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Source: Florida Entomologist, 87(3) : 386-390

Published By: Florida Entomological Society

URL: https://doi.org/10.1653/0015-4040(2004)087[0386:SMAASG]2.0.CO;2

SOIL MACROINVERTEBRATES ALONG A SUCCESSIONAL GRADIENT IN CENTRAL FLORIDA

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Soil macrofauna are a diverse group of biota that play important roles in many ecosystem processes. Soil macrofauna succession has been the subject of several studies in the temperate zone (Strüve-Kusenberg 1981; Tajovsky 1990; Pižl 1992; Frouz 1997). However, few data are available concerning succession of soil macrofauna in tropical and subtropical areas of the world (Silva Del Pozo & Blandon 1991a,b), including subtropical Florida, USA. The present study was undertaken to quantify changes in soil macrofauna during secondary succession in north-central Florida.

The study was conducted at the University of Florida's Natural Area Teaching Laboratory (NATL) at Gainesville, Florida (29°41'N, 82°19'W). This undeveloped area located at the southwest corner of the university campus covers 19 ha and is maintained to demonstrate local natural habitats, primarily three Florida upland ecosystems, including upland hammock, upland pine, and old-field. Five plots of different successional stage were selected for the study. These included two earlier stage plats, disturbed 2 and 7 years earlier by disking as a part of the old-field succession project of NATL. The other three plots are considered to have been subjected to clear-cutting combined with burning and mechanical disturbance, i.e., with a history typical of forest lands in this region. By comparing aerial photographs of this area taken every 10 years since 1949, we determined the appearance of different succession stages. From this and examination of the trees in the plots, we estimated that the last major disturbances in the three plots took place 20-30 years ago, 60-90 years ago, and more than 150 years ago, respectively. The last two sites appear on the oldest aerial photography as young forest about 10-30 years old (former site) or as an old growth hardwood (latter site). The study plots area extended over 1.2 ha for 2- and 7-years-old plots, 0.3 ha for 20-30-year-old plot, and ca. 3-4 ha for the two oldest plots. The first three plots were quite close to each other, whereas the last two plots bordering with each other were relatively distant.

The plot most recently disturbed (2 years) supported a dense cover of weeds, with soil covered by a discontinuous thin layer of litter. The second plot, disturbed 7 years earlier, was dominated by blackberries (*Rubus cuneifolius* Pursh.) and dog fennel (*Eupatorium capillifolium* [Lam.] Small). In this plot the soil surface was covered by a continuous 3-5 cm thick layer of shrub and herb litter. The third plot, not disturbed for 20-30 years, was dominated by Loblolly pine (*Pinus taeda* L.), with soil covered by a 5-7 cm thick layer of pine litter. The fourth plot, not disturbed for 60-90 years, was covered by 1-2 cm thick layer of litter and was dominated by hardwoods, including sweetgum (*Liquidambar styraciflua* L.), oaks (*Quercus hemisphaerica* Bartr. ex Willd and *Quercus nigra* L.), plus hop hornbeam (*Ostrya virginiana* (Mill.) K. Koch) and *P. taeda*. The last sampling plot located in an area undisturbed for > 150 years was very similar to the fourth plot in terms of vegetation and litter cover.

All plots were sampled in February, September, and October 2001, with a circular corer 11 cm in diameter. In each plot, soil samples were collected from three locations. Individual sampling locations were 20-70 m apart from each other. Except for the oldest plot, the distance between two most distant sampling locations selected on the same plot was typically greater than the distance between any two closest sampling locations existing on different plots. At each plot location, three 16-cm-deep core samples were collected. Each core sample was divided into two depth classes: 0-8 cm (top) and 9-16 cm (bottom). Thus, a total of nine cores for each depth class were taken from each plot. The top and the bottom core samples at each location were separately combined. Only apparently sandy soil in each plot was sampled, whereas clay soil patches were avoided, as were apparent soil depressions or elevations in a plot. The collected samples were extracted for 7 days in the laboratory for soil macrofauna with the Tullgren-type extraction apparatus. Extracted material from each sample was fixed in 2% formaldehyde, transferred to 80% ethanol and sorted under various magnifications of a dissection microscope to separate morphologically distinguishable morphospecies (Beattie & Oliver 1994). Morphospecies represent here morphologically distinguishable forms, which are assumed to represent separate species but which cannot be adequately determined. Morphospecies were determined to lowest practical level and these data were used for grouping into trophic groups. Morphospecies were grouped into higher taxa, dried at 40°C for 24 h, and weighed to determine

dry biomass (OHAUS AS120, Florham Park, NJ, accuracy 0.1 mg). If some higher taxa consisted of several trophic groups, these were grouped and weighed separately. The statistical package, SPSS 10.0 (SPSS, 1999) was used for ANOVA and *t*-tests; nine replicates per plot were used unless mentioned otherwise.

