# INVERTEBRATE COMMUNITY STRUCTURE AND FOREST MANAGEMENT IN THE MISSOURI OZARK LANDSCAPE

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**Abstract**—Disturbance is important in the context of ecosystem diversity, but little is known about the effects of forest management on invertebrate insect communities. We estimated arthropod species diversity in terms of species richness, abundance and evenness at several spatial scales under clearcutting, single-tree selection, and preservation management regimes in the Missouri Ozarks. A total of 121 taxonomic groups and 22,000+ arthropods were identified and catalogued. Overall species diversity among treatments was not significant either at the micro-scale or meso-scale level. However, principal components analysis effectively segregated the clearcut community from the other two communities. Results suggest that the type of forest management practiced does significantly affect overall forest and leaf litter arthropod community structure in terms of scale and diversity. The single-tree selection harvest within Pioneer Forest generates a spatial gradient throughout the landscape, creating conditions most suitable for diversity to be maximized.

## INTRODUCTION

The current paradigm in ecology is that disturbance plays a critical role in maintaining diversity within ecosystems (Sousa 1979, Pickett and White 1985, Willig and others 1998, Schowalter 2000, Camilo and Zou 2001). Too little disturbance may displace poor competitors whereas too much may create conditions unfavorable for most organisms (Sousa 1979, Runkle 1985, Filser and others 1995, Bengtsson and others 1997). The scale, intensity, and frequency of disturbance, then, contribute greatly to how communities are structured (Willig and others 1998). Less commonly known is how disturbance is transferred into spatial gradients (Wootton 1998). Macroscale studies have illustrated that change in the plant community along environmental gradients also induces change in the composition of the microarthropod community (Hagvar 1982). On a smaller scale, the arthropod community in microclimate conditions is affected by spatial heterogeneity (Poole 1962).

Critical to a forest ecosystem is the role that the invertebrate community plays in the decomposition of organic matter and maintenance of soil structure. It is estimated that up to 90 percent of a forest's net primary production returns to the soil where leaflitter and topsoil faunas aid microbial and fungal decomposers (Swift and others 1979, Coleman and Crossley 1996, Weaver and Heyman 1997). Biological and biochemical energy can be dissipated back into the soil along shorter time scales than by chemical or physical avenues that, via soil formation processes, may take at least 10,000 years. The specific properties of soil invertebrates, as well as environmental factors, determine the rates at which this energy flows through the soil ecosystem (Swift and others 1979, Jenny 1980, Lavelle and others 1995). By studying the ecology of these animals, scientists have come to understand that there are suites of interaction integral to maintaining forest processes (Swift and others 1979, Faber and Verhoef 1991, Ananthakrishnan 1996).

Forested systems are under extreme pressure to be harvested (Annand and Thompson 1997, Herbeck and Larsen 1999, Guyette and Larsen 2000). In western Oregon, the impact of clearcutting has had an effect on the spatial patterns of soil arthropods. Forest stand composition appeared to contribute significantly to the spatial structuring of soil properties and, therefore, invertebrate spatial structuring (Torgersen and others 1995). It is the purpose of this research to analyze how various forest management practices have affected the community composition of leaflitter invertebrates over ecological time. Our working hypothesis is that the type of forest management practiced over recent history has shaped the structure of the leaflitter arthropod communities. Our objectives are to characterize leaflitter invertebrate communities at each site and to determine how changes in scale affect community parameters.

## MATERIALS AND METHODS

### Study Sites

The Ozark Highlands are characterized by high plateaus, carved by centuries of erosion; spring-fed streams have cut deeply into the plateaus, shaping moderately rolling hills with local relief of 50-150 m, sometimes reaching 300 m. Soil composition ranges from shallow unconsolidated materials over bedrock to very deep, highly weathered soils in hillslope sediments or residuum or both (Kabrick and others 2000). Oak-hickory and oak-shortleaf pine forests and woodlands, oak savannas, bluestem prairies, and glades make up the natural vegetation of the Ozark Highlands. Bottomland and mixed upland hardwood forests reside in large valleys and on adjacent sideslopes whereas the prairies and savannas are situated on gentler slopes (Kabrick and others 2000).

