

Recovery of Decomposition and Soil Microarthropod Communities in a Clearcut Watershed in the Southern Appalachians

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Introduction

The recovery of ecosystems after disturbance remains a productive theme for ecological research (Holling 1973; DeAngelis 1992; Pimm 1984; Lindenmayer et al. 2004). Numerous studies have focused either on the reestablishment of biological communities (e.g., Elliott and Swank 1994; Niemela 1997; Kotanen 2004) or on the recovery of ecosystem processes after perturbations (Covington 1981; Mann et al. 1988; Elliott and Swank 1994; Likens and Bormann 1995; Knoepp and Swank 1997; Qualls et al. 2000; Elliott et al. 2002). In the case of decomposer organisms and the processes of organic matter decay and the mineralization of nutrients, the recovery of the biota and ecosystem process can be usefully considered together. To what degree must the organismal community recover before associated processes are restored to predisturbance levels? The question is an important one, especially in the context of ecosystem restoration, where emphasis is often placed on measuring the elements of ecosystem structure (expressed often as mean species composition) or the levels or rates of a key ecosystem function, but rarely on both simultaneously (Ehrenfeld and Toth 1997). Restoration ecology, in practice, has largely been a botanical science (Young 2000), and success is often measured by an evaluation of the recovery of a target plant community over one or two subsequent seasons; data investigating the long-term community viability is rarely documented. A clearer understanding of the link between the community and ecosystem processes needed for resilient communities may lead to and justify greater attention in restoration

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practice to a larger suite of variables. One model for this relationship can be found in soil microarthropods and leaf-litter decomposition processes.

Factors determining the rate of leaf-litter decomposition are both biotic (microbes and decomposer fauna) and abiotic (climate, edaphic factors, substrate resource quality). Both biotic and physical factors prevail in all terrestrial ecosystems; however, their relative importance may vary along environmental gradients (Lavelle et al. 1993). A large physical disruption on the scale of a watershed, such as the clearcutting of a stand, will have a dramatic impact on all these factors, including changes arising from soil compaction (Corns and Maynard 1998; Startsev et al. 1998; Lindo and Visser 2004). Clearcutting is likely to have a long-lasting impact since the disturbance will impose modifications to soil structure, changes in site hydrology, altered litter input, and solar radiation flux changes as succession proceeds, which will continue to influence decomposition factors beyond the duration of the actual disruption event. Both direct and indirect impacts on soil biota can be expected after a clearcut. Direct effects result from the physical disruption of the soil. Indirect effects stem from modification of the abiotic habitat factors regulating communities in the soil. In turn, modified soil communities affect rates of decomposition and mineralization of key nutrients.

Soil fauna have been shown to have an important regulatory role in a variety of ecosystem processes including decomposition and nutrient dynamics (Seastedt 1984; Verhoef 1996; Heneghan et al. 1999; Johnston and Crossley 2002). Microarthropods, mainly free-living mites, Collembola, and Protura, are relatively small contributors to ecological energetics, but they appear to have a disproportionately prominent role in determining soil fertility through their regulatory effect on soil microbial communities (Lussenhop 1992). Although they are by no means the only fauna of importance in the process of decomposition, microarthropods have been implicated as playing a major role in the decomposition of dead organic matter because of their ability to regulate belowground food webs (Seastedt 1984; Lussenhop 1992). Reduction of microarthropod populations can reduce rates of decomposition and can result in modified patterns in nutrient leaching in forest soil (Heneghan and Bolger 1996). Some studies on the recovery of decomposition in clearcut watersheds in northern hardwoods have demonstrated, or at least implied, that decomposition rates accelerate after the disturbance (Covington 1981; Aber et al. 1978). In contrast, studies on the decomposition of leaf litter and wood in many other temperate locations, including in clearcut watersheds at Coweeta Hydrological Laboratory, have indicated that decomposition rates and/or CO₂ efflux were initially lower than in an adjacent undisturbed control watershed (Abbott and Crossley 1982; Seastedt 1979; Blair and Crossley 1988; Gemesi et al. 1995; Pumpanen et al. 2004; Zerva and Mencuccini 2005). Blair and Crossley (1988) established that decay rates remained depressed 8 years after the disturbance by as much as 46% for *Cornus florida*, the most rapidly decomposing leaf species they examined. All three leaf species they employed in the study decomposed more slowly in the disturbed watershed than in the control. Investigations of the response of decomposer organisms and microbial processes to tree harvesting have been similarly equivocal. Houston et al. (1998) showed very slight microbial responses to clearcutting in two Ontario hardwood forests. Striegl et al. (1998)

reported a reduction in soil respiration rates (measured as CO₂ evolved) as a consequence to clearcutting in Saskatchewan. Siira-Pietikäinen et al. (2001) concluded that forest harvesting had little impact on decomposers at a variety of trophic levels. These studies suggest that no generalizations can be made concerning the impact of clearcutting (Whitford et al. 1981; Will et al. 1983; Binkley 1984).