A total of 71 soil macrofaunal morphospecies was recorded during the study, with 23-38 morphospecies identified from individual sites (Table 1). Mean number of morphospecies occurring per sample in individual plots, total number of morphospecies per plot as well as Shannon-Weiner diversity index increased with time since last disturbance. These findings agree with those of Loranger et al. (1998) who reported that the species diversity increased with successional age of plots in the Martinique (Caribbean).

Density of soil total macrofauna ranged from 512 to 962 individuals/m^2 (Table 1). These values are comparable with those given for soil under a mixed forest in France (Geoffroy et al. 1981), or a mountain forest in Ecuador (Silva del Poso & Blandon 1991a,b). However, substantially higher densities (than in our study) of soil macrofauna have been reported for some wet tropical areas (Decaens et al. 1994, Loranger et al. 1998, Höfer et al. 2001). In our study, omnivores represented mainly by Formicidae were the most abundant among soil macrofauna at the investigated sites (Table 1). In the 2-year post disturbance plot, Hymenoptera, larval Coleoptera, larval Diptera, and adult Coleoptera were the most abundant. In other studies, high abundance of soil insects with flying adults, especially Diptera larvae, in initial succession stages has been reported by Strüve-Kusenberg (1981), and Frouz (1997); such an abundance has been attributed to high migration potential of the insects (Strüve-Kusenberg 1981; Frouz 1997). Omnivores and the highest proportion of phytophagous organisms, such as insect larvae, were recorded in the earliest stage. With post-disturbance time increase, the proportion of herbivores decreased and the number of saprophagous organisms increased (Table 1). Diplopoda (Julidae) were abundant among saprophagous groups in the 7- and 20-30-years post-disturbance plots. Isoptera were abundant in the 60-90-year post-disturbance hardwood plot and Diplopoda (mostly Polyxenidae) were abundant in the oldest site. The relatively lower number of saprophagous groups, in comparison with their reports from temperate zone studies (Axelon et al. 1984) may be attributable to the occurrence of oligochaetes in low densities. In sandy soils, oligochaete densities are usually low because of the lower water holding capacity as well as lower organic matter content of such soils (Hendrix et al. 1992; Kalisz & Powell 2002 a,b).

The proportion of macrofauna occurring in the deeper (9-16 cm) soil layer was greatest in the 7-year post-disturbance plot and generally decreased in older plots, with only slight increase in the oldest hardwood plot. Vertical distribution of macrofauna differed seasonally. More invertebrates were recorded in the upper soil layer during September ($P < 0.05$, paired *t*-test, all plots). However, no significant differences were noted between invertebrate densities in the two soil layers collected in February and October 2001. Temporal differences were most pronounced in the 7-year post-disturbance plot, where 55 and 60% of all soil macrofauna were recorded in the deeper layer in February and October, respectively, but only 23% in September. In contrast, the proportion of macrofauna in the deeper soil layer of the 60-90-year post-disturbance hardwood remained fairly constant, and ranged between 8-12% during the observation period. We postulate that vertical distribution in our plots reflects changes in shelter against soil desiccation during succession. As the vegetation and litter layer develop during succession, the topsoil layer is protected against desiccation, thus decreasing the necessity of downward faunal migration during the dry season. The sandy soil may be more conducive to this process because it can desiccate easily, and also because burrowing in sandy soil is likely easier than in clay soil. Contrary to this observation, Silva Del Pozo & Blandon (1991a) observed an increase in proportion of macroinvertebrates inhabiting deeper soil layers during succession.

