CHANGES IN FOREST PRODUCTIVITY AND NITROGEN CYCLING ASSOCIATED WITH DECLINE OF EASTERN HEMLOCK

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Chapter 1

Ecological Impacts of Invasive Insects on Forest Communities and Ecosystems

Introduction

Invasive organisms pose a critical threat to plants and plant communities (Wilcove et al. 1998). For example, invasive insects and pathogens have altered the composition of forests in the northeastern US by causing widespread declines of American chestnut (*Castanea dentata* (Marsh.) Borkh.; Keever 1953), American elm (*Ulmus americana* L.; Parker and Leopold 1983), American beech (*Fagus grandifolia* Ehrh.; Runkle 1990), and ash species (*Fraxinus* spp.; Oliver 1981, Smallidge et al. 1991). However, while the negative impacts of invasive plants and abiotic disturbances on plant communities have been widely recognized and studied (Vitousek and Walker 1989, D'Antonio and Vitousek 1992, Malecki et al. 1993, Crooks 2002), less attention has been given to impacts of invasive insects (Castello et al. 1995, Schowalter et al. 1986). Because disturbances caused by invasive insects are continuing to impact plant communities worldwide (Tilman and Lehman 2001), it is imperative to understand the impacts of these organisms on community structure and ecosystem function.

The impacts of invasive insects on plant communities are likely to vary spatially with the relative dominance of the host species prior to an invasion, and with the extent of defoliation and mortality occurring during an invasion (Kulman 1971, Schowalter et al. 1986). In addition, the impacts of invasive insects are likely to vary through time depending on insect-host interactions. However, existing studies of invasive insects and other disturbances generally emphasize long-term patterns, such as changes to successional processes, forest growth, or disturbance regimes (Foster and Zebryk 1993). In contrast, short-term impacts, especially those of invasive insects, are often not

emphasized (Boring and Swank 1984, Carson and Root 1999, Yorks et al. 2003). A better understanding of patterns of plant disturbance or mortality is critical because community responses to the disturbance may be constrained by important processes that occur in the time period immediately following a disturbance (Clebsch and Busing 1989). In addition, short-term changes often foreshadow changes to the future community composition (Egler 1954).

This dissertation details the short-term effects of the loss of a dominant host tree species, eastern hemlock (*Tsuga canadensis* L. Carr.), on composition, productivity, and nitrogen cycling, as a function of spatial patterns in the dominance and decline of hemlock. This system is an excellent case study to examine the roles of host dominance and decline because hemlock is currently declining throughout much of the eastern US due to the introduction of an invasive non-native insect, the hemlock woolly adelgid (HWA; *Adelges tsugae* Annand.). The decline of eastern hemlock is expected to have far-reaching effects because eastern hemlock is a dominant species in much of its range (Braun 1950). A good deal of the current research on the introduction of the HWA focuses on the direct interactions between HWA and hemlock. For example, studies observed the specific tree/needle level effect of the HWA on hemlock (McClure 1991b), or life history and morphology traits of the HWA (Skinner et al. 2003). Comparatively less is known about the changes to communities and ecosystems that result from the direct effects of the HWA on eastern hemlock. In order to fully explore the short-term effects of the loss of a dominant tree, it is important to discuss what is known about the impacts of invasive species and abiotic disturbances on community structure and ecosystem function. In the following sections of this chapter, I will (1) address patterns of impacts of different disturbance types on community structure, ecosystem function, (2) provide background information on the relationship between eastern hemlock and the HWA, and (3) address my hypotheses and objectives.

Patterns of Impacts on Community Structure

The impact of invasive insects on community composition depends on the severity (Runkle 1990, Davidson et al. 2001), size (Hibbs 1983), and duration of the disturbance. The extent of disturbance, in turn, is a function of the dominance and distribution of the host species, the degree of defoliation or mortality, and the specificity of insect-host interactions (Elton 1958, Kulman 1971, Crawley and Akhteruzzaman 1988, Erbilgin and Raffa 2002). Thus, the patterns of community change are likely influenced by the relative composition of particular host and non-host trees (Egler 1954).

Shifts in community composition associated with host species decline may be a function of the severity of interactions between the invasive insects or pathogens and the host species (Crawley and Akhteruzzaman 1998, Erbilgin and Raffa 2002). While some insects or pathogens cause widespread host mortality, as in the case of the American chestnut, other insects cause extensive defoliation without causing mortality (Schowalter et al. 1986). Widespread host mortality may lead to larger shifts in community composition relative to shifts associated with invasions that do not cause mortality. For example, the severity of spruce and fir defoliation (>67%, 34-66%, <33% defoliation) by spruce budworm in Quebec influenced the severity of mortality (89%, 62%, 0% mortality, respectively; Kulman 1971). This ultimately changed the forest composition by shifting dominance from severely defoliated trees to unaffected trees co-occurring with spruce and fir. Similarly, extensive mortality associated with root rot led to substantial shifts in the composition of understory grass tree (*Xanthorrhoea australis*) in eucalyptus forest in Australia. Specifically, plots with root rot incurred a 43% decrease in tree density, while tree density in forests without root rot increased by 10% (Weste 1986). Therefore, the severity of the host-insect interaction, and the relative abundance of the host tree, will influence the effect of invasive insects on community structure.

Successional dynamics are also influenced by the duration of the disturbance (Krasny and Whitmore 1992). Disturbance duration can vary from abrupt declines to gradual declines. An abrupt disturbance is generally associated with abiotic factors, such as weather related wind that cause immediate damage to tree boles. Conversely, gradual changes associated with an insect or pathogen may occur over an entire growing season or over several years. While both abrupt and gradual disturbances allow more light to reach the forest floor (Glitzenstein et al. 1990, Jenkins et al. 1999) and alter soil and stream chemistry (Swank et al. 1981, Hutchens and Benfield 2000), gradual disturbances alter communities more slowly over time as insects or pathogens cause mortality to their host trees.

Compositional change also reflects the effects of disturbance size on successional dynamics (Schowalter et al. 1986, Runkle 1990, Davidson et al. 2001). In areas of widespread decline, forests were colonized by fast-growing species with superior dispersal abilities (Hibbs 1983), whereas in areas of more localized disturbances, co-occurring species generally expand into the canopy (Canham 1989, Krasny and Whitmore 1992). For example, beech bark disease caused greater American beech decline in areas of greater host tree density. The small disturbance size associated with the clumped distribution of beech trees influenced the composition of the forest by allowing localized increases in light availability and shifting resources to co-occurring species (Houston et al. 1979, Runkle 1990). By contrast, the large disturbance size following the decline of the American chestnut caused more widespread light and resource availability. These areas of decline were colonized by fast-growing early-successional species in much of the former chestnut-dominated areas (Stephenson 1986). However, in areas where chestnut was co-dominant with or subdominant to other species, these co-occurring species had a competitive advantage over colonizing species. Thus, the size of the disturbance and the composition of former chestnut-dominated forests influenced the composition of species observed following chestnut decline. Therefore,

the patterns of impacts of an invasive insect on community structure will depend on a suite of interactions: the community composition prior to the disturbance, the specificity of the insect for the host species, the severity, the size, and the duration of the disturbance.

Patterns of Impacts on Ecosystem Function

Through the impacts of insects on host species dominance and decline, invasive insects often alter ecosystem functions, such as net primary production (NPP) and nutrient cycling (Vitousek et al. 1997, Symstad et al. 1998, Gordon 1998, Jackson et al. 2002). These ecosystem functions are linked because, in terrestrial ecosystems, NPP is often constrained by nitrogen availability. Invasive insects directly and indirectly affect both NPP and soil nitrogen dynamics by prematurely removing foliage (Mattson and Addy 1975) and transferring organic matter from the leaves to the forest floor (Lovett et al. 2004). Defoliation directly decreases NPP by removing photosynthetically active leaf material. However, defoliation may also indirectly increase NPP by increasing the amount of nutrients in the soil available for tree growth or by stimulating growth of more productive plant parts (Kulman 1971). It is imperative to understand the separate and integrative responses of NPP and nitrogen cycling because these ecosystem functions will change as a result of the impacts of an invasive insect on its host species.

Net primary production is commonly assumed to decrease in forest ecosystems with increasing defoliation and mortality (Romme et al. 1986). However, invasive insects may promote ecosystem NPP by selectively removing either less-productive tree components or less viable trees that have decreased resistance to herbivory (Mattson and Addy 1975, Romme et al. 1986). The selective defoliation or mortality creates greater light and nutrient availability for the surviving plant tissues and co-occurring plants (Mattson and Addy 1975). In fact, studies comparing growth rates of defoliated and

unaffected trees observed greater growth rates of defoliated trees five to ten years following defoliation (Schowalter et al. 1986). Under such circumstances, plants will continue to grow at a greater rate compared to normal conditions until the elevated resource availabilities diminish (Chapin et al. 2002). The impacts of invasive insects on NPP will influence the growth and recovery of ecosystems as well as other community and ecosystem processes.

As forest composition and NPP change because of the introduction of invasive insects, forest nitrogen cycling will likely change because of the transfer of carbon and nitrogen from the tree pool to the forest floor pool (Chapin et al. 2002, Lovett et al. 2002). The rate and amount of nutrient transfer or loss is likely dependent on the disturbance type. The overall effect of insect defoliation and abiotic disturbance both increase light and heat to the forest floor (Mladenoff 1987, Jenkins et al. 1999). Along with increased transfer of organic matter associated with the disturbance, the increase in light and heat will also increase microbial activity, and subsequently, available nutrients (Zak et al. 2003). But unlike abiotic disturbance, insect defoliations cause relatively little immediate disturbance to the soil, and forests recover more quickly after defoliation events (Lovett et al. 2002). As a result, invasive insects likely cause slower effects on nutrients compared to abiotic disturbances because of the temporal variability of defoliation and mortality of host species.

Increased defoliation and mortality caused by invasive insects alter nitrogen cycling by increasing the rate and amount of foliage being transferred from the leaves to the forest floor (Schowalter et al. 1986, Lovett et al. 2004). The overall impact on ecosystem function and recovery depends on (1) the amount of nitrogen lost from the ecosystem and (2) whether ecosystem is nitrogen-limited. The severity of defoliation and mortality may determine the amount of nitrogen leached from the ecosystem. Nitrogen losses may be small following small disturbances because nitrogen is rapidly immobilized by the microbial community and the excess nitrogen can be recovered by

surviving trees (Lovett et al. 2002). But if defoliation causes widespread mortality of host species, changes in nitrogen cycling may be greater. In this scenario, nitrogen may be lost via leaching because there are no trees available to utilize excess nitrogen (Swank et al. 1981) and the microbial community may not be able to immobilize the excess nitrogen (Lovett et al. 2002). Thus, the interaction between the extent of the disturbance and nitrogen cycling affects the responses of forest communities and ecosystems following disturbances.

