentially colonize fresh litter material; the decline in density at later stages suggests that these microarthropods are becoming increasingly limited by resources at later stages of decay. Generally, the density of microarthropods did not differ significantly between litter types indicating that soil microarthropods are little specialized. Feeding experiments by Schneider and Maraun (2005) also confirmed low specialization in soil microarthropods such as oribatid mites. Including a wider range of litter species, however, Hansen and Coleman (1998) provided evidence that oribatid mite diversity (but not abundance) increases with tree litter diversity but the increase was only moderate.

Collembolan density was highest in *G. emarginata* and mixed litter at 1850 m altitude indicating that compared to *P. nutans G. emarginata* is of superior food quality. At 2280 m the differences in densities between the three litter materials were less pronounced indicating that at high altitudes abiotic factors covered the effect of litter type. Densities of Uropodina and Pro-+ Astigmata at 1850 m decreased from *G. emarginata* and mixed to *P. nutans* litter but were similar in each of the litter types at 2280 m. Low densities of microarthropods in general at high altitudes suggest that they suffer from harsh environmental conditions and/or are limited by resources of low quality.

Results of the principal components analysis showed that *Tectocepheus velatus sarekensis*, *Truncozetes sturmi* and species of the genus *Scheloribates* quickly colonized the fresh litter

material. *Tectocepheus* spp. have been suggested to be fast colonizers which may be related to its parthenogenetic mode of reproduction (Domes *et al.* 2007c, Maraun and Scheu 2000, Norton 1994). *Cultroribula zicsii* also preferentially colonised the fresh litter material whereas *Cultroribula argentiniensis* predominantly colonised the more decomposed litter after 12 months. This indicates that niche requirements can differ between closely related species (Schneider *et al.* 2004). Most of the oribatid mite taxa and also juveniles colonized the 12 month old litter supporting the view that oribatid mites usually exhibit K-style life history traits (Norton 1994). Oribatid mite communities were generally dominated by Poronota and Gymnonota, i.e. higher derived oribatid mites; especially abundant were Scheloribatidae. Since stable isotope data ($\delta^{15}N$) indicate that derived taxa of oribatid mites are fungal feeders or predators (Chapter 5.1.) our results support the conclusion of (Chapter 5.1.) that in tropical mountain rain forests litter feeding microarthropod taxa are rare.

In our study mixing of litter of different tree species did not result in a significant increase in diversity of soil microarthropods which is in contrast to the results of Anderson (1978) and Hansen and Coleman (1998). It has been assumed that litter diversity reflects microhabitat diversity and be correlated with soil animal diversity. However, this is not necessarily true since the generalistic life history tactics of soil animals prevent close correlation between habitat diversity and species diversity (Maraun *et al.* 2007a). Wardle *et al*. (2006) also concluded that soil animal species predominantly are generalist feeders colonizing a wide habitat spectrum and may therefore be rather unresponsive to litter mixing.

CHAPTER 6 GENERAL DISKUSSION

Tropical mountain rain forests as biodiversity hotspots

For most animal and plant taxa, the neotropical region is known to be extremely species rich (Gentry 1988, Wilson 1992) Especially tropical mountain rain forests are known to be among the most species rich regions of the world and are therefore called "biodiversity hotspots" (Meyers *et al.* 2000). Our study site is located in one of these hotspot regions in the Ecuadorian Andes at an altitude between 1000 and 3000 m. At this site around the Reserva Biológica San Francisco (RBSF; 1850 m) the diversity of plants (especially bryophytes and trees) and above-ground animals (especially birds, bats and arctiid and geometrid moths) has been investigated in detail indicating that the region indeed is a biodiversity hotspot for those taxa (Brehm 2005, Werner *et al.* 2005, Liede-Schumann and Breckle in press.). Only few taxa (e.g. ants) do not have their highest diversity in the mountain regions but instead their diversity is likely to peak in lower regions (Brehm *et al.* in press). However, a large number of taxa are not yet well investigated including amphibians, reptiles, molluscs, beetles, hymenopterans, dipterans and soil animal taxa in general. The abundance, diversity, community structure and functioning of soil animals were the topic of the present work.

Soil animals

Soil or litter dwellers, dominated by insects and arachnids, presumably comprise about 1/4 of all described living species of the world (Decaëns *et al.* 2006). Even most above-ground animal species of terrestrial habitats are soil inhabitants for at least one stage of their life cycle. Soil animals are important components of all terrestrial ecosystems, in many, such as base rich forests, consuming virtually all of the litter material. By consuming dead organic material they affect litter decomposition, nutrient cycling and soil formation (Behan and Hill 1978, Moore *et al.* 1988, Maraun *et al.* 1998b).