We sampled three forest management regimes in the Missouri Ozarks; preservation (Current River Natural Area, 37°15'N, 91°15'W), single-tree selection (Pioneer Forest, Inc., 37°18'N, 91°23'W), and clearcutting (Reis Biological Station, 37°56'N, 91°10'W), each of which has maintained their respective treatments since the early 1950s.

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### Experimental Design

Within each site, three 20- by 20-m (= 400 m²) plots were demarcated with flags and PVC stakes. Each plot was further subdivided into 16 smaller subplots (5 by 5 m). Forest structure was estimated measuring abiotic parameters, vegetative composition, and understory vegetation profiles. Ambient temperature (°C) and percent relative humidity were recorded at the base of each subplot corner using a digital thermometer. Percent canopy cover, using both convex and concave mirrored densiometers, was also estimated for each point. Within every 5- by 5-m subplot, trees were identified to species and diameter at breast height (d.b.h.) was measured. Foliar volume was measured using a 3-m PVC pole with 0.5-m dowels attached perpendicularly at 0.5-m intervals along the length of the pole. Rotating the pole 360° at each flag, the number of touches made at each height increment was recorded (Secrest and others 1996).

Within each 400-m² quadrat, we collected litterbag samples at random from 10 of the 16 subplots. The sampling area in each subplot was approximately 0.25 m by 0.25 m (or .06125 m²). Within each transect, 20 of the 32 subplots were randomly sampled in the same manner. These leaflitter collections were taken once each summer for 1999 and 2000. Each leaflitter sample was processed through Berlese funnels, a high-gradient extractor (Winter and Voroney 1993), which separates the fauna from the litter. Eventually, the litter desiccated, and the fauna dropped down into a 70- percent ethanol solution. After separation, these specimens were identified and cataloged to at least family. Mites, an ubiquitous group of organisms with up to 50,000 described species (Walter and Proctor 1999), easily qualified as a candidate for morphospecies identification (Camilo and Zou 1999). The concept of "taxonomic sufficiency" identifies organisms to a level of taxonomic resolution adequate enough to satisfy a study's objectives (Ellis 1985). Studies have shown that this concept can be applied to ecological studies of terrestrial invertebrate communities without sacrificing estimates of species diversity or species turnover (Pik and others 1999).

### Species Diversity Estimates

Analyzing arthropod species diversity in terms of species richness, abundance, and evenness provides baseline descriptions about community composition. In community order studies, there are two types of information collected: (1) the number of species and (2) the number of individuals in each species. The Shannon-Weiner Index takes into account the proportional abundance of species within a community giving more weight to rarer species (Magurran 1988, Krebs 1989). This function assumes that all species are represented from random samples and measures the uncertainty of correctly predicting the species of the next individual collected (Krebs 1989). Although the experimental design does not randomly distribute subplots throughout the forest stands, the sampling area used (0.0625 m²) is small enough relative to the landscape that it could be considered random. Information indices such as Shannon-Weiner are widely used because no assumption is made about the underlying species abundance distribution curve (Magurran 1988). Rank abundance curves, on the other hand, plot the proportional abundance against rank of abundance utilizing all the information gathered about the community (Magurran 1988). This provides a more complete picture of species abundance distribution among treatments than using diversity indices alone (Krebs 1989, Stiling 1996). Distribution curves can be likened to one of four main models (log normal distribution, log series, geometric series, broken-stick) with each highlighting a specific pattern of species richness and evenness (Magurran 1988, Stiling 1996).

### Ordination Analyses

Ecological data are often multi-dimensional and can be arranged in a matrix (e.g., with species as rows, treatments as columns, and abundance as entries). Because there may be a lot of redundant information (e.g., many species responding to the same environmental gradient), only the most crucial dimensions must be extracted. These techniques can provide diagrammatic expressions of species composition pattern variation as well as the relationship between species and environmental variables (Palmer 1993). Principal Components Analysis (PCA) is an indirect ordination method that is used to order arthropod species and the three forest treatments in successive dimensions without regard to environmental variability (Digby and Kempton 1987).

