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GEOGRAPHIC VARIATION OF HABITATS IN COSTA RICAN VELVET WORMS (ONYCHOPHORA: PERIPATIDAE)

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ABSTRACT.- Habitat characteristics were compared for 20 onychophoran localities in Costa Rica, from the seasonally dry western Pacific forest to the rainforests of the Caribbean. Everywhere, rainfall is more variable than temperature and than relative atmospheric humidity. A microhabitat study of *Epiperipatus biolleyi* Bouvier, 1902 was done for comparison with the only other species for which equivalent data are available, the Brazilian *Peripatus acacioi*. The Costa Rican species was found (1) in sandy, not clay rich soil, (2) closer to the surface and (3) in burrows whose temperature is more similar to the external air temperature. For both species the soil humidity (mean 35 %) and acidity (pH=5.2-6.2) were similar. The *E. biolleyi* population density was 0.25 individuals/m^2. No clearcut trends in associated flora and fauna were found. In the laboratory, the animals preferred rotten to non-rotten wood, and water-soaked soil to oven-dried soil, during periods of inactivity.

KEY-WORDS.- Onychophora, Habitat, Biogeography, Ecology

RESUME.- Sont comparées les caractéristiques des habitats de 20 localités à Onychophores dans le Costa Rica, depuis la forêt sèche saisonnière du Pacifique occidental jusqu'à les forêts humides de la région Caribe. Globalement, la pluviosité est plus variée que la temperature et l'humidité relative. Une étude du microhabitat de *Epiperipatus biolleyi* Bouvier, 1902 est réalisée comparativement à la seule autre étude disponible, pour laquelle les données sont équivalentes, c'est-à-dire celle de l'espèce brésilienne *Peripatus acacioi*. L'espèce du Costa Rica a été trouvée (1) dans des sols arenoux, pauvre en argile, (2) plus près de la surface et (3) dans des cavités où la temperature est davantage similaire à celle de l'air extérieur. Pour les deux espèces l'humidité du sol (moyenne 35%) et l'acidité (pH=5.2-6.2) était similaires. La densité de population de *E. biolleyi* est de 0.25 individus/m^2. Aucun trait clairement défini n'a pas été observé en association avec la flore et la faune. Au laboratoire les animaux préferent des bois pourris au bois non-pourris, et des sols trempés à des sols très secs, ceci pendant les périodes d'inactivité.

MOTS-CLÉS.- Onychophora, Habitat, Biogéographie, Ecologie

INTRODUCTION

Onychophorans ("peripatus" or "velvet worms") are famous for their rarity and morphological conservatism (BOUVIER, 1905; RUHBERG, 1985). Their main habitat is the dark forest floor, where humidity is high and temperature relatively constant. MANN (1951) generalized that animals found in this type of habitat tend to be slow, parthenogenic, detritivores, have flattened bodies and move by legs. Onychophorans fit the generalization, except that only one species is known to be parthenogenetic (READ, 1985) and that they are predatory. Other authors suggest that parthenogenesis is associated with unpredictable environments, but there is no general agreement (HAMILTON, 1967; LOURENÇO and CUELLAR, 1994).

For most onychophoran species, ecological information is limited to a few natural history comments on collectors' labels. The two exceptions are a general description of the habitat occupied by *Peripatus acacioi* (LAVALLARD *et al.*, 1975) and preliminary ecological observations about *Macroperipatus torquatus* (READ, 1985; READ and HUGHES, 1987). Nevertheless, the scarcity of these animals makes most attempts at ecological study difficult, and little has been added to the early conclusions by CLARK (1915) that uniform temperature and high humidity are important biogeographic factors (MONGE-NAJERA, 1994a). Furthermore, the literature on onychophorans is difficult to obtain, hiding such surprising observations as daytime migrations and probable predation by fishes during floods (CARVALHO, 1942).