Density of decomposer soil macrofauna, such as earthworms, millipedes and isopods, at our study site is low indicating that the quality of the organic material is not sufficient for maintaining populations of these taxa. Additionally, the pH at the study site is rather low (Wilcke *et al.* 2002, Soethe *et al.* 2006) which may also limit the distribution of decomposer macrofauna, in particular that of earthworms and isopods (Edwards and Bohlen 1996).

The density of soil microarthropods at the study sites was also low which is similar to other tropical mountain ecosystems (Plowman 1979, Holt 1985, Olson 1994). We suggest that the

low quality of the organic material in tropical mountain rain forests is the most important factor for the low densities of soil microarthropods. The low pH is probably not detrimental for the soil microarthropods since they occur in high densities in base-poor temperate forests (Maraun and Scheu 2000). In addition of being generally low, the density of microarthropods declined with altitude which supports the assumption that resource quality is of prime importance for soil microarthropods since the quality of the organic material as indicated by the C-to-N ratio declines with altitude. Low temperatures, high precipitation and waterlogging may additionally be detrimental for soil microarthropods at high altitudes.

Oribatid mites are the dominant group of microarthropods in temperate and tropical forest soils. Their species number is high (10,000 described species) and their abundance in most forest ecosystems is also high (up to 200,000 ind./m² in base-poor forests). Oribatid mites contribute to decomposition processes and nutrient cycling by feeding on dead plant material, microorganisms and by dispersal of microbial propagules (Behan and Hill 1978, Moore *et al.* 1988, Maraun *et al.* 1998b).

At our study site 193 species/morphospecies of oribatid mites from 48 families were recorded; some of them new to science (e.g. Niedbala and Illig 2007a,b). This diversity is high but not extraordinary high; similar numbers have been recorded from the Central American Cordillera de Talamanca (165 species; Schatz 2006). Therefore, oribatid mites are a species rich taxon at our study sites but do not form a hyperdiverse taxon such as geometrid and arctiid moths (Brehm *et al.* 2005, Fiedler *et al.* 2007, Maraun *et al*. 2007b). The proportion of undescribed oribatid mite species is estimated to be about 40 %, but may be higher due to a high number of rare species. Many species are restricted to tropical regions indicating specific community structures in the tropics. Indeed, the community structure in the studied mountain rain forests differed markedly from that in temperate forests, in particular derived groups of oribatid mites, such as Poronota and Pycnonotic Apheredermata, dominated indicating that they are well adapted to the biotic and/or abiotic conditions in tropical mountain rain forests. Furthermore, the oribatid mite community differed along the elevation gradient from 1850 to 2270 m indicating distinct oribatid mite communities at different altitudes. At the larger gradient in particular the ptyctimous mite fauna differed strongly between Bombuscaro (1000 m) and Cajanuma (3000 m).

In general, the diversity of soil decomposer animals is not well understood (Anderson 1975b, Maraun *et al.* 2003a). Especially the high local diversity has often puzzled soil ecologists since it points to the existence of a large number of niches on a very small scale (i.e. on one square meter of soil there may be up to 1000 soil animal species; Wardle 2002).

Since decades researchers have tried to identify the niches of the different oribatid mite species (and those of other decomposer taxa); only a limited number of microhabitats have been shown to be function as niches, e.g. the bark of trees (Behan-Pelletier and Winchester 1998). However, in our study the oribatid mite community on bark did not differ significantly from the community in soil. This suggests that microhabitat differences between the soil and the bark of trees in tropical mountain rain forests are less pronounced than in temperate forests (Aoki 1973, Proctor 2002, Lindo and Winchester 2006, Erdmann *et al.* 2006).

In our study the density of oribatid mites was similar to that of other tropical forests (Plowman 1981) but lower than in most temperate forests (Maraun and Scheu 2000). Generally, according to Giller (1996) density of soil microarthropods in the tropics is lower than in temperate regions. The density of oribatid mites was about 34,400 ind. m^{-2} at 1000 m and decreased further to 20,000 ind. m^{-2} at 2000 m and to 5,400 ind. m^{-2} at 3100 m. This decline was particularly unexpected since the thickness of the organic layers increases with altitude and in temperate forests the density of microarthropods increases with the thickness of the organic layers (Maraun and Scheu 2000). Low densities of microarthropods are probably caused by low temperatures and/or higher temperature fluctuations at higher altitude. Also, low quality litter associated with lower microbial biomass at higher altitudes is likely to contribute to lower densities of microarthropods.