The Eastern Hemlock and Hemlock Woolly Adelgid

The eastern hemlock is a dominant late-successional species that occurs throughout eastern North America. Hemlock is characterized as a late-successional species based on the slow growth, dense canopy (Canham et al. 1994), and strong competitive ability of hemlock for light and nutrients. Hemlock is also associated with acidic soils (Finzi et al. 1998) and a deep litter layer that both promotes hemlock regeneration (McIntosh 1972, Keever 1973) and limits the growth of most other species (Rogers 1978). The cool, moist conditions that occur in hemlock-dominated forests provide habitat for a variety of animals, such as deer and goshawks (Rooney and Dress 1997, Griesemer et al. 1998, McWilliams and Schmidt 1999). Because of the unique combination of environmental characteristics associated with hemlock-dominated forests, hemlock decline may have far-reaching effects on community structure and ecosystem function.

The hemlock woolly adelgid was introduced from Japan in the 1920s to the west coast of North America (McClure 1990). By 1950, the HWA was observed in Virginia. Subsequently, the HWA has spread northeast as far as Connecticut and Rhode Island, where outbreaks began in the mid-1980's (Orwig and Foster 1998). Over the past 15 years, eastern hemlock has declined dramatically in the northeastern US, associated with

the expansion of the range of HWA (McClure 1991b). The eastern hemlock has no known defense against HWA and hemlock mortality occurs within approximately four years after initial infestation (McClure 1991a).

The HWA disperses via wind, birds, and humans (McClure 1990). Winter temperature and the mode of HWA reproduction may limit its growth and expansion. Parker et al. (1998) observed higher mortality of HWA associated with colder winter temperatures. The lack of a suitable host for sexual reproduction (discussed below) may also limit HWA growth or genetic variability. Yet, even with these limiting factors, the HWA has increased its range over the past 10 years (Orwig 2002).

The HWA has a complex polymorphic life cycle that includes wingless parthenogenetic generations on hemlock and winged sexual generations on spruce. The parthenogenetic generations consist of sistens and progrediens (McClure 1989). Sistens produce cottony sacks that contain approximately 50 eggs, of which about half become progrediens and the other half become sexupara (winged migratory adults). Progrediens also lay eggs within a cottony sack. These eggs become the next generation of sistens. Adult-winged HWA mature on hemlock, but must migrate to spruce to lay eggs. In the US, no eggs laid by winged adults hatch because the appropriate spruce species for successful sexual reproduction does not occur (McClure 1989). Thus, the parthenogenetic cycle of sistens and progrediens is the only mode of survival and expansion of the HWA in the US. Because of the short generation time of the species, the HWA reproduces twice per year in the US.

Impacts of the HWA on forest ecosystems in the eastern US vary greatly within and between forests, reflecting spatial variation in infestation, individual tree variation in susceptibility, and a delay between infestation and defoliation (e.g., Orwig and Foster 1998). However, the widespread impact of the HWA on forest communities and ecosystems has been the focus of few studies (Orwig and Foster 1998, Jenkins et al. 1999). More information on the potential roles of hemlock dominance and decline is

critical to understand and predict the potential impacts of the HWA on forests within the current range of eastern hemlock.

Hypotheses and Objectives

Much of the literature on disturbance ecology focuses on impacts on many species across large landscapes (Reich et al. 1997). Few studies have examined the responses of communities and ecosystems during the decline of a single dominant species in response to an invasive insect (Schowalter et al. 1986, Castello et al. 1995). Studies that have assessed impacts of invasive insects on forests generally compare areas with high versus low host-species mortality, but do not consider the role of relative host dominance on communities and ecosystems (Orwig and Foster 1998, Jenkins et al. 1999). Host dominance is particularly important because natural ecosystems are dynamic, developing as a mosaic of trees across different environmental gradients (Braun 1950, Bray and Curtis 1957). In this dissertation, I explored how the decline of a dominant tree species affected forest composition, net primary productivity, and nitrogen cycling across gradients of hemlock dominance. In order to assess the effect of hemlock dominance on forest response to hemlock decline, I compared areas with high, intermediate and low relative dominance of hemlock. Areas with greater relative host dominance will likely have greater effects compared to areas with lower relative host dominance.

The primary objectives of this dissertation were to assess the roles of hemlock dominance and extent of decline in moderating the impacts of hemlock decline on short-term changes (1-3 years) in: (1) basal area and forest community properties; (2) NPP and biomass; (3) and net mineralization and nitrification, and changes in soil and tree carbon and nitrogen pools. The factors that influence the decline of hemlock, mainly the HWA, may have direct control over hemlock mortality. However, changes in community and ecosystem properties, especially associated with non-host trees, primarily depend on the

defoliation or mortality of hemlock as opposed to the density of HWA. Therefore, the indirect impact of HWA on communities and ecosystems may exceed the direct impact of HWA on hemlock populations. I hypothesized that in plots with greater hemlock dominance and mortality, basal area, density, and richness would decrease, whereas diversity and equitability would increase. I hypothesized that there would be a greater effect of dominance and mortality on NPP in hemlock-dominated stands and stands with greater hemlock mortality. While it may take many years for biomass to recover following the mortality of a dominant tree species, productivity associated with the replacement species may increase rapidly due to subsequent increases in available resources. Therefore, I hypothesized that there would be greater decreases of hemlock basal area and greater increases of co-occurring species in hemlock-dominated stands from 1985 to 2000. Finally, nitrogen dynamics were expected to change as a result of dominant species decline (Mattson and Addy 1975). I hypothesized that plots with greater hemlock dominance and greater hemlock decline would experience an increase in nitrogen mineralization and nitrification rates, as well as an increase in pools of carbon and nitrogen.

These objectives were addressed by measuring growth changes of all live trees > 15 cm diameter at breast height (DBH) in hemlock-dominated, mixed, and hardwood-dominated stands within three watersheds in southern New York and northwestern New Jersey/northeastern Pennsylvania. Initial measurements of community properties (density, richness, diversity, and equitability), hemlock mortality, and hemlock crown defoliation were necessary to determine initial compositional characteristics as well as subsequent measurements assessed the impacts of hemlock dominance and decline on community properties, NPP, and nitrogen cycling.

In chapter 2, short-term effects of hemlock decline and dominance on changes in basal area, density, richness, diversity, and equitability were assessed. By analyzing these variables, I could determine the short-term changes associated with the impact of

the HWA. In chapters 3 and 4, I considered ecosystem properties that were affected by the decline of hemlock. Specifically, in chapter 3, I assessed whether NPP and biomass changed as a result of changing hemlock relative importance, defoliation, and mortality. I also compared short- and long-term growth patterns of hemlock and trees co-occurring with hemlock to assess whether the introduction of the HWA affected tree growth. Finally, in chapter 4, I measured nitrogen mineralization and nitrification rates, as well as total soil carbon and nitrogen, in order to assess whether soil nitrogen changed as a result of hemlock decline. I additionally measured leaf and leaf litter carbon and nitrogen levels to assess whether hemlock dominance and decline affected the changes in the pools of nitrogen. This study considered the impact of an invasive insect on communities and ecosystems by assessing changes in community structure, biomass, and nitrogen cycling associated with the decline of a dominant tree species.

Chapter 2

Impacts of Hemlock Decline and Dominance on Changes in Forest Composition and Community Properties

Introduction

The decline of forest species has been widely discussed as an important ecological, economic, and cultural concern since the beginning of the 20th century (Davis et al. 1996, Orwig 2002). In addition to the effects of changes in climate and land use patterns, one of the largest impacts on forest composition and tree health has been the introduction of non-native, invasive insects and pathogens (Liebhold et al. 1995). Although some non-native insects and pathogens create small disturbances on a local level (Lynch 2004), invasive organisms lead to extensive mortality of large forested areas covering thousands of hectares (Mackey and Sivec 1973, Agrawal and Stephenson 1995). These disturbances may dramatically alter composition by creating gaps and changing forest communities. However, few studies have measured short-term forest responses of invasive insects in terms of host species dominance or decline.

Invasive insects directly affect host tree species. Yet, the decline or loss of a dominant tree species due to the indirect effects of invasive insects on community structure is also important. Such indirect effects cause either positive or negative responses to species richness and community diversity, two common indices used in describing community structure. For example, the decline of American chestnut was associated with an increase in species richness because other tree species were able to disperse into former chestnut-dominated areas (Stephenson 1986). On the other hand, the decline of American elm did not significantly change community structure because the asymmetrical distribution of the host and pathogen caused a more localized disturbance

(Parker and Leopold 1983). These two examples illustrate how the indirect effects of host tree decline, as well as the size of the disturbance, influence community structure (Runkle 1981, Canham 1989) and the post-disturbance responses of the community (Egler 1954).

Disturbance size is a key factor regulating forest community responses to invasive insects (Chapin et al. 2002). The direct effect of an invasive insect on tree species mortality will cause different degrees of disturbance depending on the distribution of the host species (Woods 2004). Thus, if forest composition is dominated by one tree species, infestations of this species will likely lead to larger, more widespread disturbances compared to infestations of a sub-dominant species. Also, host relative abundance influences the dispersal of an invasive organism, further affecting disturbance size (Basset 1999). For example, the distribution of American beech influences the disturbance size because beech mortality occurs in localized areas where the host and pathogen are abundant. By contrast, isolated, inaccessible host trees are often unaffected (Runkle 1990, LeGuerrier et al. 2003) because pathogen dispersal is inhibited by the presence of non-host species. As community responses to the invasive insects depend of the disturbances size (Chapin et al. 2002), disturbance size further influences gap formation, successional processes (Hibbs 1982, Platt and Strong 1989), and forest recovery (Frelich and Graumlich 1994). Generally, small gaps are filled by trees that are "released" from competition (Canham 1989). By contrast, large gaps are typically colonized by fast-growing species or species that reproduce vegetatively (Whitmore 1989). Therefore, both initial community composition and host-herbivore interactions affect the size of the disturbance. Consequently, disturbance size will have a large effect on the subsequent forest community.

