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Phytoparasitic nematodes associated with the rhizosphere of the aquatic weed *Hygrophila polysperma*

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ABSTRACT

Hygrophila (*Hygrophila polysperma* [Roxb.] T. Anders; Acanthaceae) is an invasive aquatic and riparian weed the southern United States. This rooted submerged or emergent plant is typically found in flowing fresh water channels and structured shorelines. In Florida, hygrophila interferes with irrigation, navigation, and flood control structures. To examine the diversity of nematode fauna associated with rhizosphere of this invasive weed, exploratory field surveys were conducted in the native (India, n = 19 sites) and invasive (Florida, USA, n = 7 sites) ranges of hygrophila during 2008–2009. Two core samples (10 cm diameter by 10 cm deep) containing moist soil and hygrophila roots were collected at each sampling site. Phytoparasitic nematodes were extracted, identified,

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and quantified to calculate diversity and evenness indices. Results showed that significantly higher densities of phytoparasitic nematodes are associated with hygrophila in India compared to Florida. In total, eight nematode species (representing seven genera), belonging to the order Tylenchida, were recorded from India. *Meloidogyne graminicola* Golden & Birchfield and *Helicotylenchus* sp. were the dominant species in the native range. In Florida, 10 phytoparasitic nematode genera were collected representing two orders, Triplonchida (n = 2 genera) and Tylenchida (n = 8 genera). *Helicotylenchus* and *Tylenchorhynchus* were the dominant genera of phytoparasitic nematodes collected across Florida. This study is the first report of phytoparasitic nematodes associated with the root zone of hygrophila.

Key words: *Hygrophila polysperma*, invasive weed, phytoparasitic nematodes, root zone

INTRODUCTION

Hygrophila (*Hygrophila polysperma* [Roxb.] T. Anders; Acanthaceae) is an invasive aquatic and riparian weed in the southern United States (US) and Mexico (EDDMaps 2010, Mora-Olivo et al. 2008). Introduced into the US as a popular aquatic plant (Innes 1947), this weed escaped cultivation and is now creating problems in warm water areas of the southern US and eastern Mexico (Cuda and Sutton 2000, Mora-Olivo et al. 2008). In the US, hygrophila is widely distributed across Florida (n = 13 counties; Cuda and Sutton 2000, EDDMaps 2010). In addition to Florida, its distribution in the US includes Alabama, South Carolina, and Texas (EDDMaps 2010). This plant is an Old World species, native broadly to Southeast Asia including India (Les and Wunderlin 1981, Cook and Cook 1996). It is listed as a Federal Noxious Weed (USDA 2006) and a Category-I invasive weed by the Florida Exotic Pest Plant Council (FLEPPC 2009). The dense stands formed by this herbaceous perennial weed interfere with irrigation, block flood control structures (Schmitz and Nall 1984, Sutton 1995), and also hinder navigation (Cuda and Sutton 2000).

Since 1990, a visible increase in the number of water bodies in Florida invaded by hygrophila suggests that current methods employed to control this weed are inadequate (Sutton 1995). The invasive characteristics exhibited by hygrophila as well as its biological and economic attributes make it a good candidate for classical biological control (Cuda and Sutton 2000). However, little information is available about the natural enemy complex associated with hygrophila in its native range. We recently undertook surveys in a range of habitats in India during 2008–2009 to collect and identify the plant's natural enemies (A. Mukherjee, unpubl. data). As a part of that survey, phytoparasitic nematodes present in the root zone of hygrophila also were extracted, enumerated, and identified. Similar surveys also were conducted in Florida, where hygrophila was introduced. Use of nematodes in classical weed biological programs is rare. For example, the leaf and stem gall nematode *Subanguina picridi* Kirja-nova (Nematoda: Tylenchidae) was released as a biological control agent of Russian knapweed (*Acroptilon repens*; Asteracee; Watson 1986, Ou and Watson 1993). However, the specific objective of this study was only to assess the diversity of phytoparasitic nematode fauna associated with the rhizosphere of this weed in its native and exotic range and to determine if hygrophila could act as an alternate host of important plant parasitic nematodes.

MATERIALS AND METHODS

Sampling and enumeration of nematodes

In September 2008, exploratory field surveys (n = 19) in India were undertaken in a range of locations in the states of West Bengal (n = 12, sites Ind-1 to Ind-12) and Assam (n = 7, sites Ind-13 to Ind-19; Figure 1), chosen for this study because they are climatically similar to the invasive range of hygrophila in the US (Mukherjee et al. 2011). Except for two sites in West Bengal (Ind-2 and Ind-8), all samples were collected from natural areas. For sites Ind-2 and Ind-8, samples were collected from irrigation channels in agricultural fields. Each survey site was geopositioned and assigned a unique accession number. Two soil cores containing hygrophila roots (10 cm diam by 10 cm deep) were collected at ~10 m intervals from each survey site. All samples were collected from shoreline ~2 m from the edge of the water and only from areas with established hygrophila plants. Cores (n = 2) collected from each survey site were pooled before extraction of nematodes. Nematodes were extracted following the sieving and specimen processing technique of Handoo and Ellington (2005). Identification of phytoparasitic nematodes to genus, and in some cases species, was performed at the Plant Health Diagnostic Laboratory, Department of Agricultural Entomology, Bidhan Chandra Krishi Viswavidyalaya, West Bengal, India.