Analysis of the natural variation in stable isotope ratios in animal tissue has shown to be a powerful tool for evaluating the trophic structure of animal communities (Minagawa and Wada 1984, Post 2002, McCutchan *et al*. 2003, Vanderklift and Ponsard 2003). Trophic niche differentiation of 32 microarthropod (mainly oribatid mite) species from *G. emarginata* litter at the RBSF forest as investigated by stable isotope ratios ($^{15}N/^{14}N$) suggests that they form a gradient from primary and secondary decomposer to predators and scavengers (four trophic levels/feeding guilds). The trophic structure of the microarthropod community in the studied mountain rain forest therefore is similar to temperate regions (Chahartaghi *et al*. 2005, Schneider *et al*. 2004). However, in contrast to temperate forests, a number of previously assumed ‘decomposer’ animals were in fact predatory or necrophagous, probably feeding on nematodes or animal carcasses.

Litter decomposition

Decomposition rates at the studied tropical mountain rain forest were generally low (average of 32 % y^{-1}) and resemble those observed by Tanner (1981) and Weerakkody and Parkinson (2006). Low litter quality (high C-to-N ratio) and low temperatures are two possible factors that may be responsible for the low decomposition rate in the studied tropical mountain rain forest. The slow litter decomposition at the study site is similar to that of beech litter in temperate forests (Anderson and Swift 1983, Albers *et al.* 2004). Presumably, similar low decomposition rates are caused by functionally similar decomposer communities developing on low quality litter despite being of very different taxonomic affiliation.

Litter types decomposed slower at higher elevation resulting in an accumulation of organic matter at high altitudes. Litter with low N concentration generally decomposes slower than litter with higher N concentration (Taylor *et al.* 1989). In general, the C-to-N ratios of litter materials increase with altitude (Leuschner *et al.* 2007). However, it is not known if the low nitrogen content at high altitudes is a consequence of the adaptation of the trees to high altitude (high level of nitrogen withdrawel into the tree before litter fall) or if it is a consequence of the plant life style (presence of thick and sclerophyllic leaves at high altitudes). Meentemeyer (1978) and Aerts (1997) provided evidence for the dominance of climate over chemical factors as major determinants of decomposition rates in ecosystems ranging from the arctic to tropical forests. Similarly, at a regional scale, Vitousek *et al.* (1994) found a strong relationship between decomposition rates and elevation (and hence mean annual temperature) on the slopes of the Mauna Loa volcano (Hawaii). Wilcke *et al.* (2002) assumed that increased waterlogging as well as lower temperatures inhibit the decomposition of organic matter at higher elevation of the studied mountain rain forest. However, the effects of temperature on decomposition rates (Q_{10}) between the studied sites at 1850 m and 2280 m were lower than in other litter materials (Vitousek *et al.* 1994). We conclude that the decomposition rate is triggered by lower litter quality together with lower temperatures and higher humidity at high altitudes.

The effect of litter type and litter mixing on decomposition processes

P. nutans litter after 2 and 6 months of exposure decomposed slower than that of *G. emarginata*, but not at the end of the experiment, after twelve months. We suggest that litter chemistry affect decomposition mainly at early stages of decomposition. Loranger *et al.* (2002) also concluded that litter decomposition in tropical forests is correlated with litter chemical parameters at different stages of decomposition. In tropical rain forests moisture is

generally not a limiting factor for decomposition processes. Therefore, the quality of the decomposing resources likely is the bottleneck for decomposition pathways and dynamics at least at early stages of decomposition. After a period of twelve months, the decomposition rate of the mixed litter treatment was higher than that of the single species treatments. This hints to a positive and "non-additive" response. Non-additive effects of mixing of litter for litter decomposition have been observed in 67% of the studied litter mixtures (Gartner and Cardon 2004); mass loss is often increased when litters of different species are mixed (see Anderson *et al.* 1983). Compared to single litter types mixed litter types contain a more complex decomposer community and this likely contributes to faster decomposition rates. However, since the time-scale of the experiment was limited (twelve months), longer lasting experiments are needed for evaluating the long-term effects of litter mixing on decomposition processes. This is particularly important in tropical regions, such as the studied mountain rain forests, where tree diversity and therefore the diversity of litter materials entering the decomposer system is exceptionally high.

