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Granite Rock Outcrops: An Extreme Environment for Soil Nematodes?

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Abstract: We studied soil nematode communities from the surface of granite flatrock outcrops in the eastern Piedmont region of the United States. The thin soils that develop here experience high light intensity and extreme fluctuations in temperature and moisture and host unique plant communities. We collected soils from outcrop microsites in Virginia (VA) and North Carolina (NC) in various stages of succession (Primitive, Minimal, and Mature) and compared soil properties and nematode communities to those of adjacent forest soils. Nematodes were present in most outcrop soils, with densities comparable to forest soils ($P > 0.05$). Nematode communities in Mature and Minimal soils had lower species richness than forest soils ($P < 0.05$) and contained more bacterial-feeders and fewer fungal-feeders ($P < 0.05$). Primitive soils contained either no nematodes (NC) or only a single species (*Mesodorylaimus* sp., VA). Nematode communities were similar between Mature and Minimal soils, according to trophic group representation, MI, PPI, EI, SI, and CI ($P > 0.05$). Forest soils had a higher PPI value ($P < 0.05$), but otherwise community indices were similar to outcrop soils ($P > 0.05$). Outcrop nematode communities failed to group together in a Bray-Curtis cluster analysis, indicating higher variability in community structure than the Forest soils, which did cluster together. A high proportion of the nematodes were extracted from outcrop soils in coiled form (33-89%), indicating that they used anhydrobiosis to persist in this unique environment.

Key words: Anhydrobiosis, community structure, diversity, ecology, granite flatrock outcrops, Maturity index, nematode survival, primary succession.

Granite flatrock outcrops are exposed slabs of rock found amidst the deciduous forests of the Piedmont region of the southeastern United States, from Southern Virginia to Alabama (Fig. 1). On these rocks, soil formation has occurred within small topographical depressions and plants establish in a well-documented sequence of primary succession (Smith, 1941; Shure and Ragsdale, 1977). Soils are initially very shallow, nutrient-poor, and have low water-holding capacity (Shure and Ragsdale, 1977). Outcrop soils host unique plant communities, including several endemic or near-endemic species (McVaugh, 1943; Baskin and Baskin, 1988; Shure, 1999). Biodiversity of plants tends to increase with increasing maturity of the depressions, as soil depth and fertility increase (Shure and Ragsdale, 1977; Houle 1990). Arthropod diversity follows this trend (Shure and Ragsdale, 1977), but very little is known about the soil's microfaunal communities (Quarterman et al., 1993).

Rock outcrops experience fluctuating and extreme environmental conditions that differ greatly from those of the surrounding deciduous forests, which are insulated by more abundant vegetation and deeper soil (Shure and Ragsdale, 1977). Trees cannot establish in the shallow outcrop soils and thus light intensity is high, contributing to high temperatures. Indeed, the rock outcrop environment has been described as "desert-like" (Shure, 1999). Granite rock outcrops also experience a greater range of daily temperatures in both summer and winter than adjacent forests, but this variation ameliorates as succession proceeds (Shure and Ragsdale, 1977). The shallow soils can be very dry seasonally, but are saturated following precipitation events due to the impermeability of the underlying rock, which causes moisture to pool in the depressions (Phillips, 1982; Shure, 1999).

Soil nematodes use a survival strategy known as anhydrobiosis to endure extreme conditions (Freckman et al., 1975; Townshend, 1984; Treonis and Wall, 2005). This ametabolic state protects the organism from environmental stress and is induced by desiccation (Crowe and Madin, 1975; Crowe et al., 1992; Wharton and Barclay, 1993). Anhydrobiosis is an inactive, cryptobiotic state characterized by an extreme loss of body water and coiled morphology, which reduces the surface area of the nematode cuticle exposed to the environment (Demeure et al., 1979; Womersley et al., 1998). Studies have shown that anhydrobiotic nematodes extracted from soils can be rehydrated, regaining motility and resuming normal metabolism (Treonis and Wall, 2005). The proportion of a soil nematode population that is anydrobiotic is correlated strongly to soil moisture content (Treonis et al., 1999, 2000; Treonis and Wall, 2005). Anhydrobiosis should be an important strategy for nematodes in habitats like granite rock outcrops where soil moisture fluctuates significantly.

