Micronesica 33(1/2):1-10, 2000

Soil Invertebrates of American Samoa

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Abstract—Soil invertebrates are largely responsible for building soil into the fertile matrix necessary for plant life, and, therefore, all animal life. Yet many of them, especially in the tropics and the southern hemisphere, are unknown. This is the first study to identify and quantify soil invertebrates in American Samoa. Pitfall traps and Berlese-Tullgren funnel extractions of soil cores were used between February 1998 and February 1999 to collect arthropods, gastropods, and turbellaria on three volcanic islands of the eastern Samoan archipelago in the south-central Pacific. The major groups collected were Acari, Amphipoda, Formicidae, and Diptera. A small number of these, and specimens from less common groups, were identified to species. The soil invertebrate composition was found to be largely a collection of species common throughout the South Pacific, usually dispersed through human commerce. Intense competition among these recently introduced species for niches relinquished by now-defunct, specially adapted indigenous species may be responsible for their much-reduced population densities, which in turn probably reduces the soil nutrient cycling efficiency for these islands.

Introduction

A census of soil invertebrates in natural environments is an important first step toward accessing the impact of agriculture on these environments. The types, numbers, and specific functions of soil organisms reflect the pedogenic status, vegetative successional patterns, and environmental perturbations of given sites (Dindal 1990).

Invertebrates are the biological foundations of every ecosystem. Soil invertebrates maintain the fertility and structure of soils and influence soil formation. The majority of soil invertebrates are found in the litter layer and in the top 5 cm of soils. They are usually grouped in aggregates of varying size and pattern, depending on species. Their numbers generally depend upon such factors as food availability, competitors, natural enemies, and temperature, moisture, and aeration levels (Edwards 1969).

Soil invertebrates are generally classified as either primary or secondary decomposers, according to their role in humus formation. Among the former are millipedes, wood lice, snails, fly larvae, springtails, oribatid mites, and earthworms. After unpalatable water-soluble materials have leached out of leaves, primary decomposers partially digest cellulose, keratin, and chitin while increasing the leaf tissue's area. Secondary decomposers, which are usually other species of springtails and oribatid mites, then flourish on the predigested material and accompanying microorganisms (Anonymous 1992).

Other invertebrates turn soil over by taking organic matter deep beneath the surface and bringing up subsoil. Earthworms, ants, termites, millipedes, wood lice, and gastropods turn over large amounts of soil by tunneling, which also helps aerate and drain compacted soils.

For some soil invertebrates, surveys in the tropics and the southern hemisphere are lacking. Faunal surveys of oceanic islands, in particular, may contribute to our understanding of biogeography and the impact of introduced species on island environments. Nearly half of the ants of Polynesia have been introduced by modern human commerce (Wilson & Taylor 1967). Consequently, many native invertebrates may have been replaced by an impoverished set of ant-resistant species. Loss of native invertebrates that served key functions in the natural community can have cascading effects that lead to severe disruptions of pollination, seed dispersal, and natural nutrient cycling with the subsequent loss of additional native plant and animal species (Wetterer 1997).

I used pitfall traps and Berlese-Tullgren funnel extractions of soil cores to collect soil invertebrates from a variety of habitats in American Samoa. Amphipoda, Diptera, Formicidae, and Gastropoda were the dominant groups in pit-fall traps; Acari and Formicidae were the dominant groups in Berlese-Tullgren funnel extractions. Nematoda were not included in this study, while Annelida are addressed elsewhere (Vargo 1999).

Most of the identified species are common throughout the region. Many of the ants have their origins in Africa and the New World tropics. These "tramp" ant species are exceptionally aggressive, prolific, and capable of profoundly influencing the composition of the faunal community by eliminating native keystone species. This suggests that the current composition of soil invertebrates in Samoa may be quite different from what it was prior to European contact over two centuries ago. Many native species may have been driven to extinction, making the present invertebrate composition a synthetic one composed of species from many parts of the world vying for niches that few, as generalists, can sufficiently exploit. This intense competition might account for the low population densities of the Samoan soil taxa. With such a short coevolutionary history, the present soil invertebrate composition may be unstable and, therefore, of special interest to evolutionists as well as ecologists.

