Effects of Soil Compaction and Organic Matter Removal on Ground-flora Diversity in the Great Lakes Forests

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Introduction

Soil is one of the key factors regulating the productivity and diversity of forest ecosystems. Soil organic matter resulting from the decomposition of leaf litter provides an important reservoir of nutrients for future forest growth. The structure of soils, in conjunction with soil texture, determines the ability of a soil to retain moisture. Forest harvest operations, through the use of heavy equipment and slash management practices, have the potential to damage soil structure and remove organic matter from the forest floor. We lack a clear understanding, however, of which soil types are most susceptible, and what degree of impact soils can sustain before the potential productivity and diversity are reduced. To address this issue, a nationwide Long-Term Soil Productivity (LTSP) study was initiated to assess the effects of logging operations on the structure and organic matter content of forest soils (Powers et al. 1990). In the Lake States, study plots were installed on the Chippewa, Ottawa, and Huron National Forests. These plots represent the range of soil textures which occur across the Lake States: silt loams, clays, and sands, respectively. Using an experimental approach, different levels of soil compaction and organic matter removal were applied to harvested aspen stands across this soil gradient. Aspen reproduction, forest biomass, and the diversity of the ground-flora layers are being monitored on an annual or biennial basis to assess their response to these treatments. The results of this experiment will allow us to predict the degree of protection required to sustain productivity and floristic diversity in aspen stands across a range of common Lake State soil types.

The Lake States LTSP study has included an analysis of floristic diversity to the suite of measurements made on the study plots. Biodiversity and forest management has become a critical issue in the Lake States Forests. In Minnesota's Generic Environmental Impact Statement, diversity was one of the key focal issues. Ground-flora has received wide use in ecological indicators and in ecological land classification systems across the Great Lakes (Spies and Barnes 1986, Host and Pregitzer 1991, Coffmann et al. 1983, Shadis et al. 1995). A primary objective of this study was assess the response of the ground-flora community to the soil compaction and organic matter removal treatments within the LTSP study. This response can be assessed not only on a year-by-year basis, but also in describing the rate and trajectory of recovery toward the compositional state of the uncut forest.

Methods

Study Sites and Sample Design

LTSP installations were located on the Chippewa, Ottawa and Huron National Forests, representing silt loam, clay loam, and sand-textured soils, respectively. The Chippewa National Forest had both a pilot installation containing a subset of treatments (Marcell; Alban et al. 1994) and a full installation. All installations were dominated by relatively mature (60-80 yr old) aspen (*Populus tremuloides* Michx., *Populus grandidentata* Michx.). Sites were carefully evaluated to ensure that they were relatively homogeneous in terms of forest cover, topography, soils, and ground-flora vegetation, and representative of the characteristic soil types of the region.

Each installation consisted of three replicates of a 3 x 3 factorial treatment with three levels of soil compaction (none, moderate and severe) and three levels of organic matter removal (bole-only removal, total aboveground tree removal, and total aboveground tree + forest floor removal (Table 1). Forest floor was removed by raking off leaf litter down to the mineral soil.

Table 1. Factorial design for an LTSP Installation. Values represent number of replicates in each treatment.

	No Compaction	Moderate Compaction	Severe Compaction
Bole-only	3	3	3
Total Tree Harvest	3	3	3
Total Tree+Forest Floor	3	3	3

There were thus 27 plots in each installation. Individual treatment plots were 40 x 40 m in size, with a 10 m buffer strip surrounding each plot. To provide baseline data, the overstory and ground-flora were sampled in all plots prior to harvest. Plots were harvested the following winter when soils were frozen to ca. 0.3 m, and treatments applied the following spring. The timing of the harvests and treatment applications for each installation is shown in Table 2.

Table 2. Timing of pre- and post-treatment sampling in the Lake States LTSP Study

	Installations			
Year	Marcell (Pilot)	Ottawa	Chippewa	Huron
1990	Pre-treat.			
1991	Year 1	Pre-treat.		
1992	Year 2	Year 1	Pre-treat.	
1993	Year 3	Year 2	NS	Pre-treat.
1994	Year 4	NS	Year 1	Year 1
1995	Year 5	NS	Year 2	Year 2

On the Chippewa National Forest, a wet spring and summer in 1993 made it impossible to apply the treatments early in the season; as a result, no floristic sampling was done in 1993; the Year 1 sampling for this installation was done on 1994.

Floristic Sampling

In each plot, four points were established for sampling vegetation and soils. Sample points were systematically located within the 40 x 40 m plots, and used as reference points for the rectangular ground-flora releve plots (Figure 1). To quantify ground-flora composition and abundance, 10 x 15 m subplots were established around each of the permanent sampling points. Percent ground cover was determined for all herbaceous and woody species in the subplot using a Braun-Blanquet cover-abundance scale (Mueller Dombois and Ellenburg 1974). Cover estimates were stratified by height class, as described in Almendinger (1988). Abundance values were determined by traversing the subplot plot several times to record the species present, and then assigning abundance values after species lists were compiled. Nomenclature for vascular plants follows Gleason (1952).

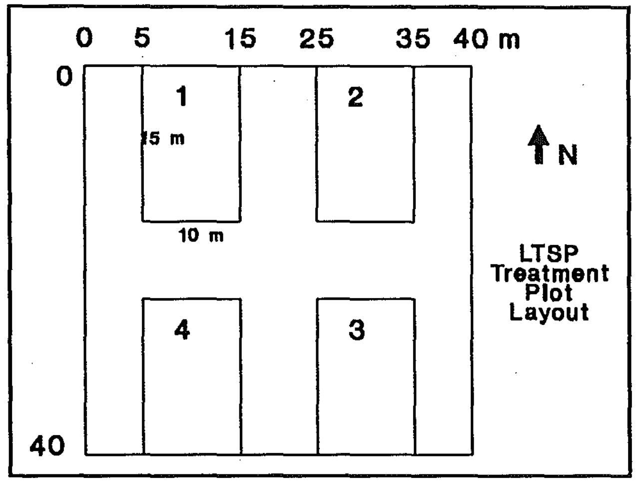

Figure 1. Subplot locations within 40 x 40 m LTSP sample plot.

Statistical Analyses

Floristic response to treatments was evaluated using a number of univariate and multivariate measures. Univariate measures included species richness (S), the number of species per plot, and Shannon's diversity index (H'). These metrics were tested using two way Analysis of Variance (ANOVA); years were analyzed with both independent and repeated measured ANOVAs. All data were tested for normality and transformed as appropriate.

Community composition was analyzed using multivariate ordination and classification techniques to determine if particular plots or treatments had different overall floristic composition. Specifically, plots were ordinated with respect to ground-flora composition using detrended correspondence analysis (DCA; Hill 1979). The primary result of a DCA is an ordination space diagram, in which plots which are close together on the plot are similar in species composition. The axes of a DCA are calculated to successively maximize variation in composition; thus DCA Axis 1 is the major compositional gradient in the data set, Axis 2 is the second dominant axis, etc. DCA also assigns weights to species, which can be used to identify which species contribute the most to the variation of the data set. Species that occurred on less that 5% of the plots were not included in the analysis, and rare species were downweighted (Hill 1979).

The statistical significance of treatment effects on species composition was tested using a multiple response permutation procedure (MRPP). MRPPs are nonparametric classification procedures for testing the hypothesis of no differences among one or more groups. The test is based on comparing actual within and between group (i.e. treatment) compositional similarities against a resampled population of similarities based on random assignments of plots to treatments. If the actual values fall within the tails of the simulated distribution of similarities, the null hypothesis is rejected. MRPP do not rely on the assumptions of multivariate normality and homogeneity of variance required in parametric tests (McCune 1995).