This paper considers the geographic variation in Costa Rican onychophoran habitats and presents quantitative habitat data for *Epiperipatus biolleyi* Bouvier, 1902.

MATERIAL AND METHODS

STUDY AREA AND FIELD SAMPLING

Climatic data for Costa Rican localities were provided by the government's Instituto Meteorológico Nacional database. They represent the majority of the sites for which specimens (mostly unidentified) occur in the Costa Rican collections (Fig. 1).

The study site is cattle grassland with patches of secondary "very moist forest" (MONGE-NAJERA *et al.*, 1993) between Las Nubes and Cascajal, Coronado, San José, Costa Rica (83°57'37" W, 10°00' 18" N).

During the 1992 rainy season, 16 square meter quadrats in a 200 m^2 area were selected with a random number generator to extract all the macroinvertebrates that could be captured manually in 10 min (animal sampling could only be done in ten quadrats). Although manual extraction is an usual procedure in onychophorology (LAVALLARD *et al.*, 1975; RUHBERG, 1985), 80 cm^3 of soil from quadrat centers were preserved in alcohol to extract the microinvertebrates visible at 10 X that were missed by manual extraction. Vegetation was collected from a 20x20 cm square in each quadrat and another soil sample (aproximately 500 g) was extracted from ten quadrats for analysis in a commercial laboratory, after separating subsamples in each for moisture analysis. Flora, fauna and soil characteristics were compared for quadrats with and without *E. biolleyi*.

LABORATORY TESTS

To supplement previous tests (MONGE-NAJERA *et al.*, 1993), choice experiments were done with 11 freshly collected individuals (length in alcohol: 1.6–4.2 cm) which had not participated in the original test series. The hypotheses were that (1) they are unable to distinguish moisture levels in the dark, (2) they are attracted to the smell of mosses and (3) they prefer rotten wood. The tests were as follows:

1. Petri dishes with the bottom covered with soil, the water-saturated half isolated from the dry half by a low plastic wall.

2. A plastic 12x8 cm (x6.5 cm high) terrarium with crumpled filter paper 3 cm deep, one half moisted with moss macerate and the other half with distilled water.

3. The same terrarium, provided with two pieces of water-saturated wood, one rotten and the other in good condition.

The animals were placed individually in the central part of the petri and allowed to move to either half; the choice was recorded after 15 min. All tests were done in darkness and repeated five times with each onychophore (individual variability was recorded considering the possibility of habituation). Moss, soil and wood originated from the natural microhabitat of the species.

A previous evaluation with controls had shown that the methods were appropriate (MONGE–NAJERA *et al.*, 1993).

Voucher specimens are deposited as follows:

Plants: Herbario, Escuela de Biología, Universidad de Costa Rica, San José, Costa Rica.

Onychophorans: Instituto Nacional de Biodiversidad (INBio), Heredia, Costa Rica; Museo de Zoología, Universidad de Costa Rica (San José) and American Museum of Natural History, New York.

Other invertebrates: Museo Nacional, San José, Costa Rica.

RESULTS

HABITAT VARIABILITY AND MICROCLIMATE

The climatic patterns for habitats of Costa Rican onychophorans are of two types, Pacific (seasonal) and Caribbean (low seasonality). Despite this variability, in all sites moisture is high and rainfall is more variable than temperature and than relative atmospheric humidity (Fig. 1).

In Coronado *E. biolleyi* has been found (1) inside and under logs; (2) under moss covering soil, stones, stumps and the base of living trees; (3) under stones and (4) in soil crevices and microcaverns, often slightly contracted. In horizontal surfaces the worms are normally found in the upper 10 cm of soil. In road banks and other vertical surfaces, they are often near the horizontal ground on the base (W. Böckeler 1994 pers. com.).

At the begining of the rainy season of 1992 (11 am) the microsites where two onychophorans were found measured 18°C (soil microcavern at a depth of 10 cm) and 17.5°C (log microcavern) when the external air temperature was 18.5°C.

