Available online at www.sciencedirect.com
ScienceDirect
European Journal of Soil Biology 42 (2006) S150–S156
EUROPEAN JOURNAL OF SOIL BIOLOGY
http://france.elsevier.com/direct/ejsobi

Original article

Long-term land-use effects on soil invertebrate communities in Southern Piedmont soils, USA

M.A. Callaham Jr.[a], D.D. Richter Jr.[b], D.C. Coleman[c], M. Hofmockel[b]

[a] *USDA Forest Service, Southern Research Station, 30602 Athens, GA, USA*
[b] *Nicholas School of the Environment and Earth Sciences, Duke University, 27708 Durham, NC, USA*
[c] *Institute of Ecology, University of Georgia, 30602 Athens, GA, USA*

Available online 14 July 2006

Abstract

Historically, a large percentage of land area in the Piedmont of the southeastern USA was under intensive agricultural management for the production of cotton. This intensive farming resulted in massive erosion, and general degradation of soil resources until insect pests and poor economic conditions forced large-scale abandonment of farmland around the 1930s. In subsequent decades, there have been four predominant land-uses in the region, and we sampled soil macroinvertebrates from three replicate sites of cultivated fields, grass-dominated fields, loblolly pine stands, and remnant hardwood stands for a period of 2 years, with the objective of examining soil invertebrate community composition in relation to these long-term land-uses. At each site we dug three or four soil pits that were 30 × 30 cm to a depth of 15 cm, and sorted the soil volume by hand for a time not more than 1 person h, collecting all invertebrates ~5 mm in length or larger. We recorded abundance data for all invertebrate taxa collected, and we calculated community indices including diversity, evenness, rank abundance and percent similarity in order to identify patterns of community assemblage within each land-use type. Results suggest that soils in hardwood stands support the most taxonomically diverse macroinvertebrate communities followed by pine stands, pastures, and cultivated fields in order of decreasing diversity. For earthworms, *Diplocardia* spp. (North American megascolecids) were most abundant in the hardwood stands, but sometimes made up a substantial fraction of the community in other land-uses; whereas lumbricid earthworms (primarily introduced *Apporectodea* spp.) were most abundant in the cultivated and pasture soils, or showed no consistent habitat preference (native *Bimastos* spp.). Scarab beetles (larvae and adults) were common in all four systems, but reached the highest densities in cultivated and grass sites. Carabid beetle larvae were collected most often from cultivated soils. Several taxa were collected either exclusively or predominantly from forested sites, including diplopods, chilopods, gastropods, and several taxa of Diptera. These results indicate that long-term soil disturbance and the attendant differences in vegetation structure have profoundly influenced the community composition of invertebrates in Southern Piedmont soils, and that more intense disturbance results in a less diverse invertebrate community composed of a few, frequently non-native, disturbance-tolerant taxa.

Keywords: Macroarthropods; Soil macrofauna; Earthworms; *Diplocardia*; *Aporrectodea*; Bimastos; Scarabaeidae; Carabidae; Immature insects; Elateridae; Land-use

1. Introduction

History is frequently under-appreciated in ecological study, and as a consequence, relatively little is understood about the legacies of land-use on soil and soil processes, but the importance of considering these legacies in terms of current ecological patterns and processes is increasingly being recognized [7,16]. The his-

1164-5563/$ - see front matter © 2006 Published by Elsevier Masson SAS.
doi:10.1016/j.ejsobi.2006.06.001

tory of the soils on the Southern Piedmont of North America is one of intensive human use beginning in the late 18th century with the advent of slave-subsidized, large-scale cotton agriculture. The soils of the Southern Piedmont provide an excellent opportunity for researchers interested in studying the effects of historical disturbances and the recovery of soil from these disturbances.

Soil invertebrates are an important component of soil systems, and may affect soil processes such as root production, nutrient cycling, and organic matter decomposition [5,6]. Additionally, soil invertebrates have been suggested to serve as indicators of "soil quality" in agricultural and pollution contexts [10–12]. The presence or absence of certain taxa, or the characteristics of the whole invertebrate community may be related to the level of disturbance that historically or is currently influencing a given soil system, and could provide valuable indications of the sustainability of management regimes.