Canonical Correspondence Analysis (CCA) is a direct ordination technique that was used to directly relate arthropod species composition to the abiotic and vegetation gradients (Palmer 1993). CCA overlays the arthropod data onto the abiotic and vegetation data resulting in a direct ordination of the environmental factors that shape community composition (Digby and Kempton 1987). What is generated, then, is a diagram termed a tri-plot in which the environmental variables that explain most of the variation within treatments are represented by arrows. The length of the vector represents the loading (i.e., how much is the arthropod community responding to the environmental gradient). The direction is the level of correlation, and the thickness is an estimate of the variation (Palmer 1993).

## RESULTS

### Species Diversity Estimates

A total of 121 taxonomic groups and 22,000+ arthropods were identified and catalogued from 112 out of 120 leaflitter collections (table 1). Overall species diversity among treatments was not significant among logging treatments either at the micro-scale (0.0625 m²) level or the meso-scale level (1600 m²; fig. 1). Rank abundance analysis revealed more insight into community structure (fig. 2). The clearcut site had a total of 104 species and followed a log series distribution ($R^2$ = 0.82). Note, however, that many of these species were rare with low abundances. The preservation site had 81 species and also followed a log series distribution ($R^2$ = 0.88). The single-tree selection site had a total of 80 species and followed a log normal distribution ($R^2$ = 0.69), suggesting that the total

**Table 1—Taxonomic listing and abundance of leaflitter invertebrates collected from three forest stands under three management regimes in the Missouri Ozarks** [a]

| Taxonomic classification | Clearcut | Preservation | Selection |
|---|---|---|---|
| **Class Arachnida** | | | |
| **Order Aranae** | | | |
| Dictynidae | 4 | 31 | 0 |
| Pholcidae | 4 | 1 | 0 |
| Thomisidae | 6 | 86 | 41 |
| Clubionidae | 115 | 248 | 104 |
| Pisauridae | 3 | 0 | 0 |
| Lycosidae | 1 | 19 | 1 |
| Salticidae | 11 | 3 | 7 |
| Pirate spiders | 1 | 0 | 0 |
| **Order Opilionida** | | | |
| Palpatores sp 1 | 1 | 0 | 0 |
| **Order Acari** | | | |
| **Suborder Ixodida** | 1 | 0 | 0 |
| **Suborder Prostigmata** | | | |
| Tetranychidae | 4 | 0 | 5 |
| **Suborder Oribatida** | | | |
| Oribatid sp 1 | 296 | 988 | 1980 |
| Oribatid sp 2 | 29 | 337 | 833 |
| Oribatid sp 3 | 3 | 19 | 0 |
| Oribatid sp 4 | 81 | 244 | 342 |
| Oribatid sp 5 | 2 | 15 | 3 |
| Oribatid sp 6 | 13 | 12 | 14 |
| Oribatid sp 7 | 52 | 224 | 511 |
| Oribatid sp 8 | 7 | 0 | 4 |
| Oribatid sp 9 | 2 | 0 | 4 |
| Oribatid sp 10 | 6 | 22 | 165 |
| Oribatid sp 11 | 15 | 14 | 75 |
| Oribatid sp 12 | 23 | 38 | 61 |
| Oribatid sp 13 | 2 | 2 | 5 |
| Oribatid sp 14 | 1 | 8 | 18 |
| Oribatid sp 15 | 0 | 3 | 22 |
| Oribatid sp 16 | 0 | 0 | 1 |
| Oribatid sp 17 | 0 | 2 | 7 |
| Oribatid sp 18 | 1 | 0 | 0 |
| Oribatid sp 19 | 0 | 8 | 68 |
| Oribatid sp 20 | 0 | 3 | 68 |
| Oribatid predator sp 1 | 6 | 22 | 17 |
| Oribatid predator sp 2 | 15 | 43 | 299 |
| Oribatid predator sp 3 | 21 | 60 | 3 |
| Oribatid predator sp 4 | 12 | 0 | 12 |
| Oribatid predator sp 5 | 12 | 49 | 59 |
| Oribatid predator sp 6 | 1 | 0 | 12 |
| Oribatid predator sp 7 | 15 | 83 | 121 |
| Oribatid predator sp 8 | 114 | 200 | 313 |
| Oribatid predator sp 9 | 257 | 217 | 342 |
| Oribatid predator sp 10 | 12 | 12 | 75 |
| Oribatid predator sp 11 | 1 | 0 | 2 |
| Oribatid predator sp 12 | 72 | 43 | 20 |
| Oribatid predator sp 13 | 1 | 0 | 0 |
| Oribatid predator sp 14 | 1 | 0 | 0 |