Differences in the response of forest community structure to invasive insects are also a function of the duration of the disturbance (Chapin et al. 2002). The duration of the disturbance will influence community change by altering the gap dynamics (Canham et

al. 1994). Insects, which cause disturbances over many months or years, typically cause a "gradual" change. By contrast, wind throw or fire generally cause "sudden" gaps that immediately alter forest composition (Krasny and Whitmore 1992). The impact of a gradual gap on community structure shifts species dominance towards co-occurring species (Krasny and Whitmore 1992) because established species can expand rapidly into small gaps and utilize excess resources. However, the result of sudden gaps typically encourages the recruitment of early successional species (Woods 2004) because few species remain in the disturbed area. Therefore, the greater temporal variability in disturbances caused by an invasive insect will affect the forest community structure by shifting resources to other co-occurring tree species.

A primary objective of this study was to assess changes in community structure, including changes in basal area, density, species richness, diversity, and equitability, in response to eastern hemlock (*Tsuga canadensis* (L.) Carr.) decline across a gradient of hemlock dominance. A second objective was to examine the patterns of hemlock defoliation and mortality that may cause changes in community structure (Orwig 2002). I predicted that forest basal area, density, richness, and diversity would differentially change over time as a function of hemlock dominance, and subsequent crown defoliation and mortality. I hypothesized that there would be the greatest decrease in basal area, density and species richness, and increase in diversity and equitability in hemlock-dominated stand-types compared to mixed or hardwood-dominated stand-types. I hypothesized that as hemlock mortality increased, there would be a decrease in basal area, density, and richness and an increase in diversity and equitability. Additionally, I hypothesized that crown defoliation was negatively correlated with changes in basal area, density, and richness, and positively correlated with diversity and equitability.

Site Description

Patterns of forest responses to the hemlock woolly adelgid (HWA; *Adelgis tsugae* Annand.) were examined at Black Rock Forest (BRF), Ward Pound Ridge Reservation (WPR), and Delaware Water Gap National Recreation Area (DWG). The three forests had similar tree species compositions and were typical of oak-dominated forests located in the northeastern US (Braun 1950). In addition to northern red oak (*Quercus rubra* L.) and chestnut oak (*Quercus prinus* L.), other dominant tree species included eastern hemlock and sugar maple (*Acer saccharum* Marsh.). Black birch (*Betula lenta* L.), red maple (*Acer rubrum* L.), white oak (*Quercus alba* L.), black oak (*Quercus velutina* Lam.), and American beech (*Fagus grandifolia* Ehrh.) were present in at least 30% of the study plots (Tables 1 and 2). Species were identified following Gleason and Cronquist (1991) and herbarium specimens from the Louis Calder Center – Biological Station, Armonk, New York.

Old growth hemlock-dominated areas were distributed among larger hardwood-dominated areas in all three forests. Plots were delineated based on the relative importance of hemlock. Species relative importance (RI) was defined by averaging the relative density and relative basal area of each species within the plot. Individual plots with greater than 50% hemlock RI at the beginning of the study were defined as hemlock-dominated plots. Mixed plots were those with 6 – 49% hemlock RI. Hardwood-dominated plots had less than 6% hemlock RI.

Black Rock Forest, Orange County, New York, USA (41°25'N, 74°01'W)

The Black Rock Forest (BRF) is a 1530 ha reserve located in the Hudson Highlands on the west bank of the Hudson River in Cornwall, New York. The area was set aside as a natural habitat in 1928 (Tryon 1943) and has served as a scientific field station for a consortium of academic institutions since 1989. The study watershed, Black

Table 1: Species relative importance† of all live and dead mature trees (> 15 cm DBH) in hemlock-dominated (E), mixed (M), and hardwood-dominated (A) plots at Black Rock Forest (B), Ward Pound Ridge (W), and Delaware Water Gap (D).

Species (Abbreviation)	B1E	B2E	B3E	B4M	B5M	B6M	B7A	B8A	B9A
Acer rubrum L. (ACRU)	1.3	9.0	8.0	2.5	2.5	1.0		2.0	
Acer saccharum Marsh. (ACSA)				2.7	2.7	4.5		11.0	5.5
Betula alleghaniensis Britton (BEAL)	1.5	0.8	3.7		3.2	7.1		6.0	9.3
Betula lenta L. (BELE)	1.1	5.3	1.3	3.2	1.3			11.2	
Carpinus caroliniana Walt. (CACA)									1.2
Carya ovata (Mill.) K. Koch (CAOV)		4.8							
Carya tomentosa (Poir.) Nutt. (CATO)									
Fagus grandifolia Ehrh. (FAGR)								5.8	3.6
Fraxinus americana L. (FRAM)			8.4				81.5	22.8	60.3
Fraxinus pennsylvanica Marsh. (FRPE)		1.1			8.8	40.7	23.1	15.1	32.0
Liriodendron tulipifera L. (LITU)	2.6		5.6		9.9	19.1	44.9		9.1
Nyssa sylvatica Marsh. (NYSY)						1.2			20.1
Ostrya virginiana (Mill.) K. Koch (OSVI)									
Pinus strobus L. (PIST)					3.0	37.6	19.4	3.4	
Platanus occidentalis L. (PLOC)			4.7						
Quercus alba L. (QUAL)		8.7							
Quercus prinus L. (QUPR)	15.8	7.1	9.8	38.8	4				
Quercus rubra L. (QURU)	5.9	8.4	14.3	29.9	2				
Quercus velutina Lam. (QUVE)		1.2	3.4						
Tilia americana L. (TIAM)	71.0	51.3	39.1	23.0	2				
Tsuga canadensis (L.) Carr. (TSCA)	0.8	2.2	1.6						
Ulmus americana L. (ULAM)									

†Relative Importance = (Relative basal area + Relative density)/2 x 100.

Table 1. Extended.

Species	W1E	W2E	W3E	W1M	W2M	W3M	W1A	W2A	W3A	D1E	D2E	D4E	D1M	D2M	D4M	D1A	D2A	D4A
ACRU				14.3			7.5				3.8	9.3	1.9			7.8	5.7	8.7
ACSA	6.5	10.1			60.0	15.5		53.0	19.8	3.0			5.8		32.8	6.6		21.2
BEAL		5.6																
BELE	12.4	5.2	11.0	13.7	4.5	7.8	15.8	6.5	8.8			4.1	17.2	15.9	13.6	11.1		
CACA				5.2		3.0	6.2								1.3		7.5	
CAOV								14.6	4.9						10.2			9.0
CATO																	8.8	
FAGR													2.1				10.5	
FRAM	6.6																	
FRPE																		
LITU															9.2			
NYSY													8.7		9.1	7.9		2.1
OSVI			3.7												2.8			12.4
PIST										33.6	20.0			8.5		10.3		
PLOC																		
QUAL				12.1									5.7	6.0		12.6	58.0	45.2
QUPR					10.7	17.9	33.5		3.8	2.9	9.3		7.4	10.2	3.8	7.6	9.4	
QURU						27.9	18.8	17.4	9.1				1.9	19.6				1.4
QUVE				16.7			12.0	8.6	48.0				18.7			36.3		
TIAM	5.4																	
TSCA	69.0	79.1	84.3	38.1	24.8	27.7	6.4		5.4	60.5	67.0	86.6	30.5	39.7	17.0			
ULAM																		

Table 2: Species relative importance† values calculated using all live and dead sapling trees (< 15 cm DBH) from the initial measurements at Black Rock Forest (B), Ward Pound Ridge (W), and Delaware Water Gap (D). Species abbreviations are defined in Table 1 except CADE = *Castanea dentata* (Marsh.) Borkh., and PRSE = *Prunus serotina* Ehrh. Hemlock-dominated, mixed, and hardwood-dominated stand-types are abbreviated as E, M, and A, respectively.

Species	B1E	B2E	B3E	B4M	B5M	B6M	B7A	B8A	B9A
ACRU	10.8	7.4	2.5	16.2	26.8	29.4	11.1	34.3	5.9
ACSA			9.1	6.6	6.5	9.2		19.9	20.2
BEAL				1.2					
BELE		13.3	2.7	10.1	6.5	11.2	6.0	29.7	36.6
CACA					0.5				
CADE			0.8	1.9		0.8			
CASPP		4.8						6.8	
FAGR			0.8	1.3				2.9	4.3
FRPE						1.2			
NYSY									
OSVI									17.4
PIST									
PRSE									
QUAL							2.0		0.6
QUPR		1.5			4.1	3.1	41.6	1.6	8.2
QURU				0.5	22.4		34.8	0.8	
QUVE									6.8
TSCA	89.2	74.8	84.0	62.1	33.3	45.2	3.0	0.7	
ULAM		3.0						3.3	

†Relative Importance = (Relative basal area + Relative density)/2 *x* 100.

Table 2. Extended.

Species	W1E	W2E	W3E	W1M	W2M	W3M	W1A	W2A	W3A	D1E	D2E	D4E	D1M	D2M	D4M	D1A	D2A	D4A
ACRU				21.9			46.5						4.2		4.2	18.6	11.0	7.2
ACSA		7.9			31.1	19.2	7.0	31.1	21.1				10.7		38.6	13.7		32.1
BEAL		2.3																
BELE	100.0	89.8		13.9	38.8	33.7	15.7		41.8				48.7	18.1	0.9	51.8		
CACA				9.1		23.8	12.7	1.4	9.1						1.2		26.5	
CADE																		
CASPP				7.8														
FAGR					8.0		9.0	9.4					6.5		2.0		24.4	4.0
FRPE																	38.0	
NYSY																9.7		
OSVI						14.9		2					9.1					53.9
PIST									27.9						20.8			
PRSE							55.2						6.9	4.3				0.8
QUAL																		
QUPR													9.4					
QURU				13.8	3.6			2.9					1.4	48.9		3.2		
QUVE					5.9								3.0					2.0
TSCA			81.2	33.6	12.6	8.4	9.2			100.0	100.0	100.0		28.6	32.3	3.0		
ULAM																		

Rock Brook, is a north-facing watershed encompassing approximately 100 ha and is the outlet from the Aleck Meadow and Upper Reservoirs. Eastern hemlock is the dominant tree species in approximately 38 ha of the watershed, as estimated by aerial photography and GIS (W. Schuster – Black Rock Forest, personal communication). Elevation ranges from 160 to 340 m above sea level (a.s.l.).

Ward Pound Ridge Reservation, Westchester County, New York, USA (41°14'N, 73°35'W)

The Ward Pound Ridge Reservation (WPR) is located in northeastern Westchester County and is the largest park in the county, covering 1902 ha. The land was protected in 1924 (B. Hurr – Ward Pound Ridge, personal communication) as a preserve for animals and as a recreational and educational area. There is an ephemeral stream and pond in the watershed. Eastern hemlock is generally distributed on slopes and moist areas throughout this watershed. The watershed is mostly north facing and ranges in elevation from 165 to 215 m a.s.l.