In August 2009, similar surveys were conducted in Florida (n = 7) to characterize the diversity of phytoparasitic nematodes associated with hygrophila in its exotic range (Figure 2). Samples were collected from natural areas in five counties, including Alachua (site Fl-7), Broward (site Fl-1), Dixie (sites Fl-5 and 6), Osceola (sites Fl-3 and 4), and Pinellas (site Fl-2). Using a metal trowel, two soil cores (10 cm diam by 10 cm deep) containing hygrophila roots were collected from each survey site at ~10 m intervals. Similar to native habitats, samples were collected from the shoreline to ~2 m from the edge of the water. Soil cores (n = 2) collected from each site also were pooled before extraction of nematodes. The geoposition of each survey site was recorded. Nematodes were extracted using aforementioned methods and identified to the genus level in the Nematode Assay laboratory, Entomology and Nematology Department, University of Florida.

Assessment of nematode dominance

To determine the dominant nematode taxa (genus or species) within the native or invasive ranges of hygrophila, a standardized index of prevalence (*Ip*, equation 1) was calculated following Zhou et al. (2003). Two criteria, density and frequency of a taxon for a given site were considered for calculation of *Ip*:

$$Ip = \left[\frac{N_i}{N} \times \frac{S_i}{S} \right], \quad (1)$$

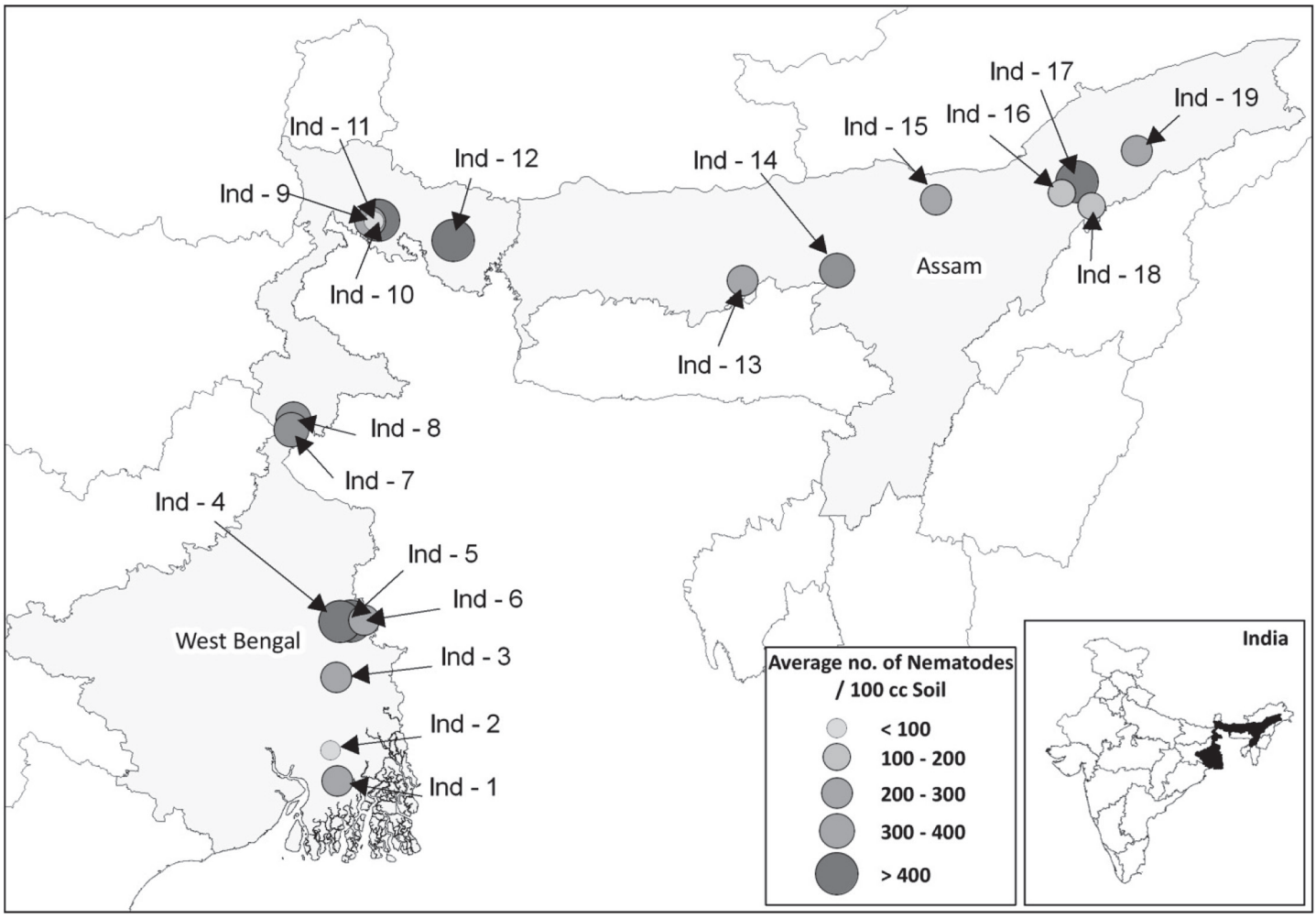

Figure 1. Survey sites in India (n = 19). Each site was assigned a unique accession number. Symbols are graduated based on average number of nematodes collected per core sample of soil.

where, N_i = total number of nematode taxon *i* collected across all sites within a range (native/invasive), N = total number nematodes collected from a given range, S_i = number of sites from which taxon *i* was collected, and S = total number of sampling sites within a given range.