Studies on decomposition in WS 2 and WS 7 at Coweeta concentrated on tracking changes in this process subsequent to the clearcut in 1977. An assumption was made that microarthropod abundance was similar on WS 2 and WS 7 at Coweeta before WS 7 was cable logged in 1977. After a year, abundance was reduced by more than 50% in the clearcut watershed compared with the control (Abbott et al. 1980; Seastedt and Crossley 1981). Blair and Crossley (1988) suggested that microarthropod abundance, which remained 28% lower in the clearcut area than in the control, may have been responsible for decreased decomposition rates.

In this present study, which was made two decades after the clearcut, we reinvestigated the decomposition dynamics of the litter types examined by Blair and Crossley (1988).

Methods

Litterbags with an internal dimension of 10 x 10 cm, constructed with fiberglass window screen, were used in this study. Recently fallen leaves of chestnut oak (*Quercus prinus* L.), red maple (*Acer rubrum* L.), and dogwood (*Cornus florida* L.) were collected from a number of low-elevation watersheds, pooled by species, and mixed thoroughly (to ensure that all the leaves in a single bag were not derived from a single tree). Approximately 2.5 g of air-dried material was placed in litterbags. Five bags were oven-dried at 95°C to establish relationship between air-dried and oven-dried mass loss. Litterbags of each species were placed in three plots in each of both WS 7 and WS 2 in January 1998. Plots matched for altitude, aspect, and slope. Five bags were taken up immediately to establish mass loss from handling. Litterbags were collected every two weeks for 18 months. Bags were oven-dried at 50°C, the litter reweighed and ground, and subsamples were placed in a muffle furnace at 500°C for four hours to obtain an estimate of ash content. This value was subtracted from oven-dried mass to obtain ash-free mass. Nitrogen and carbon percent of the litter at the beginning of the study were determined by combustion using a Carlo Erba C/N analyzer (instrument NA1500).

Decomposition rates were determined using the single negative exponential decay model (Olson 1963). Significant differences in mass remaining were determined using paired one-tailed t-tests on the decomposition rates determined from the model. These tests assessed the null hypothesis that decomposition rate remained lower in the clearcut area than in the paired control watershed. Using paired t-tests, the first-year decomposition rate of each substrate was compared among years, contrasting results of this study with the study conducted by Blair and Crossley (1988). All statistics were performed on SAS.

Six samples of litter measuring 27 cm by 27 cm were collected from randomly chosen points in each of the two watersheds in July 1998. The litter samples

primarily consisted of leaf material, but no attempt was made to separate out coarse woody debris. Prior studies (Heneghan, unpublished) had demonstrated that there were no differences in the volume of litter when the two watersheds were compared. These observations were based upon three replicates from quadrats measuring a meter squared. Microarthropods were extracted from the samples using Tullgren funnels, and the fauna were stored in 70% ethanol before being separated into Prostigmata, Mesostigmata, Oribatei, Collembola, and Protura. Oribatei were sorted to morphospecies. Total abundance of each taxonomic group was recorded and species richness, Shannon diversity, and Shannon evenness were measured for Oribatei. Assemblages of oribatids in each of the samples from both watersheds were analyzed using principal components analysis using Multivariate Statistical Package (MVSP). Similarities among these samples were analyzed using Jaccard's index (Magurran 1988). Differences between proportions of microarthropods were tested using t-tests (arcsine transformed). Potential differences between measures of richness and diversity were also examined using t-tests, after a test for homogeneity of variances.

Results

Twenty-one years after the clearcut, the decomposition rates of all three leaf species were either the same, or in the case of *C. florida* greater than, that of the control watershed (figure 8.1). Decay rates were lower a year after the disturbance and remained lower than in the control watershed 8 years afterward by as much as 46% for *C. florida* (Blair and Crossley 1988) (table 8.1). A comparison of the decomposition rates of each leaf species 8 years and 21 years after the clearcut revealed some differences between these years in decomposition rates in the clearcut watershed and the same leaf species in the control watershed. Differences in decomposition rates of chestnut oak in the cleared watershed were marginally significant between years ($t = 2.26$, $P = 0.087$). No differences were detected in the control watershed. Differences for *C. florida* were significant when our results were compared with Blair and Crossley's (1988) data from the clearcut watershed ($P = 0.0004$) and the control watershed ($t = 11.34$, d.f 4, $P = 0.003$). Differences were detected between maple decomposition rates between years in the clearcut watershed ($P = 0.03$) and the control watershed ($P = 0.004$).