Materials and Methods

I sampled from February 1998 to February 1999, mainly on Tutuila Island and once on Aunu‘u and Ta‘u Islands. These rugged volcanic islands lie between 14º10' and 14º25' S and between 168º and 171º W in the south-central Pacific Ocean. The hot, humid climate supports a variety of native tropical vegetation ranging from coastal strand, littoral scrub, and mangrove areas to montane and cloud forests (Whistler 1980). The highest elevation on Tutuila Island, Mt. Matafao, is 653 m; the highest elevation in the archipelago, Mt. Lata on Ta‘u Island, is 965 m. The climate is humid-tropical with over 3,000 mm of rain annually and an average year-round temperature of 26º C.

To minimize differences in invertebrate densities owing to differences in soil moisture levels, I collected soil cores only after at least 3 mm of rain fell for more than half the days over a two-week period. Specimens of the most common invertebrates were sent to experts for identification.

Twenty sites were selected for coring, primarily from undisturbed areas ranging from about 10 to 50 m^2. Twenty soil cores, 5 cm x 6.5 cm dia., were taken from a given site with a standard corer. Each core was placed, inverted, in a Berlese-Tullgren funnel made from a 7-cm dia. polypropylene Büchner funnel with five 1-cm dia. holes symmetrically arranged in the floor. The funnels were snugly inserted into a stage which was then placed in a box equipped with an overhead bank of 40 W lamps. These provided heat to slowly dry the soil from top to bottom, repelling mobile animals downward into jars containing 70% ethanol with a few drops of glycerol to retard evaporation (Edwards 1991; Ausden 1996). The upper rim of the jars was about 2 cm from the funnel base. For weakly aggregated soils, a single layer of coarse gauze was placed on the floor of the funnel in order to minimize soil, detached during drying, from falling into the jar. Closing the front panel rendered the box air-tight, except for small vents at the top. The closed box was divided into two sections by the stage. Air temperature in the upper section was maintained between 30 and 35º C by controlling the lamps with a variable transformer. The bottom section of the box was connected to an air conditioner via a 10-cm dia. duct. This gently forced 14º C air up through the floor of the funnels, further attracting animals downward. After 4 to 6 days the contents of each jar was filtered, and the specimens, remaining on the filter paper, were sorted by group and counted.

Stones or dense root mats prevented coring at three sites, so soil was collected with a hand trowel and treated as above. Owing to the undetermined area sampled, specimens were examined but not counted.

A pitfall trap consisted of a 7.5 cm x 11.5 cm dia. plastic tub buried to its rim and covered with a 25 cm dia. plate to keep out rain and debris (Ausden 1996). Plates were raised about 4 cm above the soil surface on spacers. Tubs were filled to 3 cm with ethylene glycol preservative and a few drops of detergent to reduce surface tension. Six traps, spaced about 3 m apart, were placed at six sites and checked after about 30 days. Pooled specimens from each collection were washed on a 2 mm-mesh sieve stacked atop a 0.85 mm-mesh sieve. Specimens from both sieves were sorted by group and counted.

Pitfall traps were also used to study the seasonal composition of the invertebrate community under a stand of timber tree, *Fleuggia flexuosa* (Muell. Arg.) Muell. Arg. (formerly *Securinega flexuosa*; **Poumuli** in Samoa). Twenty-one traps were spaced 3 m apart along a 3 x 7 grid and checked monthly for a year. Rainfall data, recorded daily at a nearby open area, was summed over the 30 days or so prior to each collection date. Abundance was expressed as "activity density" (AD), the mean number of specimens of a taxon captured by one trap for a standard period of 10 days (Lasinio & Zapparoli 1993).

Results and Discussion

Over 10,500 specimens were collected, about 5,100 by Tullgren funnel extraction and 5,400 by pitfall trapping. Taxonomic groups, ranked from highest to lowest in number of individuals, included Acari, Amphipoda, Formicidae, Diptera, Gastropoda, Gryllidae, Coleoptera, Isopoda, Collembola, Araneida, Hemiptera, Dermaptera, Chilopoda, Lepidoptera, Diplopoda, and Apocrita. Acari and Formicidae were the dominant groups in Berlese-Tullgren funnel extractions; Amphipoda, Diptera, Formicidae, and Gastropoda dominated in pitfall traps.

The majority of mites were Oribatida belonging to the families Galumnatidae, Carabodidae, Camisiidae (Figure 1), and Nanhermaniidae. Mites of the suborders Gamasida and Actinedida, which are principally predators, parasites, fungivores, or algavores, were less abundant. Mite density, as measured by Berlese-Tullgren funnel extraction of soil cores, was greatest under turf grass, particularly Siglap grass, and annual grasses near streams (Table 1). The shallow, fibrous roots of grasses provide an extensive rhizosphere capable of supporting large densities of mites. At near water-saturated conditions, such as in wetland taro and a marsh, mite densities were drastically reduced owing to flooding of soil macropores. The large sample standard deviations, relative to sample means, reflect the aggregated distribution of these arthropods.

