

Nematode Assemblages in Native Plant Communities of Molokai, Hawaii

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Abstract: Four native plant community types (in decreasing elevation: montane bog, rain forest, wet mesic forest, drier forest) on Molokai were sampled for nematodes. Six samples of 10 cores each were gathered from each community. Nematodes were extracted from 200 cm³ soil by elutriation. All extracted nematodes were counted and identified to species-level taxa. Sixty-seven species were identified among the four plant communities; only eight species occurred in all four communities. Species diversity and evenness were greater in the rain forest and mesic forest than in the bog and the drier forest, but the drier forest and mesic forest had similar species communities. The bog nematode community was not similar to the other three sites. In a presence/absence cluster analysis, all six bog sample assemblages clustered together. The rain forest samples also clustered together but were associated with the mesic forest sample closest to the rain forest edge. Of 11 nematode orders collected, Tylenchida accounted for 40% to 73% of all individuals, followed by Dorylaimida (5% to 17%). Diplogasterida were absent. No plant-parasitic nematodes of known Hawaiian agricultural importance or occurrence were collected in these native plant communities. Calculated nematode densities (76,000 to 321,300/m²) were comparable to those reported for some other Pacific tropical forests.

Key words: biodiversity, biogeography, bog, community structure, cluster analysis, diversity, Hawaii, island, Molokai, nematode, rain forest, survey.

The Hawaiian island chain is recognized as an important biological laboratory for the study of biotic dispersal, speciation, and biogeography (Carlquist, 1970; Gressitt, 1963; Juvik and Austring, 1979; Zimmerman, 1970), but little attention has been paid to these aspects for soil-dwelling nematodes. Few records exist of nematodes collected from indigenous Hawaiian plant communities (Andrassy, 1986; Cohn and Sher, 1972), although much attention has been devoted to the phytoparasitic nematodes of coffee, pineapple, sugarcane, and other important Hawaiian crops (Caswell and Apt, 1989; Holtzmann, 1968; Schenck and Schmitt, 1992; Tashiro et al., 1977). The nematodes typically found in Hawaiian agroecosystems include *Meloidogyne incognita*, *M. javanica*, *Pratylenchus* spp., *Radopholus similis*, and *Rotylechulus reniformis*. These taxa are common, global species that likely have been dispersed by human activity.

In 1991 we conducted an extensive survey of nematodes in native plant communities of the islands of Hawaii, Kauai, Maui, Molokai, and Oahu. The goals of this survey were to determine if nematodes in undisturbed Hawaiian plant communities differed from those in agricultural sites and whether aggressive crop pests were spreading into native vegetation, and to study the relationship of nematode assemblage composition to plant communities. The objective of this research was to de-

termine the biodiversity of nematode assemblages in a series of plant communities on the island of Molokai.

MATERIALS AND METHODS

Sampling sites: Soil samples were collected from four distinct plant community types in the Kamakou Nature Preserve, Molokai, Hawaii. The sites descended in elevation from bog to relatively dry forest (approximately ESE to WNW: N21°07'08" W156°53'50" to N21°07'50" W156°55'10") and were linked by the Pepe'opae trail. The highest site was Pepe'opae (elevation 1,280 m), a cool, montane bog overlaid with a dense, 1-m-thick cover of ferns and dwarfed woody plants, especially 'ō'hia (*Metrosideros polymorpha* Gaud.) and pukiawe (*Styphelia tameiameia* (Cham. & Schlectend.) F. v. Muell.). Below and sharply demarcated from the bog was rain forest (1,250 m) that received constant runoff from the bog. Vegetation consisted mostly of tree ferns (*Cibotium* spp.) and arborescent 'ō'hia covered with epiphytic mosses and ferns. The third site, below the rain forest, was a wet mesic forest (1,190 m) dominated by 'ō'hia and *Cheirodendron trigynum* (Gaud.) A. Heller, with an open, mixed tree fern and hau (*Hibiscus tiliaceus* L.) understory. The lowest site (1,005 m) was superficially similar to the wet mesic forest but was more open, slightly drier, lightly disturbed by tracked machinery, and contained an additional understory tree, *Pelea* sp.