A 95% confidence interval (CI) of the mean *Ip* was calculated using a technique by Buonaccorsi and Liebhold (1988). As emphasized earlier in Buonaccorsi and Liebhold (1988) and later by Beyene and Moineddin (2005), calculation of confidence interval of *Ip* is necessary because it is a product of two criteria. According to Zhou et al. (2003), a taxon was considered dominant if its *Ip* > upper limit of 95% CI, taxa with *Ip* intermediate between upper and lower limit of CI were considered common, and taxa with *Ip* < lower limit of CI were classified as occasional.

Assessment of nematode diversity

The diversity of the phytoparasitic nematofauna was assessed for each sampling site (n = 19 for native range, n = 7 for invasive range). In addition, data from all sampling sites within a given range (native or invasive) were pooled to calculate the overall diversity of the nematodes. Following techniques reported by Bernard and Schmitt (2005), Shannon diversity (H'; equation 2) and evenness (E_H; equation 3) indices were calculated to measure the α diversity (within site diversity) of each sampling site and habitat (Magurran 2004) using the following equations:

$$H' = -\Sigma p_i(\ln p_i), \quad (2)$$

$$E_H = H'/\ln S, \quad (3)$$

where p_i = relative abundance of each species, calculated as the proportion of individuals of the ith species (n_i) to the total number of individuals (N) in the community, or $p_i = \frac{n_i}{N}$; and S = total number of species present in the community or the species richness. The range of values for E_H is 0 to 1, with 1 being complete evenness.

For each geographical region sampled, the diversities and sample densities (number/100 cc soil) of nematode taxa were analyzed. The Kruskal-Wallis analysis of variance (here-

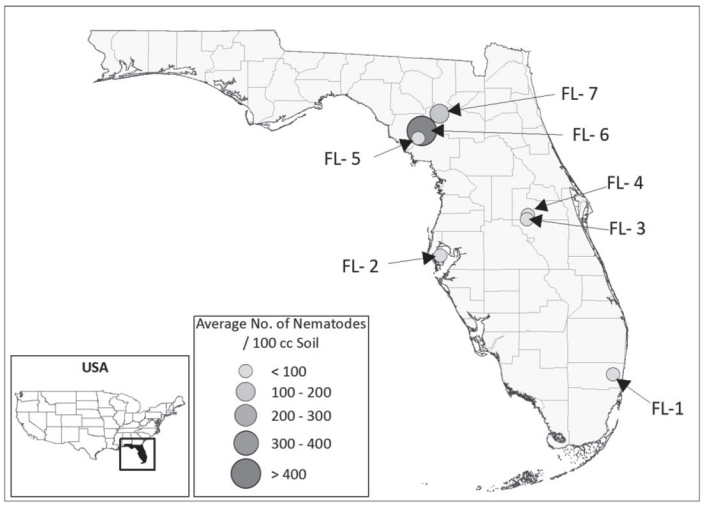

Figure 2 Survey sites in Florida (n = 7). Each site was assigned a unique accession number. Symbols are graduated based on average number of nematodes collected per core sample of soil.

after Kruskal-Wallis test; Corder and Foreman 2009) was used to test the difference in density and diversity of phytoparasitic nematodes between exotic and native ranges. Statistical tests were performed using the open source statistical software R (version 2.11.1) at $\alpha = 0.05$.

