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# Understory Plant Responses to Uneven-Aged Forestry

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UNDERSTORY PLANT RESPONSES TO UNEVEN-AGED FORESTRY

ALTERNATIVES IN NORTHERN HARDWOOD-CONIFER FORESTS

A Thesis Presented

by

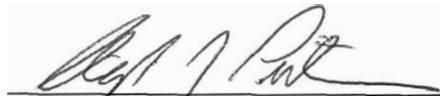Kimberly J. Smith

to

The Faculty of the Graduate College

of

The University of Vermont

In Partial Fulfillment of the Requirements
for the Degree of Master of Science
Specializing in Natural Resources

October, 2007

Accepted by the Faculty of the Graduate College, The University of Vermont, in partial fulfillment of the requirements for the degree of Master of Science, specializing in Nutrition and Food Sciences.

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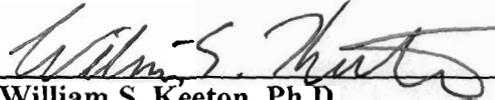
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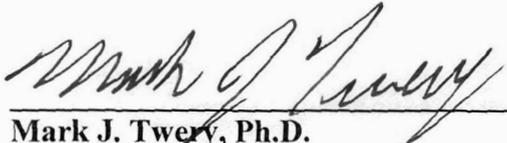
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# Abstract

In northern hardwood-conifer forests, alternatives to conventional forest management practices are being developed in order to maintain biodiversity and ecosystem functioning while providing for timber revenue generation. The understory layer of vegetation encompasses the major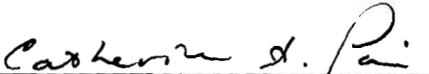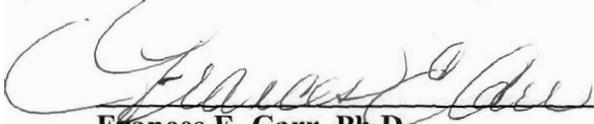ity of plant species diversity in forested ecosystems and may be sensitive to timber harvest disturbance. Thus, monitoring the response of forest understories to new silvicultural techniques may provide a means for evaluating their intensity. In this study, we hypothesize that i) uneven-aged, low-intensity silvicultural systems can maintain understory plant diversity and support late-successional species through harvest disturbance; ii) retaining and enhancing stand structural complexity can increase understory plant diversity in northern hardwood-conifer forests; and iii) plant responses are influenced by interactions between canopy structure, soils, and exogenous climate processes. Experimental treatments include two conventional uneven-aged prescriptions (single-tree selection and group selection) modified to increase structural retention, and a third technique designed to promote late-successional forest structure and function, termed structural complexity enhancement (SCE). Four replications of each treatment were applied to 2 ha management units at three sites in Vermont and New York, U.S.A. Understory vegetation was monitored over 2 years pre- and 4 years post-treatment. We used a linear mixed effects model to evaluate the effects of treatment, soil properties, and drought stress on understory diversity and abundance. Compositional changes among treatments were assessed with non-metric multidimensional scaling (NMS), an ordination technique. Model results show that over time, understory responses were strongly affected by overstory treatment and less influenced by soil chemistry and drought stress. All treatments were successful in maintaining overall composition and diversity. However, late-successional diversity increased significantly in SCE units compared to group selection units. These results indicate that while conventional uneven-aged systems are capable of maintaining understory plant diversity, variations that retain or enhance structural complexity may be more efficient at retaining late-successional species. Increased microsite heterogeneity as a result of these techniques may also increase understory plant diversity, at least during the initial post-harvest recovery period.

## Acknowledgements

# Table of Contents

## List of Tables

## List of Figures

## Chapter 1.  Comprehensive Literature Review

Understory plant communities are a species-rich component of forest ecosystems that contribute to ecosystem functioning and support higher trophic levels. Therefore, understanding the response of forest understories to silvicultural disturbance can help guide management strategies that aim to maintain ecological integrity.  This study examines understory plant responses to alternative, uneven-aged forestry practices in northern hardwood-conifer forests.  Three major themes are integrated in this research: disturbance and the successional dynamics of forest understories, conventional and alternative silvicultural systems, and understory responses to forest management practices.  This comprehensive literature review discusses the current understanding of these topics within the scientific community, and provides a brief overview of an experimental research program called the Vermont Forest Ecosystem Management Demonstration Project (FEMDP).

### 1. Disturbance and the successional dynamics of forest understories

There are many theories on the mechanisms driving succession and how plant assemblages respond to and reorganize following disturbance.  One of the earliest theories was the community concept, which described the plant community as a complex organism and succession as a temporal sequence of communities culminating in a climax assemblage for a given climatic region (Clements 1916).  The community concept was challenged by the individualistic plant species concept, which proposed that plants respond independently to their surroundings and their co-occurrence is

coincidental (Gleason 1917). Building upon this idea, Egler (1954) defined the initial floristics model of succession, whereby individual species can arrive, colonize, and assume dominance at any time following disturbance. Connell and Slatyer (1977) later described inhibition, facilitation, and tolerance as the important forces driving successional change, while Tilman (1988) argued that long-term successional dynamics were controlled by differences in species' responses to multiple resources such as soil nutrients, moisture, and light.

Recent studies examining different aspects of these theories on succession have revealed complex patterns, feedbacks, and interactions that influence post-disturbance plant community composition (Halpern 1988; Tilman 1988; Halpern 1989; Berger and Puettmann 2000; Marby et al. 2000; Roberts 2004). Many of these models stress the controlling influence of natural disturbance regimes (Franklin et al. 2002). For example, succession is influenced by the type, frequency, intensity, and size of disturbance (White and Pickett 1985). These factors determine the severity and extent of canopy, understory, and forest floor that is removed or disturbed and subsequently, how the understory vegetation responds. Roberts (2004) defined eight factors that may influence understory response to natural disturbance, depending on the degree to which forest strata are disturbed. These include: 1) competition with higher strata, 2) competition within the herb layer, 3) microclimate, 4) coarse woody debris substrate, 5) pits and mounds, 6) mineral soil substrates, 7) damage to pre-existing plants, and 8) propagule availability. The relative importance of these eight response factors changes over time. In the initial stages of succession, direct effects of

the disturbance such as physical damage to plants and soil disturbance are likely to have the greatest influence on understory composition. Over the long-term, indirect effects of stand structure, microclimate, and propagule availability may become more important (Halpern and Spies 1995).

Post-disturbance vegetation dynamics are influenced by the plant strategies, life history traits, and functional characteristics of residual and colonizing species (Halpern 1989). Plant strategies are the evolutionarily developed patterns of response to the elements of the environment encountered in a plant's habitat (Bazzaz 1996). The r-K continuum described by MacArthur and Wilson (1967) identified r-strategists, species that occupy disturbed habitats, and K-strategists, density-dependent species that persist longer. In the classification scheme of Grime (1977), species are identified as competitor, stress-tolerant, and ruderal according to their ability to deal with varying levels of stress and disturbance. Disturbance response has also been linked to specific life history or functional characteristics, including life forms (Raunkiaer 1934), vital attributes (Noble and Slatyer 1980), functional types (Smith et al. 1997) and life-history traits (McIntyre et al. 1995). These characteristics influence a plant's ability to compete and reestablish following disturbance, and are commonly used to model forest succession (Bazzaz 1996).

Plant species composition and diversity are also controlled at broad scales by abiotic factors such as climate, elevation, topography, light, and soil resources (Leach and Givnish 1999) and with soil resource gradients, overstory characteristics, and microtopographic features at fine scales (Beatty 1984; Gilliam 2002). By altering

3

abiotic factors, disturbance can indirectly influence composition and distribution of understory plants. For example, disturbances that uproot trees can create a complex pit and mound topography, and provide microhabitats for certain plant species by exposing large amounts of mineral soil and coarse woody debris substrate (Beatty 1984). Overstory removal can change the microclimate of a site, typically causing increases in solar radiation, mean temperature and temperature fluctuations, and decreases in relative humidity and moisture on the forest floor (Collins et al. 1985). The heterogeneity of light and coarse woody debris that develops later in succession has also been linked to spatial patterns of understory species (Scheller and Mladenoff 2002).

Studies have shown that nutrient availability can influence plant heterogeneity (Hutchinson et al. 1999; Fraterrigo et al. 2006). For example, soil cation concentrations, particularly calcium, have been shown to control spatial distributions of understory plants (Gilliam and Turrell 1993; Kolb and Diekmann 2004; Graves et al. 2006), and plant growth is commonly limited by availability of nitrogen and phosphorus (Marschner 1995). Disturbances can alter soil nutrient availability, although the intensity and duration of these changes vary with the soil and forest type, as well as the type of disturbance (Grigal 2000). For example, disturbances that result in high organic matter inputs can lead to local increases in soil nutrient availability. In contrast, a decrease in soil nutrients is often the result of disturbances that remove biomass and disturb forest soils (Johnson et al. 1997; Elliott and Knoepp 2005). While silvicultural disturbances frequently lead to an overall decline in soil nutrients,

elimination of overstory competition can also temporarily increase the availability of these nutrients (and light) to understory vegetation (Roberts 2004), resulting in increased productivity and diversity.

Calcium is one of the elements most susceptible to depletion following timber harvesting because of its high concentration in tree wood and bark (Schaberg et al. 2001).  In contrast, nitrogen supply to plants increases greatly following disturbance, and then may continue at low levels throughout succession (Matson and Vitousek 1981; Robertson and Vitousek 1981).  Net nitrification and mineralization can increase following forest harvesting, leading to elevated concentrations of ammonium and nitrate, but also potential for overall nitrogen loss through leaching (Bormann et al. 1977).  Later in succession, accumulated organic matter can increase the ability of the soil to hold moisture and retain soil nutrients important to understory plants (Bazzaz 1996).

The influence of soil nutrient availability on understory plant communities may change along successional gradients.  For example, Gilliam et al. (1995) observed that herb layer development was linked with soil characteristics in early-successional forests but that it declined with stand age.  In contrast, the patchy availability of soil resources, particularly nitrogen, that develops through succession has been shown to influence the abundance and pattern of understory plant species (Mladenoff 1990).  Christensen and Gilliam (2003) argue that soil chemistry accounts for much of the variation in herbaceous species composition at nearly every stage of succession.

Anthropogenic land-use has also been shown to influence successional dynamics and forest stand development (McLachlan and Bazely 2001; Bellemare et al. 2002; Foster et al. 2002; Hall et al. 2002). Studies have demonstrated strong and persistent effects of historical land-use on vegetation composition and forest structure (Foster 1992; Foster et al. 1998; Fuller et al. 1998; Motzkin et al. 1999; Gerhardt and Foster 2002; Hall et al. 2002), as well as changes in the availability and heterogeneity of soil nutrients (Fraterrigo et al. 2006). In the understory, the ability and rate of forest herbs to recolonize a site is a major factor driving vegetation patterns following natural and anthropogenic disturbances. Forest herbs with limited dispersal mechanisms are well adapted for growth in stable forest ecosystems characterized by local, small-scale disturbances such as gap-phase dynamics, but are not able to rapidly recover following severe land-use changes, such as tilling for agriculture (Bellemare et al. 2002).

The wide-ranging variability in disturbance and response factors has led to the concept of multiple pathways of succession for understory communities (Noble and Slatyer 1980; Pickett et al. 1987; Halpern 1988; Inouye and Tilman 1988; Collins 1990; Frelich and Reich 1995; Bazzaz 1996; Frelich and Reich 1999). The direction of a successional pathway depends on variation in the life history characteristics of the available species and competitive relationships, as well as the timing, intensity or frequency of disturbance, the availability of species, and the local environment (Halpern 1988). Knowledge of disturbance and response factors for a specific forest

type can help forest managers predict changes in understory vegetation as a result of forest management practices.

## 2. Forest management practices: Conventional silvicultural systems and proposed alternatives

Conventional silvicultural systems include five standard methods used to regenerate forest stands. The scale and intensity of the disturbance generated varies considerably among these different methods. For example, clearcutting, seed tree, and shelterwood systems are relatively intensive methods that produce even-aged stands. These silvicultural treatments are often used to regenerate pioneer or early-successional species, although in the northern forest region they are adapted for intermediate and shade-tolerant regeneration purposes through either patch cutting or higher levels of shelterwood retention. Clearcutting, the most severe method, involves removing all trees within a designated boundary, resulting in an area with the light and temperature regime of an open field. The seed tree method is a slight variation of the clearcut, with remnant mature trees left to provide a seed source for regeneration. The shelterwood system involves retaining a sheltering overstory to protect regenerating seedlings and saplings in addition to providing a seed source for a new cohort. Depending on the amount of overstory retained, shelterwoods are often described as two-aged systems, and can be used to regenerate mid- to late-successional species (McEvoy 2004).