Delaware Water Gap National Recreation Area, Pike County, Pennsylvania, USA and Sussex County, New Jersey, USA (41°31'N, 74°49'W)

The Delaware Water Gap National Recreation Area (DWG) covers 28,340 ha and encompasses a 50 km expanse of the Delaware River. The plots used in this study were located in the Adams Creek (41°14'N, 74°52'W) and Van Campens Brook (41°05'N, 74°55'W) watersheds, which were chosen for a long term study on HWA in 1993 because of their mature hemlock stands (Battles et al. 2000). The Adams Creek watershed has approximately 36 ha of hemlock along steep ravines ranging from 120 to 280 m a.s.l. The Van Campens Brook watershed includes approximately 18 ha of hemlock on the north and northwest ravine sides. The elevation ranges from 250 to 350 m a.s.l. (Battles et al. 2000).

Methods

To compare community responses associated with hemlock dominance, plots were established in hemlock-dominated, mixed and hardwood-dominated stands in each of the three forests. At BRF, three hemlock-dominated plots, three mixed composition plots, and three hardwood-dominated plots were chosen from long-term plots initially established in 1985. These plots were randomly located within stand-types that were delineated using aerial photographs. Distances between plots varied. Some plots from different stand-type classifications were adjacent across an altitudinal and compositional gradient, while other plots were as much as 1 km apart. In order to incorporate all trees in the long-term plots established in 1985, 40 x 40 m (0.16 ha) plots were necessary. At WPR, nine 0.04 ha (20 x 20 m) plots were established in 2000. Because no long-term plots had previously been established at WPR, three groups of hemlock-dominated, mixed, and hardwood-dominated plots were haphazardly located along a transitional gradient from hemlock to hardwood-dominated areas. Haphazard sampling was required in order to ensure proper delineation of hemlock-dominated, mixed, and hardwood-dominated stand-types. The three groups of plots were within a radius of approximately 1 km. At DWG, three 0.04 ha (20 x 20 m) hemlock-dominated plots were established in 2001 within or near previously established hemlock-dominated plots (R. Evans – Delaware Water Gap National Recreation Area, personal communication). In conjunction with each hemlock-dominated plot, one mixed and one hardwood-dominated plot were haphazardly located along transitional gradients from hemlock- to hardwood-dominated areas, so that each group of plots consisted of a hemlock-dominated, a mixed, and a hardwood-dominated plot. The three groups of plots ranged from 1 km to 16 km apart. The variation in plot sizes between BRF and the other sites was due to: (1) plot size restrictions at BRF and (2) logistical constraints of maintaining the larger plot size at

all forests. To reduce variability between stand-types, plots with similar characteristics within and across forests were chosen.

Plots were assigned to stand-types based on the relative importance of hemlock within each plot. Relative importance was assessed using measurements of all live and dead trees > 1 cm diameter at breast height (DBH) at the start of the sampling period for each forest (BRF = 1999, WPR = 2000, DWG = 2001). Standing dead trees were included in initial measurements to account for recent mortality and infer the forest composition prior to the introduction of the HWA (Battles et al. 1992, Jenkins et al. 1999). In general, hemlock-dominated plots had greater hemlock frequency in all size classes; mixed plots were dominated by oaks in the larger size classes (> 15 cm DBH) and hemlock in the smaller size classes (< 15 cm DBH); and hardwood-dominated plots were dominated by hardwoods in all size classes, primarily oaks in the larger size classes and black birch or red maple in the smaller size classes (Tables 1 and 2).

In order to test for the effects of forest and stand-type on basal area, density, richness, diversity, and equitability, all live trees > 15 cm DBH were measured at the end of the growing season annually from 1999 to 2002 at BRF, from 2000 to 2002 at WPR and from 2001 to 2002 at DWG (Table 3). This approach is not uncommon as many studies measure only trees within or near the canopy of the forest (Romme et al. 1986, Agrawal and Stephenson 1995, Keever 1973, Dunn 1986, Abrams and Orwig 1996). These and similar studies on changes in basal area and community properties measured only subcanopy and canopy trees because changes in these trees often are comparable to changes in the overall forest community. In addition, trees > 15 cm DBH account for approximately 90% of the basal area of these forests.

An indicator of hemlock decline, specifically mortality, was also used as a treatment effect on community change. Relative hemlock mortality was measured to assess the effects of hemlock decline on community structure. Hemlock mortality was calculated as: (1) the ratio of standing dead stems at the beginning of the study to the

Table 3: Sampling dates for plots at Black Rock Forest (B), Ward Pound Ridge (W), and Delaware Water Gap (D). Hemlock-dominated, mixed, and hardwood-dominated stands are abbreviated as E, M, and A, respectively.

Forest	Stand	Plot	1999	2000	2001	2002
Black Rock Forest	Hemlock	B1E	++	++	0	+
		B2E	++	++	++	+
		B3E	++	++	++	+
	Mixed	B4M	++	++	0	+
		B5M	++	++	++	+
		B6M	++	++	0	+
	Hardwood	B7A	++	++	++	+
		B8A	++	++	++	+
		B9A	++	++	++	+
Ward Pound Ridge	Hemlock	W1E	N/A	++	++	++
		W2E	N/A	++	++	++
		W3E	N/A	++	++	++
	Mixed	W1M	N/A	++	++	++
		W2M	N/A	++	++	++
		W3M	N/A	++	++	++
	Hardwood	W1A	N/A	++	++	++
		W2A	N/A	++	++	++
		W3A	N/A	++	++	++
Delaware Water Gap	Hemlock	D1E	N/A	N/A	++	+
		D2E	N/A	N/A	++	+
		D4E	N/A	N/A	++	+
	Mixed	D1M	N/A	N/A	++	+
		D2M	N/A	N/A	++	+
		D4M	N/A	N/A	++	+
	Hardwood	D1A	N/A	N/A	++	+
		D2A	N/A	N/A	++	+
		D4A	N/A	N/A	++	+

++ all trees > 1 cm DBH sampled.
+ all trees > 15 cm DBH sampled.
N/A plots were not sampled during the specified year.
0 data were lost due to a computer malfunction.

total number of stems (i.e., initial mortality); and (2) the ratio of trees that died during an annual cycle compared to the number of living trees at the beginning of the cycle (i.e., mortality over time). The extent of hemlock defoliation may be correlated with forest community characteristics. Crown defoliation class (CDC) was subjectively measured based on the amount of hemlock defoliation on a scale from one to six: (1) = 0-5% defoliation; (2) = 5-25%; (3) = 25-50%; (4) = 50-75%; 5 = 75-99%; and (6) = dead (Table 4; Orwig and Foster 1998).

To assess changes in basal area (BA) and community characteristic over time, total basal area of all tree species, density, species richness, diversity (Shannon Diversity Index), and equitability were calculated using measurements of all living trees > 15 cm DBH (Table 5). Total plot basal area was calculated as the sum of the basal area of the individual trees, which was calculated using the standard equation for the area of a circle based on its diameter:

$$\mathbf{BA} = \sum [\pi\ (0.005*\mathbf{DBH})^2] \qquad \text{EQ. 1}$$

Tree DBH was measured at approximately 1.37 m above the soil (Newbould 1970). Density was calculated as the sum of the number of individual tree stems in a plot expressed in units of stems per hectare. Species richness was calculated as the total number of tree species observed within a plot. Diversity (H') was calculated using the following formula (Begon et al. 1996):

$$H' = -\sum_{i=1}^{S} P_i \ln P_i \qquad \text{EQ. 2}$$

where H' = Shannon diversity index, P_i = the relative proportion of the ith species, $\ln P_i$ = the natural log of the proportion of the ith species, and S = the total number of species in the community. Equitability (J), or the proportionality of the species, was calculated as follows (Begon et al. 1996):

Table 4. Site description of hemlock-dominated, mixed, and hardwood-dominated plots at Black Rock Forest (B), Ward Pound Ridge (W), and Delaware Water Gap (D). Initial descriptors were assessed in 1999 at B, 2000 at W, and 2001 at D. RI = Hemlock relative importance, CDC = mean crown defoliation class.

Forest	Stand	Plot	Elevation (m a.s.l.)	Aspect	RI	Cumulative Hemlock Mortality†	CDC††
Black Rock Forest	Hemlock	B1E	290	NNE	73.9	0.20	4.06
		B2E	310	WNW	60.3	0.26	3.59
		B3E	210	N	50.6	0.42	4.64
	Mixed	B4M	260	NE	38.1	0.09	3.82
		B5M	300	N	32.0	0.05	3.50
		B6M	260	NE	29.1	0.06	3.17
	Hardwood	B7A	340	N	3.1	0.01	1.67
		B8A	310	NE	0.3	-	-
		B9A	340	SW	0.0	-	-
Ward Pound Ridge	Hemlock	W1E	180	SSE	62.9	0.00	5.00
		W2E	165	S	53.0	0.09	5.00
		W3E	215	NE	84.8	0.31	4.92
	Mixed	W1M	180	S	38.1	0.00	5.00
		W2M	165	W	19.9	0.00	4.60
		W3M	215	W	27.7	0.08	4.86
	Hardwood	W1A	180	SE	5.4	0.04	-
		W2A	165	S	0.0	-	-
		W3A	215	SE	3.6	0.03	-
Delaware Water Gap	Hemlock	D1E	300	NW	65.1	0.00	2.46
		D2E	180	N	74.5	0.05	4.33
		D4E	500	W	86.3	0.00	3.29
	Mixed	D1M	480	W	17.8	0.00	1.00
		D2M	340	SW	40.8	0.03	3.27
		D4M	540	S	21.1	0.00	1.17
	Hardwood	D1A	500	W	0.0	-	-
		D2A	380	S	0.0	-	-
		D4A	600	NE	0.0	-	-

† Sum of relative number of dead trees to total number of live trees from 1999-2002 at B, 2000-2002 at W, and 2001-2002 at D.

††CDC = subjective measure of hemlock defoliation on a scale from one to six: (1) = 0-5% defoliation; (2) = 5-25%; (3) = 25-50%; (4) = 50-75%; 5 = 75-99%; and (6) = dead.

- hemlock not present in these plots.

Table 5. Community characteristics of hemlock-dominated, mixed, and hardwood-dominated plots at Black Rock Forest (B), Ward Pound Ridge (W), and Delaware Water Gap (D). Community properties were calculated on all live and standing dead trees > 1 cm DBH and all live trees > 15 cm DBH. BA = Basal Area, H' = Shannon diversity index, J = equitability.