Results

Chippewa National Forest

Pretreatment conditions

The dominant ground-flora species in the pretreatment plots were sugar maple (*Acer saccharum*), rice grass (*Oryzopsis asperifolia*), beaked hazel (*Corylus cornuta*) and Pennsylvania sedge (*Carex pensylvanica*). Species richness data at the subplot level were not normally distributed, nor would they be transformed to normality; as a result ANOVA could not be used with subplot-level data. Plot level averages were normally distributed, however, and subsequent analyses were thus based on plot level data. Species richness and Shannon diversity were not significantly different in the pre-treatment plots. Mean species richness (S) at the subplot level was 50, mean Shannon diversity (H') was 3.96. Full details of all statistical tests are presented in Appendix A.

The abundance of species followed a truncated log-normal distribution as described by Preston (1948): a few common species (e.g. *Populus tremuloides*, *Aster macrophyllus*) dominate the plots, while the majority of species are present at low abundance values (Figure 2). Statistics on species richness alone can therefore be deceptive, in that they do not account for the relative within the community. To account this effect, both composition and abundance were included in the ordinations described below.

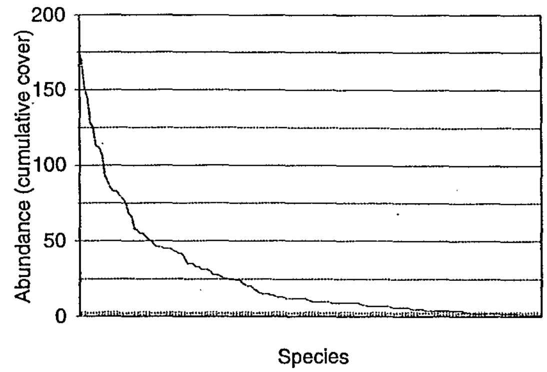

Figure 2. Species abundance relationship from the 1992 Chippewa sample plots.

Detrended correspondence analysis showed that there were distinct differences in initial ground-flora composition among the three installations (Figure 3a). Installation 3 was separated from Installations 1 and 2 on DCA Axis 1. Two violets (*Viola incognita* and *V. adunca*) received strong positive weights on the Axis 1, along with alder (*Alnus viridis*), asters (*Aster spp.*), and pyrolas (*Pyrola spp.*). Three species of horsetail (*Equisetum spp.*), greenbriar (*Smilax herbacea*), and lady-slipper orchid (*Cypripedium calceolus*) received strong negative weights on this axis (e.g. they were dominant members of Installations 1 and 2). Installations 1 and 2 separated along DCA Axis 2. The strong positive dominants on this axis were bloodroot (*Sanguinaria canadensis*), greenbriar (*Smilax herbacea*), and *Rosa spp.* Negative dominants were *Lycopodium obscurum*, *Viola incognita*, *Ostrya virginiana*, and *Carex gracilis*. Differences among plots within each installation were relatively minor (Figure 3a).

Post treatment Analyses

Species Richness

In the 1994 sampling period, there was a significant increase in species richness with increasing levels of OM removal ($p<0.05$); S increased by 11 or 12 species in the uncompacted and heavily compacted plots (Table 3). In plots where organic matter was not removed, there was in fact a decrease in species richness between 1992 and 1994 (Figure 4). There were no significant effects of compaction or interactions among the factor levels, and differences in species richness did not persist into 1995. The increase in 1994 in treated plots likely reflects a short-term response of annual and biennial species to the opening of the forest floor. The repeated measures analysis also indicated a significant effect of OM removal over time (Appendix A).

Table 3. Average species richness (S) by treatment level on the Chippewa National Forest

OM	Compaction Level								
	None			Moderate			Heavy		
Removal	1992	1994	1995	1992	1994	1995	1992	1994	1995
None	53	40	52	55	53	57	49	45	52
Moderate	44	51	48	47	58	55	49	56	51
Heavy	49	52	54	51	54	55	50	57	54

Shannon Diversity

While the effects of OM removal were expressed in terms of species richness, treatment effects on Shannon diversity were related to compaction. H' differed among compaction treatments in the 1995 sampling period. Post-hoc tests showed that the no compaction H' was significantly lower than the moderate compaction treatment (4.0 vs 4.21, respectively). The heavy compaction had an H' of 4.12, not significantly different from the moderate or uncompacted treatments. These results were corroborated with the repeated measures analysis, which indicated a significant effect of compaction over time (Appendix A).

Community Composition

There was a strong response of community composition to soil compaction. Soil compaction exerted a dominant effect on DCA Axis 1 in the 2nd and 3rd years after treatment. There was a clear separation on DCA Axis 1 between the uncompacted sites and those with moderate or high levels of compaction (Figure 5). There was also moderate discrimination between moderately and highly compacted plots in year 2, which became more pronounced in year 3 (Figure 5). The compositional distinctions between the installations were retained in the DCA, but now appear on

Axis 2. Species heavily weighted on the first axis include two species of honeysuckle (*Lonicera canadensis* and *L. dioica*), red baneberry (*Actaea rubra*), blue-bead lily (*Clintonia borealis*), and downy arrow-wood (*Viburnum rafinesquianum*). Negatively weighted species include the speedwells (*Veronica spp.*), evening-primrose (*Oenothera biennis*), asters (*Aster spp.*) and wild mint (*Mentha arvensis*).

The significant of compositional differences were tested using Multiple Response Permutations Procedures. Pretreatment composition and changes resulting from the OM removal were not significant; post-treatment effects from compacted plots were highly significant (Table 4)

Table 4. Probability levels for MRPP tests of species composition on the Chippewa National Forest

	1992	1994	1995
OM Removal	0.546	0.530	0.665
Compaction	1.000	0.000	0.000

The top ten dominant species for each compaction treatment from 1994 are shown in Table 5 ; because of the log-normal distribution of abundance, these species account for 25 to 30% of the total coverage in the plot. The top two dominants differed between compacted and uncompacted sites: *Populus tremuloides* and *Aster macrophyllus* are the dominants in uncompacted sites, whereas *Carex pensylvanica* and *Conyza canadensis* dominate compacted sites. In addition, several species present in the uncompacted plots did not occur in the upper quartile of species in the compacted plots: *Oryzopsis asperifolia, Thalitricum dioicum, Corylus cornuta, Acer saccharum, Aralia nudicaulis* and *Acer spicatum.* These were replaced in the compacted plots by more ruderal spccies: *Fragaria virginiana, Cirsium vulgare* and *C. arvense, Rubus strigosus, Carex bebbii, Epilobium coloratum,* and *Vicia americana.* There is thus a floristic response to soil compaction that seems to be related to species life history: species capable of establishment on disturbed sites may have a competitive advantage over those which occur after harvest under uncompacted conditions.

Table 5. Upper quartile dominant species on the 1994 Chippewa National Forest plots under three compaction levels.

No Compaction	Moderate Compaction	Heavy Compaction
Populus tremuloides Michx.	Carex pensylvanica Lam.	Carex pensylvanica Lam.
Aster macrophyllus L.	Conyza canadensis (L.) Cronq.	Conyza canadensis (L.) Cronq.
Carex pensylvanica Lam.	Aster macrophyllus L.	Aster macrophyllus L.
Oryzopsis asperifolia Michx.	Fragaria virginiana Duchesne	Fragaria virginiana Duchesne
Thalictrum dioicum L.	Cirsium vulgare (Savi) Tenore	Rubus strigosus var. strigosus Michx.
Corylus cornuta Marsh.	Rubus strigosus var. strigosus Michx.	Carex bebbii (L. Bailey) Fern.
Fragaria virginiana Duchesne	Cirsium arvense var. arvense (L.) Scop.	Vicia americana var. americana Muhl. ex Willd.
Acer saccharum Marsh.	Epilobium coloratum Biehler	Scirpus cyperinus (L.) Kunth
Aralia nudicaulis L.	Vicia americana var. americana Muhl. ex Willd.	Epilobium coloratum Biehler
Acer spicatum Lam.	Carex bebbii (L. Bailey) Fern.	Cirsium arvense var. arvense (L.) Scop.