In contrast, uneven-aged stands contain trees with a wide range of ages and have more than two age classes, or cohorts (Nyland 1996). Examples of uneven-

aged silvicultural systems include group selection, in which small patches (usually 0.05 to 0.25 ha) of trees are removed, and single-tree selection, in which individual trees are removed from the stand.  The diversity of age structures maintained in uneven-aged systems results in a complex stand structure.  For example, uneven-aged stands typically contain vertically differentiated canopies and considerable horizontal heterogeneity resulting from a mosaic of open canopy gaps and closed-canopy interior forest patches.  In northern hardwood-conifer forests, uneven-aged systems more closely approximate the naturally occurring structural characteristics of unmanaged late-successional forest stands than even-aged systems (McGee et al. 1999; Seymour et al. 2002).

The recognition of the global loss of biodiversity (Wilson 1988; Ehrlich and Wilson 1991; Noss and Cooperrider 1994) has led to the development of forest management strategies that include objectives for ecological conservation.  These strategies are often focused on the creation of large reserves; however, nonreserve matrix lands can also play an important role in biodiversity conservation by providing habitat, buffering reserved areas, and increasing connectivity across the landscape (Lindenmayer and Franklin 2002).  Thus, the development of ecologically sustainable techniques for managing the matrix of unprotected forest land is essential to the conservation of forest biodiversity at multiple scales.  A number of variations of uneven-aged stand management strategies have been proposed and variously termed green tree retention (Franklin et al. 1997), ecological silviculture (Benecke 1996), continuous cover forestry (Garfitt 1995), near-natural forestry (Benecke 1996), multi-

aged (O'Hara 1996) and multicohort (Oliver and Larson 1996) forestry. These techniques offer alternatives to conventional silvicultural systems that provide for ecological functions as well as timber productivity.

Structural enrichment (Franklin et al. 1997) or structure-based (Franklin et al. 2002; Keeton 2006) forestry is another alternative that has been proposed for the sustainable management of matrix lands. Structure-based forestry involves active management of stands to create spatial heterogeneity and specific structures that represent the different stages of stand development. The goal is to create a managed landscape with forest structures and age classes represented in densities and spatial distributions similar to those associated with natural disturbance and successional dynamics (Aplet and Keeton 1999; Franklin et al. 2002; Seymour et al. 2002). Structure-based approaches currently applied in some managed forests include structural retention, longer rotations, and active creation of structural complexity (Carey et al. 1999; Franklin et al. 2002; Keeton 2006).

Variable retention harvesting is another approach based on the concept of retaining structural elements of the harvested stand to achieve specific management objectives. This approach provides structures that support functions similar to those provided by biological legacies left by natural disturbances (Franklin et al. 2002). Specifically, variable retention harvest systems can retain species and processes through the silvicultural disturbance, enrich forest stands with structural features that would otherwise be absent, and enhance connectivity in the managed landscape. Retained structures can include live trees, snags, coarse woody debris, and intact

patches of forest floor that serve as biological legacies in the regenerating forest (Franklin et al. 1997). Structures are retained indefinitely (e.g. over multiple rotations or entry cycles), in contrast to shelterwood methods, which only retain structures until a new cohort has regenerated.

Another proposed alternative to conventional forest management is disturbance-based forestry, which involves modeling silvicultural systems after the scale, frequency, and pattern of natural disturbances (Mitchell et al. 2002; Seymour et al. 2002). In northern hardwood forests, common forms of disturbance including wind, pathogens, and insect herbivory create small canopy openings (Seymour et al. 2002). Numerous studies have investigated the size, frequency, and spatial distribution of these natural canopy gaps in hardwood-hemlock forests (Runkle 1982; Foster and Boose 1992; Kimball et al. 1995; Dahir and Lorimer 1996; Ziegler 2000; Boose et al. 2001; Seymour et al. 2002; Ziegler 2002, 2004), providing a guideline for the development of silvicultural analogues.

In addition to considering the pattern and intensity of harvesting practices, ecologically sustainable forest management practices involve mitigating the negative impacts of harvesting. This entails adopting methods that prevent soil erosion, soil compaction, and damage to residual trees. For example, careful design of the access system, choice of harvesting equipment, and the seasonality of logging can minimize the impacts of silvicultural disturbance (McEvoy 2004). The degree to which negative impacts are avoided, the specific level and pattern of retention, and the type of structural features retained can be altered depending on the forest type and the

management plan.  This flexibility inherent in uneven-aged forestry alternatives enables them to encompass a broad spectrum of ecological and economic objectives.

**3. Understory responses to forest management practices**

Silvicultural disturbances in managed forests vary in spatial pattern, intensity, and frequency of application.  Because of their sensitivity to disturbance, the response of forest understories to these variations can be a useful tool in assessing their ecological impact (Gilliam 2002).  To date, research in North America has focused on evaluating understory composition and diversity following conventional treatments, including plantation forestry (Ramovs and Roberts 2005), clearcutting (Gilliam et al. 1995; Halpern and Spies 1995; Liu and Ashton 1999), fire (Halpern and Spies 1995), and thinning and fertilization (Thomas et al. 1999).  In northern hardwood forests of North America, understory plant responses to opening size and age in experimental canopy gaps (Collins and Pickett 1988a, 1988b) and in even- and uneven-aged conventional silvicultural treatments (Jenkins and Parker 1999; Scheller and Mladenoff 2002) have been evaluated.

A common finding in studies of understory response is that plant communities are largely resilient to silvicultural disturbance.  Studies of even-aged approaches frequently show immediate post-harvest increases in diversity (Gilliam et al. 1995; Halpern and Spies 1995), followed by return to a state similar to the pre-harvest condition (Metzger and Schultz 1984; Jenkins and Parker 1999; Ruben et al. 1999).  In northern hardwood forests in Michigan, Metzger and Schultz (1984) found that composition and diversity showed the greatest change four to five years after even-

and uneven-aged harvest, whereas after 50 years, vegetation was similar to initial

conditions.  Similarly, Ruben et al. (1999) found substantial residual effects of

clearcutting in northern hardwood forests after 25 years, but not after 60 years.

However, opening size may be more important than opening age in determining

species composition, as the size of the initial opening affects the rate of recovery

(Collins and Pickett 1988a).  For example, forest understory composition in a northern

hardwood forest in Wisconsin recovered after 10 years in uneven-aged stands and

after 40 years in even-aged stands (Kern et al. 2006).

Although the resiliency of forest understories has been widely reported, their

sensitivity to silvicultural disturbance has also been documented.  The degree of

overstory removal influences availability of light and nutrients for understory plants

(Palik and Engstrom 1999; Berger and Puettmann 2000) and subsequently their rates

and patterns of persistence, colonization, and establishment.  Studies have identified

relationships between overstory structure and understory species diversity,

composition, and spatial patterning (Berger and Puettmann 2000; Gilliam 2002;

Scheller and Mladenoff 2002).  The pattern and intensity of soil disturbance can also

influence the recovery of understory plant communities (Berger et al. 2004).  A study

by Reader (1987) found that both soil disturbance and loss of understory species

increased with cutting intensity in mature deciduous forests of Ontario.  Post-harvest

inventories in a number of forest types have documented declines in species richness

(Hix and Barnes 1984; Duffy and Meier 1992; Goebel et al. 1999; Moola and Vasseur

2004), decreased abundance (Roberts 2002; Moola and Vasseur 2004), and local extirpations (Ruben et al. 1999; Halpern et al. 2005; Ramovs and Roberts 2005).

Loss of diversity and lack of recovery in the understory following logging may be due to a number of factors, including physical damage, physiological stress, competition with ruderal species, low reproduction, slow growth rates, limited dispersal capabilities, and loss of suitable habitat (Meier et al. 1995). In particular, forest management has been shown to affect uncommon and vernal plant species (Metzger and Schultz 1981, 1984; Meier et al. 1995; Ruben et al. 1999; McLachlan and Bazely 2001). Rare species and small populations may be particularly susceptible to genetic degradation, as well as the direct impacts of forest management such as physical damage and altered resource conditions (Roberts and Zhu 2002).

Late-successional species have also exhibited sensitivity to harvest disturbance (Moola and Vasseur 2004; Halpern et al. 2005). Post-harvest increases in diversity are commonly due to an increase in ruderal species and may mask the loss of late-successional species (Halpern and Spies 1995). Late-successional species often reproduce clonally or have biotic modes of dispersal, causing them to recover slowly from disturbance (Moola and Vasseur 2004). While once comprising 60-80% of the forested landscape (Lorimer and Frelich 1994; Lorimer 2001; Lorimer and White 2003), there are very few old-growth forests left in eastern North America and typical late-successional microhabitats such as canopy gaps or decayed coarse woody debris are rare (Runkle 1981). These remnants have been shown to be important refugia for late-successional plants (Bratton et al. 1994). As a result, logging methods that mimic

natural gap-phase dynamics may be less damaging than clearcutting for sensitive and rare plant species (Meier et al. 1995). Forest management alternatives that retain structural legacies, such as intact areas of forest floor and coarse woody debris, may also provide a means for maintaining understory diversity and retaining late-successional species.

The inconsistent results of post-disturbance studies that describe vegetation communities as either resilient or sensitive may reflect the site-specific nature of understory responses to forest management. For this reason, Roberts and Gilliam (1995) emphasize the importance of in-depth studies of understory responses for different forest types and different management practices. The intensity, frequency, and seasonality of the sampling scheme employed in studies of post-harvest understory response can also influence the study outcome (Ristau et al. 2001). Measures of species richness and diversity can differ in their sensitivity to sampling techniques and sample sizes, but generally tend to increase with sampling intensity (Magurran 2004). In some instances, observations of local extirpations of understory species following timber harvesting may be the product of a low sampling intensity (e.g. Meier et al. 1995). In addition, because the aboveground abundance of many understory plant species varies seasonally, the time of sampling can also greatly affect study results (Ristau et al. 2001).

The variation in study outcomes may also be partially explained by methodological differences. Chronosequencing, which involves sampling vegetation in stands that are in varying stages of post-harvest recovery, is the most common

method used to evaluate the impact of silvicultural treatments on understory vegetation. This approach assumes comparable initial site conditions, harvesting techniques, and post-disturbance influences, and may not capture the dynamics of short-lived species or populations with episodic fluctuations (Halpern 1989). Few studies of understory vegetation response in northern hardwood forests have utilized pre-disturbance data to evaluate actual changes over time (see Metzger and Schultz 1984; Hughes and Fahey 1991). This approach can minimize external variability and allow forest managers to assess the resilience of individual species and plant communities. Variability in abiotic factors, including soil properties and climatic conditions, may also be contributing to the divergent findings in studies of post-disturbance forest understories. Several years of pre-treatment data collection can establish a baseline for environmental conditions particular to a site and help isolate effects of disturbance, thus providing a more accurate picture of understory responses to forest management practices.

## 4. The Vermont Forest Ecosystem Management Demonstration Project (FEMDP)

The Vermont Forest Ecosystem Management Demonstration Project (FEMDP) is an on-going study that explores a balanced management approach by integrating ecological and economic objectives. The FEMDP is testing the hypothesis that "structure-based" and "disturbance-based" forestry practices can sustain a broader array of biodiversity and ecological functions, while providing opportunities for timber revenue generation (Keeton 2006).

Three modified uneven-aged silvicultural techniques that include aspects of both structure- and disturbance-based forestry are being tested by the FEMDP. Treatments include two conventional uneven-aged prescriptions, single-tree selection and group selection, which have been modified to increase structural retention and approximate the scale and pattern of natural disturbances. Modifications were based on a target residual basal area of 18.4 $m^2$/ha, maximum diameter of 60 cm, and a q-factor of 1.3. This prescription was applied in a dispersed (single-tree selection) or aggregated (group selection) spatial pattern (Keeton 2006). The approximate size of individual group selection patches (0.05 ha) was based on estimates of fine-scale natural disturbances in New England (Seymour et al. 2002). In both of the conventional treatments, slash and unmerchantable tree boles were retained.

The third treatment is "structural complexity enhancement" (SCE), a technique that promotes accelerated development of late-successional forest structure and function. This is achieved through the development of vertically differentiated canopies and variable horizontal density, re-allocation of basal area to larger diameter classes, and increased large snag and downed log densities (Keeton 2006). These attributes were encouraged with several methods. A target basal area (34 $m^2$/ha) and maximum diameter (90 cm) characteristic of old-growth structure were used to develop a guiding curve (Keeton 2006). The curve was also based on a rotated sigmoid target diameter distribution, one possible distribution of eastern old-growth forests (Goodburn and Lorimer 1999). The distribution was applied as a non-constant q-factor: 2.0 in the smallest size classes, 1.1 for medium sized trees, and 1.3 in the

largest size classes. Accelerated growth in larger trees was promoted with full and partial crown release. Snag and coarse woody debris (CWD) volume was enhanced based on stand potential and literature derived targets, and in some cases involved uprooting trees to mimic the pit and mound topography characteristic of natural disturbance in old-growth northern hardwood-conifer forests (Dahir and Lorimer 1996). The occurrence of these important structural characteristics is limited in forests managed with conventional even- and uneven-aged silvicultural systems (Gore and Patterson 1985; McGee et al. 1999; Crow et al. 2002; Angers et al. 2005).