Using the Morisita-Horn index of community similarity (C_{MH}; equation 4), cluster analysis of nematode assemblages was performed on all sampling sites within each region following the unweighted pair group average (UPGMA) method (Bernard and Schmitt 2005). C_{MH} is a measure of β diversity (between site diversity), which calculates the similarity in species composition between two sites. Walda (1981) investigated a number of similarity indices and recommended the use of C_{MH} because it is not influenced by the effects of sample size and species diversity. The limiting values of C_{MH} are 0 (completely dissimilar) and 1 (completely similar). The Morisita-Horn index of community similarity is calculated by the following equation:

$$C_{MH} = \frac{2\Sigma(a_i b_i)}{(d_a + d_b) \times (N_a \times N_b)} \quad (4)$$

where a_i and b_i are the i^{th} species of sites A and B, respectively; N_a and N_b represent the number of individuals collected, respectively, from site A and B; and d_a (and d_b) is calculated as $d_a = \Sigma a_i^2 / N_a^2$

RESULTS AND DISCUSSION

Nematode diversity

Native range: In total, eight phytoparasitic nematode species, representing seven genera were collected from India (Table 1; Figure 3A). The number of nematode species in the sampling sites varied between two (sites Ind-7, 8, 11, and 15) and seven (site Ind-12). Densities of nematodes extracted (number/100 cc soil) varied between 94 (site Ind-2) and 1130 (site Ind-12; Figure 1B), with an average (mean ± SD) of 609.3 ± 293.8 nematodes/100 cc soil (Figure 3B, black bar). The Shannon diversity (H') of nematodes in the native range (pooled data) was 1.82, with sampling sites ranging between 0.29 (site Ind-8) and 1.53 (site Ind-6; Figure 3C). Overall, a high evenness (E_H = 0.88, black bar Fig 3D) of nematode distribution was recorded across native habitats. The E_H value calculated among sampling sites ranged between 0.42 (site Ind-8) and 1.0 (site Ind-11).

Exotic range: In total, 10 phytoparasitic nematode genera were collected from Florida (Table 2; Figure 4A), with seven genera collected from site Fl-7 and one genus from site Fl-2. Nematode densities were found to be low in most of the sites, with an average density of 141.9 ± 307.7 nematodes/100cc soil, with the highest density (830 nematodes/100cc soil) recorded from site Fl-6, located in Dixie County, Florida (Figure 2 and 4A). The highest Shannon diversity index was calculated from site Fl-7 (H' = 1.27), with an overall habitat H' of 0.8 (Figure 4C). Evenness (E_H) of nematode distribution across exotic habitats was low (0.35; Figure 4D black bar). Because only a single genus was collected from site Fl-2 (Figure 4A), both calculated H' and E_H were zero (Figure 4C and 4D).

There were no differences in H' between exotic and native ranges (Kruskal-Wallis test, χ^2 =3.53, p = 0.06). Similarly, no difference was observed in E_H (χ^2 = 0.24, p = 0.62). In contrast, densities of phytoparasitic nematodes recorded from the na-

Table 1. Phytoparasitic nematode species associated with root zone of hygrophila in Assam and West Bengal, India.

Order, Taxon	Index of prevalence (Ip)†*	Sites collected
Tylenchida		
Meloidogyne graminicola Golden & Birchfield	0.18 [a]	Ind-1, 3, 5-7, 12, 14, 15, 18
Helicotylenchus sp. Steiner	0.17 [a]	Ind-1-11, 13-19
Meloidogyne incognita Chitwood	0.05 [b]	Ind-3, 5, 6, 13-15, 17, 19
Rotylenchulus reniformis (juvenile) Linford & Oliveira	0.05 [b]	Ind-2, 4-6, 8, 10, 12, 15, 16
Hirschmanniella oryzae Luc & Goodey	0.05 [b]	Ind-3, 5, 6, 8, 9, 11, 12, 19
Criconemoides sp. Taylor	0.03[b]	Ind-4, 5, 7-11, 14, 15
Tylenchorhynchus mashhoodi Siddiqi & Basir	0.02 [b]	Ind-1, 8, 9, 13
Hoplolaimus indicus Sher	0.002 [c]	Ind-1, 4, 5, 19

†Index of prevalence was calculated using equation 1.
*Upper and lower bounds of 95% confidence interval of Ip are 0.11 and 0.02, respectively.
[a]Dominant species, [b]common species, [c]occasional species (see methods for assessment of nematode dominance for classification criteria).