*continued*

**Table 1—Taxonomic listing and abundance of leaflitter invertebrates collected from three forest stands under three management regimes in the Missouri Ozarks [a] (continued)**

| Taxonomic classification | Clearcut | Preservation | Selection |
|---|---|---|---|
| Torymidae | 7 | 147 | 1 |
| Pteromalidae | 20 | 57 | 0 |
| **Superfamily Formicoidea** | | | |
| **Formicidae** | | | |
| *Aphenogaster* | 31 | 4 | 0 |
| *Crematogaster* | 1 | 0 | 60 |
| *Iridomyrmex* | 2 | 6 | 0 |
| near *Iridomyrmex* | 0 | 33 | 0 |
| near *Forelius* | 0 | 0 | 44 |
| *Procertium* | 0 | 0 | 1 |
| *Prinopelta* | 0 | 27 | 0 |

[a] Forty (0.0625 $m^2$) samples were collected from each study site and processed via Berlese funnel extraction. Specimens were counted and identified to at least family.

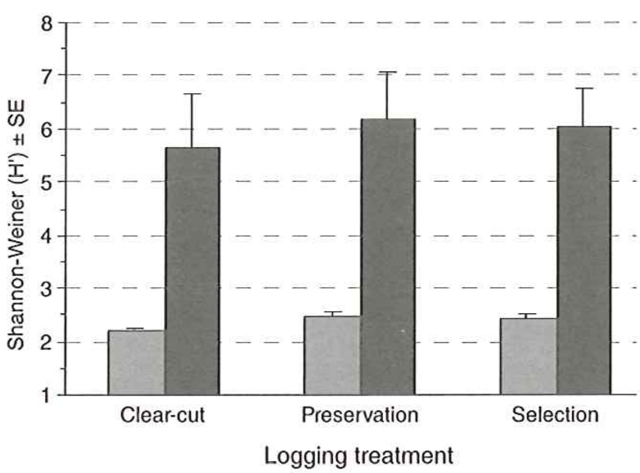


Figure 1—Leaflitter arthropod diversity of three forest management regimes in the Missouri Ozarks.

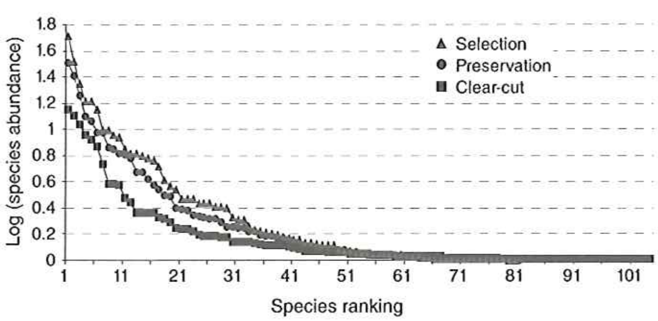


Figure 2—Rank abundance curve of arthropod species abundance for three forest management regimes in the Missouri Ozarks (1999).

number of species was large and that the community was well established (May 1975, Magurran 1988).

### Arthropod Community Structure

Principal components analysis effectively segregated the clearcut community from the other two communities along two principal components (fig. 3). Based on a loading of three Oribatid morphospecies and three families of Collembola, 42.4 percent of the variability was explained along the first principal component and 11.5 percent was explained by the second component. However, no clear separation could be made between the single-tree selection and preservation communities along either of these axes.