In this study we hypothesized that land-use legacies would have implications for the abundance and composition of the soil invertebrate community in soils from the Southern Piedmont in South Carolina, USA. Objectives for our study were to compare patterns of abundance, diversity, and other community characteristics for soil invertebrates in the four dominant land-cover types in this region.

2. Material and methods

2.1. Site description and sampling design

Invertebrate collections for this study were made in and around the Calhoun Experimental Forest near Union, South Carolina, USA (34.5°N, 82°W). Calhoun Experimental Forest is administered by the USDA Forest Service, Southern Research Station, and has served as a site for long-term experiments in forestry, hydrology, and soil science since 1947. The site was established as a laboratory for examining land management practices aimed at improving hydrologic and soil recovery from the legacy of cotton agriculture that dominated the landscape for nearly 150 years [13,17]. Plantation farming of cotton dominated the economy of the region until the time of the US Civil War (1861–1865), with smaller scale cotton farming thereafter until the combined effects of 100+ years of soil resource degradation, the vast expansion of cotton pests (boll weevils), and the international economic depression of the 1930s caused many land owners to abandon their attempts to farm cotton [17]. Since the time of farm abandonment, land-use patterns have been dominated by reforestation of old fields either through natural successional processes (leading to old-field pine or pine–oak–hickory mixed forests) or by active planting of yellow pine stands (*Pinus taeda* L., *Pinus echinata* Mill., and *Pinus virginiana* Mill.). Other major land-uses include managed pastures for livestock grazing or hay production, and continued cultivation for production of row crops.

For the sampling in this study we selected three sites in each of four land-use types that represent the management and use of a large percentage (> 85%) of the land area in the region. The selected study sites included: 1) cultivated fields (annual conventional tillage production of wheat, sorghum, and corn planted as feed for wildlife by US Forest Service), 2) permanent grass managed for pasturage of livestock or production of hay, 3) planted loblolly pine (*P. taeda*) forests, and 4) relict or regenerated mixed hardwood forests (predominantly *Quercus* spp. and *Carya* spp.). These sites were selected on the basis of soil type, landscape position, and proximity to one another, with sites as similar as possible in every regard except land-use. Sites were within 0.25–10 km of one another with the exception of one cultivated site which was ~30 km south of the other sites. All of the sites sampled had been under the given land-use for at least the past 50 years (see Table 1 for details about soils and land-use history for each site). All soils sampled in the study were derived from coarse-textured, granitic-gneiss, partially metamorphosed rock that is the predominant bedrock under the entire Southern Piedmont. Predominant soils at the 12 sites were from the Cecil, Appling, and Madison series (all classified as Fine kaolinitic thermic Typic Kanhapludults), and all sites but one have < 10% slope (i.e. all on nearly level interfluves). In each of these sites we established a permanent sampling location, where on six dates (approximately every 3–4 months) from May 2002 through December of 2003 we dug three or four pits that measured 30 × 30 cm. For the first three sample dates we dug three pits to a depth of 30 cm. We observed that invertebrates were almost never collected from the 15 to 30 cm depths in these pits, and therefore, we adapted our sampling to include only the 0–15 cm depths for the remainder of the study. This change allowed us to maximize our recovery of invertebrates and to include a fourth pit from each sampling to help capture the variability in the community within sites. Soil from each pit was carefully hand sorted in the field for approximately 60 min. All invertebrates (at

Table 1
Soil characteristics and land management history for sites sampled for soil invertebrates in and near the Calhoun Experimental Forest, Union County, SC, USA

Site type	Latitude longitude (decimal)	Age (years)	Soil C O-horizon (%)	Soil C 0–15 cm (%)	Soil N O-horizon (%)	Soil N 0–15 cm (%)	Soil pH water
Hardwood #1	34.648°N 81.732°W	> 100	45.84	2.23	1.087	0.115	5.79
Hardwood #2	34.605°N 81.723°W	> 80	46.13	2.83	1.171	0.121	4.62
Hardwood #3	34.574°N 81.663°W	> 75	45.60	2.36	0.942	0.128	5.87
Pine #1	34.647°N 81.734°W	~ 50	49.73	1.59	0.542	0.066	5.00
Pine #2	34.608°N 81.721°W	~50	49.22	0.81	0.584	0.031	4.26
Pine #3	34.605°N 81.716°W	~ 50	48.77	1.48	0.665	0.054	4.33
Grass #1	34.621°N 81.743°W		42.12	1.10	1.150	0.090	5.42
Grass #2	34.630°N 81.763°W		42.01	1.866	1.129	0.145	6.11
Grass #3	34.637°N 81.667°W		42.57	0.90	1.020	0.071	5.28
Cultivated #1	34.610°N 81.727°W		33.92	1.01	1.065	0.080	5.13
Cultivated #2	34.603°N 81.772°W		34.13	1.51	0.926	0.117	6.47
Cultivated #3	34.420°N 81.561°W		42.63	0.89	1.726	0.070	4.92