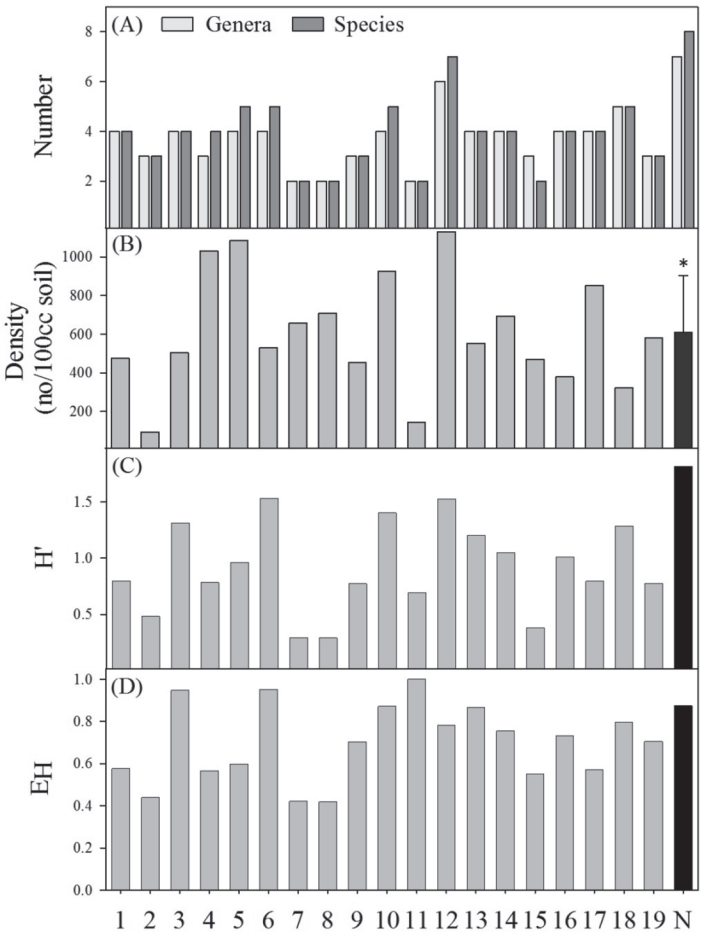

Figure 3. Nematode genera and species, density, Shannon diversity (H'), and evenness (E_H) calculated across sampling sites in India. Black bars represent values for native range (India, pooled data). Number labels on x-axis correspond to site numbers in Figure 1. N = native habitat. *For Figure B, black bar denotes the average number of nematodes/100 cc soil (609.3 ± 293.8), calculated across all sampling sites.

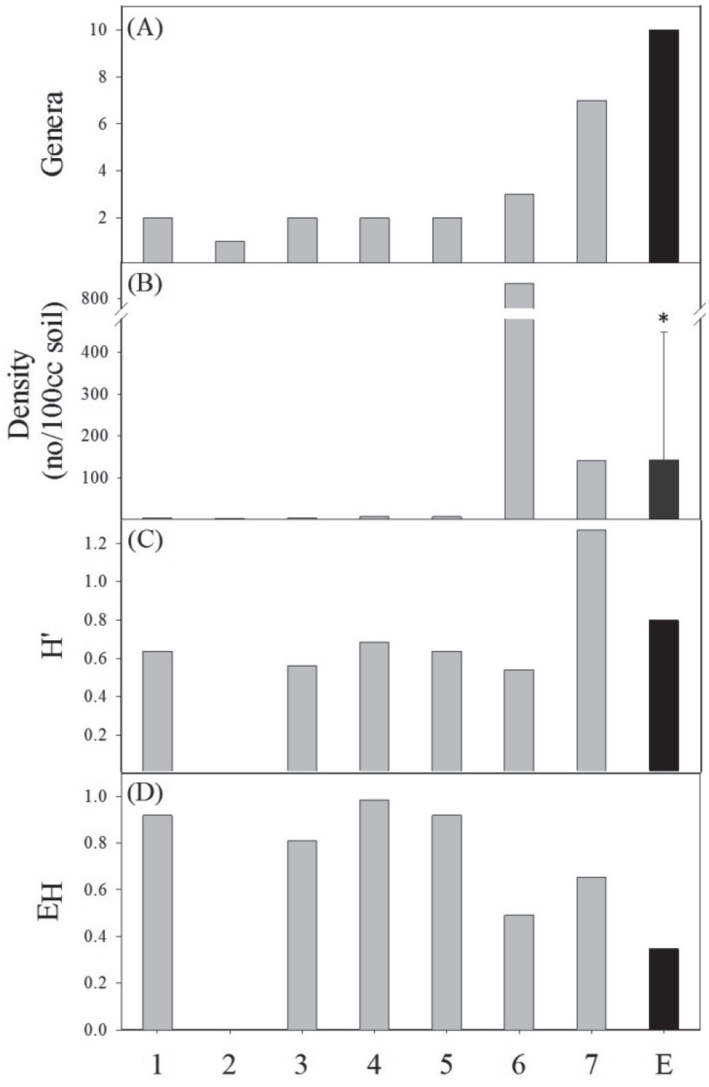

Figure 4. Nematode genera, density, Shannon diversity (H'), and evenness (E_H) calculated across sampling sites in Florida. Black bars represent values for exotic range (Florida, pooled data). Number labels on x-axis correspond to site numbers in Figure 2. E = Exotic habitat. *For Figure B, black bar denotes average number of nematodes/10 cc soil (141.9 ± 307.7), calculated across all sampling sites.

tive range were significantly higher than that of the exotic range ($\chi^2 = 8.86$, $p = 0.003$).