Late-successional structure was historically more prevalent in the northern hardwood region (Davis 1996; Cogbill 2000); widespread forest clearing for agricultural land-use during the 19th century resulted in the current predominance of young to mature forests across the landscape. Forest management techniques such as SCE that promote late-successional structural characteristics can re-establish the variable age structures characteristic of northern hardwood forests (Keeton 2006), and may be important for a number of other reasons. For example, research has shown that the structural heterogeneity provided by older forests promotes some aspects of biodiversity and sustains ecosystem processes (Lindenmayer and Franklin 1997; McGee et al. 1999; Lindenmayer et al. 2006). Increasing late-successional forest structure can also improve wildlife habitat (Keddy and Drummond 1996; McGee et al. 1999), carbon storage (Harmon et al. 1990; Krankina and Harmon 1995; Turner et al. 1995; Houghton et al. 1999), and riparian functions (Keeton et al. 2007). Horizontal heterogeneity and complexity of vertical structures increase as forests mature, directly

affecting food availability and habitat for plants and animals. Complex vertical structure affects stand microclimates by influencing light, wind, humidity, and temperature, factors which directly and indirectly affect multiple forest taxa. The diverse microclimates and microhabitats created by multi-layered canopies can support more biological diversity (Brokaw and Lent 1999).

The understory layer of vegetation represents the majority of plant species diversity in forested ecosystems (Roberts 2004) and can be an important indication of the intensity of forest harvesting (Lindenmayer et al. 2000). The FEMDP provides a unique opportunity to assess changes in understory diversity and composition as a result of alternative forest management practices. Greater retention of overstory structure and limited soil disturbance associated with these techniques may reduce physical damage and physiological stress for established plants. In addition, the late-successional stand structure created by SCE may increase heterogeneity of light and resources and provide greater variation in microtopography on the forest floor, potentially diversifying microhabitats for understory plants. Botanical diversity and its associated ecological functions may be sustained and even augmented as a result of these structural changes. Consequently, research associated with the FEMDP's low-impact silvicultural approaches may contribute to the development of conservation-oriented management strategies in the northern hardwood region.

# Chapter 2. Understory plant responses to alternative forestry practices in northern hardwood-conifer forests

**Abstract**

The understory layer encompasses the majority of plant species diversity in forested ecosystems and may be sensitive to timber harvest disturbance. We hypothesize that i) uneven-aged, low-intensity silvicultural systems can maintain understory plant diversity and support late-successional species following harvest disturbance; ii) retaining and enhancing stand structural complexity can increase understory plant diversity in northern hardwood-conifer forests; and iii) plant responses are influenced by interactions between canopy structure, soils, and exogenous climate processes. Experimental treatments include two conventional uneven-aged prescriptions (single-tree selection and group selection) modified to increase structural retention, and a third technique designed to promote late-successional forest structure and function, termed structural complexity enhancement (SCE). Four replications of each treatment were applied to 2 ha management units at three sites in Vermont and New York, U.S.A. Understory vegetation was monitored over two years pre- and four years post-treatment. We used a linear mixed effects model to evaluate the effects of treatment, soil chemistry, and drought stress on understory diversity and abundance. Compositional changes among treatments were assessed with non-metric multidimensional scaling (NMS), an ordination technique. Model results show that over time, understory responses were strongly affected by overstory treatment and less influenced by soil chemistry and drought stress. All treatments were successful in maintaining overall composition and diversity. However, late-successional diversity increased significantly in SCE units compared to group selection units. These results indicate that while conventional uneven-aged systems are capable of maintaining understory plant diversity, variations that retain or enhance structural complexity may be more efficient at retaining late-successional species. Increased microsite heterogeneity as a result of these techniques may also increase understory plant diversity, at least during initial post-harvest recovery period.

## 1. Introduction

Understory vegetation comprises the majority of plant species diversity in forested systems and affects ecosystem-level processes such as nutrient cycling and energy exchange (Roberts 2004). Intensive silvicultural systems can alter the composition and diversity of understory communities by influencing the availability of

light and nutrients, creating soil disturbance, and introducing vigorous competitors (Meier et al. 1995). Species adapted to late-successional forest stand structure or with limited modes of dispersal may be particularly sensitive to harvest disturbance (Halpern and Spies 1995; Roberts 2002). There is considerable previous research on understory responses to conventional even- and uneven-aged silvicultural treatments in northern hardwood forests (Metzger and Schultz 1984; Jenkins and Parker 1999; Scheller and Mladenoff 2002; Kern et al. 2006). These studies have primarily compared silvicultural systems with relatively dramatic differences in post-harvest canopy retention. Recent silvicultural research is exploring more subtle differences in post-harvest canopy structure associated with variable levels of retention (Franklin et al. 1997; Aubry et al. 1999) and uneven-aged approaches modified to enhance structural retention (Seymour 2005; Keeton 2006). Understory responses to these approaches are less well understood.

Management strategies for forested ecosystems are increasingly focused on promoting biodiversity conservation and ecosystem functioning while sustaining economic productivity (Lindenmayer et al. 2006). To meet this objective, silvicultural models that attempt to mimic the natural disturbance regimes and structural complexity of forested ecosystems are being developed (Franklin et al. 2002; Mitchell et al. 2002; Seymour et al. 2002; Keeton 2006). In Vermont, researchers from the Forest Ecosystem Management Demonstration Project (FEMDP) are testing a technique that utilizes disturbance-based forestry principles (see Mitchell et al. 2002) to accelerate development of late-successional structural characteristics, termed

Structural Complexity Enhancement (SCE) (Keeton 2006). The FEMDP study

compares SCE against conventional uneven-aged approaches also modified to increase

post-harvest structural retention. A central question of this research is whether

different types of uneven-aged prescriptions can be modified to achieve similar

biodiversity objectives, or if even slight modifications of the type, magnitude, and

spatial configuration of structural retention will alter biodiversity responses. New

silvicultural systems are often specifically designed to minimize impacts on

biodiversity; effects on plant communities can be a key indicator of their effectiveness

in this regard.

Studies evaluating the response of understory plants to silvicultural

manipulations in northern hardwood forests have commonly found understory

vegetation to be very resilient (Hughes and Fahey 1991; Scheller and Mladenoff 2002;

Kern et al. 2006). Species richness and diversity are often maintained and even

increase following harvest disturbance (Metzger and Schultz 1984; Jenkins and Parker

1999). However, diversity as a measure of community response can be deceiving if

there are compensatory increases and decreases in different plant groups. For

example, the loss or decline of late-successional species, defined here as species that

reach maximum abundance in mature, closed-canopy, interior forests, may be

obscured by increases in ruderal species (Halpern and Spies 1995). In many forest

types, decreased abundance or local extirpation of late-successional species has been

observed following intensive harvest disturbance, indicating that certain species may

be sensitive to overstory removal and soil disturbance (Ruben et al. 1999; Halpern et al. 2005; Ramovs and Roberts 2005).

Post-harvest composition of the understory layer is influenced by the interaction of disturbance intensity, timing, and extent, as well as the life history characteristics of persisting and colonizing species (Halpern 1989; Ramovs and Roberts 2005). Similar complex interactions affect recovery dynamics and regeneration responses following natural disturbances (Carlton and Bazzaz 1998; Franklin and MacMahon 2000). Environmental site factors such as climate, elevation, topography, light, and soil resources can also shape the composition and diversity of the understory layer (Huebner et al. 1995; Schumann et al. 2003; Roberts 2004). In particular, the influence of overstory structure on understory vegetation has been demonstrated in many forest types (Rubio et al. 1999; Moola and Vasseur 2004; Halpern et al. 2005; Macdonald and Fenniak 2007), including northern hardwood-conifer forests (Huebner et al. 1995; Brosofske et al. 2001). Disturbance can alter overstory characteristics and microtopographic features, such as coarse woody debris, that influence microsite conditions for plant species (Beatty 1984; Gilliam 2002). Similarly, relationships between understory vegetation and climatic and edaphic factors have been established (Pregitzer et al. 1983; Graves et al. 2006). Fratterigo et al. (2006) demonstrated that disturbance history influences patterns of soil nutrient availability in cove-hardwood forests, which in turn affect the spatial heterogeneity of understory plants. Plant community composition is also affected by moisture availability (Davis et al. 1998; Hutchinson et al. 1999; Schumann et al. 2003);

extended periods of drought have been shown to induce declines in plant species richness and cover (Yurkonis and Meiners 2006). While these findings have contributed to a broad understanding of the factors controlling plant responses, few studies have investigated the relative importance of below-ground (e.g. soil nutrient availability) and above-ground (e.g. canopy structure) influences on post-harvest understory composition and diversity (Brosofske et al. 2001; Gilliam 2002; Macdonald and Fenniak 2007).

The most common technique used to evaluate the impact of silvicultural treatments on understory vegetation is chronosequencing, which involves sampling vegetation in stands that are in varying stages of post-harvest recovery. This approach assumes comparable initial site conditions, harvesting techniques, and post-harvest disturbance history, and may not capture the dynamics of short-lived species or populations with episodic fluctuations (Halpern 1989). In northern hardwood-conifer forests, few studies of understory vegetation response have utilized pre-harvest data combined with post-harvest data from more than one year (e.g. Metzger and Schultz 1984). Here we report on a data set spanning six years, including four years of post-treatment monitoring, which provides a comparatively longer time period over which to assess recovery dynamics, such as lagged responses. Furthermore, there is little information available on plant responses to low-intensity, uneven-aged systems with variable levels and spatial patterns of post-harvest structural retention. Assessing initial understory responses to these variations may help to identify which combinations are capable of meeting criteria for biodiversity conservation, and if there

is a critical threshold for the local persistence of certain plant species (Halpern et al. 2005).

Our research objective was to evaluate changes in the diversity, composition, and abundance of understory plant communities following three uneven-aged forestry practices modified to increase post-harvest structural retention: single-tree selection, group selection, and SCE. Pre- and post-disturbance understory communities were monitored to assess initial compositional changes including species persistence and colonization, as well as local extirpations of sensitive species. To further understand the factors driving changes in the understory, we explored the relationships between plant responses and overstory structure, soil properties, and drought stress. We hypothesize that i) variants of uneven-aged, low-intensity silviculture can maintain understory plant diversity and support late-successional species through harvest disturbance; ii) retaining and enhancing stand structural complexity can increase understory plant diversity in northern hardwood-conifer forests; and iii) plant responses are influenced by interactions between canopy structure, soils, and exogenous climate processes.

## 2. Methods

### 2.1. Study Areas

The study was conducted at three study areas: the Mount Mansfield State Forest, the University of Vermont's Jericho Research Forest, and the Forest Ecosystem Research Demonstration Area (FERDA) in Paul Smiths, New York. The FERDA is a collaborative research effort among the Northern Research Station of the

USDA Forest Service, Paul Smith's College, and the Adirondack Park Agency Visitor Interpretive Center. The Vermont Forest Ecosystem Management Demonstration Project (FEMDP) established the experimental treatments and long-term monitoring project at Mount Mansfield State Forest and the Jericho Research Forest. All three sites are mature (ca. 70-100 years), multi-aged northern hardwood-conifer forests with a documented history of timber management. Mount Mansfield State Forest is situated on the western slopes of Mount Mansfield in northern Vermont at elevations ranging from 470 to 660 m; soils are primarily Peru extremely stony loams. The Jericho Research Forest is located in the foothills of the northern Green Mountains of Vermont at 200 to 250 m; soils are Adams and Windsor loamy sands or sandy loams. The FERDA sites are located at approximately 500 m elevation in the northwestern section of the Adirondack Park in New York. The soils are Adams loamy sands. At all three study sites, the dominant overstory species include sugar maple (*Acer saccharum)*, American beech (*Fagus grandifolia*), and yellow birch (*Betula alleghaniensis)*. At the Jericho Research Forest and the FERDA, eastern hemlock (*Tsuga canadensis)* is also co-dominant and there are minor components of red maple (*Acer rubrum*) and red oak (*Quercus rubra).* Red spruce (*Picea rubens)* is a minor element of the canopy at Mount Mansfield State Forest.

*2.2. Experimental Design*

Four replicates of each treatment and eight untreated controls were established across the three study areas. Treatments included two conventional uneven-aged manipulations, single-tree selection (STS) and group selection (GS), and structural

complexity enhancement (SCE). Experimental units were 2 ha in size and separated by 50 m (minimum) unlogged buffers to minimize cross-contamination of treatment effects. All three treatments were designed to retain a high degree of post-harvest forest stand structure. However, the treatments have different effects in terms of spatial patterning, level of retention and the specific type of features retained (see Keeton 2006).

At the FEMDP sites, logging was conducted on frozen ground in winter of 2003. Experimental units received one of three manipulative treatments or were designated as an untreated control. The conventional treatments were modified to increase post-harvest structural retention. Modifications were based on a target residual basal area of 18.4 $m^2$/ha, maximum diameter of 60 cm, and a q-factor of 1.3. This prescription was applied in a dispersed (single-tree selection) or aggregated (group selection) spatial pattern (Keeton 2006). The approximate size of individual group selection patches (0.05 ha) was based on estimates of average fine-scale natural disturbance pattern in New England (Seymour et al. 2002) and resulted in eight to nine groups per experimental unit. In both of the conventional treatments, slash and unmerchantable tree boles were retained.