Total macrofaunal biomass varied from 1.87 to 3.71 g/m^2 (Table 2). Similar values were recorded in a Kentucky forest (Kalisz & Powel 2000a) and in a rain forest in the Amazon (Höfer et al. 2001). However, Decaens at al. (1994) recorded substantially higher biomass of soil fauna during the rainy season in tropical West Africa. In the 2-year post-disturbance plot, Coleoptera (mostly Tenebrionidae) formed the highest proportion of total biomass, while in the 7- and 20-30-year post-disturbance plots, Diplopoda (Julidae) dominated. Coleoptera formed the largest proportion of total biomass in the 60-90-year post-disturbance plot, whereas oligochaetes dominated the total biomass in the oldest plot. In our study, phytophagous macroinvertebrates dominated total biomass during early succession, while the proportion of saprophagous macrofauna increased with post-disturbance age (Table 2).

Gratitude is expressed to the Board of the Natural Area Teaching Laboratory at the University of Florida for research permission. We thank two anonymous reviewers and Dr. F. W. Howard for constructive criticism of earlier versions of the manuscript.

Summary

Density, biomass, and community structure of soil macroinvertebrates were studied in five types of plots developing by secondary succession at 2,

TABLE 1. DENSITY AND DIVERSITY OF SOIL MACROINVERTEBRATES IN UP TO 16- CM DEPTH IN FIVE SUCCESSIONAL OLD-FIELD PLOTS AT THE NATURAL AREA TEACHING LABORATORY, UNIVERSITY OF FLORIDA, GAINESVILLE, FL (FEBRUARY-OCTOBER 2001).

	Successional Stage (post-disturbance years)				
	2	7	20-30	60-90	>150
Taxa	Mean ± SE (individuals/m^2)				
Annelida					
Lumbricidae	0 ± 0	19 ± 15	0 ± 0	8 ± 7	16 ± 11
Arthropoda					
Crustacea					
Isopoda	4 ± 4	0 ± 0	43 ± 25	47 ± 27	4 ± 4
Amphipoda	4 ± 4	0 ± 0	8 ± 4	0 ± 0	0 ± 0
Chelicerata					
Arachnida	8 ± 5a	12 ± 11 a	19 ± 10 ab	31 ± 10 b	16 ± 6 ab
Myriapoda					
Symphyla	0 ± 0	4 ± 4	12 ± 5	12 ± 8	0 ± 0
Chilopoda	0 ± 0	8 ± 7	4 ± 4	4 ± 4	16 ± 8
Diplopoda	12 ± 11 a	276 ± 163 b	241 ± 68 ab	23 ± 8 a	66 ± 21 ab
Hexapoda					
Diplura	4 ± 4	0 ± 0	27 ± 15	31 ± 15	12 ± 8
Insecta					
Thysanoptera	0 ± 0	0 ± 0	4 ± 4	8 ± 7	4 ± 4
Hemiptera					
Auchenorrhyncha	0 ± 0 a	0 ± 0 a	4 ± 4 ab	16 ± 8 b	0 ± 0a
Sternorrhyncha	0 ± 0	0 ± 0	0 ± 0	8 ± 7	12 ± 11
Heteroptera	43 ± 32	54 ± 27	0 ± 0	16 ± 8	27 ± 12
Isoptera	0 ± 0	39 ± 37	43 ± 36	101 ± 95	0 ± 0
Blattodea	0 ± 0	0 ± 0	4 ± 4	0 ± 0	16 ± 11
Dermaptera	0 ± 0	4 ± 4	4 ± 4	0 ± 0	0 ± 0
Hymenoptera	257 ± 143	393 ± 88	397 ± 157	408 ± 189	198 ± 88
Coleoptera—adult	47 ± 19	47 ± 26	47 ± 23	89 ± 43	70 ± 26
Coleoptera—larvae	78 ± 26	82 ± 42	43 ±15	27 ± 9	47 ± 10
Lepidoptera	51 ± 40	12 ± 8	0 ± 0	4 ± 4	0 ± 0
Diptera—larvae	74 ± 43 a	12 ± 8 b	8 ± 5 b	8 ± 5 b	8 ± 5b
Total macrofauna	582 ± 144	962 ± 185	904 ± 160	841 ± 230	512 ± 90
% in 9-16 cm[1]	36.2 ab	47.8 b	23.4 ab	10.4 a	19.5 ab
Phytophagous (%)[2]	30	14	7	10	18
Predator (%)	13	6	7	9	12
Saprophagous (%)	13	39	40	33	31
Other (%)	44	41	46	48	39
Species no. total[3]	23	31	26	38	38
Exclusive species no.[4]	7	4	2	2	8
Species no. mean[5]	4.5	5	5.9	6.5	6.7
Shannon-Weiner Diversity	3.62	3.72	3.55	3.81	4.18

Values in the same row followed by the same letter are not significantly different (ANOVA, Tukey's test, $P<0.05$), and values in the same row without any letters are not significantly different.