Changes in litter decomposition by microarthropods

The densities of microarthropod in the litterbags were generally low. As discussed above, lower microarthropod densities at the studied mountain rain forests comparison to temperate deciduous forest ecosystems (Maraun and Scheu 2000) are due to low litter quality. Microarthropods in the litterbags were more abundant at 1850 m than at 2280 m. We assume that this is due to lower temperatures at higher altitudes. It has been shown that the richness and abundance of invertebrate species in the tropics declines with elevation (Janzen *et al.* 1976, Olson 1994, Richardson *et al.* 2005). This suggests that the importance of physical factors for structuring soil arthropod communities are becoming more important at higher altitude.

The density of microarthropods in total did not differ between litter types, however, the density of Collembolans, Uropodina, and Prostigmata + Astigmata was lower in *P. nutans* litter at 1850 m indicating more sensitive responses to low quality substrate under specific (more favourable) environmental conditions.

Similar decomposition of litter materials in litterbags of different mesh size (48 µm and 1 mm) suggest that microarthropods affect the decomposition of litter at the studied mountain rain forests only little. Unexpectedly, the data suggest that microarthropods reduced litter decomposition at 1850 m. This indicates the relevance of altitude, i.e. changing environmental factors, for the effects of decomposers on litter decomposition processes. In part, these

differential effects might be due to changes in microarthropod density. Indeed, as discussed above, microarthropods were more numerous at 1850 m than at 2280 m. The high number of microarthropods at 1850 m may have reduced fungal densities and thereby decreased litter decomposition rates. In contrast, lower grazing rates at 2280 m of fungal hyphae by microarthropods may increase fungal growth and accelerate decomposition. Lensing and Wise (2006) also found no consistent effect of arthropods of different size on litter decomposition rates within different rainfall treatments; however, they assumed that the frequency of heavy rainfall is important.

At the studied mountain rain forest primary decomposers, i.e. litter feeding species, were rare but densities of secondary decomposers were high suggesting that soil animals may affect decomposition processes at later stages of decomposition. Indeed, Joo *et al.* (2006) found an increasing effect of microarthropods on the decomposition rate of needle litter, from 12 % in the first year to 21 % in the second year. However, microarthropods feeding on the microfauna (i.e. protozoa and nematodes) may compensate effects of microbial feeders on litter decomposition resulting in difficulties to measure the real impact of microarthropods on decomposition processes.

Colonization of litterbags by oribatid mites

With respect to the higher diversity of oribatid mites and the higher density of juvenile oribatid mites after 12 months we conclude that oribatid mites usually exhibit a K-style life history strategy (Norton 1994). Since soil microarthropod communities respond to land management on both local and regional scales (Minor and Cianciolo 2007), microarthropods in tropical mountain rain forests may function as bioindicators (Behan-Pelletier 1999, Lavelle *et al.* 2006). However, oribatd mites presumably are of limited use as bioindicators due to the generalistic life style of most species.

High biodiversity may be due to the presence of a high number of microhabitats (e.g. litter types), but results of the present study and from temperate forest ecosystems suggest that the diversity of decomposer animals is only little affected by the diversity of leaf litter types. Wardle *et al.* (2006) also concluded that most soil animal species are generalists in terms of feeding and habitat preference and therefore rather unresponsive to changes in the availability of resources due to litter mixing.

As indicated by a number of studies the abundance of decomposers is more important for decomposition processes than their diversity (Hansen and Coleman 1998, Kaneko and Salamanca 1999, Wardle *et al.* 2002, Schädler and Brandl 2005, Hättenschwiler *et al.* 2005).

In line with these findings, the trophic structure of the decomposer community of the studied mountain rain forest also indicates high functional redundancy of microarthropod species (Illig *et al.* 2005). Furthermore, studies on grassland decomposer systems by Cragg and Bardgett (2001) suggest that changes in the diversity of the decomposer fauna do not alter decomposition processes in a predictable way.

Prospects

The diversity of oribatid mite species in the studied tropical mountain rain forest was high (193 species). However, the diversity was not as high as that of other taxa such as birds, moths, epiphytes and trees. There are a number of explanations for this phenomenon. First, there may be a large number of cryptic species, i.e. species that can only be separated using molecular methods. Second, a large number of microhabitats may exist that have not been sampled in this study, e.g. the canopy. Future studies have to investigate these questions.