Note: Age of forested sites was determined by counting annual growth rings on trees. Based on horizonation, soils in hardwood sites are thought to have never been cultivated for cotton. Age of pastures and cultivated fields is not possible to determine with good accuracy, but they are known to be at least four decades old, and possibly have not supported forest vegetation since the time primary forest was cleared for cotton agriculture > 200 years ago.

least 5 mm in length) were collected and preserved in 70% ethanol. Colonial invertebrates occurring in very high numbers, such as ants and termites, were assessed for presence or absence only, and were not collected quantitatively.

All collected specimens were identified to the finest taxonomic resolution practical—usually species for earthworms, family for abundant insect orders (such as Coleoptera and Diptera), and order or suborder for other insects and arthropods [18,14,15,3]. Community indices were calculated for each of the sites in each land-use.

2.2. Statistical methods

We calculated the frequency of occurrence for each taxon in each land-use by counting the number of pits out of the total (for all dates) where that taxon was collected, and we generated rank–abundance curves for the invertebrate community in each land-use type.

For each pit we calculated diversity, richness, and evenness indices for each site. To calculate Shannon's diversity index (H') we used the formula:

$$H' = \bar{s} \sum_{i=1} p_i * ln(p_i)$$

where s is the total number of taxa collected, and p_i is the proportion of individuals that are taxon i relative to all individuals from all taxa collected [4]. Evenness (J') was calculated as:

$$J' = H'/\ln(s)$$

A community similarity index (percent similarity = PS) was calculated to assess the amount of overlap in the communities from each land-use over the course of the entire study as follows:

$$PS = 1 - (\sum|p_i - q_i|/2)$$

where for all taxa $i \cdots s$, p_i is the proportion of taxon i in the whole community of land-use p and q_i is the

Table 2
Major taxa collected from soil pits in and near the Calhoun Experimental Forest, South Carolina, USA. Data shown are the proportion of the total number of pits where each taxon was collected in each land-use

Taxon	Cultivated	Grass	Hardwood	Pine
Oligochaeta				
Lumbricidae				
A. trapezoides	0.25	0.22	0.05	–
Aporrectodea caliginosa	0.05	0.03	–	–
Octolasion cyaneum	–	0.02	–	–
Dendrobaena octaedra	–	0.02	–	–
Bimastos tumidus	0.02	0.02	–	–
Bimastos heimbergerii	–		0.02	–
Bimastos longicinctus	0.10	0.03	0.06	0.02
Megascolecidae				
Diplocardia spp.	0.21	0.27	0.48	0.11
Microscolex spp.	0.05	0.02	–	0.02
Enchytraeidae	0.05	0.02	–	0.02
Gastropoda	0.02	0.05	0.33	0.10
Diplopoda	–	0.14	0.43	0.49
Chilopoda	0.19	0.13	0.78	0.52
Geophilomorpha	0.16	0.13	0.75	0.35
Scolopendromorpha	0.03	–	0.30	0.17
Lithobiomorpha	0.02	–	0.10	0.06
Diplura	–	0.02	0.30	0.08
Araneae	0.21	0.40	0.38	0.32
Insecta				
Coleoptera	0.75	0.81	0.97	0.76
Scarabaeidae	0.38	0.49	0.57	0.44
Elateridae	0.16	0.22	0.46	0.32
Carabidae	0.43	0.32	0.13	0.08
Curculionidae	0.06	0.14	0.40	0.19
Staphylinidae	0.38	0.21	0.13	0.03
Tenebrionidae	0.02	–	0.46	0.21
Alleculidae	–	0.05	0.21	0.24
Chrysomellidae	0.06	0.05	0.10	0.21
Coccinellidae	0.10	–	–	0.02
Lampyridae	–	–	–	0.03
Ptilodactylidae	–	–	–	0.02
Diptera	0.16	0.08	0.63	0.35
Assilidae	0.02	0.02	0.10	0.24
Xylophagidae	–	–	0.24	–
Tabanidae	–	0.02	0.16	0.03
Empidae	–	0.02	0.11	–
Tipulidae	0.02	0.02	0.08	–
Rhagionidae	–	–	0.05	0.06
Fugivoridae	0.06	–	0.02	–
Stratiomyidae	0.02	–	0.02	0.03
Muscidae	–	–	0.02	0.02
Dolichopodidae	0.02	–	–	0.02
Therevidae	0.02	–	0.02	–
Bibionidae	–	–	0.02	–
Formicidae	0.37	0.33	0.49	0.33
Isoptera	0.06	0.02	0.13	0.21
Lepidoptera	0.16	0.16	0.13	0.02
Hemiptera	0.19	0.13	0.11	0.10
Homoptera	0.08	0.10	–	0.18
Blatodea	0.02	0.03	0.29	0.22
Orthoptera	0.08	0.13	0.06	0.03