Microarthropod Inventory

Twenty-one years after the clearcut watershed, total microarthropod density was greater in WS 7 than in the control watershed (table 8.2). Among the constituent groups of microarthropods, significant differences were detected only for oribatid mites (table 8.2). Oribatid mites were the most prevalent microarthropods, representing almost 50% of the fauna in WS 2 and approximately 57% in WS 7. There were no significant differences detected in the proportion of animals in any of the microarthropod groups (table 8.3). Jaccard's similarity index shows a consistent similarity in oribatid assemblage between samples drawn from the same watershed (figure 8.2).

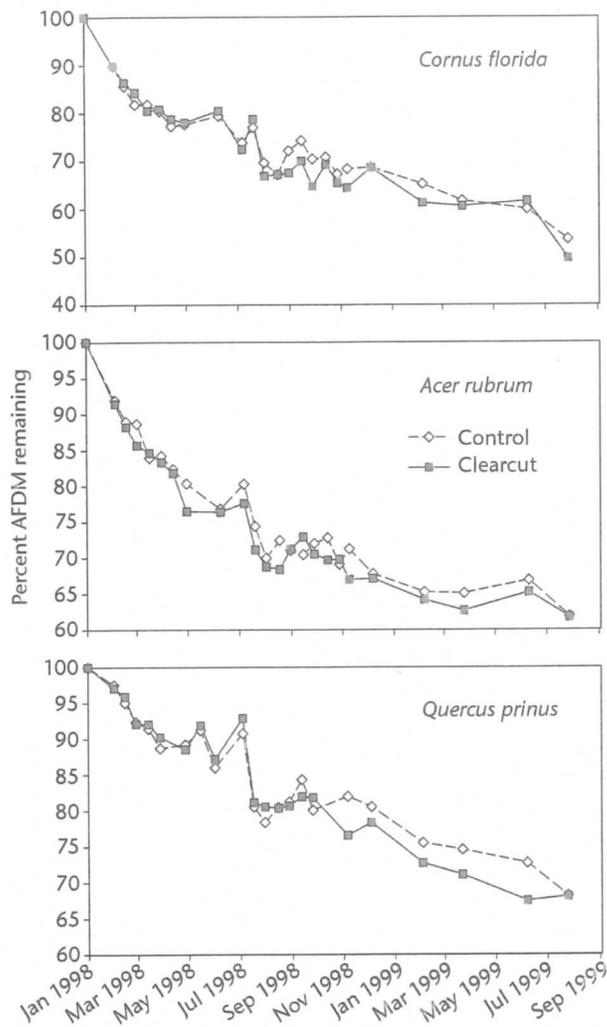


Figure 8.1 Mass loss of *Quercus prinus*, *Cornus florida*, and *Acer rubrum* in clearcut and control watershed at Coweeta Hydrologic Laboratory, North Carolina.

Oribatid diversity in the two watersheds differed (figure 8.3). There was elevated species richness of oribatid mites in the clear-cut watershed ($P = 0.04$). Differences in Shannon diversity were marginally significant ($t = 2.33$, d.f. = 6.3, $P = 0.056$) (table 8.4). No differences were found in Shannon evenness.

Discussion

Twenty-one years after the clearcut, decomposition rates in WS 7 had reconverged with or surpassed (in the case of one substrate, *C. florida*) the decomposition rates

Table 8.1 Decomposition rates (y^{-1}), percent original mass remaining after 12 months in parentheses.

	Precut		Year 1 (1978)	
	Clearcut (1974-75)	Control (1975-76)	Clearcut	Control
<i>Quercus prinus</i>	0.37 (69.3)	0.29 (72.2)	0.29 (76.7)	0.43 (65.2)
<i>Cornus florida</i>	1.31 (27.8)	0.71 (47.8)	0.63 (55.6)	1.17 (34.3)
<i>Acer rubrum</i>	0.53 (49.0)	0.48 (57.9)	0.37 (70.5)	0.62 (53.7)
	Year 8 (1985)		Year 21 (1998)	
	Clearcut	Control	Clearcut	Control
<i>Quercus prinus</i>	0.19 (78.1)	0.27 (73.1)	0.28 (72.73)	0.24 (75.54)
<i>Cornus florida</i>	0.71 (51.3)	0.85 (45.8)	0.38 (61.32)	0.32 (64.98)
<i>Acer rubrum</i>	0.55 (62.4)	0.64 (52.9)	0.34 (65.22)	0.35 (64.16)

Sources: Precut and year 1 data, Abbott and Crossley (1982); year 8 data, Blair and Crossley (1988).