Ottawa National Forest

Pretreatment conditions

The pretreatment ground-flora on the Ottawa plots was dominated by bracken fern *(Pteridium aquilinum)*, large-leafed aster (*Aster macrophyllus*), serviceberry (*Amelanchier spp.*), and barren strawberry (*Waldsteinia fragaroides*). There were no initial differences in species richness or Shannon diversity among the pretreatment plots, with a mean S of 19.1 and mean H' of 3.00. Compositionally, there were also no strong differences among plots; treatments were scattered uniformly within the DCA ordination space (Figure 6a)

Post treatment Analyses

Species Richness

Species richness increased on all plots following treatment, with mean species richness of 32.7 and 52.6 for 1992 and 1993 respectively. Over the two post-treatment years, there was a trend toward increasingly significant differences due to treatments (Appendix A). By the third year, there was a significant effect of OM removal ($p = 0.023$); the compaction effect was very close to the $p = 0.05$ cutoff ($p = 0.066$). Post-hoc comparisons using Fisher's protected LSD ($p < 0.05$) showed that in 1993 the total tree harvest+forest floor removal had significantly fewer species than the total tree harvest alone. Because the compaction treatment was so close to the 0.05 significance level, compaction effects should also be considered: the highest species richness observed was under heavy compaction and the bole-only OM removal (Table 6), counter to the trend observed when analyzing the data using OM removal only. In the repeated measures analysis, both organic matter and compaction treatments were significant, at $p=0.023$ and $p=0.046$, respectively.

Table 6. Average species richness (S) by treatment level on the Ottawa National Forest

OM	Compaction Level								
	None			Moderate			Heavy		
Removal	1991	1992	1993	1991	1992	1993	1991	1992	1993
None	20.1	33.6	45.7	19.6	38.4	55.0	20.7	37.2	63.7
Moderate	19.8	32.7	55.3	18.7	35.9	56.7	19.5	35.1	55.7
Heavy	21.2	34.6	48.2	20.1	28.5	50.6	20.7	30.1	48.5

[1] Row means not followed by the same letter are significantly different using Fisher's LSD ($P < 0.05$)

Shannon Diversity

In the second year after sampling, both organic matter removal and compaction had significant effects on H' (Appendix A). There was no significant interaction between the two factor levels.

The effects of compaction on species diversity were most pronounced in the bole-only OM Removal treatment, where mean H' ranged from 3.98 under no compaction to 4.25 under heavy compaction (Table 7). These were the extreme values in the data set. Under the Total Tree+FF removal treatment, H' was consistently low across compaction levels. Finally, under heavy compaction, h" was inversely related to degree of OM removal: diversity was highest under the bole-only treatment and lowest under Total Tree+FF removal. In the repeated measures analysis, only the OM effects were significant.

Table 7. Average Shannon diversity (H') by treatment from the 1993 sampling period on the Ottawa National Forest.

	Soil Compaction			
	None	Moderate	Heavy	Grand Total
Bole-only	3.98	4.16	4.25	4.09
Total Tree	4.14	4.18	4.16	4.15
Total Tree + FF	4.01	4.07	4.06	4.04
Grand Total	4.06	4.13	4.13	4.10

Community Composition

There were also strong effects on floristic composition following treatment. As in the Chippewa plots, the dominant gradient on DCA Axis 1 was related to the degree of soil compaction. Uncompacted sites received high scores on DCA Axis 1, moderately compacted sites received intermediate scores, and heavily compacted sites received low scores (Figure 7a,b). Discrimination among compacted plots increased in year 3, although the separations among plots were not as clear as in the Chippewa analysis. Species heavily weighted on Axis 1 (i.e. important in uncompacted plots) in 1992 and 1993 were red baneberry (*Actaea rubra*), twinflower (*Linnaea borealis*), nodding trillium (*Trillium cernuum*), sweet cicely (*Osmorhiza claytoni*), and balsam fir (*Abies balsamea).* Negatively-weighted species include clovers and horsetails (*Trifolium spp.* and *Equisetum spp.*, respectively), the grasses *Agrostis* (*A. hyemalis* and *A. stolonifera,*) and *Danthonia, Luzula acuminata*, and the composites *Erigeron annuum* and *Solidago flexuosa*. As on the Chippewa, DCA Axis 1 represents a gradient of species characteristic of closed forest canopy on uncompacted sites to species characteristic of disturbed environments. No strong treatment effects were evident in Axis 2, but Axis 3 showed some discrimination between moderately and heavily compacted sites in 1993 (Figure 7c). This first DCA axis was also related to organic matter removal in 1992 (Figure 7b), separating the total tree+forest floor removal from the other two treatments, but this discrimination was not evident in the 1993 data.

The MRPP corroborated the results of the ordination. There were significant differences in composition related to both organic matter removal and compaction in the two years following treatment (Table 8)

Table 8. Probability levels for MRPP tests of species composition on the Ottawa National Forest

	1991	1992	1993
OM Removal	0.966	0.001	0.002
Compaction	0.697	0.012	0.000

Huron National Forest

Pretreatment conditions

The dominant species on the Huron plots prior to treatment was bracken fern (*Pteridium aquilinum*), followed by red maple (*Acer rubrum*), wintergreen (*Gaultheria procumbens*), raspberry (*Rubus canadensis*), rice grass (*Oryzopsis asperifolia*) and red oak (*Quercus rubra*). There were no initial differences in species richness or diversity among the pretreatment plots, with a mean S of 30.9 and H' of 3.55 (Appendix A). Detrended Correspondence Analysis revealed strong initial differences in species composition related to installation. Specifically Installation 1, which is physically separated from 2 and 3 by approximately 2 km, was compositionally distinct from Installations 2 and 3.

Post treatment Analyses

Species Richness/Shannon Diversity

Plot-level ANOVA indicated that there were no significant treatment-level differences in S or H' in either of two post-treatment sampling periods (Appendix A). Repeated measures also revealed no significant trends related to treatment. Mean species richness dropped from 30.9 to 25.9 in year 2, but recovered to 29.6 in year 3.

Community Composition

Similar to species richness and Shannon diversity, there were no significant trends in species composition related to treatments, either from analysis of the ordinations, or in the MRPPs (Table 9. The installation effect evident on DCA Axis 1 under pretreatment conditions persisted into the first and second years following treatment (Figure 8). To determine if the installation effect was masking any treatment effects, a second ordination was conducted using only Installations 2 and 3

(Figure 9). Again, plots were separated by installation, but not by treatment. Finally, ordinations of individual installations revealed no significant treatment effects. These results were borne out in the MRPP analysis, in which no significant treatment effects were observed (Table 9).

Table 9. Probability levels for MRPP tests of species composition on the Huron National Forest

	1993	1994	1995
OM Removal	0.821	0.269	0.141
Compaction	0.962	0.524	0.766

Marcell Pilot Installation

The Marcell Pilot Installation consists of an unreplicated set of selected treatments. The treatments at the Marcel site were 1) Total Tree - No Compaction, 2) Total Tree+Forest Floor - No Compaction, 3) Total Tree - Severe Compaction, and 4) Total Tree+Forest Floor - Severe Compaction. Mean species richness prior to treatment ranged from 20 to 31; because of this relatively wide range in the pretreatment conditions, both S and the change in S from year to year were considered. In general, plots with Total Tree+Forest Floor removal maintained the highest numbers of species and were most dynamic in terms of year to year change (Figure 10). The Heavy Compaction treatment had the highest number of species. Trends in H' were similar but less pronounced.

Unlike the replicated installations, the Marcell Pilot plots have five years of continuous data. This time record allows an assessment of compositional trajectories among treatments. Plots from all years were coded by both plot number and year (e.g 591 for Plot 5 in 1991) and included in a single ordination. By connecting plots by years, the shifts in composition over time can be documented by treatment. The resulting ordination shows strong differences in compositional trajectories by treatment (Figure 11). After 5 years, treatments arranged themselves along a gradient of impact severity. The uncut control plots (7 and 8) showed a relatively short trajectory in species space, and remained closest to the starting composition of the 1990 data. Most similar to these was Plot 5, the Bole-only - No Compaction treatment. Next was Plot 4, the Uncompacted total tree+forest floor removal. The replicate plots 1 and 4, the Bole-only - Heavy Compaction treatment had similar trajectories, and Plot 2, which received heavy compaction and forest floor removal, had the longest trajectory and provided the 'outer loop' in ordination space. Plot 2 was consistently distinct through the 5 years of sampling. Plot 6, which received identical treatment, occurred in the 'heavy compaction' region of the ordination space, but did not respond as strongly as Plot 2.