Enumeration: Nematode samples were collected 5 August 1991 from six locations within each plant community. At each location, 10 to 12 soil cores (2.5-cm diam. × 20-cm deep) were taken in a circular pattern about 1.5 m in diam. Dominant vegetation was identified on site, by reference to photographs taken at the time of sampling, or by plant samples. In the laboratory, each soil sample was mixed thoroughly and nematodes were separated from 200 cm³ with elutriation (Byrd et al., 1976) and centrifugation (Jenkins, 1964). All specimens from each sample were fixed in hot 4% formalin, processed to glycerol (Seinhorst, 1959), mounted on slides, counted, and identified to species-level taxa.

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Most specimens did not fit currently described species and were categorized simply as morphospecies 1, 2, 3, etc.

Analysis: Nematode population densities were calculated by pooling counts from all samples within each site and extrapolating these sums to nematode density per square meter, assuming a 0–20-cm depth. Basic community indices (Shannon-Weiner diversity index, H' , and evenness, Hill's ratio $E5$) were calculated for each site (pooled data), and each sample within a site (for H' , MVSP Plus 3.1, Kovach Computing Services, Pentraeth, Wales; for $E5$ components, Ecological Methodology 5.1, Exeter Software, East Setauket, NY; Krebs, 1999):

$$\text{Shannon-Wiener diversity index: } H' = -\sum P_i(\ln P_i),$$

where P_i = proportion of species i in the total nematode community, and

$$\text{evenness (modified Hill's ratio } E5): E5 = (N_2 - 1) / (N_1 - 1),$$

where N_1 is the Shannon-Wiener index expressed as:

$$N_1 = e^{H'}, \text{ where } e \text{ is the base of natural logarithms;}$$

and N_2 equals the reciprocal of Simpson's index (D):

$$N_2 = 1/D = 1/\sum (n_i/N)^2,$$

where N = total individuals in the data set and n_i = number of individuals in each species.

The Morisita-Horn Index (Wolda, 1981) was calculated for estimation of nematode community similarity among sites (EstimateS, Vers. 7, R. K. Colwell <<http://purl.oclc.org/estimates>>). Seven estimators (ACE, Bootstrap, Chao1, Chao2, ICE, Jack1, Jack2) for predicted numbers of species were calculated for the Molokai collection as a whole with EstimateS. Cluster analyses based on presence-absence (binary) data were performed on all 24 samples for total nematodes, plant-parasitic nematodes, and Dorylaimida by means of an unweighted pair group average (UPGMA) and the Baroni-Urbani Buser binary coefficient (MVSP Plus 3.1).

RESULTS

Numbers of species in a site varied from 24 to 44 (Table 1). Shannon-Wiener diversity was greatest in the

TABLE 1. Species-level taxa (N), Shannon-Wiener diversity (H' , \log_e basis), evenness (modified Hill's ratio $E5$), and density per square meter of nematodes in four plant communities in the Kama-kou Nature Preserve, Molokai, Hawaii.

Community	N	H'	$E5$	Density/m ^{2a}
Bog	34	2.201	0.341	153,600
Rain forest	44	2.772	0.506	227,000
Mesic forest	24	2.671	0.668	76,000
Drier forest	29	2.179	0.495	321,300

^a Calculated to a 20-cm depth.

rain forest and mesic forest sites, but species were most evenly distributed in the mesic forest site. Extracted nematode population densities among the sites ranged from 76,000/m² (mesic forest) to 321,300/m² (drier forest). Within sites, diversity, evenness, and total species varied widely (Fig. 1). No individual sample contained more than 23 species, and one sample contained only two species. Two samples in the bog and one drier forest sample predicted diversity of their sites, but only in the drier site sample was evenness also predicted. No single sample was sufficient for characterization of an entire site with regard to numbers of species, diversity, or evenness.