There were 63 pits excavated for each land-use over the course of the study.

proportion of taxon i in the whole community of land-use q [4]. Because ants and termites were only assessed for presence or absence in collections, we excluded these two taxa from this analysis, as their relative proportion of the total community at a given site was not possible to calculate. Percent similarity was calculated for every possible comparison of land-uses.

To test for statistical differences in diversity and evenness, we performed one-way analyses of variance (ANOVA) with land-use as the treatment variable in a completely randomized experimental design. Density of each invertebrate taxon was averaged across the three or four pits from each site, and this average was used as the replicate value in ANOVA calculations (i.e., $N = 12$ for ANOVA).

3. Results and discussion

3.1. General macrofaunal distributions

A total of 62 distinct invertebrate taxa were collected over the course of the study. The frequencies at which the most abundant of these taxa were encountered in each land-use are presented in Table 2. For oligochaetes we found that the most abundant introduced earthworm species (*Aporrectodea trapezoides*) was most often collected from cultivated fields or from pastures; whereas the most common native North American earthworm genus (*Diplocardia* spp.) was collected from all four land-uses, but was most commonly collected from the hardwood forest stands. Several species from another native North American genus (*Bimastos* spp.) were collected from all four land-uses, but these were considerably less frequent than *Diplocardia* spp. in the samples (Table 2). This pattern of earthworm distribution (introduced species common in disturbed soils, and native species more common in undisturbed soils) has been observed previously in southeastern soils [9] as well as in the neotropics [19]. The exact mechanism behind the apparent preference of introduced earthworms for disturbed soils in not clear, but may be related to characteristics associated with the management of these soils such as fertilizer, lime, or organic inputs, or a general tolerance of disturbance, or decreased competition from native species displaced by the disturbance [8].

For non-insect arthropods there were several taxa that showed strong preferences for the reforested soils in our study. Diplopoda and Chilopoda were both much more commonly collected from the hardwood and pine forest stands than from cultivated or pasture sites (Table 2). For diplopods, this is most likely a function of resource availability as they are detritivores, and there is a scarcity of leaf litter or humus present in the cultivated and pasture systems. Likewise, for the predatory chilopods, the availability of a larger number of prey items in the forested stands may explain their greater abundances in these systems. Interestingly, the only chilopod suborder regularly collected outside the forested stands were the Geophilomorpha—also the only collected suborder that can be truly mineral soil dwelling and not necessarily living and feeding in the organic soil layers [14].

Insects were the most common taxa collected from the soil pits over the course of the study, and the Coleoptera were the most common insects collected (Table 2). At least 75% of all pits had larval or adult coleopterans present throughout the study, with the highest frequency observed in the hardwood forest plots where only two out of 63 pits did not have beetles present. Scarabaeidae and Elateridae were the most common beetles collected, and these families showed no clear trend with respect to land-use although both were most frequently collected from hardwood forest soils. The predacious families Carabidae and Staphylinidae were also very common, but were collected from the cultivated and pasture sites more often than from the forested sites, whereas the wood boring beetles in the Tenebrionidae were collected almost exclusively from the hardwood and pine forest sites.