Mt. Palapalaoa harbored more mites and fewer ants than the other three summits. It has a montane forest with a high diversity of native tree species. The summit of Mt. Lata is a cloud forest with a dense ground cover of grasses and a coarse-leaf climber, *Freycinetia* spp. (**Ie'ie**), and the summits of Mts. Matafao and Tau are montane scrub with ground covers of ferns, grasses, and sedges. Mite densities under *Rhus taitensis* Guillemin (**Tavai**) and *Barringtonia asiatica* (L.) Kurz (**Futu**) trees were considerably lower than under *Fleuggia flexuosa* (**Poumuli**) and *Pandanus tectorius* (**Lau fala**). *R. taitensis* and *F. flexuosa* are lowland forest trees, while *B. asiatica* and *P. tectorius* predominate in littoral forests.

Oribatid mites are one of the numerically dominant arthropod groups in the organic horizon, where densities in temperate soils commonly reach several hundred thousand individuals per square meter (Norton 1990). Never during my

Table 1. Densities of ants and mites under various vegetative covers.

	Ants m^{-2}		Mites m^{-2}	
Vegetation Type	x	s	x	s
Turf, Bermuda grass[a]	2 460	3 300	3 750	2 780
Turf, Bermuda grass			6 930	4 460
Turf, Siglap grass[b]	105	200	13 400	6 050
Taro, upland			1 700	940
Taro, upland	390	520	6 720	5 550
Taro, wetland			380	600
Summit, Mt. Matafao	1 580	3 840	1 020	840
Summit, Mt. Palapaloa	560	800	2 710	1 930
Summit, Mt. Tau	6 070	19 300	1 270	770
Summit, Mt. Lata	1 480	4 270	1 140	1 180
Stream bank, Malaota	270	440	4 690	11 400
Stream bank, Leafu	1 090	1 010	3 430	2 300
Marsh, Faimulivai	140	270	830	710
Forest, **Futu**[c]			330	380
Forest, **Poumuli**[d]			2 020	1 800
Forest, **Lau fala**[e]			2 670	1 840
Forest, **Tavai**[f]			380	600

"x" is the sample mean; "s" is the sample standard deviation; n = 20 in all cases.

[a] *Cynodon dactylon*; [b] *Zoysia* sp.; [c] *Barringtonia asiatica* (L.) Kurz; [d] *Fleuggia flexuosa* (Muell. Arg.) Muell. Arg.; [e] *Pandanus tectorius*; [f] *Rhus taitensis* Guillemin. (Whistler, 1984).

study did mite densities approach this value. The greatest density was under Siglap grass (13,400 mites m^{-2}) growing in sandy soil along the coast.

Abiotic factors generally delimit a species' distribution, while biotic factors generally determine a species' abundance. The stream bank soils contain 4 to 8 percent organic matter and the summit soils between 3 to 10 percent. All have moderately rapid permeability (Nakamura 1984). Food availability and aeration, therefore, should not be limiting factors, nor should temperature and moisture levels. Competition, predation, or some other biotic factor may be limiting mite densities in Samoa.

Several species of ants were collected in Berlese-Tullgren funnel extractions, including *Pheidole megacephala* (Fabricius), *Tapinoma melanocephalum* (Fabricius), and *Paratrechina* spp. These "tramp" ants associate with and are inadvertently spread by humans. Pitfall traps, however, contained almost exclusively one species–*Odontomachus simillimus* Fr. Smith–except near the coast, where the dominant species was *Anoplolepis gracilipes* (Jerdon) (formerly *A. longipes*) (Figure 1).

One remote peak, Mt. Taumata, yielded eight ant species within one square meter. These species, collected by aspiration bottle and by Berlese-Tullgren funnel extraction of leaf litter, were *Ponera incerta* (Wheeler), *Technomyrmex albipes* (Fr. Smith), *Strumigenys rogeri* Emery, *Pheidole oceanica* Mayr, *Solenopsis papuana* Emery, *Paratrechina minutula* (Forel), *Pa. vaga* (Forel), and