Discussion

Soil compaction and differential removal of organic matter from the forest had strong significant effects on several aspects of floristic diversity and composition. The expression of these effects varied across the three National Forests, and within a forest, different treatments affected different attributes of floristic diversity. On the loamy soils of the Chippewa and the clay soils of the Ottawa, the removal of organic matter significantly increased the number of species found on the plots. A likely explanation is that OM removal opened up the forest floor for colonization by ruderal (weedy) species, particularly the thistles (*Cirsium* spp.), raspberry, clovers *(Trifolium spp.)* and horsetails (*Equisetum spp.*).

It is important to note that species richness is probably the least robust of the diversity indices. As a simple tally of the number of species, it is sensitive to measurement error, taxonomic resolution, and 'chance' occurrences of infrequent species. In addition, species richness is insensitive to differences in the relative abundance of species: a single grass stem receives the same weight as 80% plot coverage of bracken fern. For this reason, multiple indices of diversity were calculated and analyzed. The Shannon diversity index integrates both the number of species and their relative abundance, and is likely the most commonly used diversity index. In this study, the Shannon Index was significantly affected by both compaction and organic matter on clay soils, and by compaction alone on loam soils. On the sandy Huron soils, neither species richness nor Shannon diversity were significantly influenced by treatments. These results suggest that not all soils respond similarly to compaction and OM impacts.

Given recent interest in 'biodiversity', the response of ground-flora to soil compaction and OM removal must be assessed carefully. In most cases, the severity of treatment tended to increase the number of species that colonized or shifted in abundance on the site. Clearly, however, the species that increased in abundance were those that have life history attributes developed for colonizing disturbed habitats, and their success was related to degree of disturbance. Thus, while these two diversity metrics increased with disturbance, they do not provide a complete picture of the shift in community composition that occurred. For this, we conducted ordination analyses to understand how community members respond to treatments, and to identify those species which appear sensitive to treatment effects.

Many of the species which were negatively impacted by compaction or OM removal were those characteristic of closed forest canopies, such as red baneberry (*Actaea rubra*), twinflower (*Linnaea borealis*), trillium (*Trillium cernuum*), and sweet cicely (*Osmorhiza claytoni*). Unlike the ruderal species, these are perennials, which emerge annually from underground storage tissues (or, in the case of *Linnaea*, are evergreen), persist in highly shaded conditions, and develop extensive root systems in the forest floor. While the ruderal species tend to be r-strategists, reproducing through the production of large numbers of small windborne seeds, the closed canopy species described above produce fewer, larger seeds, effectively acting as k-strategists (Odum 1971). Physiologically, the closed forest canopy species are more efficient at photosynthesizing under low light intensities (e.g. have high photosynthetic efficiencies) compared with the ruderal species, which generally require full sunlight. There are thus fundamental differences in life history strategies which are impacted by the experimental treatments. Even though all plots were harvested, the plots that did not receive compaction or OM removal treatments retained more of the k-selected species than the treated plots. Hix and Barnes found similar results in a comparing clearcut with 46 year old stands: a decrease in the Clintonia ecological species group on clearcut plots (Hix and Barnes 1984). The Clintonia group contains species with similar life histories to those described above.

While some clear results have emerged in the two years after treatment, these results must be considered with respect to the long term development of the stand. The response to OM removal on the Chippewa (Figure 4) was quite transient; it was not evident in year 2. Other responses appeared to be becoming more apparent, such as the trend toward increasing significance observed on the Ottawa sites. The continued long-term monitoring of these plots is important for tracking the trajectories of recovery and response over time. Plots should be resampled on a 2 or 3 year basis in order to provide an adequate time series for analysis. The Marcell pilot study shows that there are distinct differences in the trajectories of ground flora communities, and that these differences persist for at least five years. In fact, Figure 11 indicates that after five years, the plots appear to be more divergent than convergent, i.e. the treatment effect is persistent.

Sites on the three Forests were selected because they represent the range of soils found across the Lake States. However, since the three sites are also separated by several hundred kilometers, they are in different climatic and biogeographic regions. As a result, the effect of soil texture may also be confounded by biogeographic differences, and interpretations of the test results must be tempered with an understanding of these confounding effects. The lack of response of any diversity metric on the sand textured soil (Huron site) provides a strong indication however, that both compaction and OM removal have less of an impact on ground-flora than on soils where soil structure may have a stronger selective effect on floristic composition. As management guidelines related to forest soil compaction and OM removal are developed, it will be important to incorporate soil texture in guideline development: a single set of guidelines will not likely apply to all soil types.

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List of Figures

and c) level of organic matter removal (B - Bole Only, T - Total Tree, X - Total Tree+Forest Floor).

Figure 10. Trends in species richness and changes in species richness on the Marcell Pilot Installation.

Figure 11. Compositional trajectories for resampled plots on the Marcell Pilot Installations. Plots are coded by Plot Number and Year (e.g. 591 = Plot 5, 1991). Arrows indicate movement of plots in ordination space over time.