The objective of this study was to compare the abundance and structure of soil nematode communities in outcrop soils at various stages of succession to that of adjacent deciduous forest. Nematodes in outcrop soils may be influenced by the same environmental factors that shape the plant communities. Alternatively, the ability to use anhydrobiosis may allow most nematode species to have a wider distribution across the outcrop. We hypothesized that early succession soils would support a lower diversity and abundance of nematode species than forest soils, but that these differences would be less pronounced in more mature outcrop soils. We also predicted that nematodes found in rock outcrop soils would need to employ anhydrobiosis during periods of

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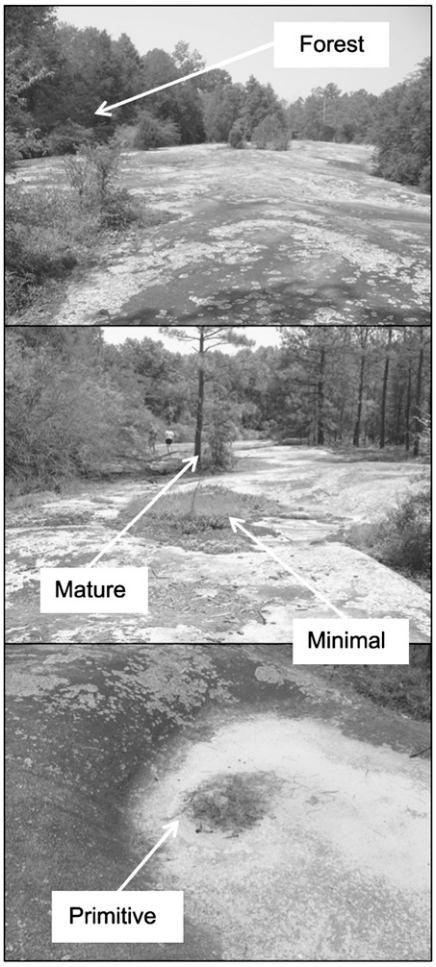

FIG. 1. Microsites on a granite flatrock outcrop (Gasburg, VA). Top panel shows most of the study site. Middle panel shows Mature and Minimal vegetation distinctions. Bottom panel shows a Primitive microsite. Photo credit: Carolyn Marks, University of Richmond.

low soil moisture. Therefore, we investigated whether soil nematodes within rock outcrop soils would be found in an anhydrobiotic state (as indicated by coiled morphology) and whether they could be revived with naturally increasing relative humidity or soil wetting.

MATERIALS AND METHODS

Two granite rock outcrop sites in the Piedmont region of the eastern United States were studied. The first, Gasburg Granite Flatrocks Preserve (Fig. 1, Gasburg, Virginia, 36°33.995′N 77°52.212′W, elevation 77 m), is protected by the Nature Conservancy of Virginia, and the second, Temple Flat Rocks (near Raleigh, North Carolina, 35°50.381′N 78°7.421′W, elevation 106 m), is protected by the Triangle Land Conservancy. Each rock outcrop is <1 hectare in area.

Soil samples were collected from May to July 2007. Six soil samples were collected from depressions on each granite rock outcrop (VA and NC) from microsites designated as Primitive (1 sample per site), Minimal (2 samples per site), or Mature (3 samples per site) (Fig. 1). Primitive microsites were sparsely vegetated at the time of sampling; only the dried stems of the pioneer species and winter annual *Diamorpha smallii* (Small's stonecrop) were present. Minimal microsites contained low-lying vegetation, primarily moss, herbaceous plants, and grasses. Mature microsites were dominated by grasses, shrubs, and small pine trees. Three soil samples also were collected from the surrounding deciduous forest within 20 m of the granite rock perimeter. A single moss sample (aboveground portion only) was collected from Minimal microsites at both sites for comparison to soils. Sample replication from the microsites varied because it was necessary to limit the impact of this research on the endemic plant species' seed banks. All samples were collected with spoons to a depth of 5 cm after scraping away surface litter. Soils at the Primitive sites did not exceed 3 cm in depth. Each sample consisted of a composite of soils collected from three separate locations within the microsite. Samples were stored in coolers for transport back to the laboratory for nematode extraction and other analyses within 48 h of collection.