Plot	All live and dead trees > 1 cm DBH					All live trees > 15 cm DBH				
	BA (m^2 ha^{-1})	Density (ha^{-1})	Species Richness	H'	J	BA (m^2 ha^{-1})	Density (ha^{-1})	Species Richness	H'	J
B1E	48.5	888	8	0.84	0.41	40.4	675	8	1.01	0.49
B2E	41.3	1113	12	1.32	0.53	36.3	525	12	1.18	0.47
B3E	35.7	725	14	1.39	0.53	34.3	369	14	1.78	0.72
B4M	31.5	1063	9	1.56	0.71	28.4	325	9	1.48	0.82
B5M	31.9	1244	9	1.66	0.76	28.8	519	8	1.14	0.71
B6M	34.5	1169	8	1.65	0.79	29.3	331	8	1.43	0.89
B7A	20.5	1394	7	1.23	0.63	14.4	488	7	0.59	0.59
B8A	24.2	1369	13	1.97	0.77	19.9	200	8	1.88	0.90
B9A	27.3	875	9	1.87	0.85	23.9	294	9	1.23	0.76
W1E	58.7	425	5	1.20	0.74	19.0	150	5	1.56	0.97
W2E	45.3	800	4	0.90	0.65	19.0	175	4	1.28	0.92
W3E	31.5	700	3	0.51	0.46	19.0	300	3	0.72	0.66
W1M	30.3	650	7	1.74	0.84	28.5	350	6	1.57	0.88
W2M	27.8	975	7	1.49	0.77	25.8	350	4	0.99	0.71
W3M	28.5	800	6	1.84	0.94	25.8	500	6	1.58	0.88
W1A	21.8	800	8	1.94	0.88	19.8	275	7	1.85	0.95
W2A	32.0	1400	8	1.25	0.60	29.8	375	6	1.30	0.72
W3A	38.1	975	8	1.94	0.88	33.5	400	6	1.55	0.86
D1E	68.0	550	4	0.88	0.63	67.3	475	4	0.95	0.69
D2E	63.8	550	4	0.66	0.48	63.0	450	4	0.76	0.55
D4E	62.5	550	4	0.55	0.40	56.3	375	3	0.63	0.52
D1M	24.0	1350	11	1.86	0.77	22.0	325	7	1.58	0.81
D2M	60.3	1050	6	1.51	0.84	47.8	825	6	1.61	0.90
D4M	36.2	1825	11	1.74	0.73	28.3	450	7	1.72	0.89
D1A	19.3	1850	8	1.20	0.58	16.3	200	4	1.07	0.77
D2A	34.5	600	6	1.64	0.92	32.0	325	5	1.18	0.73
D4A	31.8	1800	8	1.40	0.67	25.3	275	4	1.16	0.72

$$J = H' / \ln S \qquad \text{EQ. 3}$$

where J = equitability value, H' = Shannon diversity value, and S = number of species present in the plot.

Data Analysis

Non-metric multidimensional scaling (NMS) was used to assess the relative similarities of the plots (PC-ORD, MjM Software, Gleneden Beach, Oregon, USA, McCune and Mefford 1999). The relative importance of all tree species in the plots was used to confirm plot classifications. These analyses followed the methods of McCune and Grace (2002). Analyses began with a preliminary assessment of species composition data using the "Autopilot mode" in order to determine the appropriate number of dimensions for the final analysis, to reduce stress ("badness of fit"), and maximize significance in the final analysis. Stress is defined as "the departure from monotonicity in the relationship between the dissimilarity distance in the original p-dimensional space and distance in the reduced k-dimensional space" (McCune and Grace 2002). The Autopilot mode analyzed the data initially with six dimensions "stepping down" or reducing toward one dimension. A randomization (Monte Carlo) test with 50 runs at each dimension was then used to compare whether the axes generated had less stress and greater significance than expected by chance. The appropriate number of dimensions as determined by the preliminary analysis was used for the final analysis. The data were re-run in the final analysis using a single run (as opposed to 50 runs) and three dimensions (no stepping down). The Sorensen's (Bray-Curtis) distance measure was used with a supplied starting configuration file (as opposed to random starting configuration). The final output of the data was graphed with a three-dimensional graph and the cumulative correlation coefficient was reported.

Prior to testing for an effect of hemlock dominance or decline on basal area and community properties, initial assessments of mortality and relative importance were used to identify whether there were differences in these variables between the six most common species in these forests. Differences in relative mortality of the six most common species were determined using Kruskal-Wallis test with $\alpha < 0.05$. If there were significant differences between species, post-hoc analysis of means using Kolmogorov-Smirnov two-sample test was used to assess differences between species. Species relative mortality was considered significantly different if $\alpha < 0.05$. Initial assessments of the relative importance for each of the six most common tree species were compared with subsequent relative importance measurements and analyzed using Wilcoxon signed-rank test. Changes in the relative importance over time were considered significant if $\alpha < 0.05$.

In order to assess differences between stand-types in changes in basal area, density, richness, diversity, and equitability over time, nested-repeated measures (RM) ANOVA was used. A nested design was used with stand-type as a subgroup within forest because stand-type is considered a random effect in this experimental design (Sokal and Rohlf 1995). Prior to all analyses, I verified the assumption of normality visually by using density displays and the assumption of homogeneity of variances by using Bartlett's Test. Because not all forests and tree sizes were sampled in all years (Table 4), separate RM analyses were conducted on data that were comparable across time intervals. The effects of stand-type or forest were considered significant if $\alpha < 0.05$.

Regression analyses were used to test the interaction between hemlock mortality and forest on changes in basal area and community properties. Analyses were conducted using the GLM function in SYSTAT. Data were examined for statistical outliers using Studentized residuals, where the criterion for elimination was $P < 0.05$. When detected, outliers were removed and analyses were re-run. If the interaction between the independent variable and forest was not significant, the regression was reanalyzed to

examine the effects of the independent variable and forest on the response variable. The effects or interactions of the independent variable and forest on the dependent variable were considered significant if $\alpha < 0.05$. Correlations between CDC and changes in basal area or community properties were tested using non-parametric correlation (Kendall's Tau statistic). Variables were considered correlated if $P < 0.05$. All analyses were conducted using SYSTAT 10 (SPSS Inc., Chicago, IL).

Results

Initial Plot Classification

Results of the NMS analysis supported the initial classification of plots into hemlock-dominated, mixed, and hardwood-dominated stand-types based on hemlock RI. The three-dimensional ordination had a cumulative r^2 value of 0.905 (Table 6). The three groups of loosely clustered points shown in Figure 1 corroborated the general pattern that the plots within a given stand-type had similar compositions and plots were generally less similar when compared to plots from other stands.

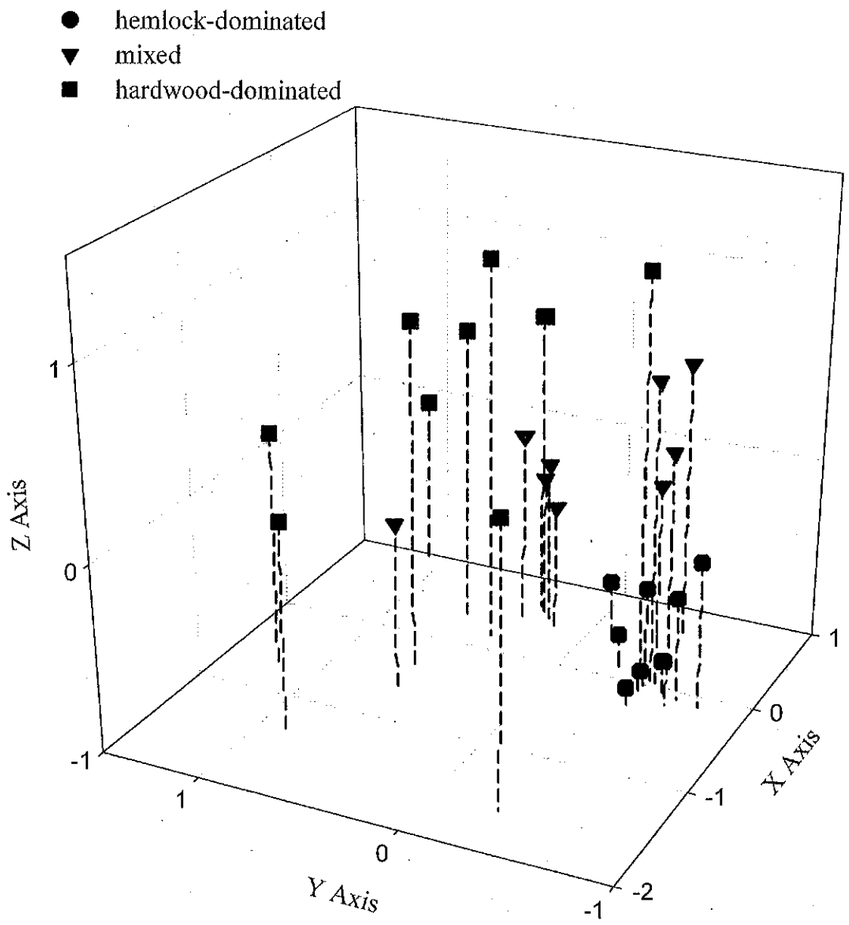
Compositional Change

Two important indicators of species decline, relative mortality and relative importance, suggested disproportionate decline of hemlock compared to the other common tree species in these forests. Species significantly varied in relative mortality between 1999 and 2002 at BRF and between 2000 and 2002 at BRF and WPR ($P = 0.013$ and 0.001, respectively). Post-hoc analysis of means showed significantly greater hemlock mortality than the other five most-common species across study sites (Figure 2). Relative hemlock mortality between 1999 and 2002 was also significantly greater in hemlock-dominated than mixed plots at BRF ($P = 0.031$; Table 7). There were no other significant effects of stand-type or forest on hemlock mortality. The relative importance

Table 6. Description and results of NMS analysis of community composition.

		All Species
Distance Measure		Sorensen
Dimensions		3
Iteration		500
Stress		9.94
Final Instability		0.009
r^2	Axis X	0.357
	Axis Y	0.198
	Axis Z	0.350
	Cumulative	0.905

Figure 1. Ordination of study plots using non-metric multidimensional scaling based on the relative importance of tree species from the initial measurements of all live and standing dead trees > 1 cm DBH.



of hemlock across stand-types and forests significantly decreased over time from a mean of 41.9 to 33.2 ($Z = -2.05$, $P = 0.040$; Table 8). No other examined species significantly changed in relative importance during this time period ($Z \leq |1.60|$; $P > 0.1$ in all cases). These data reflect the six most common species; no other species were examined because of an insufficient number of trees per plot to include in the analysis.