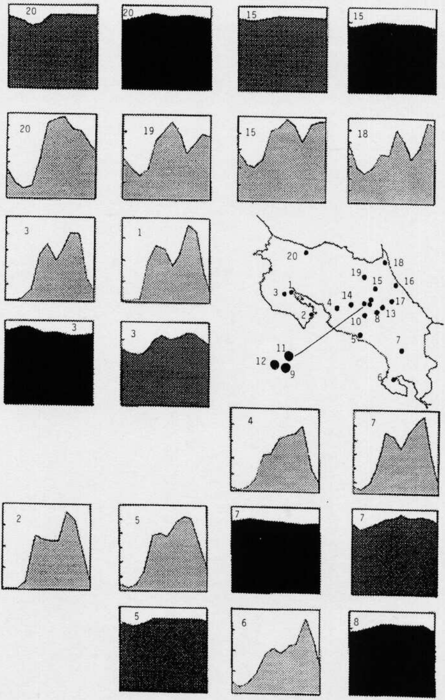
Although most animals are seen alone, clusters of as many as ten individuals have been found in a single stump. Once two were found intertwined in a soil microcavern. The population density was 0.25 individuals/m^2 (Fig. 2).

THE SOIL AND BIOTIC FACTORS OF HABITAT

The soil in Coronado is of volcanic origin. There were no differences in the soil samples from quadrats with and without onychophorans. All were franco–sandy and there were no statistically significant differences in % humidity and composition (MANN–WHITNEY U tests, Table I).

With the exception of two plants (Poaceae 4 and *Pilea* sp.) and chilopods, neither plant nor animal taxonomic composition appeared to be correlated with the occurrence of *E. biolleyi* in the quadrats (Tables II and III).

In the laboratory and excluding the cases in which the animal made no choice, there were significant preferences for moist versus dry soil and for rotten versus intact wood; the preference for moss extract over distilled water was not statistically significant (0.05 level, binomial tests, Table IV).



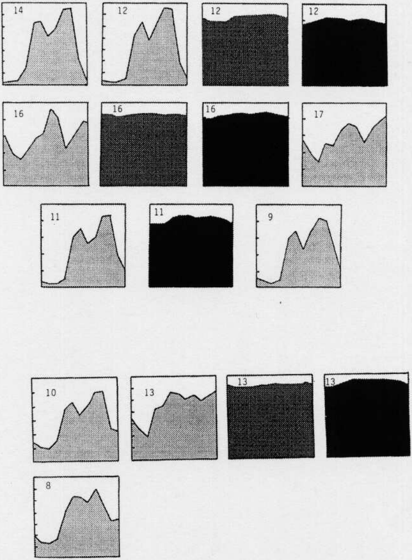


Fig. 1. Costa Rican localities where onychophorans have been found and yearly distribution of climatic parameters (numbers in climatograms refer to locality numbers in the map). Black: temperature in ^{o}C, gray: relative humidity (%), light gray: rain precipitation in mm. Maximum values in climatogram vertical axes: temperature 30 ^{o}C except in localities 8, 12 and 13 (where it is 25 ^{o}C); relative humidity 100 % in all localities; rain precipitation 800 mm in locality (loc.) 6, 700 mm in loc. 18, 600 mm in loc. 4, 5 and 7, 500 mm in loc. 3, 9, 11, 15–17 and 19, 400 mm in loc. 1 and 2, 350 mm in loc. 8, 12–14 and 20, and 300 mm in loc. 10. Key to locality names and climatic classification in the HERRERA and GOMEZ (1994) biotic zone system (**co** cold, **dm** dry months, **te** temperate, **hu** humid, **sh** subhumid, **st** subtropical, **tr** tropical, **vh** very humid, **wds** without dry season). **Pacific slope**: **1** Barra Honda (tr tr sh 5–6 dm), **2** Curú, **3** Nicoya (locs. 2 and 3 as loc. 1), **4** Orotina (tr tr hu 5–6 dm), **5** Quepos (tr tr vh 3–4 dm), **6** Rincón de Osa (tr tr vh 1–2 dm), **7** Buenos Aires (tr tr hu 3–4 dm). **Central highlands**: **8** Cachí (te tr hu 1–2 dm), **9** Coronado (te tr hu 3–4 dm), **10** La Estrella (as loc. 8), **11** Rancho Redondo (te co tr hu 3–4 dm), **12** Sabanilla (te tr hu 5–6 dm), **13** Turrialba (st tr hu wds), **14** Turrúcares (tr tr sh hu 5–6 dm). **Caribbean slope**: **15** Guápiles (tr tr vh wds), **16** Parismina, **17** Siquirres, **18** Tortuguero, **19** Puerto Viejo (localities 16–19 as loc. 15), **20** Upala (tr tr hu 3–4 dm).