Nematode Community Analysis: A Baermann funnel technique was used to extract live nematodes from 50 g soil over 72 h (Freckman and Baldwin, 1990). Nematodes were preserved in 10% formalin solution and stored at 4°C. An inverted light microscope was used to determine the total nematode count per sample and to classify nematodes into recognized morphospecies. Soil moisture (gravimetric) and soil organic matter (loss on ignition, 450°C) were measured for each sample.

Nematode Anhydrobiosis: On 25 June 2008 granite rock outcrop microsites at the Gasburg, VA site were used for an anhydrobiosis experiment. First, soils were collected at 19:00 h, a very warm and low humidity (RH) period of the day (n = 4 composite samples per Minimal and Mature microsite, n = 1 per Primitive site, 5 cm depth). The same plots were sampled again eleven hours later (06:00 h), a very cool and high RH period. Our objective was to determine whether nematodes in anhydrobiosis responded to fluctuating environmental conditions over a short time scale. Second, to determine the response of soil nematodes to a simulated precipitation event, soils were wetted at 20:00 h with enough water to reach saturation (100-300 ml). Water was applied to an area of soil within a 9 x 13 cm plastic collar that retained the water in a specific area during drainage into the soil. These soils were sampled 10 h later at 06:00 h. All soils collected for anhydrobiosis studies were transferred to 1.25 M sucrose solutions at the time of sampling to fix the status of the nematodes (anhydrobiotic or active, Treonis et al., 2000). To extract nematodes from these solutions, a sieving and flotation/centrifugation extraction technique was used with high molarity sucrose solutions replacing water to prevent rehydration (Freckman et al., 1977). Extracted nematodes were observed with an inverted light

microscope within 24-72 h of extraction. Nematodes were classified as coiled when the tail end of the body curled sufficiently to touch another part of the body. Soil moisture was measured gravimetrically (48 h, 110°C). Companion soil samples also were collected from each microsite for extraction of nematodes with standard sucrose flotation/centrifugation techniques to determine nematode density and the proportion alive based on motility in water following extraction (Jenkins, 1964; Byrd et al., 1966). Dataloggers recorded environmental conditions (temperature and relative humidity) and temperature within the soil (3 cm depth) over the course of the experiment (HOBO®H8 RH/TEMP/LIGHT loggers with 6′ Temperature Probe Cable, Onset Computer Corp., Pocasset, MA, USA). Dataloggers were also used to record spot measurements of air and soil temperature on other dates during summer 2008.

Computational and statistical analyses: The Shannon–Wiener diversity index was calculated using the following:

$H' = -\sum P_i (\ln P_i)$, where P_i = the proportion of species i in the total nematode community (Shannon and Weaver, 1949).

The Maturity Index (Bongers, 1990) is a nematode community analysis that is based upon life-history characteristics of nematode taxa. Each nematode taxa has been assigned a c-p value from 1-5, based upon whether it is considered to have "colonizer" or "persister" life history characters, with the former containing taxa that tend to proliferate in disturbed, enriched soils, and the latter considered to establish in more stable systems (Bongers, 1990). The MI excludes plant-parasitic nematodes, which are treated separately in the calculation of the PPI (Plant Parasite Index).

MI = $\sum v_i \,.\, f_i$, where v_i was the c-p value and f_i was the frequency of the ith family (free-living taxa only)

PPI = $\sum v_i \,.\, f_i$, where v_i was the c-p value and f_i was the frequency of the ith family (plant-parasite taxa only)

Ferris et al. (2001) expanded the use of the c-p scale by including trophic information into the calculation of the Channel Index (CI), Enrichment Index (EI), and Structure Index (SI). These indices provide information regarding the food web structure and decomposition pathways and were calculated for this study as described by Ferris et al. (2001).

A Bray-Curtis cluster analysis (single link) was performed to construct a hierarchical cluster dendogram of the nematode communities from the various sites using BioDiversity Pro V.2 (http://www.sams.ac.uk/research/software). The Bray-Curtis similarity coefficient that is used to construct the dendogram is based on species numbers (i.e., not presence/absence data; Bray and Curtis, 1957; Hodda, 1986).