CCA revealed that percent relative humidity was the most important environmental gradient in the clearcut to which the arthropod communities were responding (fig. 4). Foliar density at 0.5 m and 1.0 m was the most important gradient within the preservation treatment. For the single-tree selection, wood volume (i.e., diameter at breast height) was the most important environmental gradient.

## DISCUSSION

Many studies have focused on the effects of disturbance on forest arthropod communities (Swift and others 1979, Schowalter 1985, Torgersen and others 1995, Greenberg and McGrane 1996, Bengtsson and others 1997, Camilo and Zou 2001). This study assumed that three different logging practices would generate three specific forest structures, thereby creating spatial heterogeneity gradients to which species communities would respond over ecological time. Results suggest that the type of forest management practiced does significantly affect overall forest and leaflitter arthropod community structure in terms of scale and diversity.

The invertebrate community analyses suggest that communities are significantly affected by the type of forest management practiced (figs. 2, 3, and 4). The purpose of this study was to look at overall community structure. Therefore, all organisms were counted and sorted. Trying to visualize what factors explain most of the variability within community ecology data sets is a daunting task (Digby and Kempton 1987, Palmer 1993). The use of ordination techniques was especially helpful in assessing how the environmental gradients and arthropod communities could be segregated by treatment and uncovering how they relate to each other. This lends itself to ask the question, "What else could be responding to these treatments?" Principal component analysis (fig. 3) sorted through an extensive data set (of richness and abundance) and determined which taxa explain most of the variability within the data set. Because this is an indirect ordination method, the relationship between species distribution and the underlying environmental gradients is not determined (Digby and Kempton 1987). CCA superimposed the arthropod data on top of the environmental data. By performing a direct gradient analysis we were able to generate a clear separation of arthropod communities and identify the most important environmental gradients to which they were responding (fig. 4).

Given these results, it seems evident that the single-tree selection and harvest within Pioneer Forest generates a spatial gradient throughout the landscape creating conditions most suitable for diversity to be maximized. Research by Iffrig and others (2004) concluded that over a 30-year period, six of seven species groups have maintained their relative proportions within the 486 (0.2 acre) permanent research plots. A study on songbird populations in the Missouri Ozarks also suggests that this type of management treatment can contribute greatly to species abundance (Annand and Thompson 1997).

This research has provided some baseline data upon which several interesting hypotheses may be tested. The scaling results suggest that the plots could be expanded in all directions to see if bigger "window sizes" will detect spatial patterns at greater scale levels. Conversely, subplots could be further divided (i.e., increase the spatial resolution) to determine if indeed the critical window size transitions around the 5- by 5-m grid level. Specific guilds or functional groups of arthropods could be studied on a more detailed level with questions relating to emergence, trophic levels, or species turnover. Litter quality and decomposition is yet another aspect to be examined. Studies have shown that nutrient cycling is highly influenced by litter inputs to the soil (Blair 1988, Blair and Crossley 1988).

Recent advances in spatial ecology have demonstrated that scale is critical to detecting and interpreting ecological patterns (Gardner 1998). Scale is crucial to analyzing community stability and persistence (Rahel 1990) and may have significant implications when it comes to sampling and conservation strategies (Milne 1992). Any efforts to preserve biodiversity must have an ecosystem level approach (Franklin 1993). Forested systems are no exception (Lertzman and Fall 1998). This study has shown that the scale at which forest management took place had significant effects on both overall forest structure and the leaflitter arthropod communities in the Missouri Ozarks. Management and research entities must work interactively to achieve conservation objectives (Hobbs 1998).