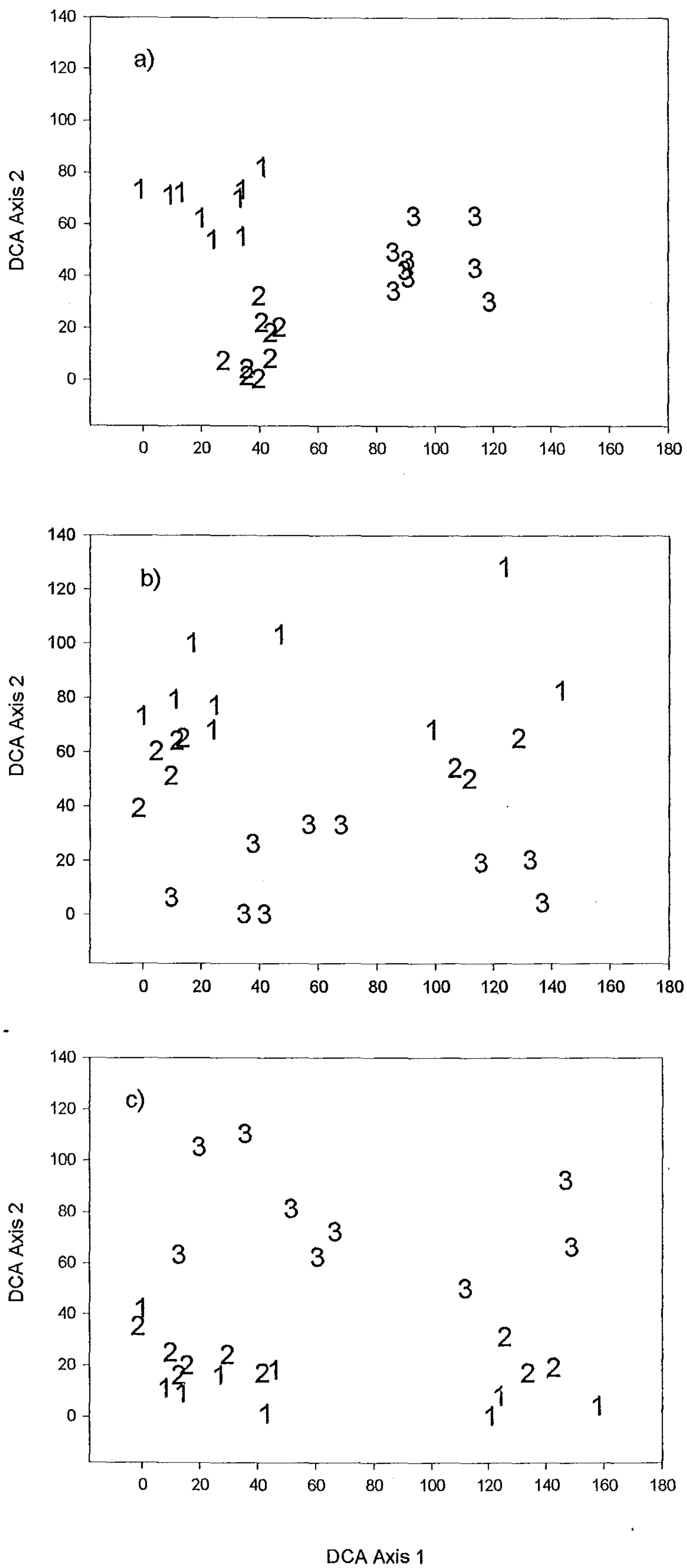


Figure 3

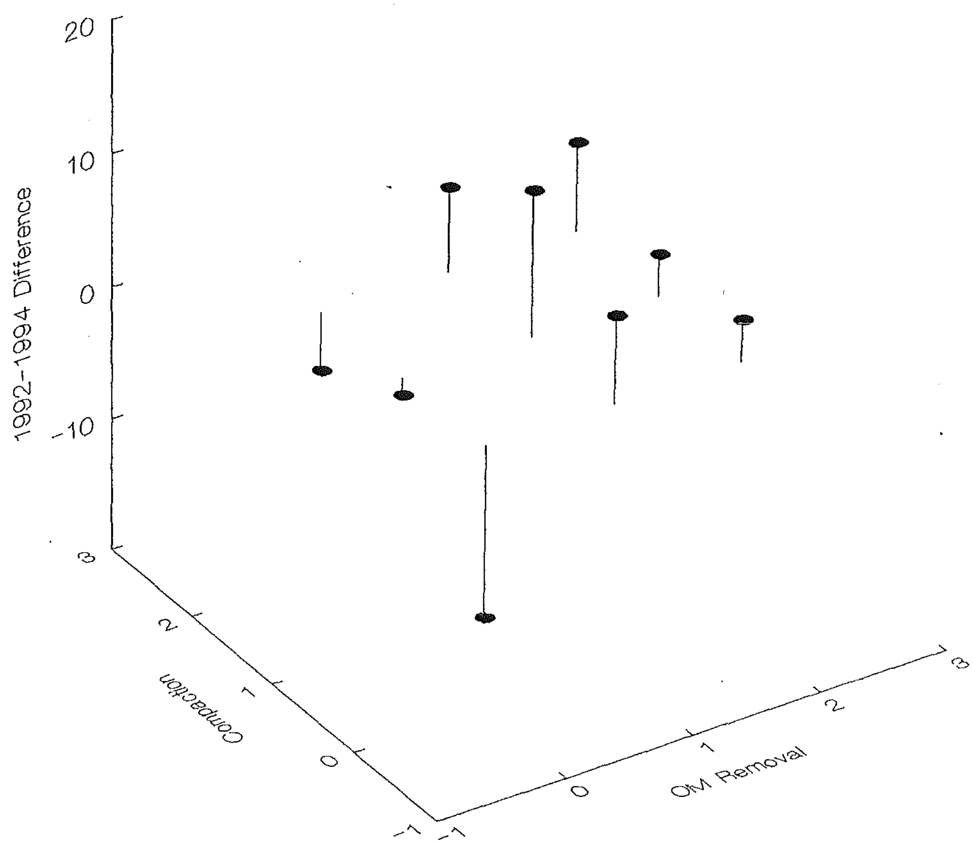

1992-1994 Difference
20
10
0
-10
Compaction
3
2
1
0
-1
OM Removal