Measured and calculated variables were compared using two-factor analysis of variance (e.g., site x microsite or treatment x microsite) performed with Statview Version 5.0.01 (SAS Institute, Inc., Cary, NC, USA). Data was transformed as needed to meet ANOVA assumptions (log-transformation for nematode density, square-root transformation for species richness, arcsine transformation for proportions; Sokal and Rohlf, 1995). Primitive and Moss samples were not included in statistical analyses due to limited replication. Means were compared using Fisher's PLSD.

Results

At both the VA and NC sites, soil moisture and organic matter were similar in soils from the outcrop microsites (Mature and Minimal) and in the adjacent Forest soils ($P > 0.05$, Fig. 2). Soils in the Primitive depressions contained very low moisture and organic matter content (Fig. 2). Temperatures on the sparsely vegetated surfaces of the rock outcrop (i.e., within Primitive depressions) routinely exceeded 50°C when spot measurements were taken in May and June 2008, while not exceeding 35°C in the forest at the same times. Beneath the soil surface, temperatures were more moderate over a 14 h period on 25 June 2008 (Fig. 3A). Temperatures within the Primitive and Minimal soils exceeded those of the Mature and Forest soils (Fig. 3A). Relative humidity was lower during the afternoon at outcrop microsites than in the forest (Fig. 3B).

Soil nematode density ranged from 0-99,479 nematodes kg^{-1} of dry soil. Outcrop soil nematode abundance was comparable to adjacent forest soils (Fig. 4A). Soils from the Minimal microsites contained fewer nematodes than Forest soils, but only at the NC site (ANOVA, significant site x microsite interaction, $P = 0.0473$). A Primitive soil in VA contained a high density of nematodes (a single species of *Mesodorylaimus*, Fig. 4A), but the homologous microsite in North Carolina contained no nematodes at all (Fig. 4A). Moss samples from both sites contained high numbers of nematodes (3,865-23,783 nematodes kg^{-1} dry moss).

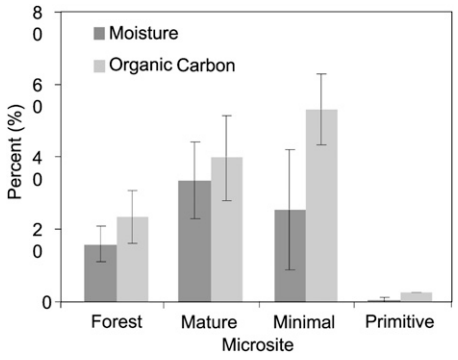

Fig. 2. Soil moisture and soil organic carbon content in the microsites sampled. Values are means ± the standard error of the mean. Differences between microsites are not statistically significant (ANOVA, $P > 0.05$).

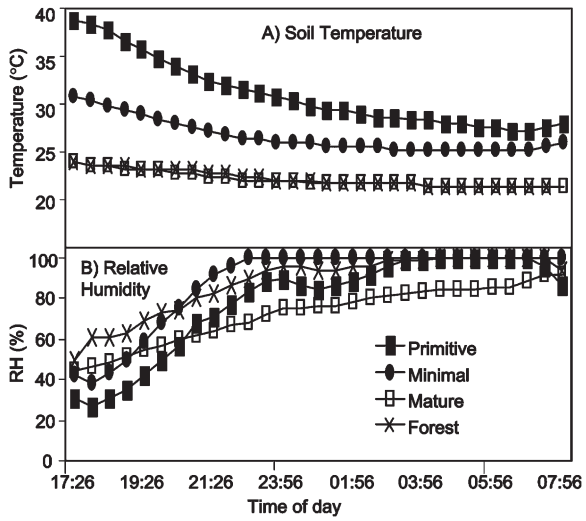

FIG. 3. Soil temperature (A) and relative humidity (B) at forest and rock outcrop microsites in Virginia (25 June 2008).

Fifty-five morphospecies, representing 24 nematode families, were found across the study sites. Morphospecies richness varied among microsites, but the patterns differed slightly between the two field sites (ANOVA, significant site x microsite interaction, P = 0.0491). Forest soils had significantly higher nematode species richness than Mature or Minimal soils at both sites, with an average of 25.3 (range 23-32) morphospecies present (Fig. 4B). The highest species richness of any outcrop soil was 22 and most were considerably lower, with the lowest richness found in Minimal soils in NC (Fig. 4B). Primitive microsites either contained no nematodes (NC) or a single morphospecies (VA), but were not included in statistical analyses due to lack of replication.