Table 8.2 Mean and standard error of abundance of each microarthropod group from six samples from both clearcut (WS 7) and control (WS 2) watersheds.

	WS 7 Abundance (Mean, S.E.)	WS 2 Abundance (Mean, S.E.)	Significance
Collembola	52, 12.04	28, 6.64	ns
Astigmata	119, 38.24	66, 27	ns
Megostigmata	27, 8.23	16, 7.96	ns
Oribatida	302, 44.73	134, 47	*
Protura	28, 26.49	6, 4.66	ns
Prostigmata			ns
Others	59, 22.09	19, 14.21	ns
Total	530, 70.68	260, 85.91	*

* = difference at $P < 0.05$ level

Table 8.3 Proportion of abundance in each microarthropod group from six samples from both clearcut (WS 7) and control (WS 2) watersheds.

	WS 7	WS 2
Astigmata	0.03%	0.13%
Collembola	9.74%	9.96%
Mesostigmata	5.25%	5.44%
Oribatida	56.90%	55.87%
Protura	5.37%	4.76%
Prostigmata	22.40%	23.03%
Others	11.06%	10.34%
Total	100.00%	100.00%

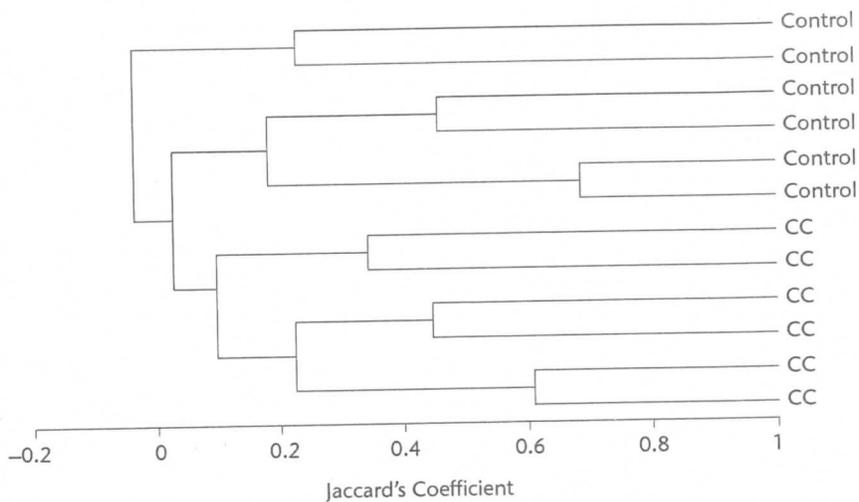


Figure 8.2 Dendrogram of Jaccard's coefficient for oribatid morphospecies from control (WS 2) and clearcut (WS 7) watersheds.

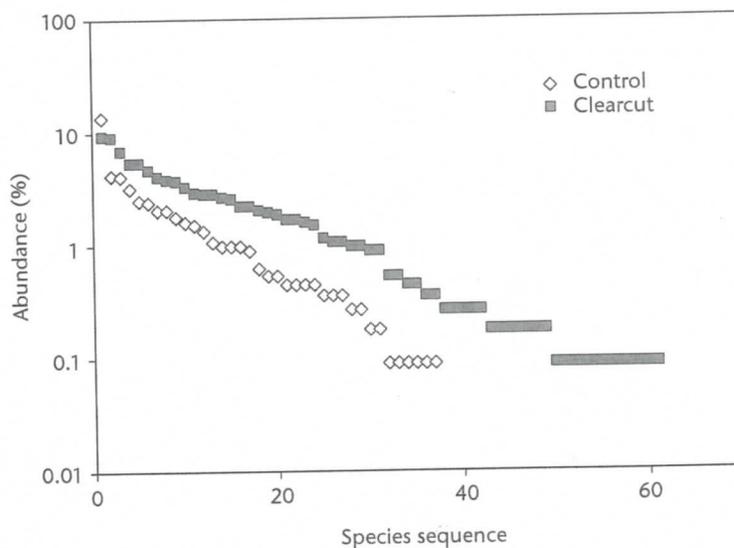


Figure 8.3 Rank abundance curves for oribatid mite assemblages from control (WS 2) and clearcut (WS 7) watersheds.