Among all sites, 67 species-level taxa were differentiated (Table 2). Most of these taxa could not be identified as any species described previously. Predicted numbers of species based on seven estimators ranged from 67 (100% of species collected) to 93 (72%). Tylenchida was by far the most diverse order, with 32 species, and was the dominant order in terms of individual numbers, in all four sites. Among the Tylenchida, three *Ditylenchus* spp. and six *Filenchus* spp. were differentiated. Eleven species of Dorylaimida and six Rhabditida were collected, but none of these species constituted more

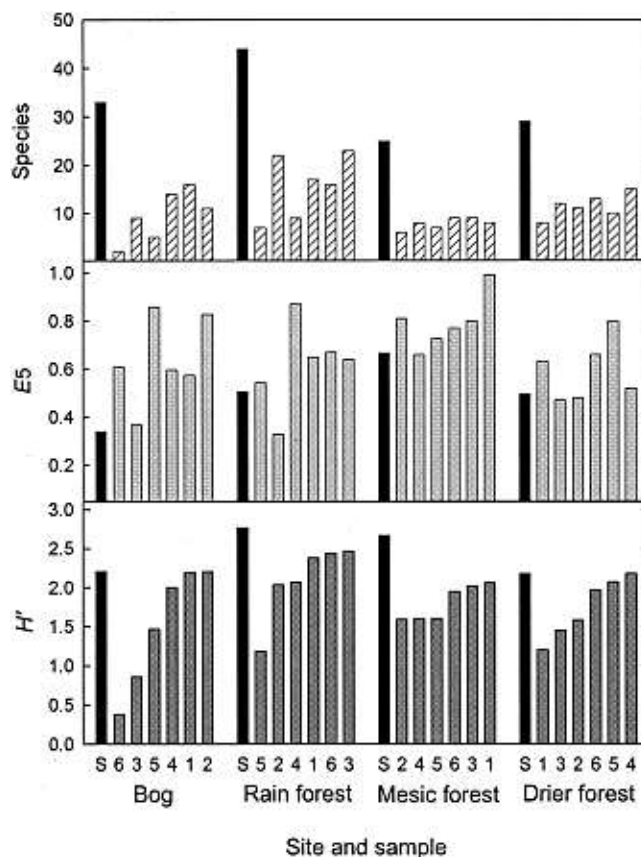


FIG. 1. Diversity (H'), evenness ($E5$), and number of nematode species in each of six samples among four sampling sites. Black bars (S) are values for each site. Bars within each site are arranged by increasing diversity. Number labels on x-axis correspond to sample numbers in Fig. 2.

TABLE 2. Proportions of individuals by order and species in four plant communities on Molokai, Hawaii.

Order, taxon	Trophic group ^a	Bog	Rain forest	Mesic forest	Drier forest
Aphelenchida					
<i>Aphelenchoides</i> sp.	H	0.009	0.003		
Alaimida					
<i>Alaimus</i> sp.	B		0.064	0.022	0.010
<i>Etamphidelus</i> sp.	B	0.009	0.006		0.002
Aracolaïmida					
<i>Bastania</i> sp.	B	0.024	0.009	0.022	0.008
<i>Chronogaster</i> sp.	B	0.021			
<i>Plectus</i> sp. 1	B	0.009	0.009		0.011
<i>Plectus</i> sp. 2	B	0.005	0.006		
<i>Wilsonema</i> sp.	B		0.003	0.045	0.024
Chromadorida					
	—	0.002	0.012		
Dorylaimida					
<i>Aporcelaimellus</i> sp. 1	O,PR	0.007	0.008	0.028	
<i>Aporcelaimellus</i> sp. 2	O,PR	0.002		0.011	0.004
<i>Belondira</i> sp.	F	0.005	0.017		
<i>Epidorylaimus humilis</i> (Thorne & Swanger) Andrassy	O		0.031	0.090	0.026
<i>Mesodorylaimus</i> sp.	O		0.009	0.011	
<i>Mylodiscoides</i> sp.	PR	0.051	0.006	0.011	
Qudsianematidae sp. 1	O				0.004
Qudsianematidae sp. 2	O				0.004
<i>Tylencholaimus</i> sp.	F	0.019	0.003	0.011	
<i>Willinema</i> sp.	F		0.009	0.011	
<i>Xiphinema</i> sp.	PPR	0.005	0.025		0.073
Enoplida					
<i>Halalaimus</i> sp.	—		0.009		
<i>Tripyla affinis</i> de Man	PR	0.021	0.059		
Monhysterida					
<i>Eumonhystera</i> sp.	B		0.015	0.011	0.022
<i>Prismatolaimus</i> sp.	B	0.009	0.015	0.214	0.413
Mononchida					
<i>Miconchus</i> sp.	PR	0.014			0.003
<i>Mylonchulus brevicaudatus</i> Cobb	PR		0.032		
<i>Truxonchus dolichurus</i> (Ditlevsen) Siddiqi	PR				0.001
Rhabditida					
<i>Acrobeloïdes tricornis</i> (Thorne) Thorne	B		0.003	0.045	0.011
<i>Bunonema</i> sp.	B		0.019	0.022	0.016
<i>Cephalobus</i> sp.	B		0.006		
<i>Diploscapter coronata</i> (Cobb) Cobb	B		0.003		
<i>Panagrolaimus</i> sp.	B	0.005	0.003		
Rhabditidae	B	0.019			
Teratocephalida					
<i>Euterocephalus</i> sp.	B	0.009	0.018	0.034	0.040
<i>Metaterocephalus</i> sp.	B	0.009			0.002
Tylenchida					
<i>Basiria</i> sp. 1	PPE		0.009		
<i>Basiria</i> sp. 2	PPE			0.011	
<i>Basiria</i> sp. 3	PPE				0.002
<i>Basirenchus</i> sp.	—		0.003		
<i>Cephalenchus leptus</i> Siddiqi	PPR	0.009		0.045	0.004
<i>Coslenchus</i> sp.	PPR		0.006	0.056	0.008
<i>Criconema</i> sp.	PPR	0.019	0.238	0.179	0.125
Criconematidae	PPR				0.001
<i>Ditylenchus</i> sp. 1	H	0.005	0.003	0.011	
<i>Ditylenchus</i> sp. 2	H	0.005	0.003		0.002
<i>Ditylenchus</i> sp. 3	H	0.005			
<i>Ecphyadophoroides</i> sp.	H			0.011	0.003
<i>Filenchus flagellicaudatus</i> Bernard	PPE	0.005			