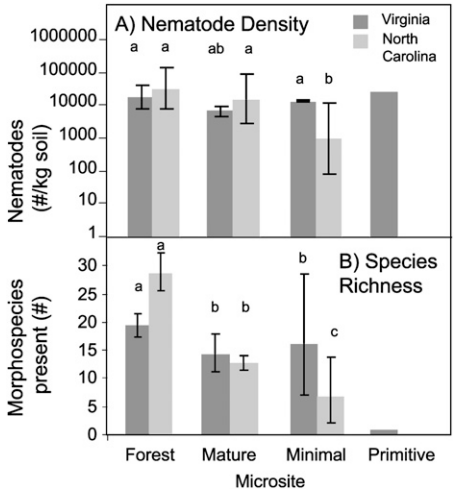

FIG. 4. Nematode density (A) and Species Richness (B) in forest and rock outcrop soils (Means with 95% confidence intervals, n = 3 for Forest and Mature microsites, n = 2 for Minimal, and n = 1 for Primitive). Means with the same letter are not significantly different (Fisher's PLSD, $P < 0.05$).

Most of the nematodes encountered (85-100%) could be placed into nine taxa (Table 1). Most of these groups had representatives in all samples, at both sites (VA and NC) and at all microsites (Forest, Mature, Minimal). Some taxa seem to be site specialists, however. For example, a *Teratocephalus* sp. was relatively abundant in the Minimal outcrop microsite soils and within moss samples themselves. The Shannon-Wiener index did not vary between sites or microsites (mean = 2.15 ± 0.102 s.e.m., ANOVA, $P > 0.05$). Bray-Curtis cluster analysis revealed a high degree of similarity between nematode communities in Forest soils (NC and VA, Fig. 5). No clear patterns were evident for the outcrop soils, however (Fig. 5).

The trophic structure of nematode communities varied among the microsites, but not between sites (VA and NC). Forest soils had higher proportions of fungal feeders (including species from the family Tylenchidae) (Table 2, ANOVA, P = 0.0160), while bacterial feeders were more abundant in Mature and Minimal rock outcrop soils (ANOVA, P = 0.0449). Plant-parasite and omnivorous nematode proportions were not significantly different between microsites ($P > 0.05$ for both ANOVAs). The F:B ratio follows the above trends, with Forest soils having a higher ratio than soils from Mature and Minimal granite rock outcrop microsites, (Table 2, ANOVA, P = 0.0053).

The MI was not significantly different between sites or microsites (Table 2, ANOVA, $P > 0.05$), but Forest soils had higher PPI than Mature and Minimal soils (Table 2, ANOVA, P = 0.0017). The Structure Index (SI) was plotted against the Enrichment Index (EI) to visualize the Faunal Profiles of the nematode communities (Ferris et al. 2001; Fig. 6). Forest soil plotted solidly into a quadrant that should characterize stressed and/or degraded soils (Ferris et al. 2001). Mature and Minimal rock outcrop soils plotted very similar to each other, but to the left of the Forest soils, suggesting these communities originate from a less-disturbed habitat. The Channel Index was 89.3 ± 10.7, 74.6 ± 14.9, 91.6 ± 3.1 for Minimal, Mature, and Forest soils, respectively, indicating that the fungal decomposition pathway is important at all sites. Statistically, the SI, EI, and CI are

TABLE 1. Proportional representation of key nematode taxa in communities from forest and granite rock outcrop microsites.

	Forest	Mature	Minimal	Primitive	Moss
Aphelenchoides	0.30	0.11	0.06	0	0.02
Acrobeloides	0.12	0.22	0.12	0	0
Teratocephalus	0.04	0.10	0.22	0	0.33
Dolichodoridae	0.09	0.01	0	0	0
Mesodorylaimus	0.02	0.12	0.08	1.00	0.25
Plectidae	0.09	0.11	0.07	0	0.17
Tylenchidae	0.15	0.09	0.14	0	0.02
Monhysteridae	0	0.01	0.08	0	0.09
Prismatolaimidae	0.01	0.06	0.05	0	0