Table 8.4 Species richness and Shannon diversity and evenness, with associated test statistic for clearcut and control watersheds.

	Clearcut (WS 7) (mean, s.e.)	Control (WS 2) (mean, s.e.)	Significance
Species richness	34, 2.64	21.66, 4.43	*
Shannon diversity	1.31, 0.04	1.05, 0.10	n.s.
Shannon evenness	0.86, 0.01	0.84, 0.04	n.s.

* = difference at $P < 0.05$ level

Table 8.5 Percent nitrogen and carbon: nitrogen mass ratios for three substrates used in 1984 and 1996 experiment.

		%N	C:N
1984	Oak	0.87	55.7
1996	Oak	0.88	55.0
1984	Dogwood	0.56	85.7
1996	Dogwood	0.96	50.7
1984	Maple	0.75	62.9
1996	Maple	0.98	47.5

of an adjacent control watershed. Previous observations up to year 8 showed slower decomposition rates in the disturbed watershed compared with the control.

Though decomposition in the treatment and control rates were similar, the rates after 21 years were slower than they were after 8 years. That is, both *C. florida* and *A. rubrum* decomposed more slowly in both the clearcut and control watersheds. *Q. prinus* decomposition rates remained the same in the control watershed but slowed marginally in WS 7. The percent N in the litter of both of these litter types was greater in year 21 (table 8.5). Percent N in leaves can vary greatly from tree to tree and from year to year for different species (Nordell and Karlsson 1995). Although there is often an increase in decomposition rates associated with elevated leaf nitrogen content, analysis of percent N does not reliably indicate substrate quality, as this nitrogen can be incorporated into a variety of recalcitrant molecules (Taylor et al. 1989). Arguably, differences in climate between the two years that we compared could be partially responsible for the differences in decomposition rates. To test this we used monthly climatic data collected from the National Climatic Data Center and made available through the Coweeta Long-Term Ecological Research (LTER) program webpage (<http://coweeta.ecology.uga.edu/>). The average temperature was warmer by about 1°C for year 21 than for year 8; but total precipitation in both summer and fall was lower in year 21 than in year 8. Lower moisture conditions have important implications for decomposition rates and may have been responsible for the observations of lower decomposition rates for *C. florida* and *A. rubrum*.

These results suggest that in the clearcut watershed there has been a trend toward a return to predisturbance levels of a variety of factors, both abiotic and biotic, that ultimately control the breakdown of leaf material. Blair and Crossley (1988) attributed the substantially lower decomposition rates after 8 years in the clearcut watershed compared to the control to differences in microarthropod abundance. In their study, they noted that microclimatic extremes were greater in the clearcut watershed than in the control. This, they argued, created a situation unfavorable for microarthropods. Though we have not presented data on microclimate here, the large abundances of microarthropods in the disturbed watershed suggest that the abiotic constraints on the growth rates of faunal populations that initially occurred after the clearcut have abated.

Prior to clearcut it is assumed that there were no significant differences between microarthropod densities in the two watersheds (Abbott et al. 1980; Seastedt and Crossley 1981). In the study by Blair and Crossley (1988), the populations were shown to have recovered somewhat from the strong reductions noted after year 1 (remaining 28% lower in the clearcut watershed in the Blair and Crossley study). There was a differential response among the microarthropod groups. Mesostigmata and oribatid mites in the clearcut site were still 50% less abundant compared to the control. Abbott et al. (1980) found that within a year of the cut, the proportional abundance of the most dominant species, *Tectocephus velatus*, was only 14.5%. The proportional abundance of the most dominant species in the control watershed, *Oppiella nova*, was 27.1%.

A comparison of microarthropod abundance in the two watersheds reveals a greater density of microarthropods in WS 7. The elevated density of oribatid mites in WS 7 was largely responsible for this overall increase. The proportions of organisms in each broad taxonomic group were similar. The proportion of oribatids was the highest of all groups examined, and this contrasts with results from 8 years after the clearcut when prostigmatid mites were proportionately the most prevalent. Blair and Crossley (1988) reported on animals extracted directly from the litterbags, whereas we looked at extractions from the forest floor adjacent to the litterbags. There is no reason to suspect that litterbags should be colonized preferentially by different microarthropod taxonomic groups (Heneghan et al. 2002). Differences in diversity were detected and the Jaccard's similarity measure suggested that samples drawn from each watershed are self-similar.