DISCUSSION

HABITAT VARIABILITY AND MICROCLIMATE

Although the results show that Costa Rican onychophorans are able to survive in habitats of contrasting precipitation seasonality and of very different temperatures, air humidity is similar in all. In comparison with the Costa Rican populations, the Brazilian *P. acacioi* occurs in harsher conditions, generally with less precipitation, as well as lower and more variable temperature. Only relative air humidity tends to be higher and more constant for *P. acacioi* than for some Costa Rican onychophorans.

The microhabitats where *E. biolleyi* has been found are typical of the phylum (BOUVIER, 1905; LAVALLARD *et al.*, 1975; RUHBERG, 1985).

In the soil this species has been found closer to the surface (upper 10 cm) than *P. acacioi* (20–50 cm deep, LAVALLARD *et al.* 1975), perhaps because the climate is less seasonal and extreme in this part of Costa Rica than in southern Brazil, although possible vertical migrations remain to be studied (LAVALLARD *et al.*, 1975; ENDRÖDY-YOUNGA & PECK, 1983).

The microhabitat of *E. biolleyi* was 0.5–1°C colder than the surface near noon, similar to the 1°C difference measured for *P. heloisae* (CARVALHO, 1942). In contrast, the burrows of *P. acacioi* may be 13.6°C warmer than the external air during cold periods (LAVALLARD *et al.*, 1975). The 17.5–18°C measured in Coronado are in the lower part of the range reported for the phylum (13.6–30°C, RUHBERG, 1985). The occurrence of clusters of animals (CARVALHO, 1942; LAVALLARD *et al.*, 1975; VAN DER LANDE, 1978), sometimes in physical contact, is thought to reduce climatic stress (RUHBERG, 1985; MONGE-NAJERA, 1995). It may help onychophorans colonize difficult microhabitats. In the laboratory, pairs of *E. biolleyi* showed physical contact half of the time (MONGE-NAJERA *et al.*, 1993).

The recorded population density of this species, which ranges from 0.25 through 2 individuals/m^2 (MONGE-NAJERA, 1995), is intermediate between the 0.037 and the 10 individuals/m^2 recorded in Trinidad and South Africa, respectively (Fig. 2). Density values can only be considered general guides until sampling methods become standard worldwide.

Adult females without visible embryos are a rare finding (BOUVIER, 1905), because neotropical females normally mate while young and store viable sperm through life (BOUVIER, 1905; MONGE-NAJERA, 1995).

THE SOIL AND BIOTIC FACTORS OF HABITAT

The relative climatic stability of the soil allows some onychophorans to survive important habitat modifications and even bushfires (VAN DER LANDE, 1978; ENDRÖDY-YOUNGA and PECK, 1983; MESIBOV and RUHBERG, 1991). The similarity of soil in quadrats with and without onychophorans suggests that texture and acidity were not important factors when the sampled animals chose their daytime resting sites, or simply that there were not enough individuals to occupy a greater variety of microhabitats. Nevertheless, the nature of this soil adds to RUHBERG's (1985) observation that many species occur in volcanic soils. In contrast with the predominance of clay in soils inhabited by *P. acacioi, E. biolleyi* was collected in sandy soil. The soil acidity range is surprisingly similar for both species (5.2–6.2 for *E. biolleyi*, 5.5–6.1 for *P. acacioi*;