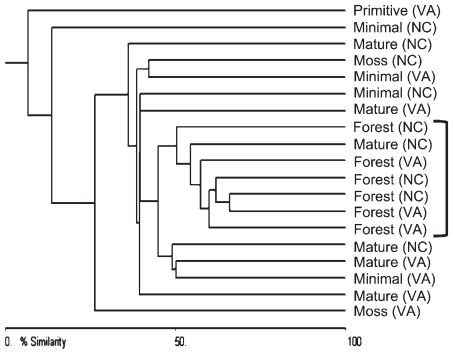

FIG. 5. Heirarchical cluster dendogram based on a Bray-Curtis cluster analysis of the nematode communities. The cluster containing all the Forest soils is indicated with the bracket. Primitive (NC) did not contain any nematodes and was not included in this analysis.

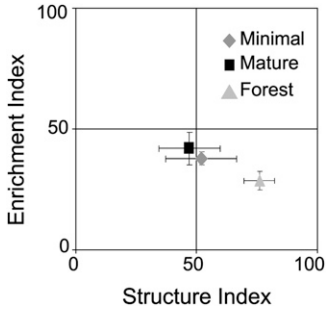

FIG. 6. Faunal Profile for Forest and Mature and Minimal granite rock outcrop soil nematode communities. Means are plotted ± s.e.m. (n = 6 for Forest and Mature microsites and n = 4 for Minimal).

not significantly different among the sites or microsites (ANOVA, $P > 0.05$ for all).

On 25 June 2008, a substantial percentage of the nematodes in VA outcrop soils (Mature, Minimal, and Primitive) were extracted in coiled/anhydrobiotic form (33-89%) (Fig. 7). There was no difference between the proportion of nematodes that were coiled at the Mature and Minimal microsites between 19:00 h and 06:00 h (Fisher's PLSD, Fig. 7), despite differences in soil temperature and relative humidity between those times (Fig. 2). The addition of water to soil in the Mature and Minimal sites raised gravimetric soil moisture content significantly (from 10.2% before wetting to 24.7% for Mature soils, 11.9 to 37.5% for Minimal, and 0.31 to 6.2% for Primitive). These increases corresponded to a significant reduction in the proportion of coiled nematodes (ANOVA, $P < 0.001$, Fig. 7). Only a fraction of the nematodes in soils from these sites were alive (motile) following extraction with water (mean = 15.3% for both microsites, range = 0–50.5%). The Primitive site had the lowest proportion of nematodes coiled following extraction with sucrose solutions, but more than 98% of the nematodes at this site failed to regain motility when extracted and rehydrated in water.

TABLE 2. Nematode community structure at Forest and Mature and Minimal granite rock outcrop microsites[a].

	Forest	Mature	Minimal
Bacterial-feeders[b]	0.32[b]	0.59[a]	0.60[a]
Fungal-feeders[b]	0.46[a]	0.20[b]	0.21[b]
Plant Parasites[b]	0.15[a]	0.02[a]	0.09[a]
Omnivores[b]	0.06[a]	0.19[a]	0.10[a]
Predators[b]	0.01	0.00	0.01
F:B[c]	0.59[a]	0.26[b]	0.26[b]
MI	1.00[a]	2.23[a]	2.02[a]
PPI	1.36[a]	0.46[b]	0.65[b]

[a]Within a row, values with different superscipts are statistically different (ANOVA, $P < 0.05$, Fishers PLSD). Due to low prevalence, predator data was not subject to statistical analysis.
[b]Proportion of total community.
[c]F:B = density of fungal feeders/(density of fungal + bacterial feeders).

DISCUSSION

Soil nematode communities in granite rock outcrop soils appear to be influenced by differences in environmental and edaphic factors among the succession stages. We hypothesized that early succession soils would support a lower diversity and abundance of nematode species than forest soils, but that these differences would become less pronounced in more mature outcrop soils. Our data mainly support this hypothesis.