The other dominant insect order collected during the study was the Diptera. We collected a total of twelve families of Diptera, with the majority of individuals being collected from the forested stands (Table 2). The Assilidae and Xylophagidae were most frequently collected flies in the pine and hardwood stands, respectively, with no other family exhibiting strong preference for any particular land-use.

Other major insect groups collected during the study included ants (Formicidae), which were collected in all land-uses in relatively high frequencies, and termites (Isoptera) which were collected with the greatest frequency from the pine stands but were also represented in collections from all the other land-uses.

Table 3
Percent similarity of the soil macroarthropod community between land-use types at the Calhoun Experimental Forest over 2 years of sampling

	Hardwood	Pine	Grass	Cultivated
Hardwood	–	0.63	0.51	0.37
Pine	0.63	–	0.52	0.35
Grass	0.51	0.52	–	0.60
Cultivated	0.37	0.35	0.60	–

3.2. Community characteristics

When assessed by the rank–abundance relationship, the communities from each of the four land-uses showed a general trend for strong dominance by a few taxa, with most groups collected falling into the rare category (arbitrarily defined for this study as 10 or fewer individuals of a given taxon collected over the study) (Fig. 1). For plant communities, this pattern is usually interpreted as indicative of a community that is in early stages of the successional process [2]. For the four communities we examined in this study, the cultivated sites showed the steepest slope on the rank abundance curve, indicating the strongest dominance by a few taxa and the fewest number of rare taxa. At the other extreme, the hardwood stands exhibited the most gradual decline in the rank abundance curve, indicating less overall rarity in the community. Interestingly, the taxon with the highest rank–abundance was different for each of the four land-uses. Carabid beetles (larvae and adults) were the most abundant in cultivated soils, Scarab beetle larvae and adults were most abundant in pasture soils, Geophilomorph centipedes were most abundant in hardwood forest soils, and millipedes were the most abundant taxa in pine forest stands. Scarabaeidae was the only taxon common to the top five most abundant taxa for all four systems (data not shown), possibly reflecting their general diversity, and their plasticity of resource use (i.e. some are detritivores, some herbivores).

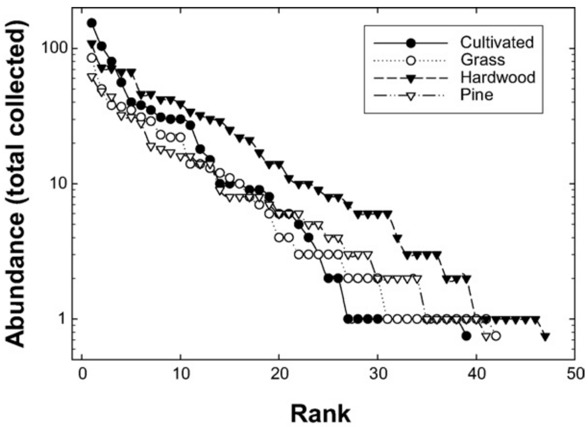

Fig. 1. Rank–abundance curves for soil dwelling macroinvertebrates at the Calhoun Experimental Forest, South Carolina, USA. Note: *y*-axis scale is logarithmic.

Shannon–Weiner diversity (H') calculations revealed that the hardwood forest soils had the greatest diversity of all the land-uses, and this difference was statistically significant ($P < 0.1$) for the fourth and sixth sampling dates (Fig. 2a). The pine stands were consistently next most diverse, but were not statistically different from the cultivated or grass sites. However, none of the soil invertebrate communities examined in the study were particularly taxonomically rich compared to other studies of this kind [1]. This general lack of diversity may be related to the severe historical disturbance that serves as the starting point for community organization for all these systems. The evenness index showed significantly ($P < 0.05$) lower evenness for the cultivated soils on the third and fifth dates indicating dominance of the community by a few taxa (Fig. 2b), similar to the patterns indicated by rank abundance curves (Fig. 1). Finally, the percent similarity measures revealed that the macroinvertebrate community in the cultivated sites had the least overlap with the forested sites, whereas the grass sites had intermediate overlap with the two forest types (Table 3). Macroinvertebrate communities from soils in pine forests and hardwood forests were most similar over the course of the study with similarity measures at 63% (Table 3).