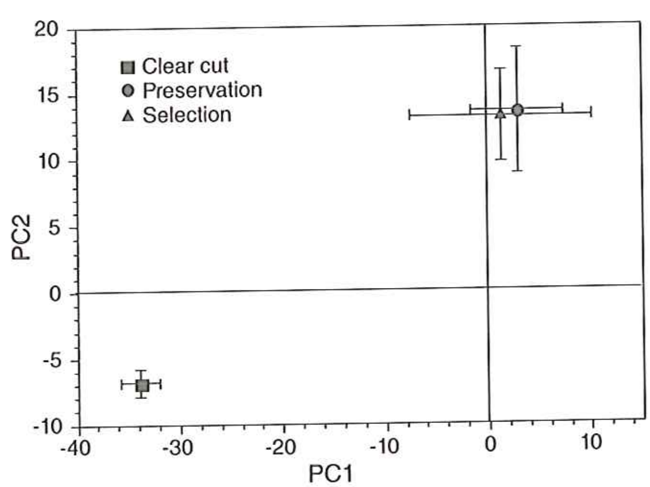


Figure 3—Principal Components (PC) analysis of arthropod species and abundance for three forest management regimes in the Missouri Ozarks.

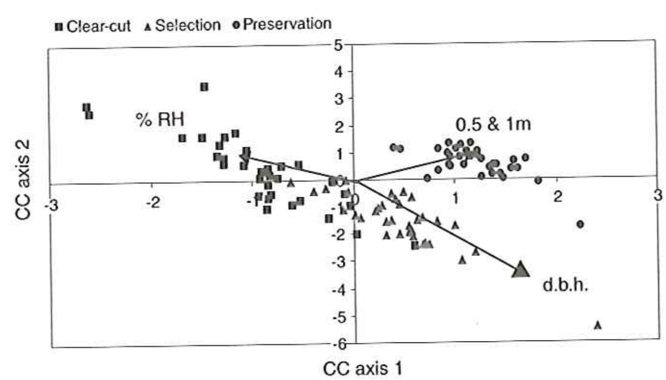


Figure 4—Canonical Correspondence Analysis (CCA) of arthropod data and forest structure variables for three forest management regimes in the Missouri Ozarks. Arrows represent the main abiotic gradient that explains the greatest amount of variation within a community.

## LITERATURE CITED

Ananthakrishnan, T.N. 1996. Forest litter insect communities: biology chemical ecology. Science Publishers, Inc., Lebanon, NH.

Annand, E.M.; Thompson, F.R. 1997. Forest bird response to regeneration practices in central hardwood forests. Journal of Wildlife Management. 61(1): 159-171.

Bengtsson, J.; Persson, T.; Lundkvist, H. 1997. Long-term effects of logging residue addition and removal on macroarthropods and enchytraeids. Journal of Applied Ecology. 34: 1014-1022.

Blair, J.M. 1988. Nitrogen, sulfur and phosphorus dynamics in decomposing deciduous leaflitter in the Southern Appalachians. Soil Biology and Biochemistry. 20: 693-701.

Blair, J.M.; Crossley, D.A., Jr. 1988. Litter decomposition, nitrogen dynamics and litter microarthropods in a Southern Appalachian hardwood forest 8 years following clearcutting. Journal of Applied Ecology. 25: 683-698.

Camilo, G.R.; Zou, X. 2001. Soil fauna in managed forests: lessons from the Luquillo Experimental Forest, Puerto Rico. In: A. Grajal, R. Fimble and J. Robinson, eds., The Cutting Edge: Conserving Wildlife in Logged Tropical Forests. Columbia University Press, Columbia, NY.

Coleman, D.C.; Crossley, D.A., Jr. 1996. Fundamentals of soil ecology. Academic Press, San Diego, CA. 1-170.

Digby, P.G.N.; Kempton, R.A. 1987. Multivariate analysis of ecological communities. Chapman and Hall. New York, NY. 206 p.

Ellis, D. 1985. Taxonomic sufficiency in pollution assessment. Mar. Poll. Bulletin. 16: 459.

Faber, J.H.; Verhoef, H.A. 1991. Functional difference between cosely related soil arthropods with respect to decomposition process in the presence or absence of pine tree roots. Biol. Biochem. 23: 15-23.