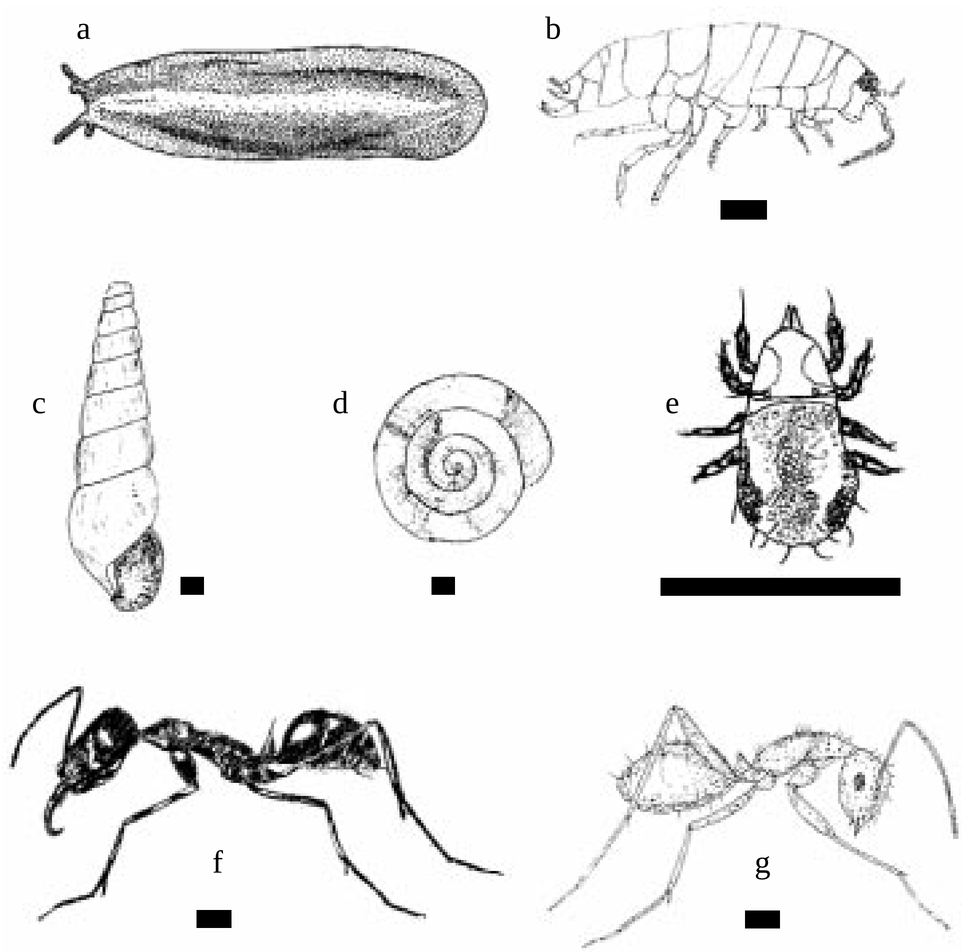

Figure 1. Some common terrestrial invertebrates of American Samoa include the following: (a) *Vaginulus plebeius* Fisher (Systellommatophora: Veronocillidae; (b) *Floresorchestia floresiana* (Weber) (Amphipoda: Talitridae); (c) *Subulina octona* (Bruguiere) (Stylommatophora: Subulinidae); (d) *Ovachlamys fulgens* (Gude) (Stylommatophora: Helicarionidae); (e) *Camisia* sp. (Acari: Camisiidae); (f) *Odontomachus simillimus* Fr. Smith (Hymenoptera: Formicidae); and (g) *Anoplolepis gracilipes* (Jerdon) (Hymenoptera: Formicidae). The bar beneath each figure corresponds to 1 mm.

O. simillimus. Such species-rich ant communities are not unusual if each species occupies a niche sufficiently different from the others. The more aggressive species dominates the others and forms the core of the community. In French Polynesia, a community of seven ant species, including *Ph. oceanica, S. papuana*, and *Pa. vaga*, was dominated by *Ph. oceanica* (Morrison 1996). *Ph. oceanica* might possibly be the dominant species, also, on Mt. Taumata.