We have suggested that studies on recovery of ecosystems from large disturbances may be instructive for restoration practice. Ecosystem successional development at WS 7 was not assisted by restoration management. The changes over time in WS 7 reported for the vegetation (see Boring et al., chapter 2, this volume), soil nutrient dynamics (see Knoepp et al., chapter 4, this volume), and hydrology (see Swank et al., chapter 3, this volume) are those that occur in the absence of deliberate human management. Although different processes may proceed at different paces, it is clear that these are mechanistically related. In the data we present here, decomposition rates and the biota that contribute to the decomposition process are linked. The recovery of the former is dependent to some extent on the recovery of the latter. It is also clear that the decomposer system is influenced by the successional patterns of the vegetation; and furthermore, that decomposition may influence primary productivity and vegetation patterns. In contrast to the postdisturbance events that we report on here, restoration management represents, by definition, an attempt to assist in the recovery of an ecosystem that has been degraded, damaged, or destroyed (SER 2002). However, since many (though by no means all) restoration projects focus on manipulating the plant community, and evaluate outcomes based on plant populations or community measures, opportunities for improving outcomes may be neglected if other available indicators, such as microarthropods and decomposition rates, are not considered. Our results suggest that, even in the absence of management, the decomposer subsystem in a hardwood forest re-established itself after two decades. Even if the plant communities differ after two decades, the recovery of decomposition will nevertheless be important in

influencing vegetation development. Incorporating soils ecological knowledge into restoration may improve restoration outcomes (Callaham et al. 2008; Heneghan et al. 2008). We suggest two avenues of research, exploring the questions: What is the impact of specific restoration practices (including trampling by project personnel and heavy equipment, etc.) on soil abiotic regimes, biota, and subsequent community development? Are restoration strategies that aim to rehabilitate soil processes more likely to produce resilient ecological results as measured, for instance, by resistance to reinvasion by exotic species, the removal of which is often a prelude to restoration practice)?

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Literature Cited

- Abbott, D. T., T. R. Seastedt, and D. A. Crossley, Jr. 1980. The abundance, distribution and effects of clear cutting on oribatid mites (Acari: Cryptostigmata) in the southern Appalachians. *Environmental Entomology* 9: 618–623.
- Abbott, D. T., and D. A. Crossley, Jr. 1982. Woody litter decomposition following clear cutting. *Ecology* 63: 35–42.
- Aber, J. D., D. B. Botkin, and J. M. Melillo. 1978. Predicting the effects of different harvesting regimes on forest floor dynamics in northern hardwoods. *Canadian Journal of Forest Research* 8: 306–315.
- Binkley, D., 1984. Does forest removal increase rates of decomposition and nitrogen release? *Forest Ecology and Management* 8: 229–233.
- Blair, J. M., and D. A. Crossley, 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.
- Callaham, M. A., C. C. Rhoades, and L. Heneghan. 2008. A striking profile: soil ecological knowledge in restoration management and science. *Restoration Ecology* 16: 604–607.
- Corns, I. G. W., and D. G. Maynard. 1998. Effects of soil compaction and chipped aspen residue on aspen regeneration and soil nutrients. *Canadian Journal of Soil Science* 78: 85–92.
- Covington, W. W. 1981. Changes in forest floor organic matter and nutrient content following clearcutting in northern hardwoods. *Ecology* 62: 41–48.
- DeAngelis, D. L. 1992. *Dynamics of Nutrient Cycling and Food Webs*. Chapman and Hall, London, United Kingdom.
- Ehrenfeld, J. G., and L. Toth. 1997. Restoration ecology and the ecosystem perspective. *Restoration Ecology* 5: 307–318.
- Elliott, K. J., and W. T. Swank. 1994. Changes in tree species diversity after successive clearcuts in the southern Appalachians. *Vegetatio* 115: 11–18.
- Elliott, K. J., L. R. Boring, and W. T. Swank. 2002. Aboveground biomass and nutrient accumulation 20 years after clear-cutting a southern Appalachian watershed. *Canadian Journal of Forest Research* 32: 667–683.