Phytoparasitic nematodes recorded

For both native and exotic ranges, the *Ip* of individual taxa (genus or species level for India, genus level for Florida) collected from the rhizosphere of hygrophila was recorded (Table 1 and 2, respectively).

Native range: In total, eight phytoparasitic nematodes species, all belonging to the order Tylenchida were collected from India (Table 1). The lower and upper limits of 95% CI of *Ip* were 0.02 and 0.11, respectively. Among all the taxa, the rice rootknot nematode *Meloidogyne graminicola* Golden & Birchfield (*Ip* = 0.18) and the spiral nematode *Helicotylenchus* sp. (*Ip* = 0.17) were recorded as dominant phytoparasitic nematode species (dominant species = *Ip* > upper limit of 95% CI) across native range samples (Table 1). The rootknot nematode *M. incognita* Chitwood, reniform nematode *Rotylenchulus reniformis* Linford & Oliveira, rice root nematode *Hirschmanniella oryzae* Van Breda de Hann, ring nematode *Criconemoides* sp., and stunt nematode *Tylenchorhynchus mashhoodi* Siddiqi & Basir were found to be common nematode species (*Ip* intermediate between upper and lower bounds of 95% CI) associated with root zone of hygrophila (Table 1). Using the criteria *Ip* < lower limit of 95% CI, *Hoplolaimus indicus* Sher was classified as an occasional species (*Ip* = 0.002).

Based on the Morisita-Horn index of similarity, sampling sites across India can be divided into two groups with low similarity in collected phytoparasitic nematofauna (<0.2; Fig 5). Among all sampling sites, highest similarity was observed between Ind-7 and Ind-15 (similarity index of 0.99; Fig 5). In both cases, two species of nematodes, *Helicotylenchus* sp. and *M. graminicola*, were collected with approximately equal densities. Overall, similarity indices across native range sampling sites documented wide variation in nematode fauna associated with hygrophila roots.

Table 2. Phytoparasitic nematode genera recorded from the root zone of hygrophila in Florida, US.

Order Taxon	Index of prevalence (Ip)†*	Sites collected
Triplonchida		
Paratrichodorus sp. Siddiqi	0.0003[c]	FL-1
Trichodorus sp. Cobb	0.0001[c]	FL-1
Tylenchida		
Helicotylenchus sp. Steiner	0.33[a]	FL-5, 6, 7
Tylenchorhynchus sp. Cobb	0.09[a]	FL- 3, 6, 7
Hemicycliophora sp. de Man	0.02[b]	FL-3, 6, 7
Mesocriconema sp. Andrassy	0.003[c]	FL-2, 5, 7
Meloidogyne sp. Goeldi	0.003[c]	FL-7
Hemicriconemoides sp. Chitwood & Birchfield	0.0004[c]	FL-4
Pratylenchus sp. Filipjev	0.0003[c]	Fl-2
Hoplolaimus sp. Daday	0.0001[c]	FL-7

†Index of prevalence was calculated using equation 1.
*Upper and lower bounds of 95% confidence interval of *Ip* are 0.04 and 0.01, respectively.
[a]Dominant taxa, [b]common species, [c]occasional taxa (see methods for assessment of nematode dominance for classification criteria).

Exotic range: Genus level nematode taxa, representing two Orders (Triplonchida and Tylenchida), were collected from Florida (Table 2). With eight genera, the Order Tylenchida was found to be the most diverse across all the sampling sites in Florida (n = 7). The Order Triplonchida was represented by two genera, *Paratrichodorus* and *Trichodorus*.

The upper and lower limits of CI of *Ip* calculated from Florida samples were 0.04 and 0.01, respectively. Based on the criteria used to determine dominant taxon (*Ip* > upper limit of 95% CI), *Helicotylenchus* was the most dominant nematode genus (*Ip* = 0.33) followed by the genus *Tylenchorhynchus* (*Ip* = 0.09). The genus *Hemicycliophora* was classified as a common phytoparasitic nematode (*Ip* = 0.02). With *Ip* < the lower limit of 95% CI, all other phytoparasitic nematode genera collected across Florida were classified as occasional (Table 2).

The Morisita-Horn index of similarity among sampling sites across Florida was found to be generally low (Figure 6). Maximum similarity (~0.91; Figure 6) was recorded between sites FL-6 and FL-7. A somewhat lower similarity index (0.86) was recorded between sites FL-2 and FL-5. In contrast, site FL-1 was distinctly different than all other sites in Florida, with no similarity in phytoparasitic nematodes collected.