Table I and LAVALLARD *et al.*, 1975). LAVALLARD *et al.* (1975) suggested that soil acidity was characteristic of the humus necessary to provide *P. acacioi* with appropriate humidity and food, because other vegetational and topographic clues failed to predict its occurrence. *P. acacioi* inhabits soil with 20.5–34.8 % humidity, lower than the mean 35 % recorded for *E. biolleyi*. The occurrence of microcaverns in the soil seems to be an important requirement because the animals apparently cannot excavate their own burrows (ENDRÖDY–YOUNGA and PECK, 1981; RUHBERG, 1985; MONGE–NAJERA *et al.*, 1993).

The results presented here seem to confirm collectors' impression that the taxonomic composition of vegetation is relatively unimportant in determining the spatial distribution of onychophorans (CLARK, 1915; RUHBERG, 1985; MESIBOV and RUHBERG, 1991; MONGE–NAJERA, 1994a). Nevertheless, because of economic limitations, it was not possible to obtain the larger sample needed for a firm conclusion. Field experience has shown that *E. biolleyi* is often found in soil associated with non–vascular plants, a limitation which does not apply to specimens collected in logs. Mosses are frequently reported by collectors as present where onychophorans were found (BRINCK, 1956; RUHBERG, 1985). Perhaps these and other non–vascular plants, as well as the soil burrows used by *E. biolleyi*, are associated with the early stages of ecological succession, a hypothesis that should be tested in the future.

Onychophorans may avoid the vicinity of ant colonies (CARVALHO, 1942; RUHBERG, 1985), but *Epiperipatus isthmicola* has been found in logs with such colonies (D. BRICEÑO, 1993 pers. comm.) and ants were more frequent in quadrats with *E. biolleyi* (Table III). Some Australian onychophorans are associated with termites (SCOTT and ROWELL, 1991). Again, my sample is too small for more definite conclusions about associations with other animals, but maybe there is a fauna associated with typical onychophoran microhabitats, rather than a fauna associated with the onychophorans themselves. B. MORERA (unpublished) has produced an interesting ecological diagram for the biota associated with *Epiperipatus hilkae* (Fig. 3). Although it was not possible to collect similar trophic data for the fauna associated with *E. biolleyi*, the energy flow pattern probably is similar in the microecosystem where it is found.

MICROHABITAT SELECTION

Behavioral experiments with onychophorans are problematic because the samples must often be small and proper experimental design is elusive (see ELIOTT *et al.*, 1993). These limitations apply to the following discussion.

There is evidence that the availability of hiding places in wood is more important for onychophorans than the condition of the wood (MESIBOV and RUHBERG, 1991), but experienced collectors believe that these animals prefer rotten wood in which to spend the daytime hours (RUHBERG, 1985). These results with *E. biolleyi* support that belief. If members of this species were attracted by the smell of moss (see MONGE–NAJERA *et al.*, 1993), the experiment would be biassed because rotten logs could have kept some moss smell despite careful cleaning, but the smell test only showed a non–significant preference for the moss extract. Besides, when ten individuals were put in a bag with moist moss and damp rotten wood during field collection, all hid in the crevices and canals of the wood.

In a previous experiment (MONGE–NAJERA *et al.*, 1993), this species showed some inability to distinguish small differences in moisture, but in this case where the choice was between extremes ("dry" vs. "water–saturated"), most animals moved to the moist section. Thus, the overall results are inconclusive and cannot be associated with differences in sex or size between the two samples, because such factors did not statistically correlate with most results, at least in the first study (unpublished reanalysis of data reported by MONGE–NAJERA *et al.*, 1993).