Filser, J.; Fromm, H.; Nagel, R.F.; Winter, K. 1995. Effects of previous intensive agricultural management on microorganisms and the biodiversity of soil fauna. In: The Significance and Regulation of Soil Biodiversity. H.P. Collins, G.P. Robertson and M.J. Klug, (eds.), Kluwer Academic Publishers, Netherlands. 123-129.

Franklin, J.F. 1993. Preserving biodiversity: species, ecosystems, or landscapes? Ecological Applications. 3(2): 202-205.

Gardner, R.H. 1998. Pattern, process, and the analysis of spatial scales. In: Ecological Scale - Theory and Applications. D.L. Peterson and V.T. Parker, eds. Columbia University Press. New York, NY. 17-34.

Greenberg, C.; McGrane, A. 1996. A comparison of relative abundance and biomass of ground-dwelling arthropods under different forest management practices. Forest Ecology and Management. 89: 31-41.

Guyette, R.; Larson, D. 2000. A history of anthropogenic and natural disturbances in the area of the Missouri Ozark Forest System Project. In: Missouri Ozark Forest Ecosystem Project: Site History, Soils, Landforms,Woody and Herbaceous Vegetation, Down Wood, and Inventory Methodsfor the Landscape Experiment. S.R. Shifly and B.L. Brookshire, (eds.), U.S. Department of Agriculture, North Central Research Station Forest Service, St. Paul, MN. 19-40.

Hagvar, S. 1982. Collembola in Norwegian coniferous forest soils. I. Relations to Plant Communities and Soil Fertility. Pedobiologia 24: 225-296.

Herbeck, L.A.; Larsen, D.R. 1999. Plethodontid salamander response to silvicultural practices in the Missouri Ozark Forests. Conservation Biology 13(3): 623-632.

Hobbs, R.J. 1998. Managing ecological sstems and processes. In: Ecological Scale - Theory and Applications. D.L. Peterson and V.T. Parker, eds. Columbia University Press. New York, NY. 459-484.

Iffrig, G.F.; Trammel, C.E.; Cunningham, T. 2004. Pioneer Forest: a case study in sustainable forest management. Pages 193-204 in S. L. Flader, ed. Toward Sustainability for Missouri forests. General Technical Report NC-239. St. Paul, Minnesota; U.S. Department of Agriculture, Forest Service, North Central Research Station. 251 p.

Jenny, H. 1980. The soil resource: origin and behavior. Ecological Studies 37. Springer-Verlag, New York, NY. 1-145.

Kabrick, J.; Meinert, D.; Nigh, T.; Gorlinsky, B.J. 2000. Physical environment of the Missouri Ozark ecosystem project sites. In: Missouri Ozark Forest Ecosystem Project: Site History, Soils, Landforms, Woody and Herbaceous Vegetation, Down Wood, and Inventory Methods for the Landscape Experiment. S.R. Shifly and B.L. Brookshire, (eds.), U.S. Department of Agriculture, North Central Research Station, U.S. Forest Service, St. Paul, MN. 41-42.

Krebs, C.J. 1989. Ecological methodology. Harper Collins Publishers. New York, NY. 1-370.

Lavelle, P.; Lattand, C.; Trigo, D.; Barois, I. 1995. Mutualism and biodiversity in soils. In: The Significance and Regulation of Soil Biodiversity. H.P. Collins, G.P. Robertson and M.J. Klug, eds. Kluwer Academic Publishers, Netherlands. 23-33.

Lertzman, K.; Fall, J. 1998. From forest stands to landscapes: spatial scales and the roles of disturbances. In: Ecological Scale - Theory and Applications. D.L. Peterson and V.T. Parker, eds. Columbia University Press. New York, NY. 339-368.

Magurran, A.E. 1988. Ecological diversity and its measurement. Princeton University Press. Princeton, NJ. 1-114.

May, R.M. 1975. Patterns of species abundance and diversity. In: Ecology and Evolution of Communities. M.L. Cody and J. Diamond, eds.. Harvard University Press, Cambridge, MA. 81-120.