A native amphipod, *Floresorchestia floresiana* (Weber 1892) (Figure 1), far outnumbered (AD = 180) other invertebrates collected in pitfall traps from a wet-

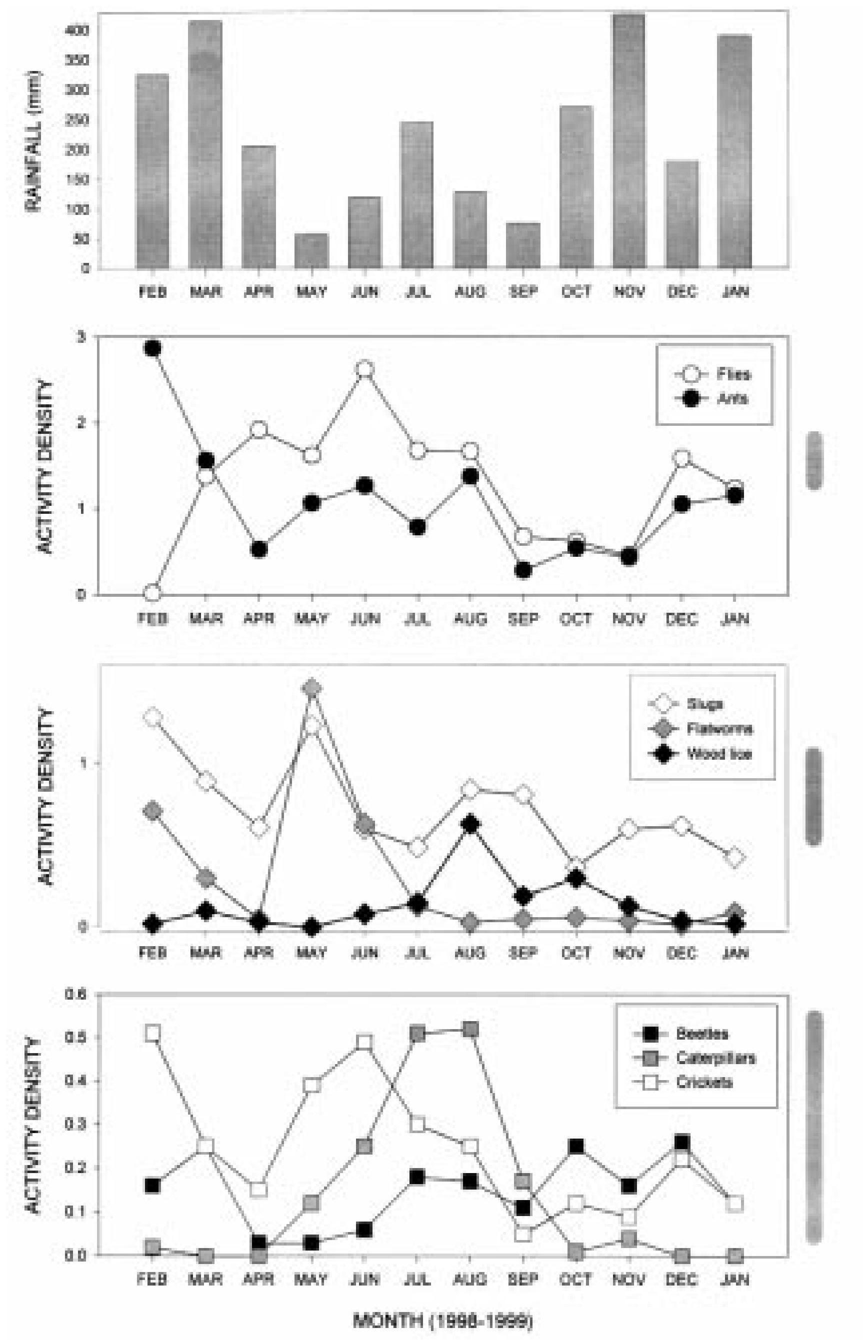

Figure 2. Rainfall data and Activity Densities for major taxa collected monthly from pitfall traps placed under *Fleuggia flexuosa* ("Poumuli" in Samoa). The gray bars on the right portray changes of the same magnitude on the three ACTIVITY DENSITY panels.

land area (**taufusi**) on Aunu‘u Island. This area is unique in all of American Samoa. It has been under the continuous cultivation of taro, *Colocasia esculenta* (L.) Schott, for more than 200 years (Uhrle, J., personal communication). Its soil is a sandy, carbonatic, isohyperthermic Typic Tropaquents (Nakamura 1984) with a high organic matter content due to mulching. Its freshwater table rests on a denser layer of sea water which fluctuates with the tide. Also abundant was a springtail that did not preserve well. Its pink cuticle was easy to see though difficult to count owing to fragmentation.

Another native amphipod, *F. anomala* (Chevreux 1901), was found at a density of 523 ± 610 individuals m^{-2} ($x \pm s$, n = 20) in soil cores taken along the bank of Leafu Stream, which flows through a long-established residential area. No amphipod was found along Maloata Stream, which drains a 1.9 km^2 forested watershed. The presence or absence of certain aquatic invertebrates often indicates the level of stream pollution. Amphipods suggest good to fair water quality (Newton, et al. 1998). Neither stream has been adequately sampled for water quality criteria, but the absence of known sources of pollution from the Maloata watershed would suggest that the absence of amphipods from Maloata Stream might be due to a factor other than water quality.