About 40 % of the species found in this study were new for science indicating that still a large number of species have to be discovered and described in the tropical regions, especially in tropical mountain rain forests.

Oribatid mite species numbers tended to decline with increasing altitude. This indicates that the number of different resources also declines with altitude. Additionally, the number of microhabitats may decline with altitude, and abiotic factors may also be more detrimental at higher altitudes. This topic deserves further attention in the future (Hammer and Wallwork 1979, Schatz 2006, Maraun *et al.* 2007).

The studied oribatid mite community was dominated by higher derived taxa which are mainly predators, scavengers or fungal feeders and reproduce sexually. This indicates that co-evolutionary forces between consumers (e.g. predators, fungal, lichen and algal feeders) and their resources have forced the taxa to maintain their ecological flexibility by reproducing sexually (Scheu and Drossel 2007). Further investigations are needed to investigate the patterns and reasons for the dominance of the higher derived sexual oribatid mites in tropical mountain rain forests.

Since larger predators of microarthropods were rare in the studied tropical mountain rain forest, soil microarthropods are unlike to be top-down controlled. Rather, microarthropod density is probably by the quality and quantity of resources. Since organic material is in ample supply at the studied tropical mountain rain forest, we assume that the quality of food is the most important factor for the low density of microarthropods.

A surprising result of the stable isotope analysis was that the number of primary decomposers (animals that feed mainly on litter) was low. The reason for this may be the fact that primary decomposers are limited by the availability of nitrogen (Yoneyama *et al.* 1997). To understand the factors that are responsible for the lack of primary decomposer taxa in the tropical mountain soil food web further studies are needed that investigate resource limitation.

Stable isotope analysis of this and other studies have shown that oribatid mite species span over about four trophic levels (Chahartaghi *et al*. 2005, Schneider *et al*. 2004). However, the exact food spectrum of these species is still not known. To allow deeper insight into the actual trophic niches of the decomposer species the analysis of fatty acid patterns of different soil animal species and a molecular study of their gut content is needed (Symondson 2000, Klamer and Baath, 2004; Ruess *et al.* 2005, Haubert *et al.*, 2006).

Litter decomposition in the studied tropical mountain rain forest was generally slow and decreased with altitude. High moisture and low litter quality may limit the decomposition process but more detailed studies including the nutrient content of the litter material at different stages of decomposition are needed. Since the effect of temperature on decomposition rate was rather low, precipitation (soil moisture) seems to be an important factor regulating decomposition processes. Manipulation of water supply may help to evaluate the importance of humidity on decomposition rates.

Results of the litterbag experiment indicated a non-additive effect of litter mixing on decomposition processes (mixed litter decomposed faster). Additional long-term experiments with more litter types from various functional groups are needed to confirm the hypothesis of litter interactions during decomposition processes.

In the studied tropical mountain rain forests necromass of roots contributes to the thickness of organic layers especially at higher altitudes (Moser *et al.* 2007). Presumably, harsh abiotic conditions and low animal and microbial activity are the main reason for the slow decomposition of dead root material. Compared with litter material dead roots must be of even lower quality.

Results of the litterbag experiment indicate that soil microarthropods in tropical mountain rain forests contribute little to litter decomposition. This is consistent with results of our food web studies suggesting that litter feeding soil meso- and macrofauna in these forests are rare. However, higher density and diversity of secondary decomposers as compared to primary decomposers suggest that soil animals may affect decomposition processes at later stages of decay. Exposure of litter for 12 month, as in the present study, may have not been long enough to evaluate the role of decomposers for litter decomposition in the studied tropical

mountain rain forest. Long-term studies are needed to investigate the effect of soil animals on decomposition processes.

Overall, the studied tropical mountain rain forests are nutrient poor systems which are limited by the availability of carbon, nitrogen and phosphorous. Carbon is probably more important for microorganisms whereas nitrogen may be more important for animals. Carbon and nutrient limitation in tropical mountain rain forests appear to be more severe than in tropical lowland rain forests. This nutrient limitation may be the most important factor for the high biodiversity of a large number of animal and plant taxa. However, soil animals are not as diverse as other animal groups supporting the view that the diversity of niches of soil invertebrates increases less towards the tropics than in aboveground invertebrates. Similar to aboveground invertebrates the density of soil animal species is low indicating that resources are in short supply, of low quality and difficult to access. Integrating belowground invertebrates into studies of tropical mountain rain forests may allow to uncover the different evolutionary forces shaping above- and belowground communities.