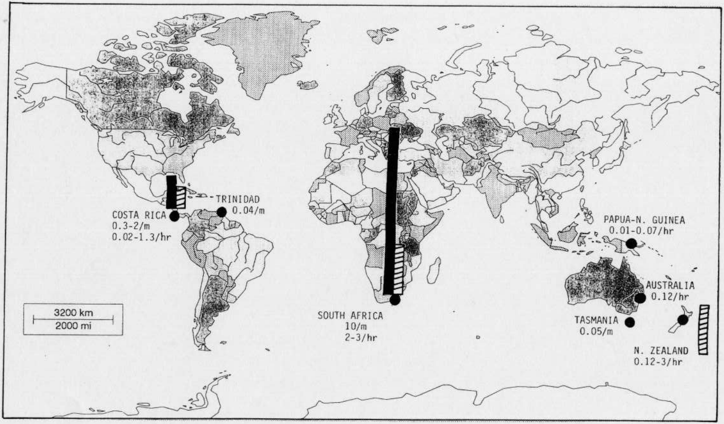


Fig. 2. Reported density of onychophorans in individuals/m^2 (black bars and numbers followed by "/m") and by collecting effort in number of specimens/hr/collector (hatched bars and numbers followed by "/hr") throughout the world (data from sources cited in MONGE-NAJERA 1995 and from van der LANDE 1993 pers. comm. and N. TAIT 1995 pers. comm.). The Papua-New Guinea numbers show the range if all searching days (0.01) or only those in which animals were found are included (0.07, V. van der LANDE 1994 pers. comm.).

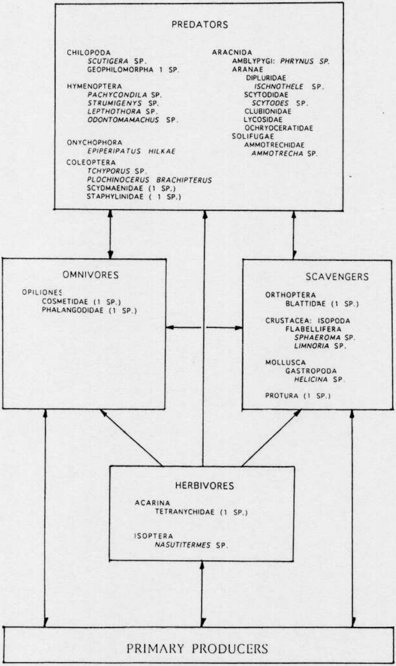


Fig. 3. Basic energy flow in the microecosystem of *Epiperipatus hilkae*. Half arrowheads refer to post-mortem consumption; additionally, predators may receive energy from plant material in prey digestive tracts and primary producers get some energy from dead animals. Based on specimens collected at Las Cascadas Forest, Barra Honda, Guanacaste, Costa Rica (10° 10' 45" N, 85° 20' 45" W). Premontane Wet Forest, Basal transition (Holdridge Life Zone System, Holdridge, 1967). Data source: B. Morera B., 1994 pers. comm.

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APPENDIX

Table I. Characteristics of soil from quadrats with (N=4) and without (N=6) *Epiperipatus biolleyi* in Coronado, Costa Rica.

	With				Without			
	X	SD	Mi	Ma	X	SD	Mi	Ma
Clay	4.2	1.79	3.0	7.0	4.2	1.79	2.0	6.0
Sand	70.6	3.36	67.0	74.0	69.8	2.59	67.0	74.0
Slime	25.2	4.21	19.0	30.0	26.0	2.91	22.0	29.0
Organic matter	7.8	1.23	5.8	8.8	8.0	2.11	6.1	0.8
pH	5.8	0.35	5.4	6.2	5.8	0.33	5.2	6.0
Humidity (%)	35.0	7.00	29.0	50.0	33.0	9.00	5.0	47.0

Key: X Mean, SD Standard deviation, Mi Minimum, Ma Maximum.