[1]Mean percent of macroinvertebrates collected from 9-16 cm depth of the total macroinvertebrates occurring in 0-16 cm soil depth.

[2]Percentage of total density.

[3]Total number of morphospecies recorded in a plot.

[4]Total number of morphospecies recorded exclusively in a plot (absent on other plots studied).

[5]Number of morphospecies per one sample.

7, 20-30, 60-90 and >150 years after last major disturbance. Formicidae, Diplopoda, and larval Diptera constituted the highest density, while Coleoptera, Isoptera, and Oligochaeta were among the most important groups in terms of total biomass. The highest numbers of morphospecies

TABLE 2. DRY BIOMASS OF SOIL MACROINVERTEBRATES IN UP TO 16-CM-DEPTH IN FIVE SUCCESSIONAL OLD-FIELD PLOTS AT THE NATURAL AREA TEACHING LABORATORY, UNIVERSITY OF FLORIDA, GAINESVILLE, FL (FEBRUARY-OCTOBER, 2001). GROUPS WHICH DID NOT REACH BIOMASS 0.5 MG/M^2 (E.G., ALL AUCHENORRHYNCHA) ARE NOT INCLUDED EVEN IF MENTIONED IN THE PLOTS (SEE TABLE 1).

	Successional Stage (post-disturbance years)				
	2	7	20-30	60-90	>150
Taxa	Mean ± SE (mg/m^2)				
Annelida					
Lumbricidae	0 ± 0	51 ± 12	0 ± 0	18 ± 4	741 ± 108
Arthropoda					
Crustacea					
Isopoda	23 ± 6	0 ± 0	12 ± 3	295 ± 44	49 ± 11
Amphipoda	2 ± 1	0 ± 0	2 ± 1	0 ± 0	0 ± 0
Chelicerata					
Arachnida	14 ± 3	23 ± 5	4 ± 1	173 ± 21	1 ± 1
Myriapoda					
Symphyla	0 ± 0	1 ± 1	4 ± 1	4 ± 1	0 ± 0
Chilopoda	0 ± 0	2 ± 1	6 ± 1	126 ± 26	26 ± 6
Diplopoda	210 ± 50	1057 ± 57	3163 ± 552	105 ± 14	298 ± 69
Hexapoda					
Diplura	1 ± 1	0 ± 0	6 ± 1	6 ± 1	5 ± 1
Insecta					
Hemiptera					
Sternorrhyncha	0 ± 0	0 ± 0	0 ± 0	11 ± 2	13 ± 3
Heteroptera	93 ± 15	237 ± 33	0 ± 0	18 ± 4	467 ± 33
Isoptera	0 ± 0	35 ± 29	56 ± 46	168 ± 8	0 ± 0
Blattodea	0 ± 0	0 ± 0	12 ± 4	0 ± 0	53 ± 40
Dermaptera	0 ± 0	1 ± 1	1 ± 1	0 ± 0	0 ± 0
Hymenoptera	83 ± 40	112 ± 74	200 ± 19	76 ± 29	53 ± 10
Coleoptera	1593 ± 664	244 ± 102	245 ± 137	1047 ± 295	307 ± 134
Lepidoptera	88 ± 72	26 ± 21	0 ± 0	36 ± 30	0 ± 0
Diptera	16 ± 13	76 ± 28	1 ± 1	1 ± 1	117 ± 92
Total macrofauna	2123 ± 155	1865 ± 60	3712 ± 585	2084 ± 132	2130 ± 150
Phytophagous (%)[1]	59	21	4	24	31
Predator (%)	18	8	3	36	8
Saprophagous (%)	19	65	88	35	59
Other (%)	4	6	5	5	2

[1]Percentage of total biomass.

were recorded in the oldest plots. The proportion of invertebrates found in deeper soil (9-16 cm) generally decreased with successional age. This may be attributed to more pronounced downward migration of soil macrofauna during drier periods of the year in earlier succession plots where the soil could be more sensitive to desiccation. This is Florida Agricultural Experiment Station Journal Series No. R-09606.

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