TABLE 2. Continued

Order, taxon	Trophic group ^a	Bog	Rain forest	Mesic forest	Drier forest
<i>F. polyhyphus</i> (Steiner & Albin) Meyl	PPE		0.006		
<i>Filenchus</i> sp. 1	PPE		0.003		
<i>Filenchus</i> sp. 2	PPE		0.003	0.003	
<i>Filenchus</i> sp. 3	PPE		0.003		
<i>Filenchus</i> sp. 4	PPE	0.005			
<i>Gracilacus</i> sp.	PPR	0.071	0.112		
<i>Helicotylenchus</i> sp. 1	PPR	0.485			
<i>Helicotylenchus</i> sp. 2	PPr		0.175		0.002
<i>Lelenchus leptosoma</i> (de Man) Meyl	PPE	0.009			
<i>L. schmitti</i> Bernard	PPE	0.061	0.003		
<i>Malenchus</i> sp.	PPE		0.006		
<i>Meloidogyne</i> sp.	PPR	0.005	0.019	0.090	0.056
<i>Miculenchus</i> sp.	PPE		0.003		
<i>Neopsilenchus</i> sp.	PPE	0.005			
<i>Notholetus spicatus</i> Ebsary	PPR	0.057			
<i>Paratylenchus</i> sp.	PPR				0.117
<i>Pateracephalanema</i> sp.	PPR				0.006
<i>Pratylenchus</i> sp.	PPR		0.003		
<i>Seriespinula</i> sp.	PPR			0.006	

^a Primarily after Yeates et al. (1993). H: hypha-feeding; B: bacteria-feeding; O: omnivore; PPE: plant-parasitic, browsing on epidermal cells and root hairs; PPR: plant-parasitic, feeding on root cortex or vascular tissue; PR: predator; -: unknown.

than about 5% of the total nematofauna in a site. Diplogasterid nematodes were not collected in this survey. *Prismatolaimus* sp. was the only non-phytoparasitic nematode forming a dominant component in any site (mesic and drier forests). Habitat segregation was apparent for several species pairs. For instance, a possibly parthenogenetic (no sperm in spermatheca) *Helicotylenchus* sp. was found only in the bog, and a presumably amphimictic (males present, sperm in spermatheca) *Helicotylenchus* sp. was collected only in the neighboring rain forest, with a trace in the drier forest. Similarly, *Notholetus spicatus* was collected only in the bog, and an unidentified *Criconema* sp. was found in the other three sites but not the bog.