Primitive outcrop depressions had the warmest and driest environment of the microsites studied, and the soils here contained the lowest organic matter. Due to the presence of several endemic or near-endemic plant species, we were obliged to minimize soil sampling from these small areas. Therefore, any inferences that can be made about the nematode communities are tentative. In the two Primitive soils sampled, we found either no nematodes (North Carolina) or only a single nematodes species (Virginia). We recorded a high temperature of 62.7°C at the surface of a Primitive rock outcrop depression in North Carolina on 11 June 2008, when the standing air temperature was 45°C (113°F). Although soil nematodes generally can avoid the effects of high surface temperature by occupying deeper soil layers, the soils in the NC outcrop depression were only about 3 cm deep, so it is not too remarkable that nematodes were

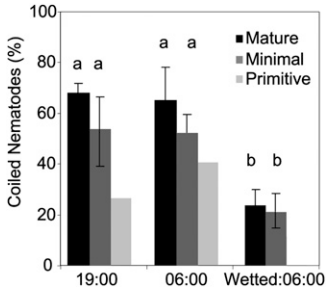

FIG. 7. Proportion of nematodes that were coiled (anhydrobiotic) in rock outcrop soils in VA (25 June 2008) at 19:00, 06:00, and at 06:00 after being wetted at 20:00 the evening before. [Means with 95% confidence intervals, n = 4 for Mature and Minimal microsites, n = 1 for Primitive (not included in ANOVA). Means with the same letter are not significantly different (Fisher's PLSD, $P < 0.05$).].

absent here. In contrast, nematode density in the VA Primitive soil was comparable to that of other microsites. We used Baermann funnels for nematode extraction, so these nematodes had to be alive at the time that the soil was collected. One year later, in June 2008, 98% of the nematodes from the same Primitive depression failed to regain motility following sugar-centrifugation extraction (i.e., they were dead). It is possible that, like the pioneering plant species, the nematode communities in these Primitive depressions are also "annual" in nature, re-establishing when conditions are favorable. Primitive depressions were colonized at both sites by the annual *Diamorpha smallii* (Small's stonecrop). We observed the living, flowering plants in Virginia in March and early May 2008, but the plants seeded and died by June. The "pioneering" nematode at the VA site was a *Mesodorylaimus* sp., a genera classified as omnivorous in its feeding habits (Yeates et al., 1993). *Mesodorylaimus* spp. can exhibit predatory behavior, using their stylets to pierce the cuticles of nematode prey (Ferris and Ferris, 1989). As the only nematode species found in Primitive outcrop soils, it seems unlikely that the species found was behaving as a predator. They may be microbivorous in this habitat or possibly root parasites.

Mature and Minimal microsite soils were more moist and contained higher organic content than expected. This could reflect the poor water holding capacity of the soils as well as the ephemeral wetland nature of these microsites. Decomposition could be limited by desiccation at some times and saturation at others, relative to forest conditions which are less variable. In Mature and Minimal soils, nematode density was similar to surrounding Forest soils. In these more developed and well-vegetated soils, the density of nematodes appears to be less influenced by conditions on the rock outcrop than was the case for Primitive outcrop soils. Morphospecies richness was lower in the Mature and Minimal outcrop soils than in Forest soils, however, suggesting that the outcrop environment is not optimal for some nematode species. One notable, virtual absence in the outcrop soils was that of members of the root ectoparasitic Dolichodoridae, which formed a significant component of the community in forest soils. Otherwise, outcrop soil nematode communities appear to contain a subset of the nematode morphospecies found in the Forest soils, with higher representation by various taxa of bacterial-feeders and fewer fungal feeders.

Few differences were detected among nematode communities when comparing Mature microsites to Minimal or homologous Mature and Minimal microsites in VA and NC. This is likely due to a high degree of variation in the data (as implied by cluster analysis), rather than because these communities actually are very similar. Shure and Ragsdale (1977) studied the density and diversity of soil microarthropods (mites and springtails) in microsites on a flatrock outcrop in Georgia, U.S.A. over a period of 20 months. In this study, soil microarthropods showed a clear pattern of increasing diversity with increasing maturity of the microsites, a pattern echoed by aboveground arthropod and plant diversity (Shure and Ragsdale, 1977). Soil microarthropod density showed high interseasonal variation, however, and tended to be high in the Primitive, *Diamorpha*-dominated microsites (Shure and Ragsdale, 1977). In contrast, we only found one nematode species at the VA Primitive microsite and none in NC. Nematodes appear to follow the same species richness patterns as the soil microarthropods, but nematode density appears to be more sensitive to conditions in the Primitive soils, possibly because their dispersal abilities are more limited, relative to arthropods.