SCE is designed to promote late-successional structural characteristics, including vertically differentiated canopies, elevated large snag and coarse woody debris (CWD) volumes and densities, variable horizontal density (including small canopy gaps), and reallocation of basal area to larger size classes. FEMDP researchers used several silvicultural methods to accelerate development of these attributes as

described in Keeton (2006). A target basal area (34 $m^2$/ha) and maximum diameter at breast height (90 cm) characteristic of old-growth structure were used to develop a target diameter distribution to which stands were cut (Keeton 2006). The diameter distribution was also based on a rotated sigmoid form, which is typical of some eastern old-growth forests, depending on disturbance history, species composition, and other variables (Goodburn and Lorimer 1999). The sigmoidal distribution was applied as a non-constant q-factor: 2.0 in the smallest size classes, 1.1 for medium sized trees, and 1.3 in the largest size classes. Accelerated growth in larger trees was promoted with full and partial crown release. Downed coarse woody debris (CWD) volumes were enhanced 140% on average over pre-harvest levels. In two of the four SCE units (one per study area), CWD enhancement involved uprooting trees to mimic the pit and mound topography characteristic of natural disturbance in old-growth northern hardwood-conifer forests (Dahir and Lorimer 1996).

The FERDA consists of fourteen 2 ha units treated with a variety of even-aged, multi-aged, and uneven-aged silvicultural methods during the winter of 1999-2000 (Rechlin et al. 2000). Data from eight units (two single-tree selection, two group-selection, and four controls) were included in this study. Approximately 30% of tree volume was removed, leaving approximately 18 $m^2$/ha in the treatment units, slash was left on site and treated to keep all branches below 1.3 m, and all standing dead trees were retained. Individual patches in the group selection units were approximately 0.04 ha in size (Wade et al. 2003). Structural retention and spatial pattern of single-tree selection and group selection units at the FERDA and FEMDP

27

sites were similar; as a result, data from these treatment types were combined in the analyses.

*2.3. Data Collection*

In the FEMDP study areas, five randomly placed 0.1 ha permanent sampling plots were established within each 2 ha treatment unit, buffered by a 15 m minimum distance from the edge of the unit.  We inventoried overstory structural characteristics by permanently tagging all live and dead trees (> 5 cm dbh and >1.37 m tall) within the sampling plots.  Species and diameter were recorded for each tagged tree. Thirteen 1 m$^2$ quadrats were established systematically along transects running north-south and east-west within each plot.  Percent cover of all vascular and non-vascular species was estimated within the quadrats.  Data were collected annually during the month of June in an attempt to capture the maximum diversity of spring ephemerals and later developing species.  Two years of pre-treatment and four years of post-treatment data are included in this study.

In the FERDA study areas, eight 0.04 ha permanent plots for sampling overstory structure were systematically located within each 2 ha treatment unit. Four 1 m$^2$ quadrats were established within each permanent plot for monitoring understory vegetation.  Percent cover of all vascular species was estimated in each quadrat during May-June for two years pre-treatment and three years post-treatment.  At all of the study areas we used an ocular method for percent cover estimation designed to increase precision and reduce error.

Soil macronutrients were sampled from four 2 m$^2$ subplots within each monitoring plot at the FEMDP study sites. A randomly located 10 cm diameter core was taken of the organic horizon (O horizon) down to the mineral layer. Samples were kept cool and prepared for processing within 24 hours. Soils analyses were conducted at the University of Vermont Agricultural Testing Lab according to the methods described in Wolf and Beegle (1995). Soil samples were dried at 55°C, ground in a mortar and pestle, and sieved through a 2-mm sieve. Available nutrients and reactive aluminum were extracted with Modified Morgan solution (ammonium acetate at pH 4.8, with a 5:1 solution:soil ratio, shaken for 15 minutes). Available P was determined colorimetrically (molybdate blue, reduced with $SnCl_2$); major cations (Ca, K, Mg, Na, Al) and micronutrients (Fe, Mn, B, Cu, Zn, S) were determined by Inductively Coupled Plasma Spectroscopy (ICP). Total % C and % N were determined by combustion analysis (Thermo Finnegan FlashEA Analyzer, Milan, Italy) as described in Bremner (1996). For ammonium ($NH_4^+$) and nitrate ($NO_3^-$), 5 g dried and sieved soil was extracted with 1M KCl. Analysis was by automated colorimetric analyzer ($NH_4^+$ by salicylate, $NO_3^-$ by cadmium reduction followed by diazotized sulfanilamide). Organic matter was estimated by weight loss on ignition (2 hr at 375°); pH was measured in a 2:1 suspension.

Climate data were obtained from the National Climatic Data Center (NCDC 2007). We utilized Palmer Drought Severity Index (PDSI) data for Vermont climate division 1 (western) and for New York division 8 (St. Lawrence

Valley). PDSI is a time bias corrected monthly value that indicates prolonged moisture deficiency or excess for a region and has been shown to reflect fluctuations in soil moisture (Mika et al. 2005). Temperature, evapotranspiration, soil moisture loss, soil moisture recharge, runoff, and precipitation are parameters used to calculate the index (Oliver and Fairbridge 1987). Use of a single index rather than multiple climatic parameters allowed us to reduce the number of explanatory variables, simplifying analyses and increasing statistical power.

*2.4. Data Analysis*

*2.4.1. Understory responses*

Quadrat-level sample data for pre- and post-harvest years at all three study sites were input into a Microsoft Access relational database. The final dataset spanned six years and included over 16,000 observations. Quality control involved evaluating each observation to ensure positive identifications and consistency across the years. Several species with inconsistent identifications were collapsed to genera. Individual species were classified into habitat guilds defined by habitat preference classes described by Ramovs and Roberts (2005). We equate their "forest class" with late-successional and their "disturbed class" with early-successional species as employed in this analysis. Habitat guilds include late-successional (species reach maximum abundance in mature, closed-canopy, interior forest), intermediate (species occupy young to mature, open or closed canopy forest but not excessively disturbed habitats) and early-successional (species reach maximum abundance in open-canopy, disturbed areas). Habitat preferences were determined according to Gleason and Cronquist

(1991).  We calculated plot level means for Hill's (1973) series of diversity indices

($N_0$, $N_1$, and $N_2$), where $N_0$ represents species richness, $N_1$ the exponential Shannon-

Weiner index and $N_2$ the reciprocal Simpson Index (Hill 1973).  The sequence

progressively downweights rare species; diversity measures are arranged according to

their tendency to emphasize either species richness (weighting towards uncommon

species) or dominance (weighting toward abundant species) (Magurran 2004).  The

indices are calculated as follows:

$N_0$ = # of species per quadrat

$N_1 = \exp(-\Sigma p_i \log p_i)$

$N_2 = 1/\Sigma p_i^2$

where $p_i$ is equal to the proportional abundance of the $i^{th}$ species.  The series of

indices, as well as percent cover, were calculated for all species and for the habitat

guilds.  Treatment level means of the diversity and abundance response variables were

calculated for pre- and post harvest years within each of the habitat guilds (Table 1).

*2.4.2. Analyses of treatment effects*

Multivariate analyses were used to determine if treatment had an effect on

trends in the understory response variables over time.  We used a linear mixed effects

model (LME) in SAS version 9.1 (SAS Institute Inc. 2003) to model diversity

response variables for all species and the habitat guilds.  Treatment, site, and year

were modeled as fixed effects and plots and units as random effects.  Plots were nested

within units and units within sites.  The model output includes parameter estimates for

the fixed effects (e.g. treatment*year interaction) and covariance estimates for the random effects.

Analysis of variance (ANOVA) models were used to further explore the effect of treatment on understory response variables. The first hypothesis, that late-successional species can persist through low-intensity treatments, was tested by calculating unit-level means of the diversity and abundance response variables for the late-successional guild and running ANOVAs on the percent change of each variable from pre- to post-harvest years. We tested for differences between the two pre-harvest years to determine if there was significant interannual variability in the pre-treatment baseline data. Because there were no significant differences between the two pre-harvest years, we defined pre-harvest as one year before harvest. Post-treatment was defined as three years after harvest, the longest time period available for all study areas. If significant treatment effects were detected, ANOVAs were followed by Tukey multiple comparison tests. The same technique was applied to the diversity and abundance response variables for species of all habitat guilds combined to determine if treatments maintained species diversity and to test the second hypothesis, that SCE increases understory plant diversity. This method was repeated for the early-successional and intermediate habitat guilds to identify other notable pre- to post-treatment trends.

We used the multi-response permutation procedure (MRPP) in PC-ORD Version 4.41 (McCune and Mefford 1999) to test for differences in overall species composition among treatments and between pre- and post harvest years within

treatments using the Sørenson distance measure. Nonmetric multidimensional scaling

(NMS), a non-parametric ordination method, was also applied in PC-ORD to interpret

compositional patterns among the treatment units. The main advantages of NMS are:

(i) it avoids the assumption of linear relationships among variables, (ii) it allows the

use of any distance measure, and (iii) its use of ranked distances tends to linearize the

relationship between distances in environmental space, relieving the "zero-truncation

problem" in most ordination methods. For these reasons, NMS is considered the most

effective ordination method for ecological community data (McCune and Grace

2002). We ran NMS on a species-by-sample matrix for pre- and post-treatment data

with random starting configurations. Both ordinations used a Sørenson distance

measure and each included 20 runs of real data. Dimensionality of the data was

assessed using the Monte Carlo permutation procedure in PC-ORD with 30 runs of

randomized data.

To determine if any species were declining or absent from treatment units in

post-harvest years, presence-absence and abundance of individual species were

evaluated throughout the study period. Species initially present in low frequencies (<

2 quadrats) or at low densities (<0.5%) were not included in this assessment.

*2.4.3. Sub-analysis of overstory structure and soil properties*

As an indicator of pre- and post-harvest stand structure, we calculated relative

density (RD) following Curtis (1982). This form of RD integrates quadratic mean

diameter and stem density, and is thus indicative of multiple attributes of overstory

structure, such as total occupation of growing space based on both tree density and

size.  The index is appropriate to both even- and uneven-aged stands (Curtis 1982).

We used RD as a surrogate for treatment in this sub-analysis.  Plot and unit-level

means for the required component forest inventory metrics were generated using the

Northeast Ecosystem Management Decision Model (NED-2) (Twery et al. 2005).

A subset of the data from the FEMDP sites was used to evaluate the effects of

soil properties on understory response variables and to determine whether local

differences in soil characteristics may have confounded treatment effects.  Five soil

chemical characteristics thought to be important to understory vegetation were

selected based on earlier studies (Pregitzer et al. 1983; Hutchinson et al. 1999; Gilliam

2002; Kolb and Diekmann 2004).  These were percent organic matter (% OM), total

nitrogen (% N), calcium (Ca), available phosphorus (P), and pH.  Due to a strong

relationship in the dataset between Ca and pH ($p = <0.001$, $r^2 = 0.339$), pH was not

included in the analyses.  Percent organic matter was included because it can be

reflective of local soil moisture and cation exchange capacity (Johnson et al. 1997).

Soil cation concentrations, particularly calcium, have been shown to control

distributions of understory plants (Gilliam and Turrell 1993; Kolb and Diekmann

2004; Graves et al. 2006), and plant growth is commonly limited by availability of

nitrogen and phosphorus (Marschner 1995).  Samples from the organic layer (first 10

cm) were used as this layer encompasses the bulk of the rooting zone of the

understory.  Plot and unit-level means were generated for each soil variable.

Pre- to post-harvest percent change was calculated for all variables and a

correlation matrix used to identify relationships among the soil variables, RD, and the

diversity and abundance response variables ($N_0$, $N_1$, $N_2$, and % cover) for all species and for the habitat guilds.  The LME model was run for each response variable with treatment, site, and year as fixed effects, unit and plot as random effects, and soil characteristics as covariates.

The effects of site variables on overall species composition were assessed using the NMS ordination in PC-ORD.  We calculated the percent of variance explained by each ordination axis and generated Kendall's Tau correlations to identify associations between ordination scores and overstory and soil characteristics, both before and after treatment.  Overlays were created in PC-ORD to interpret the results.

*2.4.4. Analysis of Moisture stress*

Moisture stress in the study areas was assessed using the Palmer Drought Severity Index (PDSI).  Monthly PDSI values were averaged into two time periods when moisture stress would likely influence understory vegetation.  PDSI_1 represents a mean monthly value for July-September of the year prior to sampling.  PDSI_2 represents a mean monthly value for April-June of the sampling year.  For diversity and abundance response variables (all species and habitat guilds), pre-treatment data were removed and unit means were standardized to +/- mean for each treatment/site.  For each treatment, simple linear regressions were used to identify relationships between PDSI_1 and PDSI_2 and standardized annual means of the response variables.