Flies and ants accounted for more than half the specimens collected during the year-round study under *F. flexuosa* (Figure 2). Many fly families were present, with Drosophilidae being dominant. In contrast, the ants were almost exclusively *O. simillimus*. Other arthropods, whose abundance exceeded 3% of the total catch, were crickets, beetles (mainly Carabidae and Staphylinidae), caterpillars, and wood lice.

The slug, *Vaginulus plebeius* Fisher (Figure 1), and an unidentified turbellarian flatworm were the major non-arthropods present. Two snails, *Subulina octana* (Bruguiere) and *Ovachlamys fulgens* (Gude) (Figure 1), constituted about 2% of the total catch in the year-long study. (The former dominated the catch of all specimens in pitfall traps from Mt. Palapalaloa.) Present individually at less than 3% of the total catch were spiders, earthworms (primarily *Pontoscolex corethrurus* (Müller)), true bugs, earwigs, centipedes, moths, millipedes, bees, and wasps.

Initial pitfall trap catches are commonly higher than subsequent catches owing to depletion of individuals (Joosse 1975). In my study this held true for ants, slugs, and crickets but not for flies, flatworms, wood lice, beetles, and caterpillars. Ignoring this “digging-in effect,” all, except beetles, had peak activity densities at some time during the drier months of May to August. Although this implies increased numbers of these invertebrates during the drier season, two other factors may be involved: invertebrates may be more mobile during this period or they may be drawn to moister conditions under the trap cover plate.

These invertebrates are primarily detritivorous or phytophagous. Drier conditions may force them to search for food or more favorable environmental conditions over a wider area. Consequently, the animals are more likely to encounter a trap, especially if they are attracted to the moister soil or the odor of ethylene glycol under the cover plate.

For beetles, peak activity density came in October and again in December. This lag may be a response of Carabidae and Staphylinidae, which are mainly predators, to increased numbers of prey.

Comparable data on the soil arthropod community in central Italy differed from my data in composition and abundance (Lasinio & Zapparoli 1993). Beetles (Carabidae and Staphylinidae), ants, and mites were the most abundant groups with much greater activity densities than the dominant groups in Samoa. For example, the peak abundance of Carabidae in Italy (AD = 35) was over ten times greater than the peak abundance of ants in Samoa (AD = 3).

As for mites, the relatively low numbers of larger invertebrates in Samoa may be due to a biotic factor. This, in turn, may be the consequence of human influence on the invertebrate composition.

Polynesian voyaging canoes first arrived in the Samoan archipelago from the west about 1000 B.C.E. (Kirch & Hunt 1988). Besides crops and domestic animals, they very likely carried an assortment of invertebrate stowaways. This heralded the initial assault on the natural island biota assembled since the islands emerged from the sea 2 to 3 million years ago.

The ants of Polynesia are unusual in that nearly half of the species were introduced into the region within the past 400 years (Wilson & Taylor 1967), coinciding with the advent of European exploration from the east. Some of these alien ants, such as *Ph. magacephala*, *A. gracilipes*, and *Paratrechina* spp., are known to transform entire biological communities (Wetterer 1997). Introduction of such keystone species had a much more serious impact on the native invertebrate fauna. Many native species may have been driven to extinction, directly or indirectly, by tramp ants and replaced by non-native ant-tolerant and ant-mutualist species.

Military exigencies during the Second World War and the introduction of one or many otherwise benign biological control agents since (Tauili‘ili & Vargo 1993) also influenced the current soil invertebrate composition into being a mainly synthetic assemblage of species that are widespread throughout the region. Having such short coevolutionary histories, Samoan soil invertebrates may be in strenuous competition for niches which few, as generalists, are suitably adapted to fully exploit. This might account for their unusually low population densities. Such a situation is necessarily in a state of flux and should be of great interest to evolutionists as well as ecologists.

Acknowledgments

I thank Makeati Utufiti, Lloyd Ali, and Raymond Tilialo for assisting in the collections. Specimens were identified by Sabina Swift (mites), Robert Cowie (molluscs), James Wetterer and Roy Snelling (ants), and Alastair Richardson (amphipods). This work was supported by a USDA grant, CRIS Accession No. 164128, administered by the American Samoa Community College.

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Received 14 June 1999, revised 20 Sep.