Changes in Basal Area and Community Properties

Effects of stand-type on changes in basal area, density, richness, diversity, and equitability were examined to assess whether hemlock dominance affected the potential impacts of the HWA on forests. A significant stand-type x time interaction (within subject effect) would indicate that changes over time did vary between stand-types. Whereas, if there was a significant effect stand-type alone (between subject effect), this result would indicate that stand-types differed in their composition, but the change in composition over time did not significantly differ between stand-types. There was significant stand-type x time interaction on total basal area at BRF between 1999 and 2002, BRF and WPR between 2000 and 2002, and at all three forests between 2001 and 2002 (summary of results in Table 9). The general pattern across forests and measurement periods showed a mean decrease in total basal area of 5 $m^2 ha^{-1}$ in hemlock-dominated plots (Figure 3). In contrast, total basal area decreased an average of 3 $m^2 ha^{-1}$ in mixed plots and increased 0.3 $m^2 ha^{-1}$ in hardwood-dominated plots. There were also significant forest effects and forest x time interactions on basal area (Tables 9 and 10). In general, basal area was the greatest at DWG compared to BRF and WPR.

There were significant stand-type x time interactions on the changes in density, diversity and equitability between 2000 and 2002 at BRF and WPR and on the change in equitability at BRF between 1999 and 2002 (summary of results in Table 9). The general pattern across forests showed density decreased by 97, 38, and 24 trees ha^{-1} in hemlock-dominated, mixed, and hardwood-dominated stand-types, respectively (Figure 4).

Figure 2. Mean (+ 1 SE) relative number of dead to live trees by species summed across years and pooled across stand-types at Black Rock Forest from 1999 to 2002. The pattern shown at Black Rock Forest was consistent with the pattern observed at Black Rock Forest and Ward Pound Ridge from 2000 to 2002. Species abbreviations are defined in Table 1. Different letters between species indicate means that are significantly different at $P < 0.05$ based on the Kolmogorov-Smirnov two-sample test. *H*: Kruskal-Wallis test statistic.

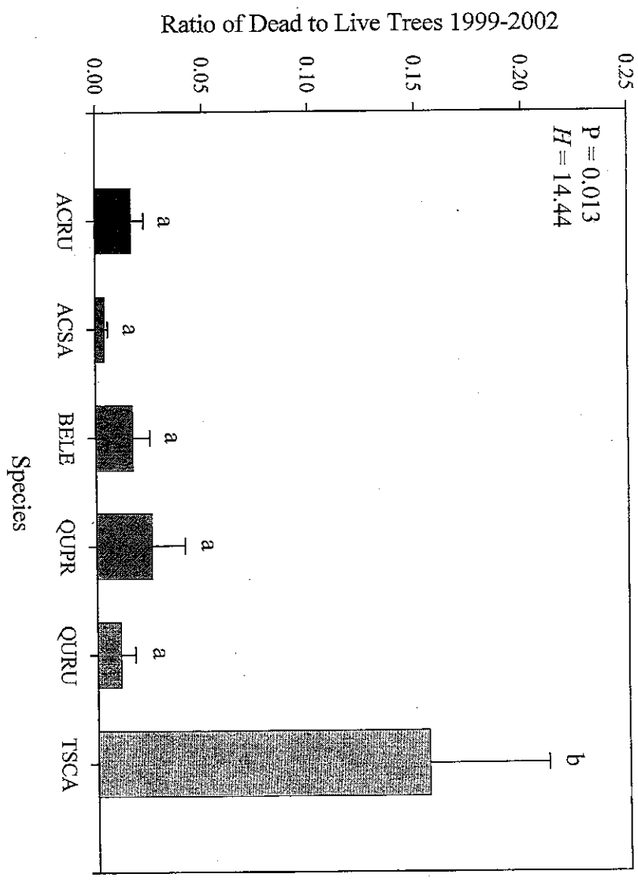


Table 7. Mean (1 SE) initial relative hemlock mortality based on the number of standing dead trees, mean annual relative hemlock mortality, and mean total hemlock mortality at Black Rock Forest (1999-2002), Ward Pound Ridge (2000-2002), and Delaware Water Gap (2001-2002).

Forest	Stand-type	Initial	Relative Hemlock Mortality			Total	
			1999-2000	2000-2001	2001-2002	1999-2002	2000-2002
Black Rock Forest	Hemlock	0.10 (0.02)	0.07 (0.03)	0.08 (0.01)	0.17 (0.04)	0.29 (0.07)	0.23 (0.06)
	Mixed	0.03 (0.01)	0.03 (0.01)	0.02 •	0.04 (0.01)	0.07 (0.01)	0.04 (0.01)
	Hardwood	0.00 •	0.01 •	0.00 •	0.00 •	0.01 •	0.00 •
Ward Pound Ridge	Hemlock	0.35 (0.11)	N/A	0.12 (0.10)	0.02 (0.02)	N/A	0.13 (0.10)
	Mixed	0.05 (0.02)	N/A	0.02 (0.02)	0.01 (0.01)	N/A	0.03 (0.03)
	Hardwood	0.02 (0.02)	N/A	0.00 (0.00)	0.03 (0.01)	N/A	0.03 (0.01)
Delaware Water Gap	Hemlock	0.06 (0.03)	N/A	N/A	0.02 (0.02)	N/A	N/A
	Mixed	0.00 (0.00)	N/A	N/A	0.01 (0.01)	N/A	N/A
	Hardwood	-	N/A	N/A	-	N/A	N/A

- hemlock not present in plots.
• 1 plots with hemlock therefore no standard error.
N/A plots were not measured over the specified time interval.

Table 8. Relative importance† of the six most common species, based on all live and dead trees >15 cm DBH at the initial sampling date at Black Rock Forest (B) in 1999, Ward Pound Ridge (W) in 2000, and Delaware Water Gap (D) in 2001, and for live trees >15 cm DBH at the final sampling date at all forest in 2002. Species abbreviations are defined in Table 1.

	ACRU		ACSA		BELE		QUPR		QURU		TSCA	
	Initial	Final	Initial	Final	Initial	Final	Initial	Final	Initial	Final	Initial	Final
B1E	1.3	1.9	-	-	1.1	2.2	20.3	15.8	5.9	8.9	71.0	59.9
B2E	9.0	9.2	0.0	1.0	5.3	5.8	8.1	7.1	8.5	10.7	51.3	36.6
B3E	8.0	0.0	0.0	12.7	1.3	0.0	13.0	9.8	14.3	17.8	39.1	20.0
B4M	2.5	2.9	2.7	4.3	3.2	3.7	38.8	28.2	29.9	36.6	23.0	13.8
B5M	-	-	-	-	1.1	1.6	45.5	35.2	16.7	16.9	45.9	33.7
B6M	1.0	2.3	4.5	1.2	7.1	6.0	19.4	23.1	44.9	42.7	19.4	23.7
B7A	-	-	-	-	-	-	78.3	81.5	15.1	17.7	3.4	4.0
B8A	2.0	1.7	11.0	9.4	6.0	5.3	10.9	22.8	32.0	29.7	-	-
B9A	0.0	1.3	5.5	4.4	9.2	11.0	59.4	60.3	0.0	2.3	-	-
W1E	-	-	5.5	15.0	12.8	41.8	-	-	-	-	69.0	15.7
W2E	-	-	11.3	21.5	5.2	29.8	-	-	-	-	76.3	35.7
W3E	-	-	-	-	11.0	24.2	-	-	-	-	85.3	60.8
W1M	14.3	14.4	-	-	13.7	13.7	-	-	-	-	38.1	38.1
W2M	-	-	60.0	59.0	4.5	4.6	11.3	10.7	-	-	24.8	25.1
W3M	-	-	15.5	9.3	7.8	4.5	24.3	17.8	27.9	25.3	27.7	29.2
W1A	7.5	7.5	0.0	6.4	15.8	15.6	33.5	33.5	18.8	19.0	6.4	6.3
W2A	-	-	53.0	50.0	6.5	6.9	-	-	17.4	18.2	-	-
W3A	-	-	19.8	17.7	8.8	5.1	4.2	3.8	9.2	18.2	5.4	0.0
D1E	-	-	3.0	3.2	-	-	3.0	2.9	-	-	60.7	59.6
D2E	4.3	4.3	-	-	-	-	9.9	3.7	-	-	61.9	64.6
D4E	5.7	11.1	4.6	0.0	4.6	5.0	-	-	-	-	85.1	84.0
D1M	-	-	5.4	5.4	-	-	11.8	6.5	5.3	0.0	40.7	40.5
D2M	-	-	-	-	13.8	13.7	-	-	14.4	11.0	37.2	39.1
D4M	-	-	27.0	24.1	20.9	21.8	5.9	5.8	-	-	7.3	7.7
D1A	-	-	-	-	-	-	7.8	7.8	-	-	-	-
D2A	4.7	4.7	-	-	-	-	12.9	12.9	-	-	-	-
D4A	6.4	11.8	5.5	0.0	-	-	0.0	0.0	-	-	-	-

†Relative Importance = (Relative basal area + Relative density)/2 x 100.
- species not present in the specified plots.

Table 9. Results of repeated measures ANOVA on effects of stand-type and forest on changes basal area, density, richness, diversity and equitability over time at Black Rock Forest (B), Ward Pound Ridge (W), and Delaware Water Gap (D). df = degrees of freedom, F = F ratio, P = probability. Significant interactions with time denote a within subject effect in the RM ANOVA. Significant treatment effects and interactions are denoted by bold typeface. Three plots from BRF in 2001 were not included in analysis due to missing data.