## 3. Results

### 3.1. Treatment effects

Analysis of understory response trends over time using the LME model showed a significant treatment*time interaction on diversity and abundance response variables for all species ($N_0$: $p = <0.001$; $N_1$: $p = <0.001$; $N_2$: $p = 0.004$; % cover: $p = <0.001$). The same interaction effect was found for late-successional and early-successional species, but not for intermediate species (Table 2). Further exploratory analyses using ANOVA models revealed differences in diversity and abundance responses among treatments from 1 year before harvest (pre) to 3 years after harvest (post) (Table 3). Multiple comparison tests showed that for all species combined, percent change in $N_0$ ($p = 0.032$), $N_1$ ($p = 0.004$), $N_2$ ($p = 0.010$) and percent cover ($p = 0.031$) were significantly higher in SCE treatment units than in control units. Percent change in $N_2$ for all species was also significantly higher in STS units than in the controls ($p = 0.010$).

When responses were analyzed separately for habitat guilds, we found that SCE units maintained significantly higher $N_0$ than GS units ($p = 0.010$), higher $N_1$ and $N_2$ than control units ($N_1$: $p = 0.009$; $N_2$: $p = 0.016$) and higher percent cover than GS, STS or control units for late-successional species ($p = 0.010$). Diversity responses of intermediate species were not different among treatments, but abundance increased significantly in SCE units compared to GS or STS units ($p = 0.03$). All three treatments showed a minor increase in early-successional species diversity and

abundance, but only the conventional treatments increased significantly ($N_1$: $p = 0.011$; $N_2$: $p = 0.006$; % cover: $p = 0.015$).

In the pre-treatment dataset, NMS found a three-dimensional solution (32 iterations; final stress of 9.17; Monte Carlo test, $p = 0.03$). The variation in species composition was explained by Axis 1 (44.8%), Axis 2 (33.2%) and Axis 3 (12.0%); the three ordination axes accounted for 90% of the total variation. The first two axes are displayed in Figure 1a. The NMS ordination and the results of the MRPP (A = 0.009, $p = 0.320$) indicated that there were no significant compositional differences among treatments. NMS also found a three-dimensional solution (23 iterations; final stress of 12.2; Monte Carlo test, $p = 0.03$) in the post-treatment dataset. The three axes accounted for a total of 75.9% of the variation in species composition: 38.2%, 25.1% and 12.6% respectively. The first two axes are displayed in Figure 1b. Although the ordination depicted stronger clustering of experimental units by treatment group, the results of the MRPP indicated that there was no significant difference in species composition among treatments (A = 0.026, $p = 0.142$). However, the average distance between SCE units ($\delta = 0.778$) was greater than the control ($\delta = 0.582$), GS ($\delta = 0.560$) or STS ($\delta = 0.609$) units, reflecting the greater compositional heterogeneity among post-treatment SCE units. The results of the MRPP within treatments revealed no significant differences in overall species composition from pre- to post-harvest years in the control or treatment units (control: A = -0.046, $p = 1.00$; GS: A = 0.028, $p = 0.232$ ; STS: A = 0, $p = 0.458$; SCE: A = -0.049 , $p = 0.855$).

In total, 108 vascular understory species were recorded in the pre-treatment monitoring plots. Twenty of these were absent from one or more units in the post-treatment surveys. Of the eleven species that were absent from treatment units, excluding controls, all were classified as late-successional species and ten had biotic (animal-mediated) modes of dispersal (Table 4). All treatment and control units experienced some local species losses. GS units lost a greater mean percentage of species (14.1%) than STS (7.3%), SCE (4.8%) or control (4.5%) units; however, there were no significant differences in mean percent species loss among treatments ($p = 0.07$).

*3.2. Effect of overstory structure and soil properties*

The effects of treatment and soil properties on overall trends in diversity responses over time were assessed with the LME model. The interaction of treatment*time had a strong effect on understory response variables for all species, early-successional species and late-successional species, while the effects of the soil covariates were not significant (Table 2). Conversely, for the intermediate species guild, the treatment*time interaction was not significant for any of the diversity or abundance response variables, while % OM and total % N did show significant effects (% OM: $N_1$, $p = 0.001$, $N_2$, $p = 0.002$; total % N: $N_0$, $p = 0.004$, $N_1$, $p = 0.001$, $N_2$, $p = 0.036$).

The correlation matrices did not reveal any consistent relationships between pre- to post-harvest percent change in soil properties and understory response variables. At the plot level, soil variables were generally not associated with diversity

and abundance responses, with a few exceptions. Change in % OM was positively correlated with intermediate species $N_0$ ($r^2 = 0.174$, $p = 0.008$) and early-successional $N_2$ ($r^2 = 0.205$, $p = 0.014$), and negatively correlated with early-successional $N_1$ ($r^2 = 0.510$, $p = 0.009$). Negative correlations were found between change in total % N and early-successional $N_0$ ($r^2 = 0.180$, $p = 0.022$), and between change in Ca and late-successional $N_2$ ($r^2 = 0.097$, $p = 0.022$). In contrast, overstory structure, represented by change in RD, was negatively correlated with changes in all response variables at the plot level, excluding late successional $N_0$ ($r^2 = 0.000$, $p = 0.976$). At the unit level, no pre- to post-harvest changes in soil nutrients were associated with the response variables. Change in RD was also not correlated with response variables, with the exception of a negative association with changes in $N_1$ ($r^2 = 0.209$, $p = 0.043$) and $N_2$ ($r^2 = 0.252$, $p = 0.024$) for all species.

Kendall rank correlation coefficients ($\tau$) for the five selected overstory and soil variables on the NMS ordination axes before and after treatment are listed in Table 5. Before treatment, none of the variables were significantly correlated with Axis 1, which accounted for most of the variation in species composition. RD ($\tau = .439$) and OM ($\tau = -0.336$) were strongly correlated with Axis 2, and RD was strongly correlated with Axis 3 ($\tau = -0.435$) (Figure 1a). After treatment, RD ($\tau = 0.368$), OM ($\tau = -0.362$) and N ($\tau = -0.336$) were significantly correlated with Axis 1 and all of the soil variables (OM, $\tau = 0.441$; Ca, $\tau = 0.520$; N, $\tau = 0.338$; P, $\tau = 0.494$) were significantly correlated with Axis 2 (Table 5).

*3.3. Effect of climate variability*

Drought indices were not strongly correlated ($p < 0.05$) with standardized diversity response variables for all species or for the habitat guilds in the control units. In the treatment units, there were no significant correlations between PDSI_1 and diversity responses or between PDSI_2 and diversity responses, with the exception of late-successional $N_0$. PDSI_2 was correlated with late-successional $N_0$ in units treated with GS ($p = 0.012$, $r^2 = 0.747$), STS ($p = 0.018$, $r^2 = 0.703$) and SCE ($p = 0.024$, $r^2 = 0.602$).

## 4. Discussion

*4.1. Understory plant responses to experimental treatments*

*4.1.1. General responses*

The results of this study support our hypothesis that in northern hardwood-conifer forests, understory plant species diversity can be maintained through uneven-aged forestry practices that retain or enhance stand structural complexity. Experimental units treated with group selection (GS), single-tree selection (STS), and structural complexity enhancement (SCE) all showed increases in diversity measures ($N_0$, $N_1$, and $N_2$) during the four years following harvest disturbance (Figure 2). We observed a significant increase in diversity response variables in the SCE units from one year pre-harvest to three years post-harvest, suggesting that enhancement of stand structural complexity may increase overall species diversity, at least during the initial post-disturbance recovery period. The lack of significant differences in post-harvest species composition among treatments and

from pre- to post-harvest within treatments indicates that all three treatments were generally capable of preserving the integrity of the understory layer. In evaluating short-term responses, it can be difficult to discern the immediate effects of disturbance from the direct and indirect effects of residual overstory structure, which may become increasingly important over time (Halpern et al. 2005). Nevertheless, initial responses, such as the ability of certain species or guilds to persist through the disturbance, may be indicative of the intensity of silvicultural systems and could have important implications for biodiversity conservation.

### 4.1.2. Response of habitat guilds

Previous studies of post-harvest forest understories have documented diversity increases immediately following silvicultural disturbance (Gilliam et al. 1995; Halpern and Spies 1995; Jenkins and Parker 1999). These increases are often attributed to an influx of early-successional species as a result of changes in light and resource availability on the forest floor. Dominance of early-successional species is generally short-lived, but with periodic disturbance their presence may impact recovery of the understory (Scheller and Mladenoff 2002). We detected an increase in early-successional species diversity and abundance in all three treatments; however, only the conventional treatments increased significantly. This may be due to increased light availability in the conventional treatment units, which retained significantly less overstory structure (e.g. canopy closure and leaf area index) than SCE treatment units (Keeton 2006). There was no difference in soil compaction among treatments, yet higher levels of scarification in the conventional treatment units (Keeton, unpubl. data)

may also have contributed to post-harvest increases in early-successional species. Additionally, greater retention and enhancement of late-successional structural characteristics in the SCE treatment units (Keeton 2006) may have reduced the amount of early-successional habitat available for post-harvest colonization.

Understory diversity commonly increases with light availability (Brosofske et al. 2001). The diversity increases in all three treatment types in this study support this relationship. However, SCE units experienced less overstory removal and showed greater increases in understory diversity than conventional treatment units, suggesting that heterogeneity may be more important for diversity response than total availability of light in the understory. The spatial heterogeneity of light created by small canopy gaps, as well as other structural characteristics such as coarse woody debris, may be particularly important for late-successional species. A study by Scheller and Mladenoff (2002) on the spatial patterning of understory communities in northern hardwood forests showed that old-growth had smaller understory community patch sizes and greater patch heterogeneity than younger forests. Community patch size was correlated with both coarse woody debris and light heterogeneity (Scheller and Mladenoff 2002). The application of SCE in this study attempted to approximate the structural heterogeneity of old-growth forests (Keeton et al. 2007) by retaining large diameter trees, harvesting trees in a variable density pattern to create a range of small gap sizes as well as undisturbed patches, creating pit and mound topography, and increasing levels of coarse woody debris (Keeton 2006). These changes may have increased microsite heterogeneity and reduced interspecific competition of understory

plants after harvest, allowing a greater diversity of understory species to persist, particularly those that require late-successional habitat. Although overall changes in species composition were not significantly different among treatments, post-treatment increases in late-successional species richness, diversity and cover were significantly higher in SCE treatment units than control units (Figure 3). This trend could become more pronounced over longer time periods, as the primary influence on understory communities shifts from the initiating disturbance to the residual structure (Halpern et al. 2005). However, although late-successional richness continued to increase, the two measures of late-successional diversity decreased slightly from post-harvest year 3 to year 4 in the SCE treatment units, suggesting that the initial increase may be unstable or transient. Alternatively, the slight decrease may represent inter-annual variability attributable to other environmental controls.

### 4.1.3. Local extirpations

Local extirpations of species that are sensitive to disturbance have been observed in intensively managed forests (Halpern et al. 2005; Ramovs and Roberts 2005). Species that reproduce clonally or have biotic dispersal mechanisms may be particularly sensitive to silvicultural disturbance (Meier et al. 1995; Mabry et al. 2000). In this study, the percentage of species lost in treatment units was not significantly different from the percentage lost in control units, although the identity and habitat preference of these species differed. Macdonald et al. (2007) suggest that the threshold for a "lifeboating" effect of variable-retention harvesting must be between 20 and 75% retention. The levels of basal area retention in the treatments

employed in this study were within or above this range (GS, STS: 64-70% retained; SCE: 81% retained; see Keeton 2006). The greater mean percentage of species lost from conventional units (GS: 14.1%, STS: 7.3%) than SCE or control units (4.8% and 4.5%, respectively) indicates that the level of retention may influence the persistence of understory species. Reader (1987) also found that percent of understory species lost increased with cutting intensity in hardwood forests of Southern Ontario. However, in contrast to our study, Reader (1987) demonstrated that size of the silvicultural openings did not influence loss of understory species. Based on our findings, the difference between GS and STS units, while not significant, suggests that the spatial pattern of retention may also be important.

The majority of species locally extirpated from one or more experimental treatment units following harvest disturbance were late-successional, perennial herbs or shrubs with biotic modes of dispersal (Table 4). Three of these species, *Lonicera canadensis*, *Oxalis acetosella*, and *Trientalis borealis*, have been previously identified as sensitive to disturbance (Ruben et al. 1999; Ramovs and Roberts 2005; Wiegmann and Waller 2006). Many similar studies (e.g. Halpern and Spies 1995) have proposed that investigations of diversity responses alone can obscure important compositional changes. Our study supports this viewpoint by demonstrating that although low-intensity, uneven-aged treatments can support late-successional understory plant diversity, populations of sensitive species may still be adversely impacted, even by timber harvests that retain very high levels of post-harvest stand structure.