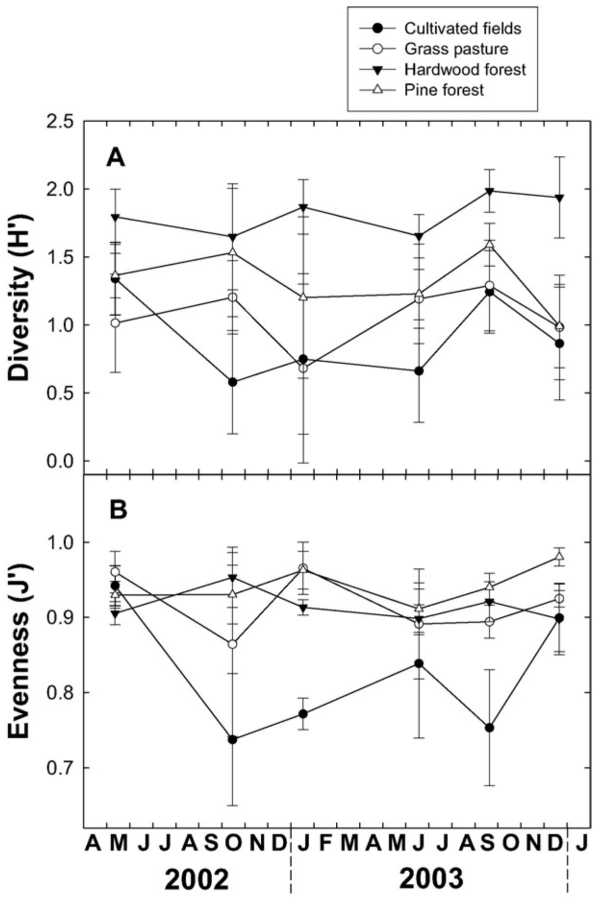

Fig. 2. A) Diversity, and B) evenness of soil macroinvertebrate collections from the Calhoun Experimental Forest, South Carolina, USA. Sampling was conducted in May and October, 2002; and in January, June, September, and December of 2003.

The long-term effects of vegetation management were evident on soil organic matter quality and quantity in this study (Table 1), and these effects may have had important influences on the soil invertebrate communities we sampled from each land-use type. For example, the C:N of SOM in mineral soils of the cultivated and grass-dominated systems was ~12 whereas this value was ~27 in the forested systems. This difference in SOM quality has probably influenced the organization and structure of the detrital foodweb in the respective systems, because lower C:N soils typically have a bacteria-based foodweb whereas higher C:N results in foodwebs based on fungal biomass [5]. In light of the fact that the pine, grass, and cultivated soils in this study all started from the same degraded condition (abandoned cotton fields), we suggest that differences in vegetation and soil are the product of a gradient of soil disturbance ranging from the least disturbed soils in the pine forests to the most disturbed soils in the annually cultivated fields. Grass systems are considered intermediate along this gradient because without repeated disturbances such as grazing or mowing they would eventually become forests though plant succession processes. The rank abundance relationships (Fig. 1) and percent similarity (Table 3) analyses presented in this study support the notion that this gradient of soil disturbance has not only influenced vegetation, but also the invertebrate community inhabiting these soils. Hardwood sites are most representative of the original, pre-cotton agriculture, condition of vegetation and soil on the Southern Piedmont. The decreasing similarity values of the invertebrate communities in the pine (63%), grass (51%) and cultivated (37%) systems relative to the hardwood sites (Table 3) seems to be at least partly a function of their relative levels of disturbance since conversion from cotton agriculture.

4. Conclusions

Soil macroinvertebrate communities in soils of the southern Piedmont were strongly influenced by land management in recent decades. Introduced earthworms were nearly exclusively collected from disturbed/managed systems whereas native North American earthworm species were most likely to be collected from less disturbed forested systems. All four ecosystems showed strong dominance by a relatively small number of taxa, but none more than the cultivated fields, reflecting their overall simplicity of system structure. The most diverse community was observed to be in the hardwood stands, but even these communities were not particularly diverse. This may be a function of the extent and severity of historical disturbance sustained by the soils of the region over more than two centuries.