The nematode faunas of the four sites were highly dissimilar according to the Morisita-Horn index, except for the visually similar mesic and drier forests, which had a similarity index of 0.778 (Table 3). In particular, the bog fauna was almost totally different from the other three faunas. In a binary cluster analysis of all species in all 24 sampling spots, the six bog samples clustered together (Fig. 2A), but the other sites did not

TABLE 3. Similarity of nematode communities among four sites on Molokai, Hawaii, according to the Morisita-Horn Index.

Site	Morisita coefficient of similarity		
	Rain forest	Mesic forest	Drier forest
Bog	0.079	0.041	0.032
Rain forest		0.490	0.261
Mesic forest			0.778



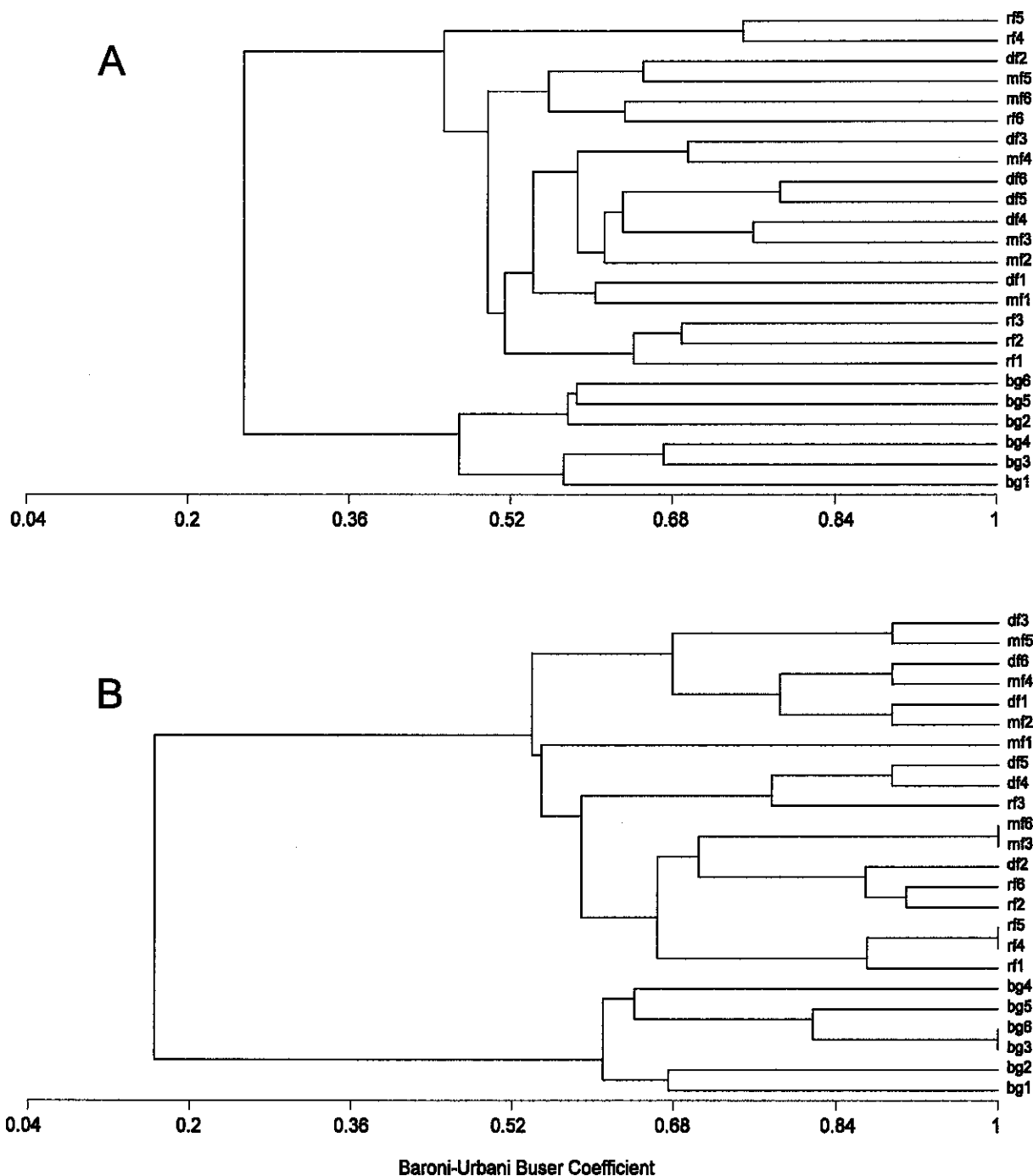


FIG. 2. Presence-absence (binary) cluster analysis of nematode assemblages from sampled areas of Molokai. A) All species-level nematode taxa. B) Plant-parasitic nematode taxa. Sites: bog (bg1 to bg6), rain forest (rf1 to rf6), mesic forest (mf1 to mf6), dry forest (df1 to df6).

cluster as well. When only plant parasites were analyzed, the bog samples again were segregated clearly, and five rain forest samples were closely aligned (Fig. 2B). This alignment of rain forest samples was not evident in the all-nematode analysis. Mesic and drier site samples, which were similar in vegetation, tended to cluster together.

DISCUSSION

Calculated nematode densities in the four sites were estimated at 76,000 to 321,300/m². These numbers are

lower than those cited by Sohlenius (1980) for tropical forest soils but are comparable to numbers determined in New Caledonian (Yeates, 1991) and Vanuatu soils (Yeates, 1973). Extraction efficiencies were not determined in this study, but presoaking of a Hawaiian agricultural soil followed by elutriation yielded three times more *Xiphinema krugi* and 16 times more Criconematidae than elutriation without presoaking (D. Schmitt, unpubl.). Similar results were found with *Meloidogyne konaensis* on coffee (D. P. Schmitt, unpubl.). Whether soaking soil samples from Hawaiian forests for



several hours would have improved extraction efficiency is unknown.

Most of the species-level taxa collected in this study could not be assigned to known species (59 of 67). Some taxa could not be identified because only juveniles were collected. Others clearly are new taxa and await description; two of these have been described recently (Bernard, 2005). In a large biodiversity inventory project in Cameroon, more than 90% of the 374 collected nematode