We recognize several uncertainties related to the observed loss of species from treatment units. The loss of species from control units suggests that irrespective of treatment, there are fluctuations in the presence and abundance of understory species. The mean pre-harvest abundances of impacted species were all very low (< 9%), suggesting that species initially present in low densities are more likely to be affected by forest management practices. The absence of a particular species in post-harvest years may be due to climatic variation, site conditions, plant life history characteristics, as well as variable sampling techniques. Species classified as locally extirpated may have been dormant or simply not detected in the four post-harvest sampling years. Others that persisted through the harvest disturbance may be gradually extirpated as a result of disturbance-related stress, inability to adapt to microclimate changes, and increased competition with ruderal species (Meier et al. 1995; Halpern et al. 2005). Finally, it is uncertain whether continued monitoring will indicate that local extirpations are only short-term in nature if recolonization proceeds from clonal expansion and seed rain from surrounding areas.

## 4.2. Influence of overstory structure and soil properties

Composition and diversity of forest understories are known to be related to local environmental and edaphic factors and can vary at different spatial scales (Brosofske et al. 2001). For instance, soil nutrient availability has been shown to influence patterns of understory vegetation (Kolb and Diekmann 2004; Fraterrigo et al. 2006). Plant distributions are affected by soil cation concentrations, particularly calcium (Gilliam and Turrell 1993; Graves et al. 2006). The soil characteristics

evaluated in this study appeared to have some influence on understory responses, yet the relationships we detected were highly variable and did not reveal consistent trends. A negative relationship between calcium and late-successional $N_2$ was detected at a fine spatial scale (plot-level); however, there were no correlations between calcium and other response variables at the fine scale, or between calcium and response variables at a coarser spatial scale (unit-level).

Total percent nitrogen and percent organic matter were also related to certain diversity responses for intermediate and early-successional species at a fine scale; however, the directionality of these associations was inconsistent and they were not observed at a coarser scale. Previous studies have also documented negative relationships between nutrient availability and plant species diversity at fine scales (Rosenzweig 1995; Brosofske et al. 2001; Gilliam 2002). Tilman (1993) hypothesized that increased productivity as a result of greater nutrient availability suppressed diversity in grasslands by reducing germination sites available to colonizing species, an idea that may also be applicable to forested systems. In this study, the negative association between certain soil nutrients and plant species diversity may be attributed to effects of the silvicultural disturbance. Forest management activities often alter soil properties, although the intensity and duration of these changes vary with the soil and forest type, as well as the type of management employed (Grigal 2000). Depending on the intensity of harvest, soil nutrient availability can increase as a result of high organic matter inputs or decrease due to biomass removal and leaching (Johnson et al. 1997; Elliott and Knoepp 2005).

While forest management may lead to a short-term decline in soil nutrients, elimination of overstory competition may temporarily increase the availability of these nutrients (and light) to understory vegetation (Roberts 2004), leading to increased productivity and diversity. Calcium is one of the elements most susceptible to depletion following timber harvesting because of its high concentration in tree wood and bark (Schaberg et al. 2001). In this study, we observed decreases in soil calcium in both treated and control units, indicating that soil calcium depletion, a widespread phenomenon in northeastern forests linked to acid deposition (Federer et al. 1989; Likens et al. 1998), is occurring in the study areas irrespective of timber harvesting. Increases in plant species diversity were limited to treated areas, suggesting that the negative association between calcium and late-successional plant species diversity involves some interaction with treatment. Similar to our study, Gilliam et al. (2002) found a negative correlation between calcium and plant species diversity, but only in clearcut stands.

The relative strength of the influence of overstory structure versus soil properties on understory vegetation is unclear. Studies have demonstrated that both timber harvest and soil properties strongly influence the understory layer (Elliott and Knoepp 2005; Macdonald and Fenniak 2007). In some instances, soil properties exert a greater control on forest understories than stand structure (Gilliam 2002), while in others, the influence of overstory characteristics can override local site factors (Brosofske et al. 2001). We observed strong relationships between pre- to post-harvest change in RD and all response variables at the fine scale, and with change in

$N_1$ and $N_2$ for all species at the coarser scale, indicating that changes in overstory structure were strongly related to understory response. Results of the LME model support this conclusion; over time, understory response variables for all species, early-successional and late-successional species were strongly affected by treatment and less influenced by soil properties (Table 2). Model results also suggest that the influence of overstory structure is less important to intermediate species, which can occupy both open and closed canopy forests; for these species, soil covariates may be more important. The ordination indicates that both overstory and soil characteristics are useful in explaining some of the variation in species composition, although much of the variation is left unexplained. As in similar studies (e.g. Macdonald and Fenniak 2007), it is likely that plant species composition was also influenced by unmeasured factors, such as elevation and microtopography, as well as historical patterns of disturbance and recovery.

*4.3. Effect of Drought Stress*

Moisture availability is often cited as a significant factor influencing vegetation dynamics in forest understories (Huebner et al. 1995; Hutchinson et al. 1999; Kolb and Diekmann 2004). In this study, periods of moderate to severe drought occurred during the pre-harvest years at the sites in Vermont and in both pre- and post-harvest years at the sites in New York (Figure 4). However, there were no significant relationships between the PDSI drought indices and understory response variables for all species or for the habitat guilds in the control units, indicating that independent of changes in overstory structure, drought stress did not have a strong influence on

understory response.  The relationships between late-successional species richness and PDSI_2 observed in the treatment units suggest that by exposing the understory to higher light levels and desiccation, silvicultural disturbance may exacerbate the effects of drought stress on late-successional species.  The relationships we observed between moisture stress and declines in late-successional species richness were stronger in conventional treatments that experienced a greater reduction in canopy closure compared to the SCE units.  This indicates that these effects may vary with the size and spatial clustering of canopy openings.  Uneven-aged practices like SCE that retain high levels of canopy closure and vertical canopy complexity (Keeton 2006) may expose understory plant communities to less post-harvest moisture stress and associated changes in plant community composition.

Recovery from pre-harvest drought conditions is one possible explanation for the large post-harvest increases in diversity and abundance in the SCE treatment units.  However, in order to return to pre-drought levels, $N_0$ would need to increase by 18.5%, $N_1$ by 15.7%, $N_2$ by 10.2% and percent cover by 12.2%.  The increases we observed, 44.9% for $N_0$, 42.6% for $N_1$, 47.5% for $N_2$ and 14.2% for percent cover, are much larger, indicating that while recovery from drought may have been partially responsible for the increases in understory response variables, the majority of the changes can be attributed to treatment effects.  This conclusion is supported by the absence of significant relationships between drought indices and understory response variables in the control units.

**5. Management Implications**

Sustainable forest management practices aim to maintain biodiversity and ecosystem functioning, while providing opportunities for timber revenue generation. Experimental research at the scale of individual forest stands provides an opportunity to assess the contribution of these practices to broader, landscape-scale conservation efforts. Assessments of how plant species respond to silvicultural treatments informs our understanding of the aggregate representation of different elements of plant biodiversity (e.g. early vs. late-successional) provided by the mix of treatments and stand conditions present at larger spatial scales. The results of our study will be useful in this context.

Our results generally support previous studies that demonstrate the capacity for uneven-aged silvicultural systems to maintain understory plant diversity in northern hardwood-conifer forests (Jenkins and Parker 1999; Scheller and Mladenoff 2002; Kern et al. 2006). The treatments in this study were modified to retain or enhance post-harvest structure, and it appears that even subtle differences in type, magnitude, and spatial configuration of the silvicultural prescription can result in varying understory vegetation responses. Techniques that enhance stand structural complexity may increase microsite variability on the forest floor and, as a result, sustain higher levels of understory plant diversity. By retaining biological legacies (see Franklin et al. 2002) in the form of undisturbed patches of forest canopy and forest floor, these techniques may preserve late-successional species and those that are slow to recolonize formerly occupied sites.

Despite overall maintenance of diversity under all of the low impact treatments investigated in this study, including conventional selection systems, we did observe local extirpations of certain plant species, predominantly those with an affinity for late-successional habitat, within experimental units of all treatment types, including the controls. However, during the four year post-treatment study period, GS units lost a greater percentage of species (14.1%) than STS (7.3%), SCE (4.8%), or control (4.5%) units. SCE experienced less overstory removal than the conventional treatments; the only difference between the GS and STS prescriptions was dispersed versus aggregated harvesting (see Keeton 2006). These results suggest that both the magnitude and spatial pattern of structural retention are important for retaining understory plant species through a harvest disturbance. This finding emphasizes the need to better predict compositional changes in understory plant communities following different types and intensities of silvicultural disturbance.

Where risks to plant populations, such as local extirpations of rare, threatened, or sensitive species, are deemed unacceptable, efforts can be made to minimize deleterious impacts on soils and plant communities. Choice of harvesting machinery as well as skidding and yarding practices are important considerations in this respect (Vossbrink and Horn 2004). Patch retention standards, no entry zones around selected locations with sensitive plants, greater post-harvest structural retention (i.e. reduced percent basal area removals), and logging during the dormant season are possible alternatives for minimizing impact (Berger et al. 2004). Other researchers have recommended that, despite the best practices of sustainable forestry, reserves may be

necessary to conserve all elements of biodiversity, including sensitive plant species (Poiani et al. 2000).

Although we did not observe many strong relationships between soil properties and understory responses in this study, other studies have documented soil-vegetation relationships (Pregitzer et al. 1983; Hutchinson et al. 1999; Graves et al. 2006). Forest management practices can indirectly affect understory plant communities by influencing the availability of soil nutrients (Gilliam 2002; Fraterrigo et al. 2006). Silvicultural disturbance often leads to loss of soil nutrients through biomass removal and leaching (Johnson et al. 1997; Adams et al. 2000; Grigal 2000). Thus, management approaches similar to those employed in this study that involve increased retention of tree biomass, minimal soil disturbance, and even augmentation of coarse woody debris inputs may have important implications for nutrient cycling and site productivity.

## 6. Conclusions

In this study, changes in understory plant species diversity and abundance following timber harvest were primarily driven by changes in stand structure, rather than changes in soil properties or moisture availability. Species composition was influenced by both overstory and soil characteristics and did not differ significantly among treatments three years after disturbance. Our results suggest that while conventional, uneven-aged treatments are capable of maintaining understory plant diversity, variations that retain or enhance structural complexity may be more efficient at preserving late-successional species. Over time, increased

microsite heterogeneity as a result of these techniques may also increase understory plant diversity.

This analysis reflects understory response over four years post-harvest and interpretations are therefore limited in scope to the initial recovery period. Continued monitoring of understory vegetation, particularly sensitive species, will help differentiate initial disturbance effects from the effects of residual structure, contributing to a more complete understanding of understory vegetation dynamics following modified uneven-aged forestry practices in northern hardwood-conifer forests.

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Table 1.  Diversity and abundance response variables by treatment for all species and for habitat guilds.  Diversity response variables include species richness ($N_0$), the exponential Shannon diversity index ($N_1$), and the reciprocal Simpson index ($N_2$).  Abundance is expressed as percent cover.  Treatments include group selection (GS), single-tree selection (STS), structural complexity enhancement (SCE) and untreated controls (CON).  Values expressed are treatment means ($\pm 1$ SE) for one year before harvest (pre) and three years after harvest (post).  Sample sizes are control: n = 8; SCE, GS, and STS: n = 4.

| | | GS | | STS | | SCE | | CON | |
|---|---|---|---|---|---|---|---|---|---|
| | | pre | post | pre | post | pre | post | pre | post |
| All Species | $N_0$ | 7.12 (0.68) | 7.88 (0.94) | 8.04 (0.66) | 10.15 (0.76) | 8.35 (1.02) | 13.85 (1.13) | 8.27 (0.58) | 7.87 (0.57) |
| | $N_1$ | 3.63 (0.32) | 4.60 (1.17) | 3.64 (0.68) | 5.60 (1.14) | 3.75 (0.68) | 6.94 (0.82) | 4.12 (0.43) | 3.61 (0.54) |
| | $N_2$ | 2.99 (0.24) | 3.83 (0.92) | 2.91 (0.55) | 4.71 (0.93) | 3.22 (0.42) | 5.53 (0.65) | 3.37 (0.3) | 2.90 (0.36) |
| | % cover | 15.35 (2.76) | 18.29 (6.60) | 22.35 (4.87) | 19.41 (4.14) | 11.77 (4.40) | 19.84 (5.90) | 19.32 (0.68) | 14.84 (3.11) |
| Late-successional Species | $N_0$ | 11.50 (0.65) | 9.75 (1.80) | 10.75 (1.60) | 17.00 (2.04) | 12.50 (2.02) | 17.00 (2.04) | 12.13 (1.49) | 12.25 (1.44) |
| | $N_1$ | 2.95 (0.33) | 2.89 (0.70) | 2.93 (0.57) | 3.61 (0.88) | 2.80 (0.61) | 3.98 (0.67) | 3.01 (0.32) | 2.64 (0.36) |
| | $N_2$ | 2.52 (0.23) | 2.72 (0.63) | 2.50 (0.48) | 3.37 (0.84) | 2.47 (0.46) | 3.62 (0.40) | 2.70 (0.28) | 2.32 (0.32) |
| | % cover | 12.24 (1.57) | 7.92 (0.96) | 18.65 (2.27) | 11.74 (1.69) | 6.69 (1.39) | 10.33 (1.88) | 18.13 (2.57) | 12.63 (1.5) |
| Intermediate Species | $N_0$ | 1.75 (0.25) | 2.00 (0.41) | 2.75 (0.63) | 3.25 (0.48) | 3.25 (0.85) | 3.75 (0.95) | 3.00 (0.50) | 3.00 (0.53) |
| | $N_1$ | 1.00 (0.00) | 1.03 (0.03) | 1.11 (0.05) | 1.15 (0.05) | 1.21 (0.09) | 1.35 (0.12) | 1.24 (0.07) | 1.19 (0.06) |
| | $N_2$ | 0.47 (0.05) | 0.56 (0.10) | 0.78 (0.12) | 0.79 (0.13) | 0.86 (0.20) | 1.12 (0.18) | 1.01 (0.15) | 0.97 (0.12) |
| | % cover | 0.56 (0.32) | 0.15 (0.03) | 1.5 (0.95) | 0.85 (0.52) | 0.91 (0.34) | 1.75 (0.73) | 1.61 (0.59) | 1.49 (0.54) |
| Early-successional Species | $N_0$ | 2.00 (0.41) | 3.00 (0.58) | 1.50 (0.65) | 3.25 (0.48) | 2.00 (0.00) | 3.50 (0.29) | 1.88 (0.48) | 1.50 (0.27) |
| | $N_1$ | 1.03 (0.02) | 1.50 (0.24) | 1.07 (0.05) | 1.42 (0.18) | 1.04 (0.02) | 1.44 (0.10) | 1.13 (0.05) | 1.02 (0.02) |
| | $N_2$ | 0.59 (0.08) | 1.21 (0.35) | 0.34 (0.17) | 1.31 (0.19) | 0.63 (0.19) | 1.30 (0.17) | 0.45 (0.14) | 0.44 (0.14) |
| | % cover | 1.32 (0.62) | 5.85 (3.46) | 0.44 (0.23) | 3.60 (1.13) | 2.50 (1.75) | 3.19 (1.90) | 0.48 (0.26) | 0.39 (0.18) |