Clay, sand, slime and organic matter as %; all by standard agricultural procedures and classifications according to Centro de Investigaciones Agronómicas, Universidad de Costa Rica.

Table II. Proportion of quadrats* with each plant species and their relation with *Epiperipatus biolleyi* in Coronado, Costa Rica. N=16 quadrats.

PLANT	With *E.biolleyi*	Without *E.biolleyi*
Amaranthaceae: *Iresine* sp.	0.25	0
Acanthaceae: undet. sp. 1	0	0.08
Apiaceae: *Hydrocotyle* sp.	0	0.25
Asteraceae: *Gnaphalium* sp.	0.25	0.17
Asteraceae: undet. sp. 2	0.5	0.33
Commelinaceae: undet. sp.	0.25	0
Cyperaceae: undet. sp.	0.5	0.25
Equisetum sp.	0.25	0.08
Hepaticae: *Taxilegeunea* sp.	0.75	0.58
Marchantia sp.	0	0.33
Musci: *Fissidens* sp.	0.75	0.58
Oxalis sp.	0.25	0.17
Plantago sp	0	0.08
Poaceae: *Cynodon* sp	0.5	0.5
Poaceae: undet. sp.	2 0	0.08
Poaceae: undet. sp. 3	0.75	0.4
Poaceae: undet. sp. 4	1.25	0.25
Poaceae: undet. sp. 5	0.25	0.25
Pteridophyta: undet. sp.	0.5	0.17
Rosaceae: undet. sp.	0.75	0.25
Rubiaceae: *Spermacoce* sp.	0.25	0
Rubiaceae: undet. sp.	0.25	0
Selaginella sp.	0.75	0.33
Undetermined sp. 1	0.5	0.25
Undetermined sp. 2	0.25	0.33
Undetermined sp. 3	0	0.08
Undetermined sp. 4	0	0.08
Undetermined sp. 5	0	0.25
Undetermined sp. 6	0.25	0.08
Urticaceae: *Pileu* sp.	0.75	0.17

Total: 30 species

* Quadrats are used because the number of specimens cannot be reliably measured for some plant species. Proportion = number of quadrats with the plant species divided by total number of quadrats in each column (totals: "with" column: 4, "without" column: 12). Undet. = undetermined.

Table III. Fauna associated with *Epiperipatus biolleyi* in Coronado, Costa Rica (in mean number of specimens per quadrat*). The list is in alphabetical order and the taxa differ in rank.

TAXON	With *E.biolleyi*	Without *E.biolleyi*
Acari	0.33	0.14
Araneae	2	0.57
Blattaria	4	1.29
Chilopoda	2.33	0.14
Collembola	1	0.14
Coleoptera	1.66	0.29
Dermaptera	0.33	0.14
Diplopoda	2	0.86
Diptera	0.33	0
Formicidae	1.66	0.29
Gastropoda	1	0
Hemiptera	1.66	0.71
Hirudinea	0.33	0
Isopoda	9.33	2.71
Oligochaeta	11.3	2.71
Opiliones	2.67	0.86
Orthoptera	0.33	0.14

* N= 3 quadrats with and 7 without *E. biolleyi*.

Table IV. Results of laboratory choice tests with *Epiperipatus biolleyi*, in number of cases in which the option was selected by the experimental animals.

1- Moisture selection test (total 63 replications):	
Made no choice (i.e. stayed in middle of petri)	1
Chose the dry section of the petri	12
Chose the moist section of the petri	50
2- Smell selection test (total 54 replications):	
Made no choice (i.e. stayed in middle of petri)	7
Chose distilled water	17
Chose the moss extract	30
3- Wood selection test (total 55 replications):	
Made no choice (i.e. stayed in middle of petri)	9
Chose fresh wood	5
Chose rotten wood	41

Number of individuals that did not make the same selection in all test replications: Moisture test: 4 (out of 11), smell test: 11 (all), wood test: 7 (out of 10).