- Gemesi, O., D. Skambracks, and W. Topp. 1995. Effects of clear-cutting on litter decomposition and the density of earthworms in mountain forests of southern Germany. *Forstwissenschaftliches Centralblatt* 114: 272–281.
- Heneghan, L., and T. Bolger. 1996. Effects of the components of “acid rain” on the contribution of soil microarthropods to ecosystem function. *Journal of Applied Ecology* 33: 1329–1344.
- Heneghan, L., C. Clay, and C. Brundage. 2002. Observations on the initial decomposition rates and faunal colonization of native and exotic plant species in a urban forest fragment. *Ecological Restoration* 20: 108–111.
- Heneghan, L., D. C. Coleman, X. Zou, D. A. Crossley, Jr., and B. L. Haines. 1999. Soil microarthropod contributions to decomposition dynamics: Tropical-temperate comparisons of a single substrate. *Ecology* 80: 1873–1882.
- Heneghan, L., S. P. Miller, S. Baer, M. A. Callahan, J. Montgomery, M. Pavao-Zuckerman, C. C. Rhoades, and S. Richardson. 2008. Integrating soil ecological knowledge into restoration management. *Restoration Ecology* 16: 608–617.
- Holling, C. S. 1973. Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics* 4: 1–23.
- Houston, A.P. C., S. Visser, and R. A. Lautenschlager. 1998. Microbial processes and fungal community structure in soils from clear-cut and unharvested areas of two mixed wood forests *Canadian Journal of Botany* 76: 630–640.
- Johnston, J. M., and D. A. Crossley, Jr. 2002. Forest ecosystem recovery in the southeast US: soil ecology as an essential component of ecosystem management. *Forest Ecology and Management* 155: 187–203.
- Knoepp, J. D., and W. T. Swank. 1997. Long-term effects of commercial sawlog harvest on soil cation concentrations. *Forest Ecology and Management* 93: 1–7.
- Kotanen, P. M. 2004. Revegetation following soil disturbance and invasion in Californian meadow: a 10-year history of recovery. *Biological Invasions* 6: 245–254.
- Lavelle, P., E. Blanchart, A. Martin, S. Martin, A. Spain, F. Toutain, I. Barois, and R. Schaefer. 1993. A hierarchical model for decomposition in terrestrial ecosystems: application to soils of the humid tropics. *Biotropica* 25: 130–150.
- Likens, G. E., and F. H. Bormann. 1995. *Biogeochemistry of a forested ecosystem*. Springer-Verlag, New York, New York.
- Lindenmayer, D. B., D. R. Foster, J. F. Franklin, M. L. Hunter, R. F. Noss, F. A. Schmiegelow, and D. Perry. 2004. Salvage harvesting policies after natural disturbance. *Science* 303: 1303.
- Lindo, Z., and S. Visser. 2004. Forest floor microarthropod abundance and oribatid mite (Acari: Oribatida) composition following partial and clear-cut harvesting in the mixed wood boreal forest. *Canadian Journal of Forest Research* 34: 998–1006.
- Lussenhop, J. 1992. Mechanisms of microarthropod microbial interactions in soil. *Advances in Ecological Research* 23: 1–33.
- Magurran, A. E. 1988. *Ecological Diversity and Its Measurement*. Chapman and Hall, London.
- Mann, L. K., D. W. Johnson, D. C. West, D. W. Cole, J. W. Hornbeck, C. W. Martin, H. Riekerk, C. T. Smith, W. T. Swank, L. M. Tritton, and D. H. Van Lear. 1988. Effects of whole-tree and stem-only clearcutting on postharvest hydrologic losses, nutrient capital, and regrowth. *Forest Science* 34: 412–428.
- Niemela, J. 1997. Invertebrates and boreal forest management. *Conservation Biology* 11: 601–610.