				Basal Area		Density		Richness		Diversity		Equitability	
Effect	**Forest**	**Year**	**df**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**
Stand-type	B	1999-2002	2	9.26	**0.015**	1.01	0.417	1.63	0.272	0.17	0.848	1.08	0.397
Stand-type x time			2	5.42	**0.045**	3.52	0.097	0.17	0.850	2.36	0.176	5.20	**0.011**
Forest	B, W	2000-2002	1	3.32	0.093	3.50	0.086	14.00	**0.018**	0.08	0.782	5.38	**0.039**
Stand-type (Forest)			4	6.89	**0.004**	2.57	0.091	1.47	0.173	0.28	0.884	0.37	0.822
Forest x time			1	2.48	0.141	11.14	**0.006**	31.25	0.109	2.72	0.125	1.24	0.287
Stand-type (Forest) x time			4	5.16	**0.012**	4.71	**0.016**	3.25	0.951	3.40	**0.044**	3.38	**0.045**
Forest	W, D	2001-2002	1	20.98	**0.001**	3.81	0.075	0.32	0.582	3.74	0.077	12.22	**0.004**
Stand-type (Forest)			4	11.36	**<0.001**	3.12	0.057	8.60	**0.002**	5.91	**0.007**	6.78	**0.004**
Forest x time			1	1.00	0.337	0.08	0.778	2.00	0.183	0.02	0.888	0.40	0.537
Stand-type (Forest) x time			4	0.59	0.679	0.33	0.850	1.00	0.445	1.55	0.249	0.54	0.708
Forest	B, W, D	2001-2002	2	13.54	**< 0.001**	2.06	0.166	13.33	**<0.001**	1.57	0.240	4.31	**0.033**
Stand-type (Forest)			6	9.42	**< 0.001**	2.28	0.092	3.92	**0.001**	2.43	0.077	2.83	**0.048**
Forest x time			2	11.21	**0.001**	7.63	**0.005**	23.35	**0.012**	0.75	0.491	1.15	0.344
Stand-type (Forest) x time			6	3.82	**0.016**	2.05	0.122	1.84	0.995	2.75	0.052	0.86	0.550

Figure 3. Changes in mean (± 1 SE) total basal area of all tree species in hemlock-dominated, mixed, and hardwood-dominated plots from (A) 1999 to 2002 at Black Rock Forest, from (B) 2000 to 2002 at Black Rock Forest and from (C) 2001 to 2002 at Ward Pound Ridge. There was a significant stand-type x time interaction observed in the repeated measures ANOVA (Table 9). Representative data from the specified forest are shown; the general pattern was consistent across forests. Note axis breaks on the *y*-axes. F: Forest; S(F): Stand-type(Forest); *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$; NS: Not significant.

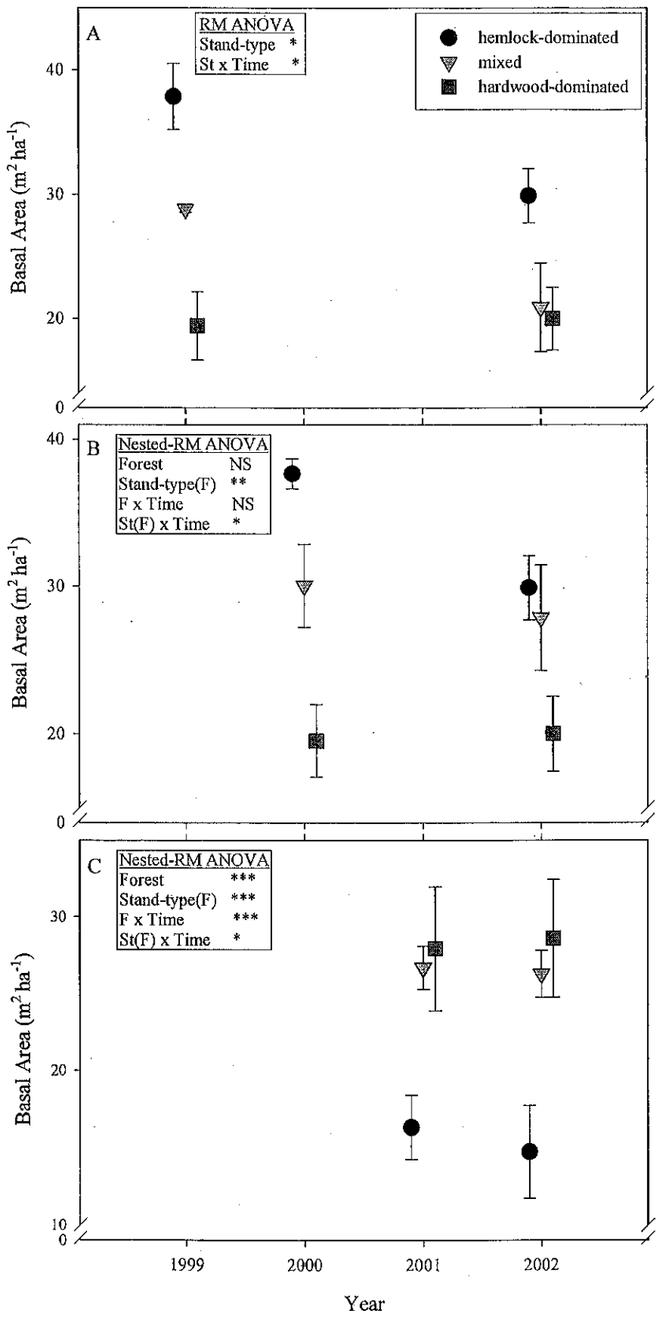
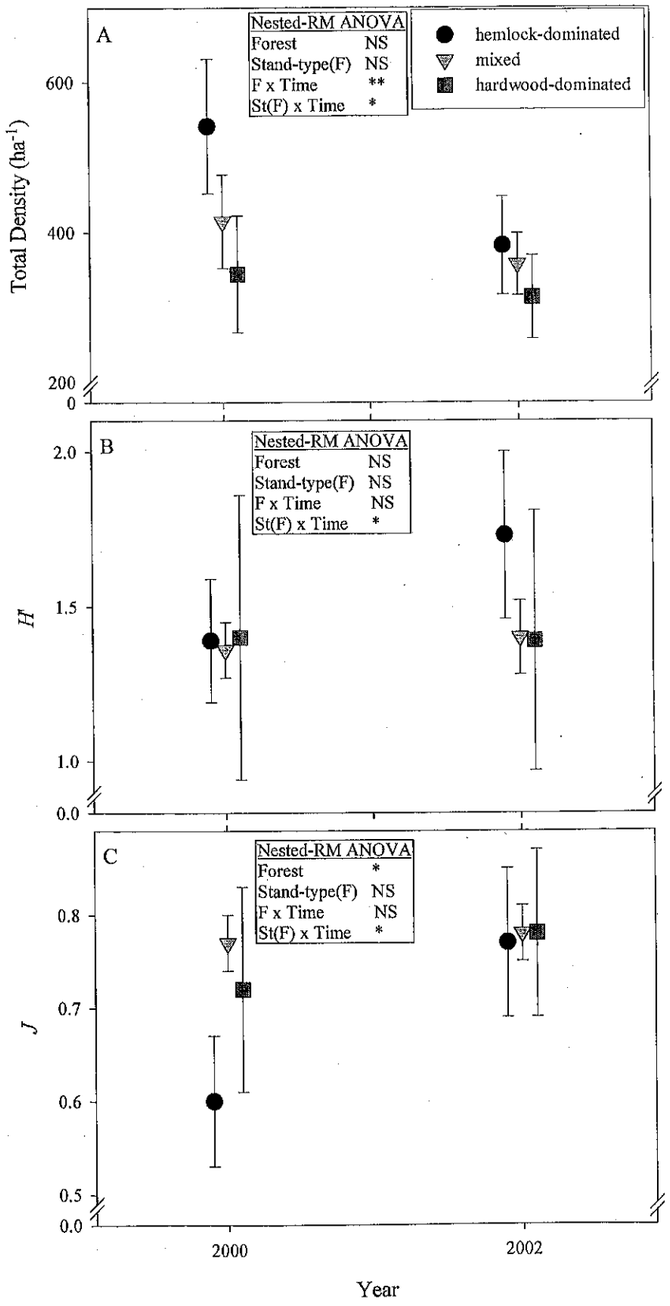


Table 10. Mean (1 SE) basal area ($m^2\ ha^{-1}$), density (ha^{-1}), richness, and equitability in 2000, 2001, and 2002 at Black Rock Forest (B), Ward Pound Ridge (W), and Delaware Water Gap (D). Refer to Table 9 for overall ANOVA results.

	Basal Area**		Density			Richness*			Equitability*		
Forest	2001	2002	2000†	2001††	2002	2000	2001	2002	2000	2001	2002
B	22.9 (1.86)	25.9 (2.07)	433 (43.9)	375 (51.9)	345 (40.5)	10.4 (1.1)	10.5 (1.2)	8.0 (1.4)	0.69 (0.05)	0.73 (0.06)	0.77 (0.05)
W	24.4 (2.58)	24.8 (2.60)	319 (24.7)	300 (38.0)	297 (36.2)	5.2 (0.4)	5.2 (0.4)	5.1 (0.4)	0.84 (0.04)	0.86 (0.03)	0.87 (0.03)
D	41.6 (6.03)	42.1 (6.10)	N/A	411 (59.8)	411 (62.1)	N/A	4.9 (0.5)	5.0 (0.6)	N/A	0.73 (0.04)	0.75 (0.05)

N/A plots were not measured over the specified time interval.
Significant forest effects are represented by *: $P < 0.05$; **: $P < 0.01$.
Significant forest x time interactions are represented by †: $P = 0.006$; ††: $P = 0.005$.

Figure 4. Changes in mean (± 1 SE) (A) total density, (B) diversity (*H'*) and (C) equitability (*J*) from 2000 to 2002 at Black Rock Forest and Ward Pound Ridge. There was a significant stand-type x time interaction observed in the nested-repeated measures ANOVA (Table 9). Representative data from Black Rock Forest are shown; the general pattern was consistent across forests. Note axis breaks on the *y*-axes. F: Forest; S(F): Stand-type(Forest); *: $P < 0.05$; **: $P < 0.01$; NS: Not significant.



Conversely, diversity increased by a mean of 0.22 and 0.02 in hemlock-dominated and mixed stand-types, respectively, but decreased by 0.02 in hardwood-dominated stand-types. Equitability increased by a mean of 0.12, 0.01, and 0.01 in hemlock-dominated, mixed, and hardwood-dominated stand-types, respectively. At BRF between 1999 and 2002, the equitability increased in hemlock-dominated stands and decreased in mixed and hardwood-dominated stands (Figure 5). There were also significant effects of forest, and forest x time interactions on density, richness, and equitability (Tables 9 and 10). In general, the greatest richness occurred at BRF and the greatest equitability occurred at WPR. There were significant forest x time interactions on density from 2000 to 2002 at BRF and WPR, and from 2001 to 2002 at all forests. In general, the greatest density change occurred at BRF.

Effects of Hemlock Mortality and CDC

Regression analysis was used to examine effects of hemlock mortality on changes in basal area, density, richness, and diversity over time. Between 2000 and 2002, an increase in hemlock mortality was associated with a significant decrease in basal area and density change, and significant increase in diversity change at BRF and WPR (Figure 6). Although there was a significant forest effect on changes in basal area, density, and richness between 2000 and 2002 and between 2001 and 2002 (Tables 9 and 10), there were no significant interactions between forest and hemlock mortality on changes in basal area, density, richness, or diversity. Crown defoliation class was not correlated with changes in basal area, density, richness, and diversity ($P > 0.05$ for all comparisons).