morphospecies could not be assigned to known species (Lawton et al., 1998). The inability to place names to specimens not only restricts our capacity to understand nematode biogeography and dispersal to Hawaii but also suggests a highly endemic fauna. This finding also lends credibility to the speculation of many nematologists that only a very small percentage of the world's nematode species are described.

Nematode dispersal to Hawaii likely has occurred in at least three ways: island-hopping along the archipelago as islands arose and then eroded and disappeared; long-distance dispersal from continents or other island groups by wind, animal transport, or rafting; and introduction by humans during waves of colonization. Wind dispersal over land is well established (Baujard and Martiny, 1994; Orr and Newton, 1971; Viglierchio and Schmitt, 1981) but its role in colonization over water has not been determined. Rafting of vegetation has been suggested numerous times to aid in island dispersal of land organisms (Howden, 1977; Jokiel, 1990) and might serve as a plausible means of island-hopping, but the effect on terrestrial nematodes of periodic immersion in seawater is unknown. Movement by birds across great ocean distances seems unlikely unless the nematodes are already anhydrobiotic; long-term retention in bird digestive systems is particularly doubtful (Clench and Matthias, 1992). Introduction in association with human migration does not solve the problem of introduction into undisturbed forest habitats, and is not consistent with the apparent lack of these nematodes in agricultural settings. None of these colonizing strategies has yet been demonstrated for any forest-endemic Hawaiian nematode. However, given initial introductions, speciation would be expected to be rapid and diverse, as is well known in Hawaii for birds, fruit flies, and other taxa. The rapid evolution of plant species would help drive nematode speciation, either directly for plant-parasitic genera or indirectly for other nematode taxa more dependent on fungi and bacteria, which themselves would be influenced by soil genesis. Nevertheless, the Molokai nematode fauna seems to be depauperate, as richness estimates suggest that 72% to 100% of the soil nematode species were collected in this survey. Among the possible explanations for this depauperate fauna are: (i) a filtering effect occurs during movement of biota along island chains in that only a fraction of the species on an island move to the next island in a given period of time; each