Milne, B.T. 1992. Spatial aggregation and neutral models in fractal landscapes. The American Naturalist. 139(1):33-56.

Palmer, M.W. 1993. Putting things in even better order: the advantages of canonical correspondence analysis. Ecology. 74: 2215-2230.

Pickett, S.T.A.; White, P.S. 1985. Patch dynamics: a synthesis. In: The Ecology of Natural Disturbance and Patch Dynamics. S.T.A. Pickett and P.S. White, eds. Academic Press, Inc., New York, NY. 371- 384.

Pik, A.J.; Oliver, I.; Beattie, A.J. 1999. Taxonomic sufficiency in ecological studies of terrestrial invertebrates. Australian Journal of Ecology 24: 555562.

Poole, T.B. 1962. The effect of some environmental factors on the pattern of distribution of soil collembola in a coniferous woodland. Pedobiologia. 2: 169-182.

Rahel, F.J. 1990. The hierarchical nature of community persistence: a problem of scale. The American Naturalist. 136(3): 328-344.

Runkle, J.R. 1985. Disturbance regimes in temperate forests. In: The Ecology of Natural Disturbance and Patch Dynamics. S.T.A. Pickett and P.S. White, eds. Academic Press, Inc., New York, NY. 17-33.Schowalter, T.D. 1985. Adaptations of Insects to Disturbance. In: The Ecology of Natural Disturbance and Patch Dynamics. S.T.A. Pickett and P.S. White, eds. Academic Press, Inc., New York, NY. 235-252.

Schowalter, T.D. 2000. Insect ecology: an ecosystem approach. Academic Press, Inc., San Diego, CA. 1-422.

Secrest, M.F.; Willig, M.R.; Peppers, L.L. 1996. The legacy of disturbance in habitat associations of terrestrial snails in the Luqillo Experimental Forest, Puerto Rico. Biotropica. 28(4a): 502-514.

Sousa, W.P. 1979. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. Ecology. 60(6): 1225-1239.

Stiling, P.D. 1996. Ecology: theories and applications, 2d ed. Prentice-Hall,Inc., Upper Saddle River, NJ. 1-449.

Swift, M.J.; Heal, O.W.; Anderson, J.M. 1979. Decomposition in terrestrial ecosystem. Blackwell Scientific Publication. Oxford, England. 1-322.

Torgersen, C.E.; Jones, J.A.; Moldenke, A.R.; LeMaster, M.P. 1995. The spatial heterogeneity of soil invertebrates and edaphic properties in an old growth forest stand in western Oregon. Pp. 225-236 in H.P. Collins, G.P. Robertson and M.J. Klug, eds., The significance and regulation of soil biodiversity. Kluwer Academic Publishers, Netherlands.

Walter, D.E.; Procter, H.C. 1999. Mites: ecology, evolution and behaviour. CABI Publishing, New York, NY. 1-268.

Weaver, J.; Heyman, S. 1997. The distribution and abundance of leaf litter arthropods in MOFEP sites 1, 2, and 3. In: Proceedings of the Missouri Ozark Forest Ecosystem Project Symposium: an Experimental Approach to Landscape Research. B.L. Brookshire and S.R. Shifley, eds. United States Department of Agriculture. 318-331.

Willig, M.R.; Secrest, M.F.; Cox, S.B. [and others]. 1998. Long-term monitoring of snails in the Luquillo Experimental Forest of Puerto Rico: heterogeneity, scale, disturbance, and recovery. In: Forest Biodiversity in North, Central, and South America, and the Caribbean: Research and Monitoring. F. Dallmeier and J.A. Comiskey, eds. UNESCO, Paris, France and The Parthenon Publishing Group, Inc., Pearl River, NY. 293-322.

Winter, J.P.; Voroney, R.P. 1993. Microarthopods in soil and litter. In Soil Sampling and Methods of Analysis. M.R. Carter, ed. Lewis Publishers. Boca Raton, FL. 319-332.

Wootton, J.T. 1998. Effects of disturbance on species diversity: a multitrophic perspective. The American Naturalist. 152(6): 803-825.