-1
0
1
2
3

Figure 4

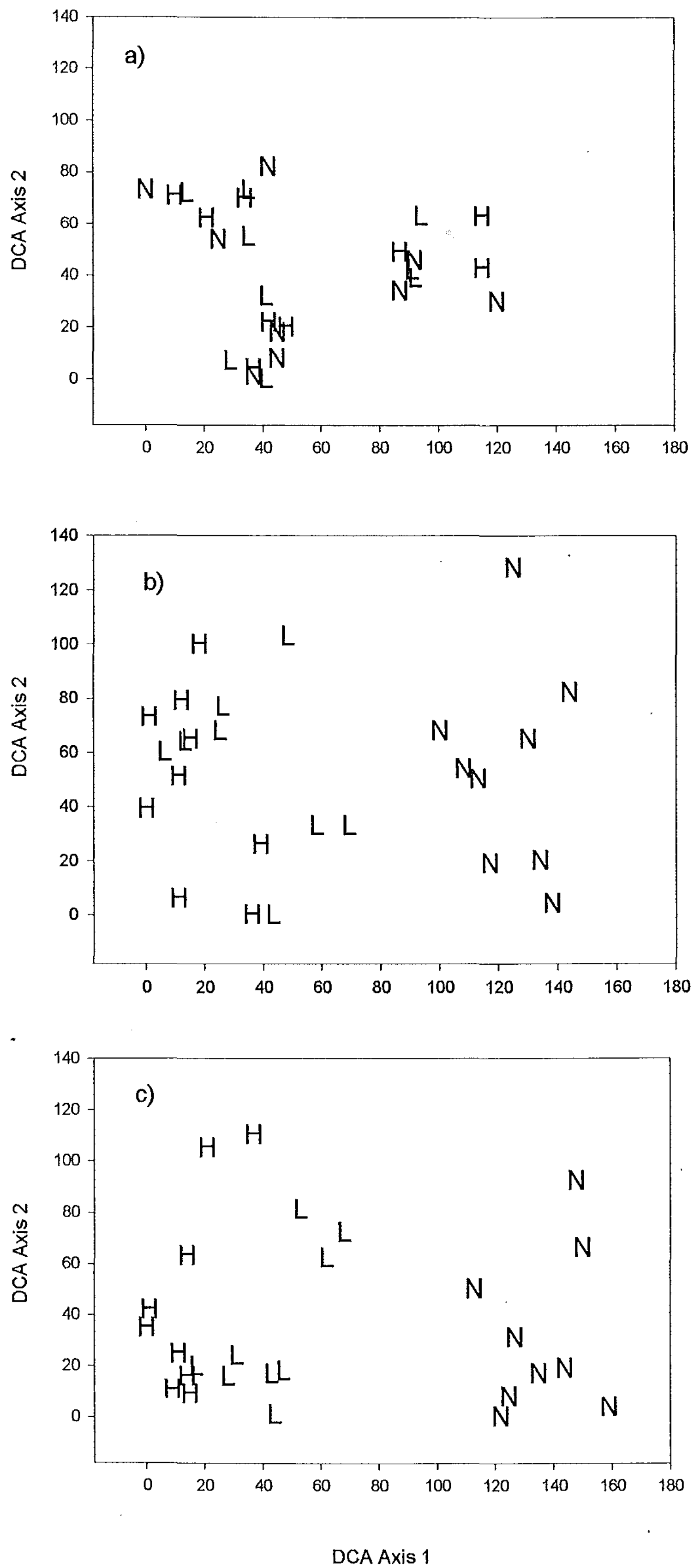


Figure 5

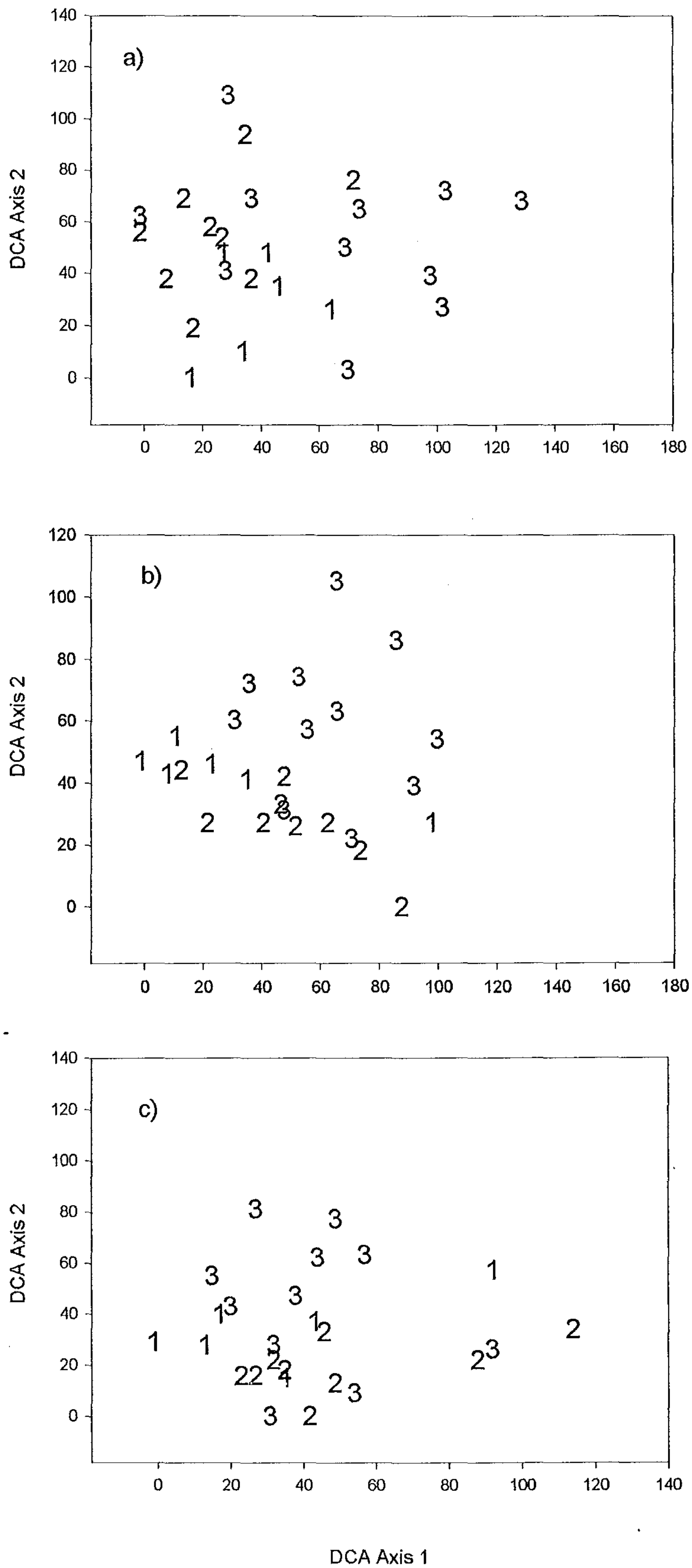


Figure 6

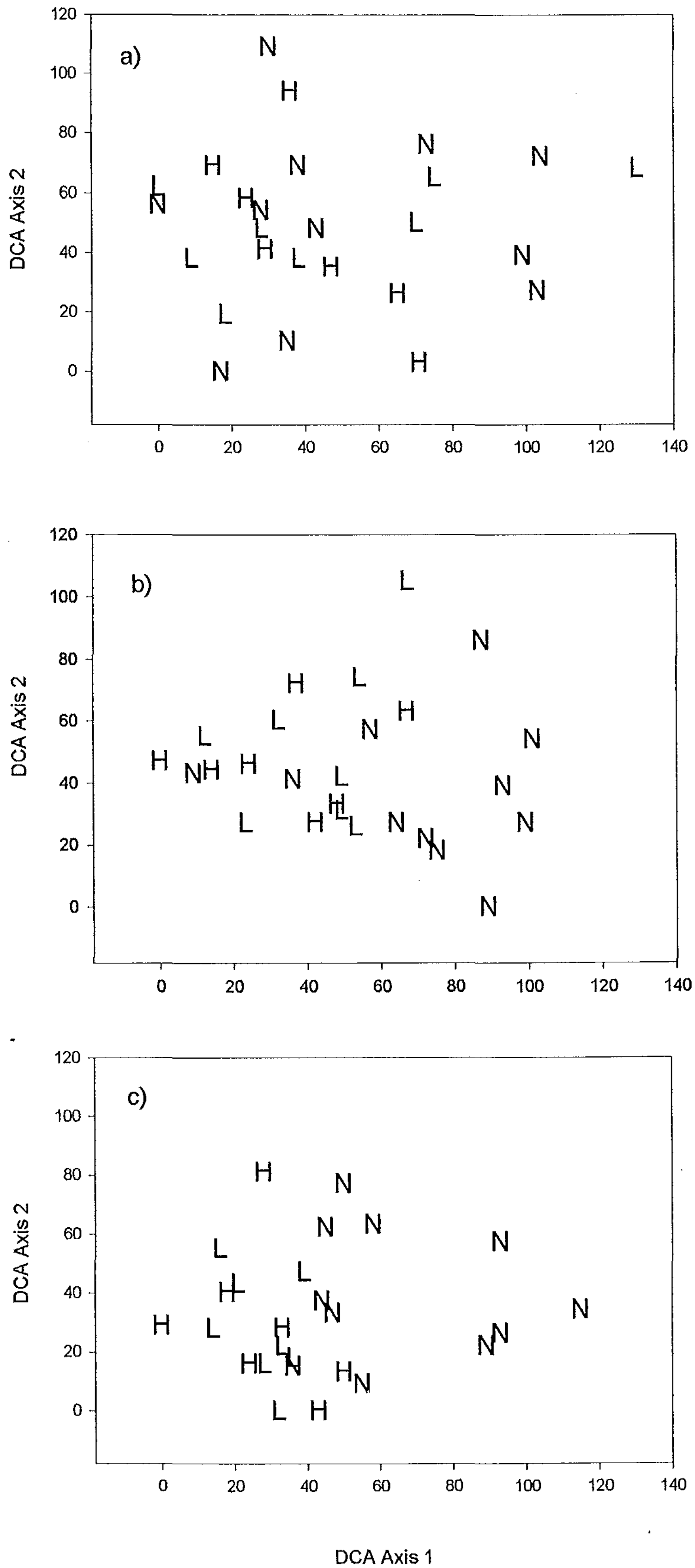