species has its own average dispersal rate, and establishment rates thus vary (Carlquist, 1970; Kobayashi, 1983); (ii) Molokai is young, having emerged from the sea about 2 million years ago, and colonization likely is not complete (Carlquist, 1970); (iii) extensive speciation of colonizer descendants has not yet occurred, due to the relatively recent formation of the island; (iv) extraordinarily high levels of glomalin (a recalcitrant glycoprotein containing high levels of carbon and iron) in Hawaiian soils (Rillig et al., 2001; Wright et al., 1996) could indicate low bacterial densities that would limit establishment of bacteria-feeding nematodes. This trophic group was uncommon in the Molokai samples. Conversely, fungal feeders would be expected to be higher in soils high in glomalin because this compound is produced by arbuscular mycorrhizal fungi. Fungal feeders, especially *Filenchus* and *Ditylenchus* spp., were diverse in the Molokai samples. However, fungal biomass was not determined for these soils.

Relationships of native Hawaiian organisms to native biotas of other land masses can be determined only if these biotas are fairly well understood. We know little about the endemic nematode faunas of most Pacific land masses, as most nematological effort has been devoted to the problems of crop protection (Bridge and Page, 1982; Kirby et al., 1978; Orton Williams, 1980). Sources of colonization can differ among different phylum and class-level taxa. For instance, most endemic Hawaiian birds are derived from the Americas, with a minor component from New Guinea (Diamond, 1984) and perhaps a few island-hopping northeast Asian species (Berger, 1981), but Hawaiian species of the arthropod class Collembola appear to have strong North American and temperate Asian components with little New Guinean input (Christiansen and Bellinger, 1994). Our knowledge of Pacific-rim and island nematodes still is far too meager to be able to make robust conclusions about nematodes, although some tentative hypotheses can be made. For example, the criconematid genus *Pateracephalanema* (Mehta and Raski, 1971), recorded in the present survey, is known from Queensland, which suggests a pan-Pacific radiation, whereas the long-tailed *Filenchus flagellicaudatus* (Bernard, 2005) seems most similar to *F. normanjonesei* from southern Chile (Raski and Geraert, 1986).

An instructive approach to understanding nematode dispersal routes might be development of a scenario for dispersal of several well-defined genera throughout the tropical Pacific, such as *Xiphinema* spp. This genus of large nematodes generally is not anhydrobiotic (Taylor and Brown, 1997) and should not be easily dispersable, yet several species have been described or reported from rain forest on Pacific islands, including *X. bacani-boia* from Fiji (Orton Williams, 1984) and *X. fagesi* from New Caledonia (Germani, 1990). In addition, *X. ensiculiferoides* (Cohn and Sher, 1972) was described from an exotic planting on Oahu, and several widespread spe-



cies are known from Hawaiian agricultural sites. Although only one species is reported in the present Molokai study, several other species have been collected from undisturbed native forest on the other islands of Hawaii and could serve as a basis for interpretation of *Xiphinema* biogeography in the Pacific. *Xiphinema* character states are well delimited (Loof and Luc, 1990), and restriction fragment length polymorphisms have proven effective for separating closely related members of the *X. americanum* species group (Vrain, 1993). Recognition of relationships among Pacific *Xiphinema* could lead to useful hypotheses on the biogeography of Pacific soil nematodes.

Additional insight into nematode dissemination across the Pacific also could be gained by examination of nematode faunas in non-agricultural plant communities of Pacific islands and archipelagos. These faunas are at least partially known for the Aleutian Islands (Bernard, 1981, 1982, 1984), Fiji (Orton Williams, 1984), New Caledonia (Germani, 1990; Yeates, 1991), New Zealand (Loof et al., 1997), and Vanuatu (Yeates, 1972, 1973). For instance, Criconematidae could serve as a model family for nematode biogeography. This family generally is easy to collect and recognizable by minimally trained lab personnel, and identification of species-level taxa is straightforward. The comparative ease at recognizing species would be of benefit to molecular taxonomic analysis in this group because painstaking observation of minute characters to separate species would not normally be necessary (cf. Tylenchidae). Hypotheses from a biogeographic model for Criconematidae then could be tested with other nematode taxa to further our understanding of nematode dispersal over time.

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