Nematode community indices (MI, PPI, EI, SI, CI) did not reveal any marked differences between the forest and outcrop soils. The Bongers' Maturity Index was originally developed as tool for using nematode community structure to assess soil health, particularly in polluted or submerged soils (Bongers, 1990; Bongers and Bongers, 1998; Bongers and Ferris, 1999). This analysis was tailored to understanding soils experiencing disturbance and recovery (secondary succession, not primary). Bongers and Bongers (1998) discuss the utility of the Maturity Index for understanding nematode community development in primary succession and suggest that the MI does not model primary successional dynamics in nutrient-poor soils very well. In our study, the only significant effect that we observed was higher PPI in Forest soils as compared to rock outcrop soils. Specifically, nematodes from the PPI Group 3 family Dolichodoridae (*Tylenchorhynchus* sp. and others) were considerably more abundant in forest soils. This could be correlated to denser root biomass in the forest soils. The EI, SI, and CI also did not reflect the differences in nematode community trophic structure that were detected between forest and outcrop soils (Table 2). Also surprising, plotting the Enrichment Index versus the Structure Index placed the outcrop soils in an area of the Faunal Profile (lower SI, slightly higher EI) suggesting more stability, less disturbance, and increased resource availability compared to forest soils (Ferris et al., 2001). This characterization seems unlikely, given the extreme variation in environmental conditions that occur on the rock outcrop. Overall, it appears that the utility of some nematode community indices across a sequence of primary succession is limited, although this does not undermine their utility in other types of soils, particularly in understanding the impact of agricultural practices and environmental change on the structure and function of nematode communities (Freckman and Ettema, 1993; Neher, 1999; Porazinska et al., 1998; Wang, 2004; Pavao-Zuckerman and Coleman, 2007; Biederman et al., 2008).

Desiccation survival strategies are available to terrestrial biota, such as seeds, mosses, and many invertebrates, during all or part of the life cycle (Alpert,

2005). We hypothesized that nematodes found in rock outcrop soils would employ an anhydrobiotic survival strategy during periods of low soil moisture. We found significant proportions of the nematode community in coiled form, supporting this hypothesis. We also predicted that nematode activity in rock outcrop soils would peak immediately after precipitation events, as has been seen in other soils (Whitford et al., 1981; Treonis et al., 2000). We simulated rainfall by saturating soils, and this proved to be a strong trigger for uncoiling of the nematodes. However, we also knew from a separate extraction of the same soils that many of these nematodes were dead, suggesting that rehydration is a passive process and that dead nematodes uncoil in water. Nonetheless, nematodes in the outcrop soils appear to be using anhydrobiosis, although this strategy may not guarantee indefinite survival.

Teratocephalus and *Acrobeles* are among the few nematode taxa that emerged in this study as particularly abundant in the rock outcrop environment, together composing about one third of the nematodes in Mature and Minimal soils. At the Minimal microsites in both Virginia and North Carolina, moss was a significant component of the vegetation, and moss samples contained considerable *Teratocephalus sp.* populations. This genus has been associated with moss in other habitats, including the Antarctic peninsula (Pickup, 1990; Pickup and Rothery, 1991), where *T. tilbrooki* is found in moss cushions. *T. tilbrooki* is capable of surviving long periods of desiccation through its ability to employ anhydrobiosis (Pickup and Rothery, 1991). It seems likely that its relative has similar ecology in the outcrop soils as it does in Antarctica. *Acrobeles* spp. and other Cephalobina are common nematodes in desert soils (Pen-Mouratov and Steinberger, 2005; Adams et al. 2007) and these have also been shown to use anhydrobiosis (Demeure et al., 1979; Freckman and Mankau, 1986; Treonis et al., 2000). Although anhydrobiosis could play a role in the success of these specific nematode taxa in the rock outcrop soils, the use of this survival strategy probably is widespread among nematode taxa. Therefore, anhydrobiosis may contribute to many nematode species having a wide distribution across the outcrop succession series. Comparative investigations of the use of anhydrobiosis by divergent nematode taxa are greatly needed to further understand the role this strategy plays in the ecology of soil nematodes (Treonis and Wall, 2005).

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