Acknowledgements

We wish to thank land-owner J.F. Burnett for graciously allowing us to sample on his properties over the course of the study. We also thank those who contributed immeasurably by assisting with digging and sorting: Ryan Fimmen, Meg Mobley, Andrea Silletti, Arlene Mendoza, Michelle Hersh, Dan Richter III, Paul Heine, Kim Crider, Rytas Vilgalys, Jason Jackson, and Jianwei Li.

References

[1] E. Barros, B. Pashanasi, R. Constantino, P. Lavelle, Effects of land-use system on the soil macrofauna in western Brazilian Amazonia, Biol. Fertil. Soils 35 (2002) 338–347.

[2] F.A. Bazzaz, Plant species diversity in old-field successional ecosystems in southern Illinois, Ecology 56 (1975) 485–488.

[3] D.J. Borror, C.A. Triplehorn, N.F. Johnson, An Introduction to the Study of Insects, sixth ed, Harcourt Brace College Publishers, Fort Worth, 1989.

[4] J.E. Brower, J.H. Zar, C.E. von Ende, Field and Laboratory Methods for General Ecology, WCB/McGraw Hill, Boston, 1998.

[5] D.C. Coleman, D.A. Crossley Jr., P.F. Hendrix, Fundamentals of Soil Ecology, second ed, Academic Press, San Diego, 2004.

[6] D.C. Coleman, P.F. Hendrix, Invertebrates as Webmasters in Ecosystems, CABI Publishing, New York, 2000.

[7] D. Foster, F. Swanson, J. Aber, I. Burke, N. Brokaw, D. Tilman, A. Knapp, The importance of land-use legacies to ecology and conservation, Bioscience 53 (2003) 77–88.

[8] P.F. Hendrix, P.J. Bohlen, Exotic earthworm invasions in North America: ecological and policy implications, Bioscience 52 (2002) 801–811.

[9] P.J. Kalisz, D.B. Dotson, Land-use history and the occurrence of exotic earthworms in the mountains of eastern Kentucky, Am. Midl. Nat. 122 (1989) 288–297.

[10] R. Kuperman, Relationships between soil properties and community structure of soil macroinvertebrates in oak–hickory forests along an acidic deposition gradient, Appl. Soil Ecol. 4 (1996) 125–137.

[11] D.R. Linden, P.F. Hendrix, D.C. Coleman, P.C.J. van Vliet, Faunal indicators of soil quality, in: J.W. Doran, D.C. Coleman, D.F. Bezdicek, B.A. Stewart (Eds.), Defining Soil Quality for a Sustainable Environment, SSSA Special Publication No. 35, Madison, 1994, pp. 91–106.

[12] L.A. Lobry de Bruyn, The status of soil macrofauna as indicators of soil health to monitor the sustainability of Australian agricultural soils, Ecol. Econ. 23 (1997) 167–178.

[13] L.J. Metz, The Calhoun Experimental Forest, Publication of the USDA Forest Service, Southern Research Station, Asheville, 1958. Available online http://www.srs.fs.usda.gov/pubs/.

[14] P. Mundel, Chilopoda, in: D.L. Dindal (Ed.), Soil Biology Guide, John Wiley and Sons, New York, 1990, pp. 819–833.

[15] A. Peterson, Larvae of insects: an introduction to the nearctic species, vols. 1 and 2, Edwards Brothers, Ann Arbor, 1967.

[16] D.D. Richter Jr., D. Markewitz, P.R. Heine, V. Jin, J. Raikes, K. Tian, C.G. Wells, Legacies of agriculture and forest regrowth in the nitrogen of old fields, For. Ecol. Manage. 138 (2000) 233–248.

[17] D.D. Richter Jr., D. Markewitz, Understanding soil change: soil sustainability over millennia, centuries, and decades, Cambridge University Press, Cambridge, 2001.

[18] D.P. Schwert, Oligochaeta: Lumbricidae, in: D.L. Dindal (Ed.), Soil Biology Guide, John Wiley and Sons, New York, 1990, pp. 341–356.

[19] X.M. Zou, G. González, Changes in earthworm density and community structure during secondary succession in abandoned tropical pastures, Soil Biol. Biochem. 29 (1997) 627–629.