Figure 7

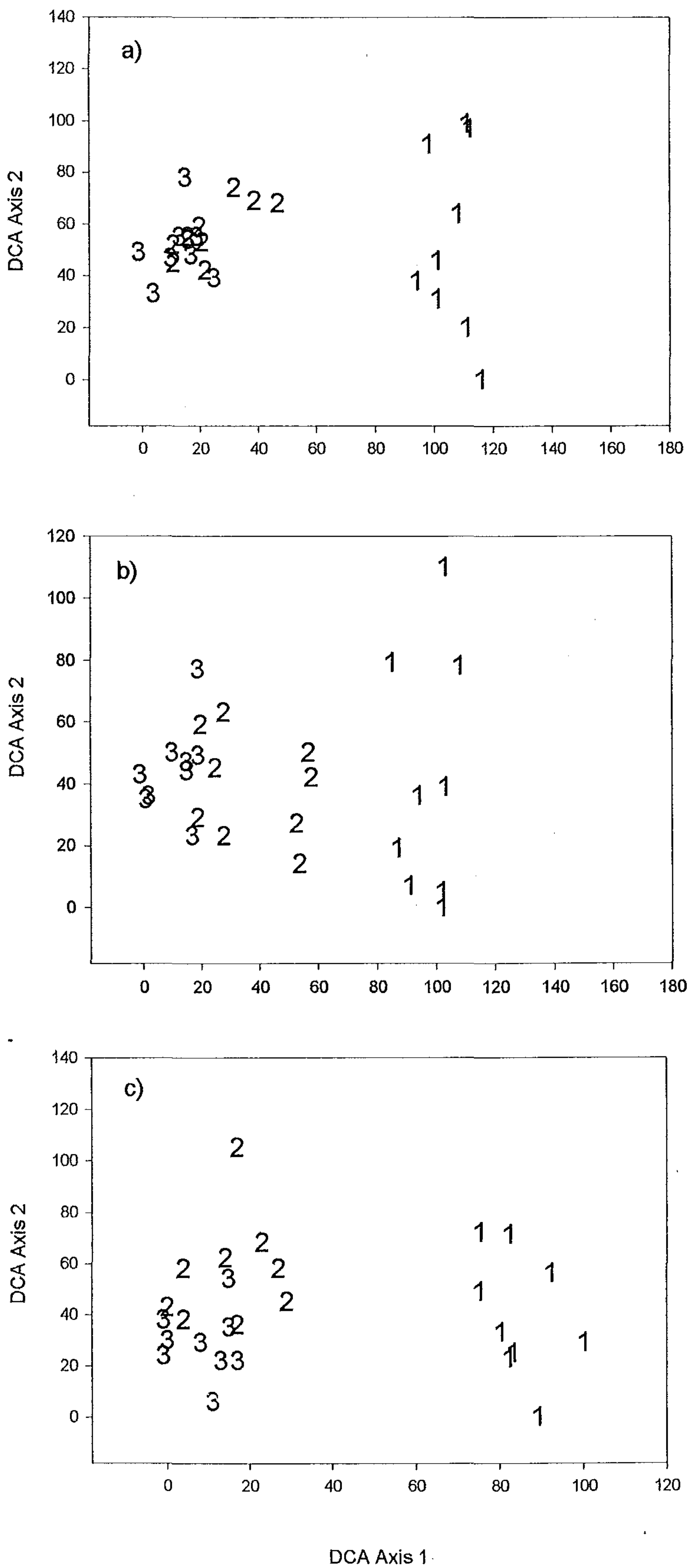


Figure 8

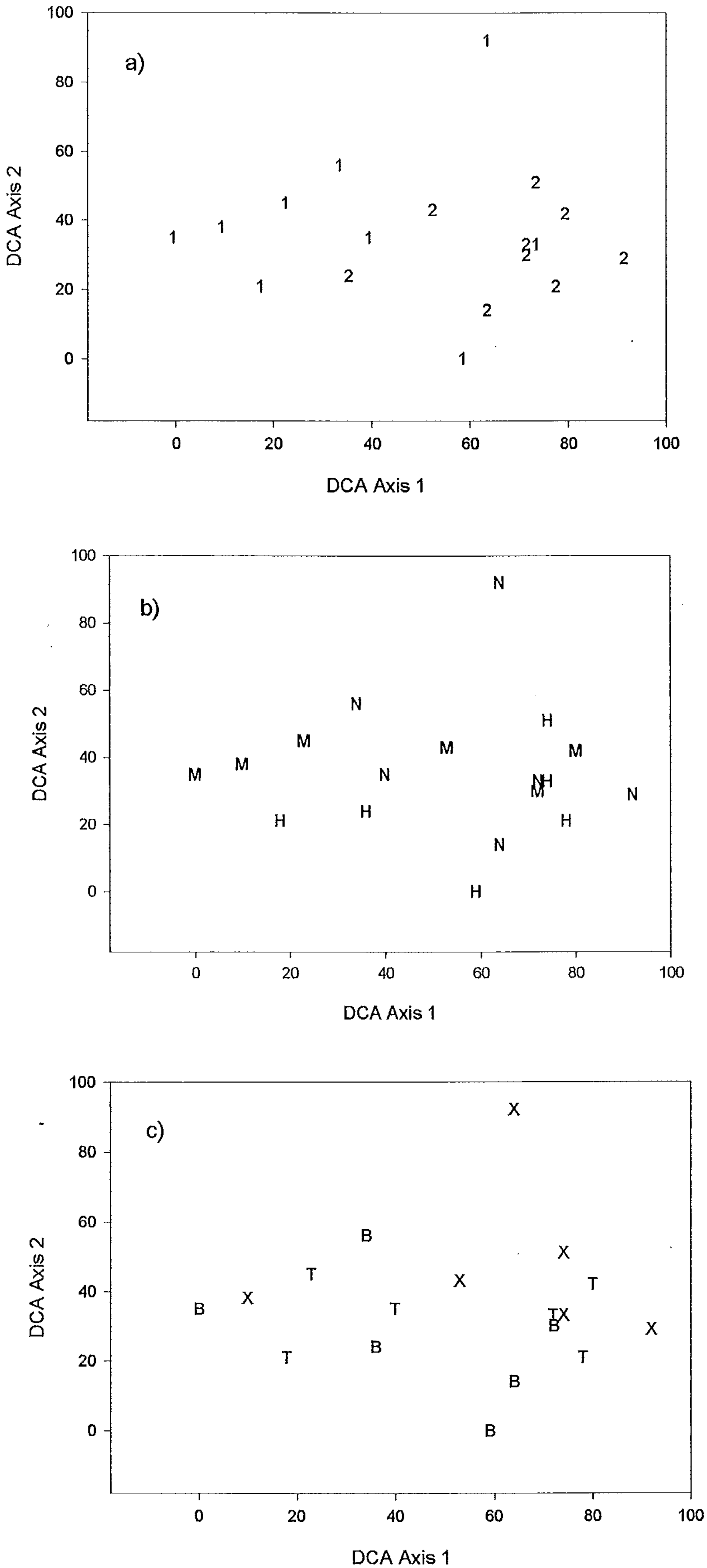
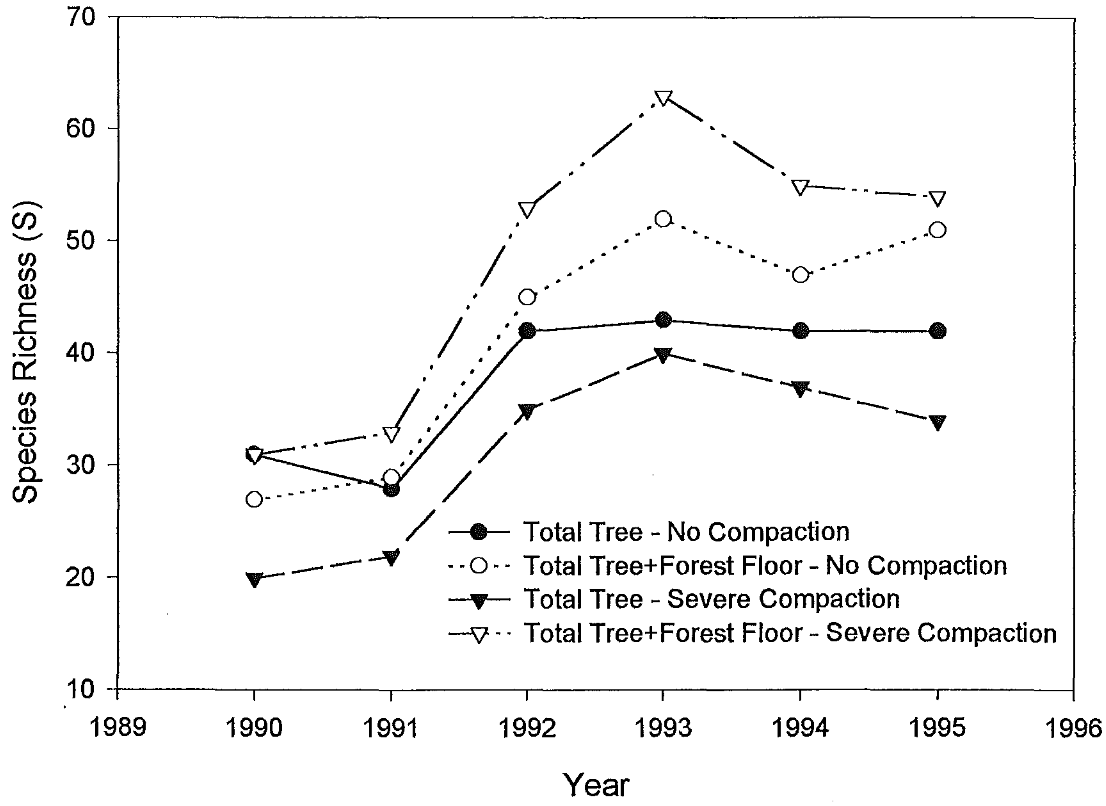