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1991 - 1992	Rettungsdienst (DRK) in Wald-Michelbach
Schulbildung	
1982 - 1991	Gymnasium (Überwald-Gymnasium) mit Abiturabschluss in Wald-Michelbach
1978 - 1982	Grundschule (Adam-Karillon-Schule) in Wald-Michelbach
Berufliche Tätigkeiten	
3. - 10. 2003	Wissenschaftliche Hilfskraft der TU-Darmstadt (AG Scheu): Forschungsreise nach Ecuador mit Etablierung von Freiland-Vorversuchen
11. - 12. 2001	Wissenschaftliche Hilfskraft der TU-Darmstadt (AG Scheu): Bodenwasseranalyse, Extraktion und Bestimmung von Oribatiden (Acarina)
Sommersemester 1998, 1999	Studentische Hilfskraft im FB Biologie der TU-Darmstadt: Betreuung der zoologischen Bestimmungsübungen
8. 1997 - 2. 1999	Auswertung zytogenetischer Präparate (Chromosomenaberration) bei RCC (Cytotest Cell Research GmbH), Roßdorf

6.- 8. 1995	Biologische Schädlingsbekämpfung bei der Kommunalen Aktionsgemeinschaft zur Bekämpfung von Stechmücken (KABS), Darmstadt

Fortbildungen

26. - 30.7. 2004	5th Symposium of the European Association of Acarologists (EURAAC): Berlin, Germany
13. - 15.6. 2003	5. GEO-Tag der Artenvielfalt im Nationalpark: Harz/Hochharz, Germany
9. - 13.6. 2003	96. Jahresversammlung der Deutschen Zoologischen Gesellschaft: Berlin, Germany

Tagungsbeiträge

14. - 16.3. 2001	17. Jahrestreffen der AG Bodenmesofauna: Gießen, Germany. "Funktionelle Reaktion, Intra-Gilde-Prädation und Kannibalismus bei *Pergamasus septentrionalis*"
26. - 28.9. 2003	4. Milbenkundliches Kolloquium: Greifswald, Germany. "Hornmilben (Oribatida) aus einem tropischen Bergregenwald in Süd-Ecuador"
6. - 9.4. 2005	21. Jahrestreffen der AG Bodenmesofauna: Göttingen, Germany. "Struktur und Funktion der Oribatida eines tropischen Bergregenwaldes (Ecuador) "
14. - 17.11. 2005	III Congreso de Conversacion de la Biodiversidad de los Andes y de la Amazonia:Loja, Ecuador. "Pattern and causes of soil microarthropod diversity in a tropical mountain forest in Ecuador"
18. 11. 2005	Conferencia sobre "Functionalidad del Bosque Tropical de Montana en el Sur del Ecuador": Quito, Ecuador. "Microarthropods en un bosque tropical de montana del Sur del Ecuador"
21. - 24.2. 2006	19th annual gtö meeting Connecting microbes, plants, animals and human impact: Kaiserslautern, Germany. "Effect of microarthropods on decomposition of two litter types (*Purdiaea nutans*, *Graffenrieda emarginata*) in a tropical montane rain forest in southern Ecuador"
21. - 26.8. 2006	XIIth International Congress of Acarology: Amsterdam, Netherlands. "The oribatid mites of a tropical montane rain forest in Southern Ecuador"

Eidesstattliche Erklärung

Hiermit versichere ich an Eides statt, dass ich die vorliegende Arbeit ohne fremde Hilfe angefertigt habe und mich keiner anderen als die von mir angegebenen Schriften und Hilfsmittel bedient habe. Kapitel 2 wurde unter Federführung von Dr. Gunnar Brehm von allen Autoren gemeinsam verfasst. Der Großteil der Daten, Ergebnisse und Diskussion von Kapitel 3 entstanden aus meiner Arbeit und wurden von mir gemeinsam mit Dr. Mark Maraun und Prof. Dr. Stefan Scheu zusammengefasst. Die Daten zu Kapitel 4.1. stammen von mir; die zugehörigen Publikationen wurden gemeinsam mit Prof. Dr. Wojciech Niedbała verfasst. Ich habe noch keinen Promotionsversuch unternommen.

Darmstadt, den 20.9.2007

Jens Illig