For both exotic and native ranges, the results of cluster analysis indicated that similarities among sampling sites were not correlated with between-site geographic distances. In India for example, high similarity was observed between sites Ind-7 and Ind-15, but similarities between sites geographically closer to these sites were low. Lack of correlation between similarity and geographic distance also was evident in Florida. Several factors, including soil characteristics, climatic conditions, proximity to agriculture fields, and surrounding vegetation can affect similarity of nematodes between sites. For example, Bernard and Schmitt (2005) found that site characteristics (bog, mesic, rain, and drier forests) influenced similarity of nematofauna in native plant communities in Hawaii. Based on our field observations, proximity to agriculture fields could explain the similarities of nematode fauna between geographically distant sites. For example, sites Ind-7 and Ind-15 were in close proximity to rice fields, and in both cases *M. graminicola* was the predominant species collected. Because no soil characteristics or vegetation data were collected during this study, no objective evaluation of why nematode similarities vary across sites was possible.

In Florida, highest nematode diversity was observed at site Fl-7 (Rum Island Springs; 29.83357, –82.67762). This is a heavily forested site, and large mats of hygrophila were

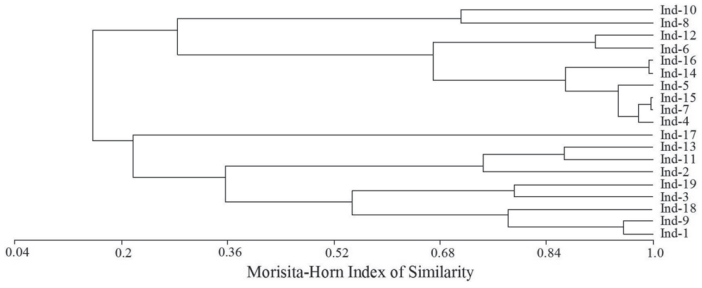

Figure 5. Cluster analysis of phytoparasitic nematode assemblage based on Morisita-Horn index of community similarity from sampled sites in India (see Figure 1 for site locations).

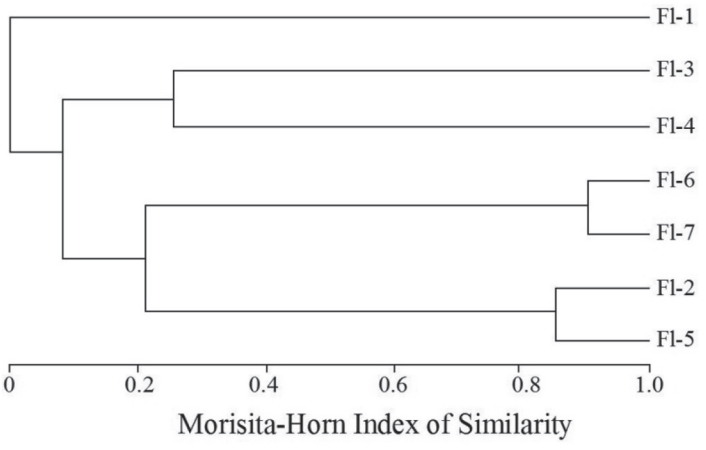

Figure 6. Cluster analysis of phytoparasitic nematode assemblage based on Morisita-Horn index of community similarity from sampled sites in Florida (see Figure 2 for site locations).

observed along the bank of the Santa Fe River. Perhaps soil conditions unique to the site and the presence of large mats of hygrophila could explain the high nematode diversity observed, but no soil data were collected to support this hypothesis. Interestingly, cluster analysis indicated high similarity in nematode assemblage between sites Fl-6 and Fl-7. Seven nematode genera were collected from Fl-7 and three from Fl-6 (Fig 4A); however, major nematode genera (genera collected in higher numbers) were the same, *Helicotylenchus*, *Tylenchorhynchus*, and *Hemicycliophora* (Table 2), explaining the similarity in nematode assemblage between these two sites.

Assessment of nematode assemblage across the native and invasive ranges of hygrophila demonstrated that significantly higher densities of phytoparasitic nematodes are associated with roots of this weed in its native habitat; however, no differences in nematode diversity were observed. This similarity of nematode diversities may indicate that in both exotic and native ranges, hygrophila can act as an alternative host to major phytoparasitic nematode genera. As mentioned earlier, except for two sites (Ind-2 and Ind-8), all samples in India were collected from natural areas; however, many of these sites were in close proximity to agriculture fields. In contrast, all sampling sites in Florida were in natural areas and not close to any agriculture sites. This observation suggests that proximity to agriculture fields may explain the higher density of nematofauna observed and also indicates that stable populations of phytoparasitic nematodes may be present in the root zone of hygrophila in India.