- Nordell, K. O., and P. S. Karlsson. 1995. Resorption of nitrogen and dry matter prior to leaf abscission: variation among individuals, sites and years in the mountain birch. *Functional Ecology* 9: 326–333.
- Olson, J. S. 1963. Energy storage and the balance of producers and consumers in ecological systems. *Ecology* 44: 322–331.
- Pimm, S. 1984. The complexity and stability of ecosystems. *Nature* 307: 321–326.
- Pumpanen, J., C. J. Westman, and H. Ilvesniemi. 2004. Soil CO₂ efflux from a podzolic forest soil before and after forest clear-cutting and site preparation. *Boreal Environment Research* 9: 199–212.
- Qualls, R. G., B. L. Haines, W. T. Swank, and S. W. Tyler. 2000. Soluble organic and inorganic nutrient fluxes in clearcut and mature deciduous forests. *Soil Science Society of America Journal* 64: 1068–1077.
- Seastedt, T. M. 1979. Microarthropod response to clear-cutting in the southern Appalachians: effects on decomposition and mineralization of litter. PhD dissertation. University of Georgia, Athens.
- Seastedt, T. M. 1984. The role of microarthropods in decomposition and mineralization processes. *Annual Review of Entomology* 29: 25–46.
- Seastedt, T. M., and D. A. Crossley, Jr. 1981. Microarthropod response following cable logging and clearcutting in the southern Appalachians. *Ecology* 62: 126–135.
- SER (Society for Ecological Restoration Science & Policy Working Group). 2002. The SER primer on ecological restoration. Available at www.ser.org.
- Siira-Pietikäinen, A., J. Pietikäinen, H. Fritze, and J. Haimi. 2001. Short-term responses of soil decomposer communities to forest management: clear felling versus alternative forest harvesting methods. *Canadian Journal of Forest Research* 31: 88–99.
- Startsev, N. A., D. H. McNabb, and A. D. Startsev. 1998. Soil biological activity in recent clearcuts in west-central Alberta. *Canadian Journal of Soil Science* 78: 69–76.
- Striegl, R., G. Kimberly, and P. Wickland. 1998. Effects of a clear-cut harvest on soil respiration in a jack pine–lichen woodland. *Canadian Journal of Forest Research* 28: 534–539.
- Taylor, B. R., D. Parkinson, W. F. J. Parsons. 1989. Nitrogen and lignin content as predictors of litter decay rates: a microcosm test. *Ecology* 70: 97–104.
- Verhoef, H. A. 1996. The role of soil microcosms in the study of ecosystem processes. *Ecology* 77: 685–690.
- Whitford, W. G., V. Meentemeyer, T. R. Seastedt, K. Cromack, Jr., D. A. Crossley, Jr., P. Santos, R. L. Todd, and J. B. Waide. 1981. Exceptions to the AET model: deserts and clear-cut forests. *Ecology* 62: 275–277.
- Will, G. M., P. D. Hodgkiss, and H. A. I. Madgwick. 1983. Nutrient loss from litterbags containing *Pinus radiata* litter: influence of thinning, clearfelling, and urea fertilizer. *New Zealand Journal of Forest Science* 13: 291–304.
- Young, T. P. 2000. Restoration ecology and conservation biology. *Biological Conservation* 92: 73–83.
- Zerva, A., and M. Mencuccini. 2005. Short-term effects of clearfelling on soil CO₂, CH₄, and N₂O fluxes in a Sitka spruce plantation. *Soil Biology & Biochemistry* 37: 2025–2036.

LTER



Long-Term Response of a Forest Watershed Ecosystem

CLEARCUTTING IN THE
SOUTHERN APPALACHIANS

EDITED BY
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"No serious student of forest hydrology or ecology can survive long without encountering the name "Coweeta." The Coweeta Hydrologic Laboratory in North Carolina has rightly become world-famous across a broad spectrum of environmental science. It is well over 20 years since the last compilation of Coweeta research appeared in book form, and this volume provides a very welcome update."

—Professor Tim Burt, Durham University

"Forest watershed research is reaching an age when some long-term trends—or the lack of them—can be evaluated. Aside from its great value as a synthesis of a comprehensive long-term research project in and of itself, this volume is a welcome scientifically objective investigation of the long-term effects of forest harvesting. This volume should reside on the bookshelves of scientists (both basic and applied), educators, policy makers, and environmental advocates.

—Dale Johnson, Emeritus Professor, University of Nevada

"This volume is a most compelling case on the value and necessity of long-term research on ecological patterns and processes. Findings summarized here are applicable way beyond the ecology and management of southern Appalachian hardwoods, by providing a framework on improving both economic and ecological values with appropriate forest management practices."

—Donald J. Leopold, Chair, Department of Environmental and Forest Biology, SUNY-ESF

Our North American forests are no longer the wild areas of past centuries; they are an economic and ecological resource undergoing changes from both natural and management disturbances. A watershed-scale and long-term perspective of forest ecosystem responses is requisite to understanding and predicting cause and effect relationships. This book synthesizes interdisciplinary studies conducted over thirty years, to evaluate responses of a clear-cut, cable-logged watershed at the Coweeta Hydrologic Laboratory in the Nantahala Mountain Range of western North Carolina. This research was the result of collaboration among Forest Service and university researchers on the most studied watershed in the Lab's 78-year history. During the experiment, a variety of natural disturbances occurred: two record floods, two record droughts, a major hurricane, a blizzard of the century, major forest diseases, and insect infestations. These disturbances provided a unique opportunity to study how they altered the recovery of the forest ecosystem. This book also shows that some long-term forest trends cannot be forecast from short-term findings, which could lead to incorrect conclusions of cause and effect relationships and natural resource management decisions.

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