Figure 9


Species Richness (S)
Year
Total Tree - No Compaction
Total Tree+Forest Floor - No Compaction
Total Tree - Severe Compaction
Total Tree+Forest Floor - Severe Compaction

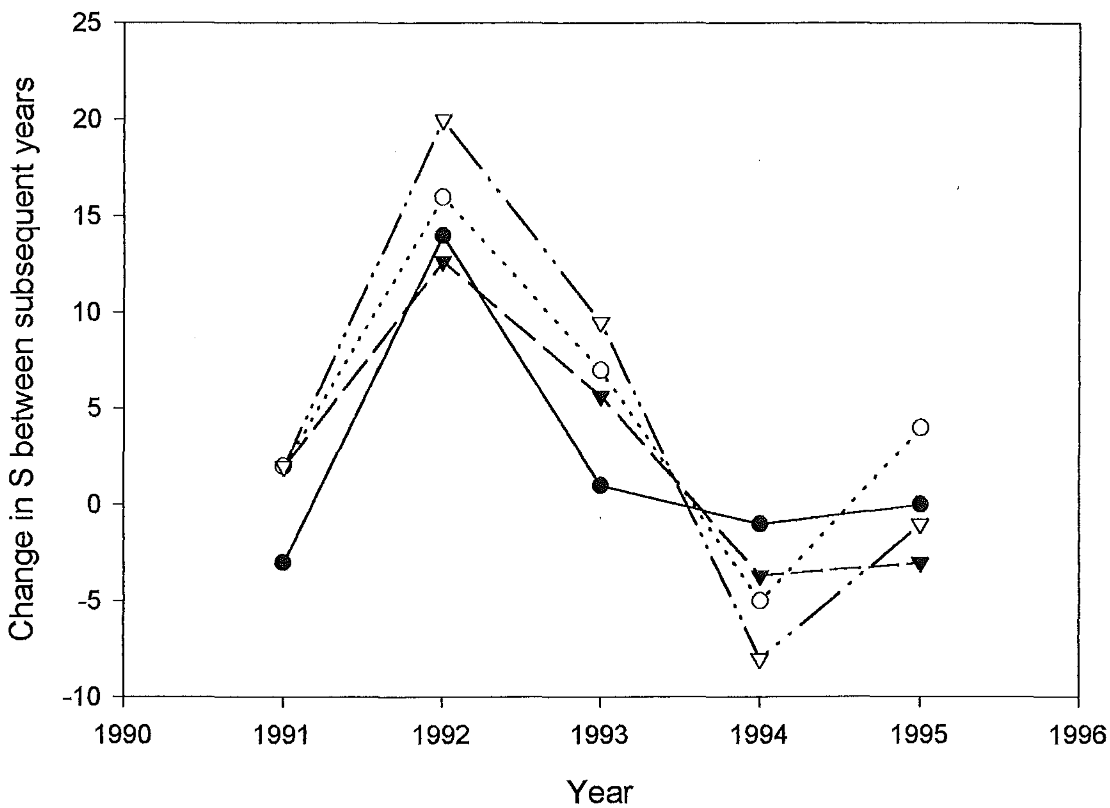
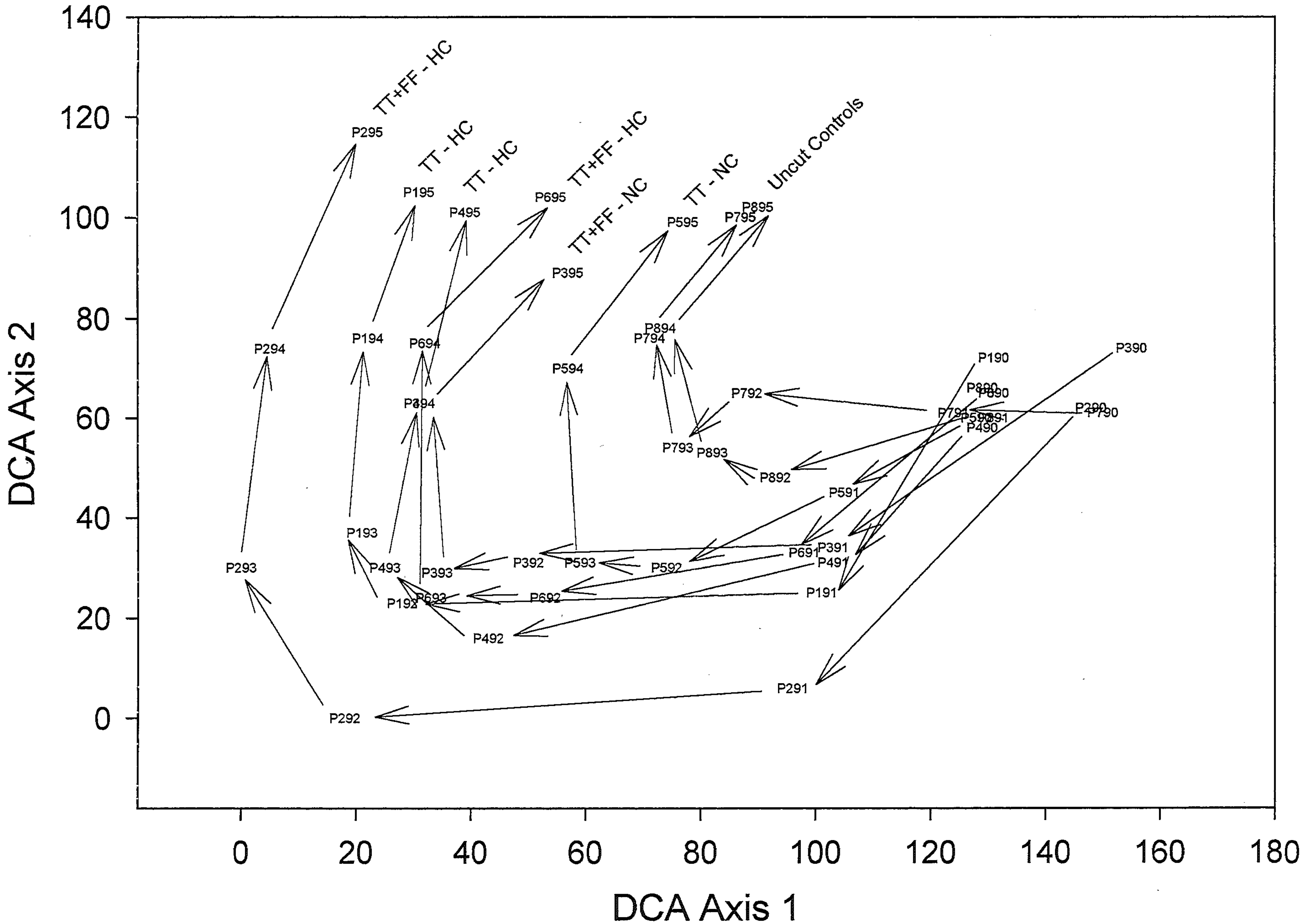

Change in S between subsequent years
Year

Figure 10


DCA Axis 1
DCA Axis 2
TT+FF - HC
TT - HC
TT - HC
TT+FF - HC
TT+FF - NC
TT - NC
Uncut Controls
P295
P195
P495
P695
P395
P595
P795
P895
P294
P194
P694
P594
P894
P794
P394
P792
P793
P893
P892
P190
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P890
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P590
P391
P490
P591
P193
P293
P493
P393
P392
P593
P592
P691
P391
P491
P191
P192
P693
P692
P492
P291
P292
0
20
40
60
80
100
120
140
160
180

Figure 11