For both regions, the nematodes collected from the rhizosphere of hygrophila are considered pests of important agricultural and horticultural crops (Table 1 and 2). For instance, the rice blind root knot nematode *Hirschmanniella oryzae* Van Breda de Hann, lance nematode *Hoplolaimus indicus* Sher, and stunt nematode *Tylenchorhynchus mashhoodi* Siddiqi and Basir, collected in the native range of hygrophila are considered as major pests of rice (*Oryza sativa* L.) (CABI 2005). In Florida, species of the sheath nematode *Hemicycliophora* de Man, lance nematode *Hoplolaimus* Sher, as well as the stunt nematode *Tylenchorhynchus* Cobb are known to be important crop pests (Anderson et al. 1991, Fortuner and Nickle 1991, CABI 2005).

Previous studies have shown that invasive weeds can act as alternate hosts for important crop pests, including fungal pathogens (Wisler and Norris 2005) and insects (Seal 2004) as well as nematodes (Davis et al. 2006). In particular, Davis et al. (2006) demonstrated that the invasive weed tropical spiderwort (*Commelina benghalensis* L., Commelinaceae) can act as an alternate host for the peanut root knot nematode (*M. arenaria* [Neal] Chitwood). The high densities of phytoparasitic nematodes found in the root zone of hygrophila, particularly in its native range, suggest that this weed could act as an alternative host of these important plant parasitic nematodes. Further studies involving inoculation with phytoparasitic nematodes to assess performance of hygrophila as a susceptible host plan can provide further insight about its suitability as a transitional or alternative host. Overall, this study, demonstrated for the first time the root association of plant pest nematodes with the invasive weed hygrophila.

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Spatial and temporal variation in duckweed and filamentous algal levels in contiguous floodplain lakes of the Upper Mississippi River

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ABSTRACT

This study examined how free-floating macrophyte cover (principally composed of duckweeds [*Lemna* spp.]) and prevalence of floating filamentous algal mats (metaphyton) varied within and among lakes within three reaches of the Upper Mississippi River. Data were collected using standard sampling approaches over the period 1998 to 2008. Duckweed cover varied primarily within and among lakes; in comparison filamentous algae prevalence varied primarily among lakes and lake-years. Duckweed cover increased with submersed aquatic vegetation (SAV) abundance at within-lake and among-lake-year scales; in comparison, filamentous algae prevalence increased with SAV abundance at within-lake, among-lake and year scales. Given adjustment for SAV, filamentous algae prevalence decreased with increasing lake connectivity but was not statistically associated with annual changes in mean river discharge; duckweed cover was not associated with either connectivity or discharge. Documenting the relatively high levels of variation within lakes and of year-to-year variation in lake means improves our understanding of the dynamic nature of aquatic plant and algal communities in the Upper Mississippi River and will assist efforts to manage or control aquatic plants and nuisance algae in this region. In particular, this work explicitly characterizes sources of variability in free-floating macrophyte cover and filamentous algae prevalence, and highlights how this variation may complicate efforts to evaluate the short-term success of management and control efforts.

Key words: free-floating aquatic macrophytes, Lemnaceae, metaphyton, submersed aquatic vegetation, variance components

INTRODUCTION

High levels of free-floating aquatic plants, including *Lemna* and *Azolla* species and filamentous algal mats, may have profound effects on aquatic ecosystems and may substantially influence food web structure, biogeochemical cycles, and the recreational use of freshwater systems (Janes et al. 1996, Scheffer et al. 2003, Pinto et al. 2007, Saunders 2009, Fontanarrosa et al. 2010).

Filamentous algae often form conspicuous mats attached to substrates or submersed aquatic vegetation (SAV) or float below or near the water surface. Algal mats that originate beneath the water surface, referred to as metaphyton (Howell et al. 1990, Wetzel 2001), may become suspended by wind-induced circulation (Wetzel 2001) or when trapped gases accumulate and float them to the surface (Saunders 2009). The establishment of metaphyton and its subsequent accumulation in littoral or pelagic regions is common in temperate eutrophic or acidic lakes (Howell et al. 1990, Makarewicz et al. 2007). Algal mats and free-floating macrophytes like duckweeds have been associated with thermal characteristics of water bodies, decreased SAV growth, and decreased dissolved oxygen concentrations (Dale and Gillespie 1977, Phillips et al. 1978, Jones et al. 2002, Morris et al. 2003, Parr and Mason 2004, Hilton et al. 2006).

The ability of free-floating plants and algae to absorb insolation and reduce incident light likely causes the most dramatic impact on other portions of the aquatic plant community (Giorgi et al. 2005). Specifically, low light availability may decrease SAV growth and photosynthetic rates, biomass, richness, and alter community composition (Phillips et al. 1978, Jones et al. 2002). Decreased SAV photosynthesis may, therefore, lead to changes in dissolved oxygen and pH. Because photosynthetically active SAV may substantially increase water pH (Spencer et al. 1994), reductions in photosynthetic activity may influence aquatic chemistry and the activity of epiphytic microorganisms (Eriksson and Weisner 1999). Finally, decreases in dissolved oxygen associated with

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