Table 2. Linear mixed effects model results for diversity indices ($N_0$, $N_1$, and $N_2$) and percent cover for all species and by habitat guilds.

| | | Treatment*time | | OM | | Ca | | N | | P | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | F | $p$ | F | $p$ | F | $p$ | F | $p$ | F | $p$ |
| All Species | $N_0$ | 4.58 | <0.001 | 2.66 | 0.104 | 0.04 | 0.838 | 1.90 | 0.169 | 1.76 | 0.186 |
| | $N_1$ | 3.29 | <0.001 | 0.07 | 0.791 | 0.00 | 0.971 | 1.15 | 0.284 | 0.00 | 0.948 |
| | $N_2$ | 2.55 | 0.004 | 0.06 | 0.802 | 0.53 | 0.468 | 0.14 | 0.705 | 0.01 | 0.920 |
| | % cover | 3.36 | <0.001 | 0.48 | 0.490 | 0.01 | 0.906 | 1.00 | 0.319 | 1.93 | 0.166 |
| Late-Successional Species | $N_0$ | 2.73 | 0.002 | 0.00 | 0.976 | 0.00 | 0.946 | 0.02 | 0.876 | 0.47 | 0.496 |
| | $N_1$ | 2.02 | 0.024 | 0.59 | 0.442 | 0.87 | 0.351 | 0.53 | 0.466 | 2.47 | 0.117 |
| | $N_2$ | 1.81 | 0.047 | 0.08 | 0.778 | 0.23 | 0.629 | 0.13 | 0.721 | 0.50 | 0.478 |
| | % cover | 3.08 | <0.001 | 0.46 | 0.498 | 1.83 | 0.177 | 5.25 | 0.023 | 0.93 | 0.336 |
| Intermediate Species | $N_0$ | 1.12 | 0.348 | 4.55 | 0.034 | 0.67 | 0.414 | 8.52 | 0.004 | 0.43 | 0.514 |
| | $N_1$ | 1.52 | 0.117 | 11.32 | 0.001 | 0.01 | 0.905 | 11.26 | 0.001 | 0.87 | 0.351 |
| | $N_2$ | 1.31 | 0.217 | 5.31 | 0.022 | 0.18 | 0.676 | 4.46 | 0.036 | 0.12 | 0.734 |
| | % cover | 0.98 | 0.467 | 0.22 | 0.640 | 0.28 | 0.597 | 1.62 | 0.204 | 1.22 | 0.271 |
| Early-Successional Species | $N_0$ | 3.77 | <0.001 | 0.12 | 0.733 | 0.00 | 0.987 | 0.01 | 0.909 | 3.22 | 0.074 |
| | $N_1$ | 3.45 | <0.001 | 1.19 | 0.276 | 0.22 | 0.637 | 0.05 | 0.830 | 2.46 | 0.118 |
| | $N_2$ | 2.87 | 0.001 | 0.72 | 0.397 | 0.00 | 0.958 | 0.20 | 0.652 | 4.59 | 0.033 |
| | % cover | 3.50 | <0.001 | 0.43 | 0.511 | 1.35 | 0.247 | 1.44 | 0.231 | 2.58 | 0.110 |

Table 3. ANOVA results of changes in diversity and abundance response variables for all species and for habitat guilds from one year pre-harvest to three years post-harvest. Treatment types include group selection (GS), single-tree selection (STS), structural complexity enhancement (SCE), and untreated controls (CON).

| | | MS | F | $p$ | Multiple comparisons ($\alpha = 0.05$) |
|---|---|---|---|---|---|
| All Species | $N_0$ | 2233 | 3.75 | 0.032 | SCE > CON |
| | $N_1$ | 7175 | 6.63 | 0.004 | SCE > CON |
| | $N_2$ | 5506 | 5.32 | 0.010 | SCE, STS > CON |
| | % cover | 6775 | 3.82 | 0.031 | SCE > CON |
| Late-successional Species | $N_0$ | 1842 | 5.06 | 0.012 | SCE > GS |
| | $N_1$ | 1868 | 5.4 | 0.009 | SCE > CON |
| | $N_2$ | 2201 | 4.67 | 0.016 | SCE > CON |
| | % cover | 5940 | 9.27 | 0.001 | SCE > CON, GS, STS |
| Intermediate Species | $N_0$ | 842 | 0.37 | 0.774 | |
| | $N_1$ | 61.3 | 1.23 | 0.333 | |
| | $N_2$ | 267 | 1.18 | 0.350 | |
| | % cover | 3479 | 3.84 | 0.030 | SCE > GS, STS |
| Early-successional Species | $N_0$ | 14389 | 1.92 | 0.167 | |
| | $N_1$ | 969 | 5.12 | 0.011 | GS > CON |
| | $N_2$ | 5694 | 6.06 | 0.006 | STS > CON |
| | % cover | 58694 | 4.75 | 0.015 | STS > CON |

Table 4. Understory species recorded pre-harvest and absent post-harvest.  X indicates the species was absent from two or more units of this treatment type for all four post-harvest years.  Treatment types include group selection (GS), single-tree selection (STS), structural complexity enhancement (SCE), and untreated controls (CON).  Life history characteristics were determined from Gleason and Cronquist (1991), Handel et al. (1981), and Mabry et al. (2000).

| Scientific Name | GS | SCE | STS | CON | Growth form | Fruit type | Dispersal | Habitat preference |
|---|---|---|---|---|---|---|---|---|
| *Actaea alba* | | X | | | perennial herb | berry | biotic | late-successional |
| *Adiantum pedatum* | | | | X | fern | spore | abiotic | late-successional |
| *Aralia nudicaulis* | X | | X | X | perennial herb | drupe | biotic | late-successional |
| *Arisaema triphyllum* | X | | X | | perennial herb | berry | biotic | late-successional |
| *Asarum canadense* | | X | | X | perennial herb | capsule | biotic | late-successional |
| *Coptis trifolia* | X | | | | perennial herb | follicle | biotic | late-successional |
| *Eupatorium rugosum* | | | | X | perennial herb | achene | abiotic | intermediate |
| *Lonicera canadensis* | X | | X | | shrub | berry | biotic | late-successional |
| *Medeola virginiana* | X | | | | perennial herb | berry | biotic | late-successional |
| *Osmunda claytoniana* | X | | X | | fern | spore | abiotic | late-successional |
| *Oxalis acetosella* | | X | | | perennial herb | capsule | biotic | late-successional |
| *Panax trifolia* | | | | X | perennial herb | drupe | biotic | late-successional |
| *Polygonatum pubescens* | | X | | | perennial herb | berry | biotic | late-successional |
| *Polygonum cilinode* | | | | X | perennial herb | achene | biotic | intermediate |
| *Pyrola elliptica* | | | | X | perennial herb | capsule | abiotic | late-successional |
| *Sambucus racemosa* | X | | | X | shrub | berry | biotic | early-successional |
| *Smilacina racemosa* | | | X | | perennial herb | berry | biotic | late-successional |
| *Trientalis borealis* | X | | | | perennial herb | capsule | biotic | late-successional |
| *Trillium erectum* | X | | | | perennial herb | berry | biotic | late-successional |
| *Viburnum alnifolium* | | X | | | shrub | drupe | biotic | late-successional |

Table 5. Kendall's tau correlations (τ) between the ordination axes and site variables.  The pre-harvest ordination included data from 1 year before harvest and the post-harvest ordination contained data from 3 years after harvest.  Bold values indicate a significant correlation at P < 0.05.

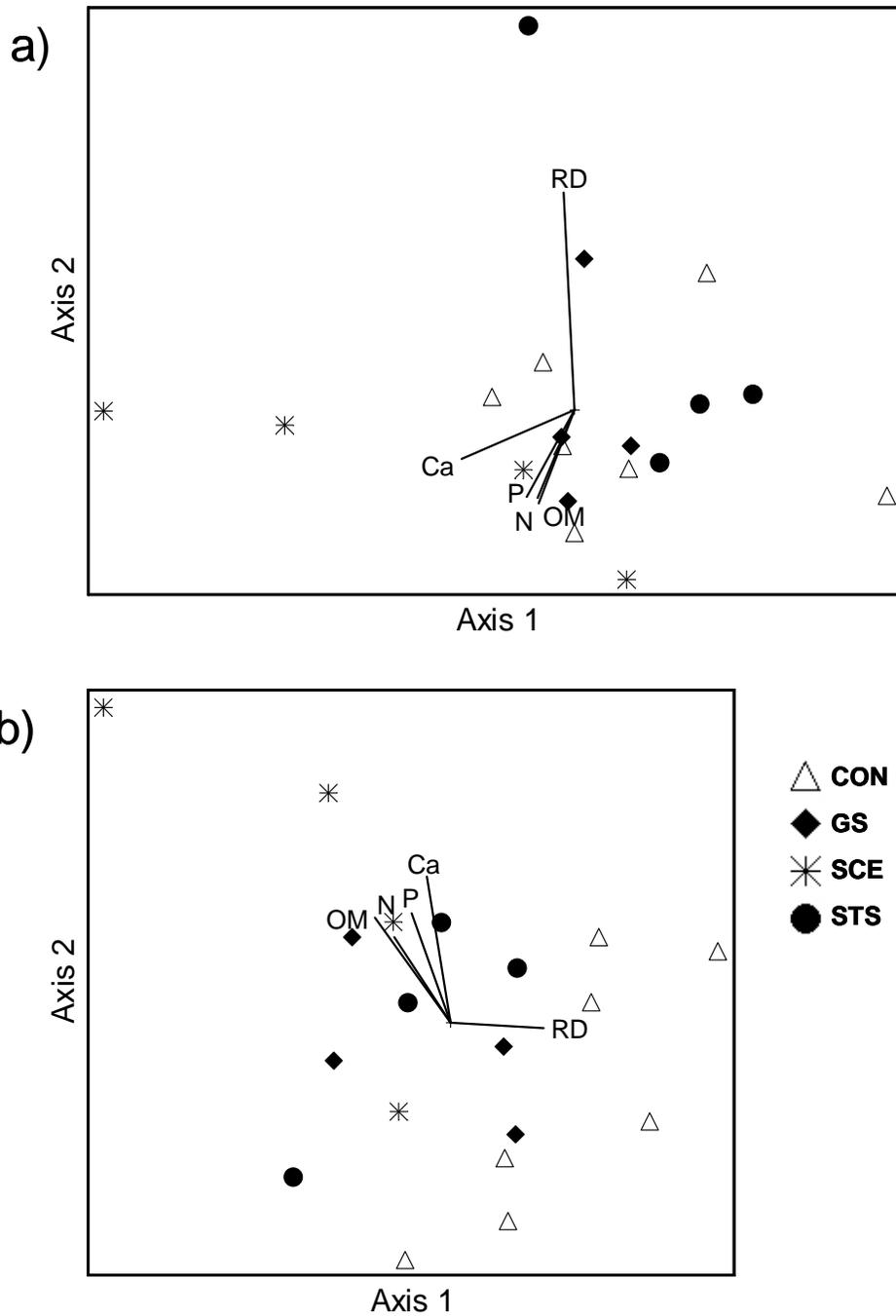| Site variable | Pre-harvest | | | Post-harvest | | |
| --- | --- | --- | --- | --- | --- | --- |
| | Axis 1 (44.8%) | Axis 2 (33.2%) | Axis 3 (12.0%) | Axis 1 (38.2 %) | Axis 2 (25.1%) | Axis 3 (12.6%) |
| RD | -0.099 | **0.439** | **-0.345** | **0.368** | -0.135 | -0.170 |
| OM | -0.072 | **-0.336** | 0.072 | **-0.362** | **0.441** | 0.230 |
| Ca | -0.230 | -0.257 | -0.112 | -0.204 | **0.520** | 0.178 |
| N | -0.086 | -0.323 | 0.086 | **-0.336** | **0.388** | 0.283 |
| P | -0.165 | -0.323 | -0.072 | -0.283 | **0.494** | 0.151 |

Figure 1. Relationship of species composition to forest structure and soil variables using nonmetric multidimensional scaling (NMS): a) pre-treatment (% of variation in species data: Axis 1 = 44.8; Axis 2 = 33.2), and b) post-treatment (% of variation in species data: Axis 1 = 38.2; Axis 2 = 25.1).
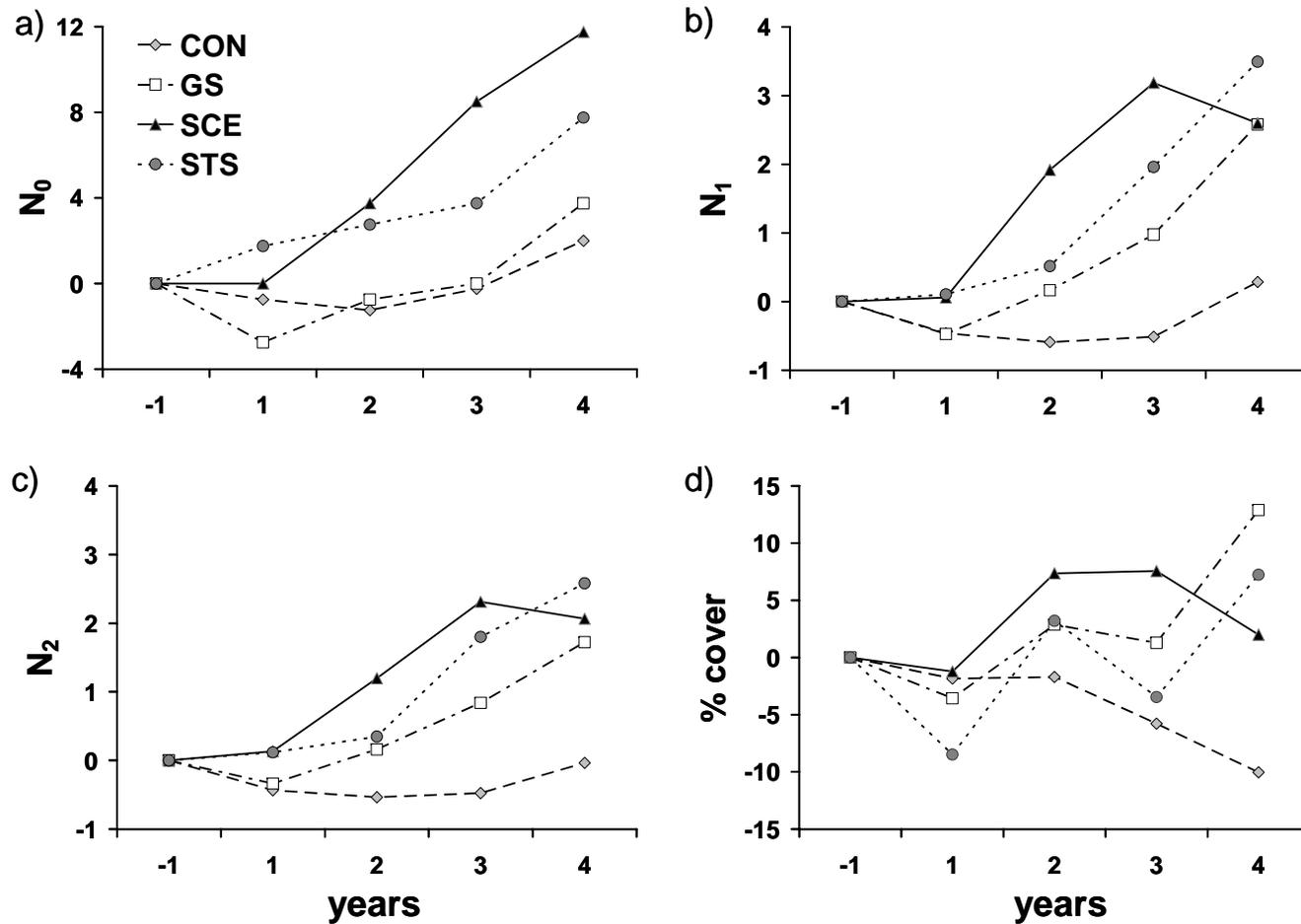
Figure 2. Change in treatment means of overall a) species richness ($N_0$), b) the exponential Shannon diversity index ($N_1$), c) the reciprocal Simpson's diversity index ($N_2$) and d) percent cover from one year pre-harvest to four years post-harvest. Data is normalized to one year pre-harvest. Year 3 is used as post-harvest in ANOVAs. Sample sizes are control: n = 8 for all years; SCE: n = 4 for all years; GS and STS: n = 4 for years -1 through 3, n = 2 for year 4.

Figure 3. Change in treatment means of late-successional a) species richness ($N_0$), b) the exponential Shannon diversity index ($N_1$), c) the reciprocal Simpson's diversity index ($N_2$) and d) percent cover from one year pre-harvest to four years post-harvest. Data is normalized to one year pre-harvest. Year 3 is used as post-harvest in ANOVAs. Sample sizes are control: n = 8 for all years; SCE: n = 4 for all years; GS and STS: n = 4 for years -1 through 3, n = 2 for year 4.
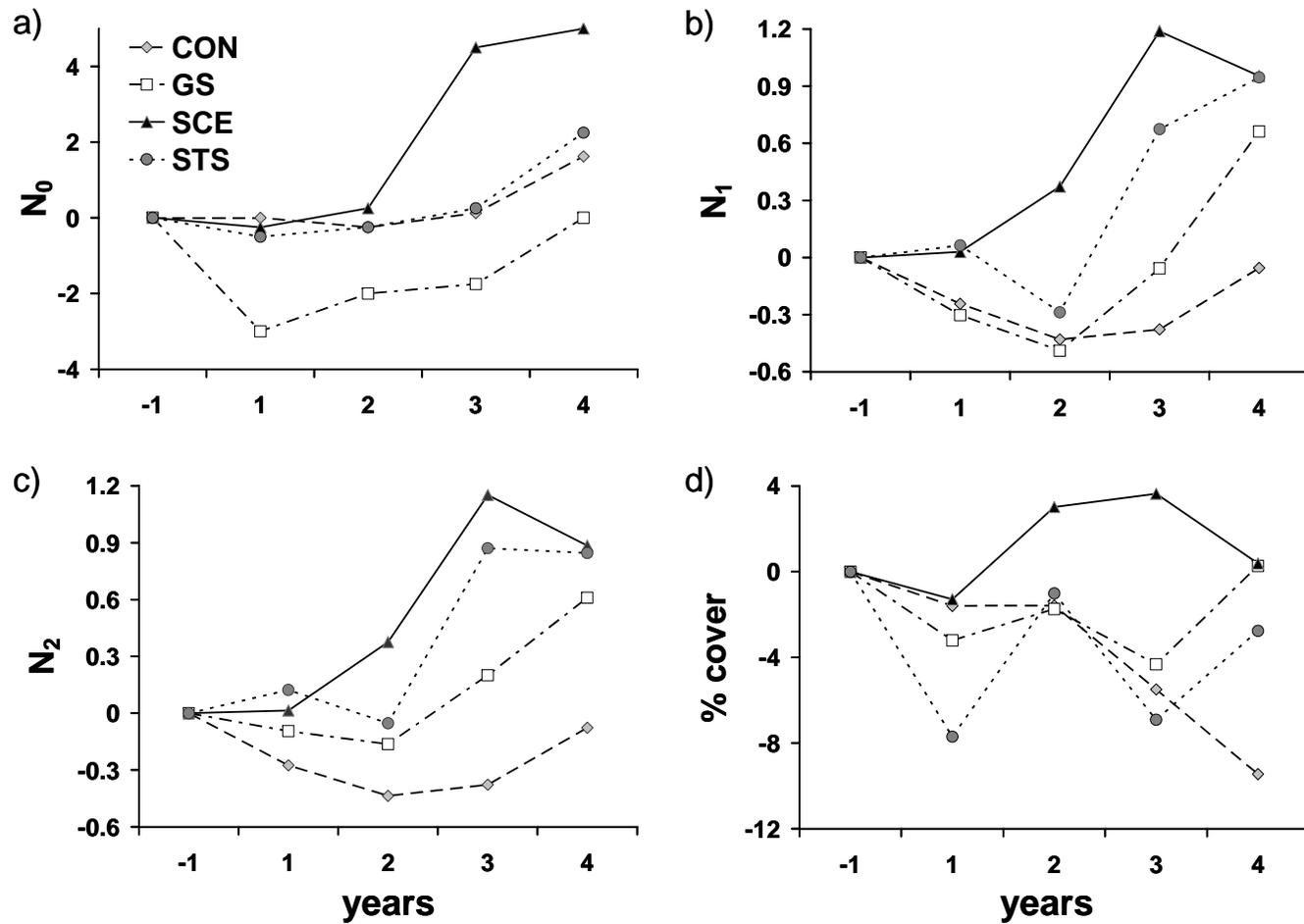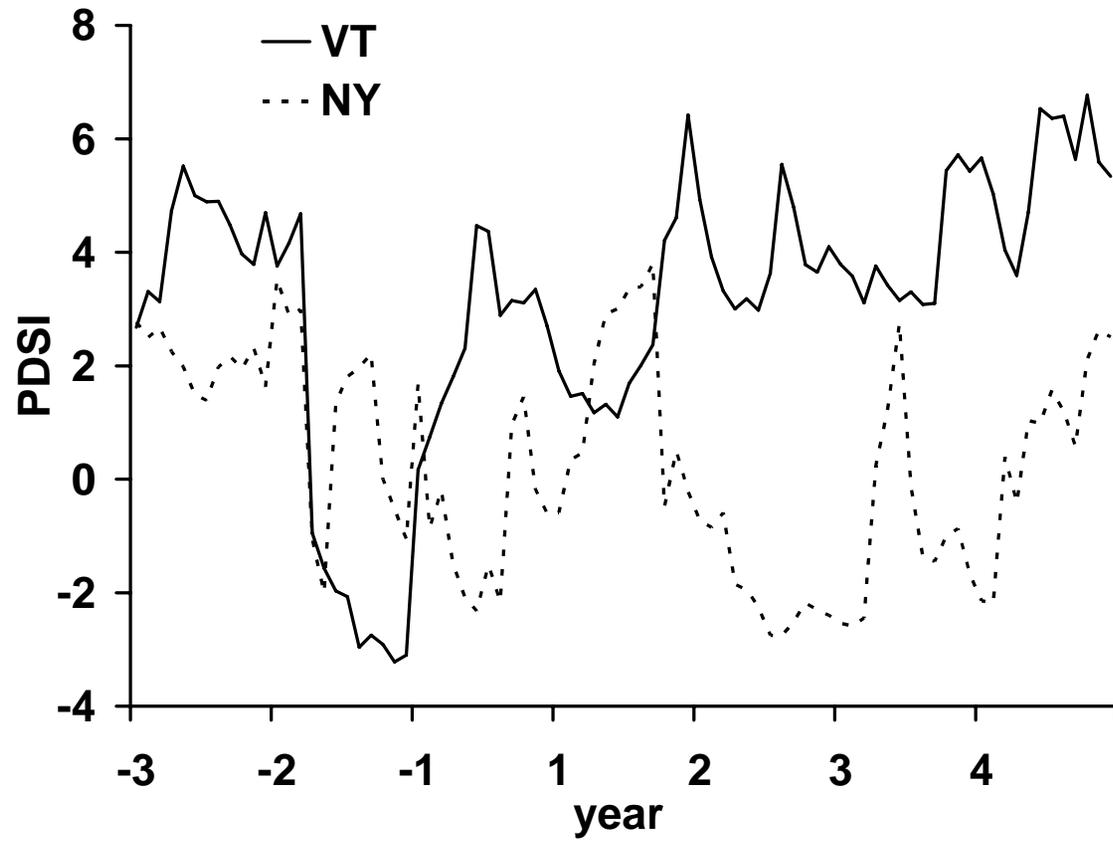
Figure 4. Fluctuations in the Palmer Drought Severity Index (PDSI) in the Vermont (VT) and New York (NY) study areas from three years pre-harvest to four years post-harvest.

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