Discussion

Across 1999 to 2002, the rate of hemlock mortality was 4 to 15 times higher than the mortality rates of the five other prevalent tree species examined (Figure 2). Another

Figure 5. Change in mean (± 1 SE) equitability (*J*) from 1999 to 2002 at BRF. There was a significant stand-type x time interaction observed in the repeated measures ANOVA (Table 9). Note axis break on the *y*-axis. *: $P < 0.05$; NS: Not significant.

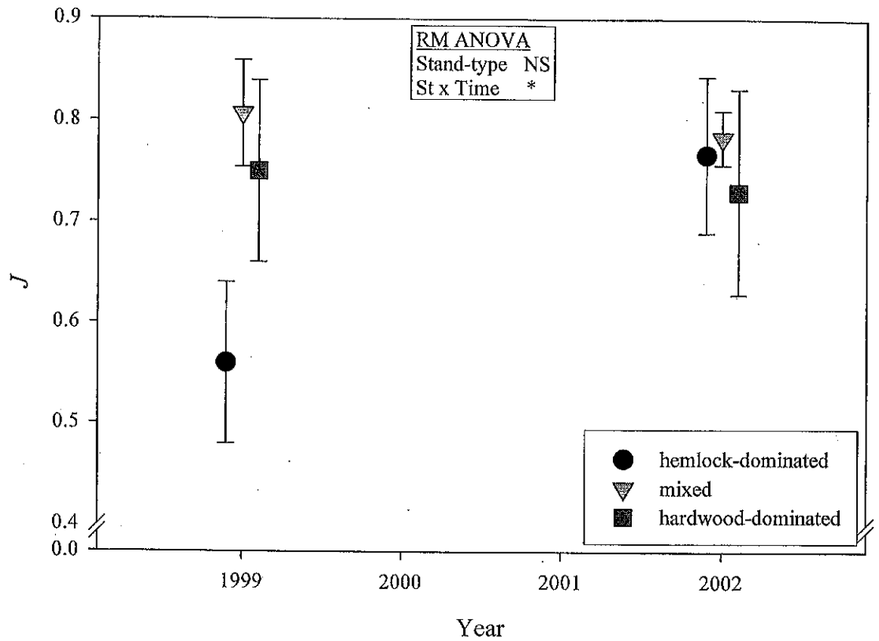
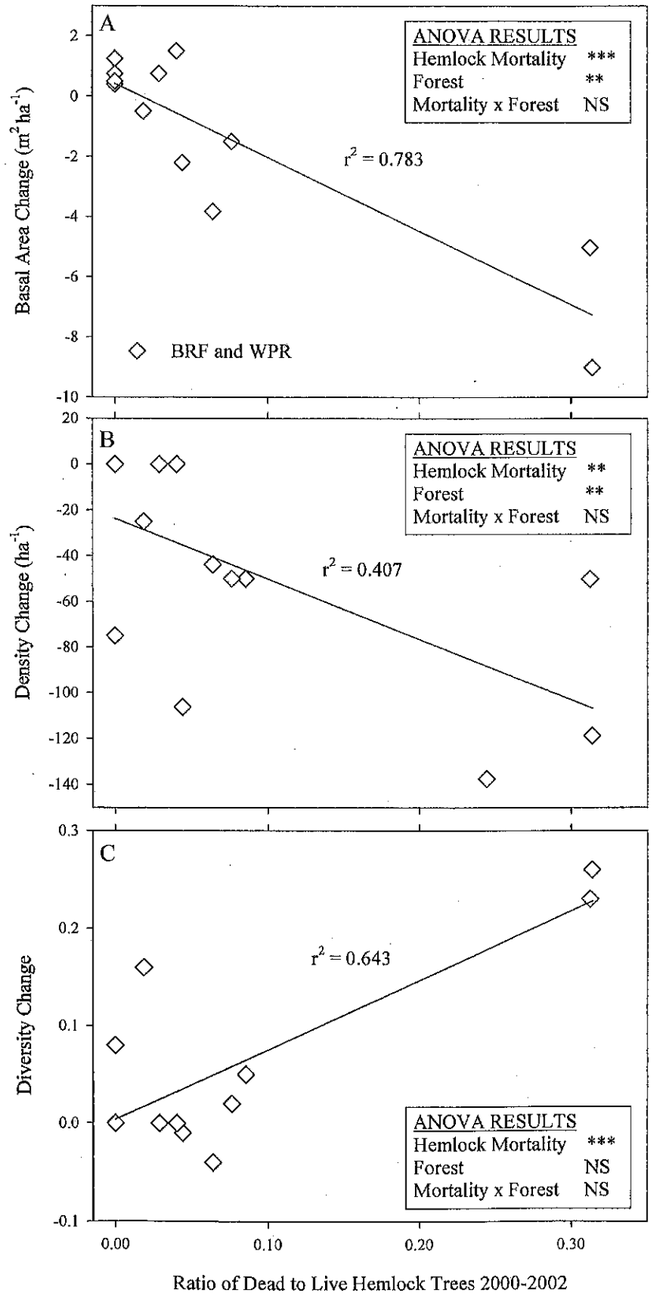


Figure 6. The effect of hemlock mortality between 2000 and 2002 on changes in (A) basal area, (B) density, and (C) diversity between 2000 and 2002 at Black Rock Forest (BRF) and Ward Pound Ridge (WPR). The corresponding regression equations were: basal area change = 0.42 - 24.49 (hemlock mortality); density change = -23.71 - 264.25 (hemlock mortality); diversity change = -0.001 + 1.15 (hemlock mortality). *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$



important indicator of hemlock decline was the greater relative decrease in hemlock relative importance compared with the other tree species measured (Table 8). I inferred that the HWA had a large effect on hemlock based on the high hemlock mortality rates and decreased hemlock relative importance (Battles et al. 2000, W. Schuster, Black Rock Forest – personal communication). HWA invasion is also associated with greater hemlock mortality relative to other species (McClure 1990, Orwig and Foster 1998, Jenkins et al. 1999). Impacts of the HWA on hemlock mortality support the hypothesis that hemlock relative importance and hemlock mortality are driving factors for community change.

The role of hemlock dominance in the response of community composition to hemlock decline was observed in the significant interactions between stand-type and time on basal area change. The greatest decreases in basal area occurred in hemlock-dominated stands while basal area generally increased only in hardwood-dominated stands (Figure 3). These results were consistent with my hypothesis that as hemlock dominance increased there would be a decrease in basal area over time. Further, the magnitude of the decrease in basal area in hemlock-dominated stands is consistent with the decreases observed in other studies of hemlock-dominated forests (Orwig and Foster 1998, Jenkins et al. 1999). For example, basal area declined 2 – 48% from pre-hemlock mortality (Jenkins et al. 1999), similar to the 5 – 21% basal area decrease observed in hemlock-dominated plots in this study. The greater decline in basal area in hemlock-dominated stands compared with other stand-types is also consistent with the greater relative hemlock mortality in hemlock-dominated stands (Table 7).

The gradient of hemlock dominance also affected changes in community properties between 2000 and 2002. The greatest changes in density, diversity and equitability occurred in hemlock-dominated stands compared to mixed and hardwood-dominated stands (Figure 4). Density decreased the greatest whereas diversity and equitability increased the greatest in hemlock-dominated stands. Hemlock mortality

influenced the disproportionate decrease in stem density with increasing hemlock dominance. Increases in diversity with increasing hemlock dominance were also associated with the increase in hemlock mortality and are consistent with other studies on the impacts of hemlock decline on community diversity (Orwig and Foster 1998, Kizlinski et al. 2002). This pattern of increased diversity with increasing mortality is due to the pattern of gap formation and successional processes. Fast-growing, early successional species grow rapidly in open areas, such as areas affected by hemlock mortality. Diversity may also increase because of the mathematical relationship between diversity and species abundance; diversity increases as species abundance becomes more even. The pattern of decreased density and increased diversity may not continue across all time intervals because, after mortality occurs, the dead trees are eliminated from the plot and the redistribution of species abundance alters the community properties. Additionally, variation in abiotic factors may influence communities over time.

Selective mortality of hemlock was associated with significant decreases in hemlock dominance (Figure 2, Table 7). Across stand-types, as hemlock mortality increased between 2000 and 2002 basal area and density decreased; whereas diversity increased (Figure 6). This pattern is consistent with other short-term impacts associated with mortality or disturbance. After insect-related disturbances, there is an initial decrease in basal area and density until (1) there is enough time for unaffected co-occurring species to compensate (Mackey and Sivec 1973) and (2) there is recruitment of new individuals (Runkle 1990). The increase in diversity after the disturbance is related to the decline in the relative importance of the affected tree species, and the increase in abundance of the co-occurring trees. Following disturbances, there may be additional increases in diversity as novel species are introduced into the area (Connell and Slatyer 1977). This increase in diversity will continue until dominant species begin to selectively eliminate sub-dominant species. However, the pattern of increased diversity after disturbance will only occur in areas where the affected species is a dominant tree.

Therefore, the influence of mortality on community structure, as well as future successional processes, depends on the species present at the time of the disturbance and environmental factors that influence the growth and establishment of species.

The effects of hemlock mortality on basal area, density, richness, and diversity were expected to be paralleled by the effects of increasing CDC on these parameters. I expected CDC to be related to changes in basal area because increasing CDC should be associated with increased light transmittance through the canopy, which in turn would increase light available for growth of co-occurring tree species. However, there was no relationship between CDC and basal area, density, richness, or diversity. The expected increases in co-occurring trees due to the increases in resource availability did not offset the loss of hemlock in hemlock-dominated stands. Other studies also did not observe relationships between CDC and species abundance (Orwig et al. 2002). The lack of correlation may be due to the pattern of HWA disturbance (McClure 1990). Because the HWA causes gradual disturbances over many years (McClure 1991b; Orwig and Foster 1998); the initial defoliation event may reduce tree vigor while the tree remains productive. However, after two cycles of infestation, mortality often occurs. This disturbance pattern causes gradual changes to forest composition and decreases basal area. Also, the impact of CDC on communities may be a function of the relative dominance of hemlock. For example, defoliation of a relatively high number of trees in hemlock-dominated areas compared to mixed areas should cause a greater decrease in tree vigor and basal area increment further influencing stand-level responses. With large stand-level changes, there will likely be greater seedling recruitment, light availability, and growth increment of trees co-occurring with hemlock in hemlock-dominated stands.

Although my study emphasized that hemlock decline would cause changes in communities in the near term, these short-term analyses may also foreshadow long-term changes to forest communities. In fact, long-term studies communities affected by insects or pathogens observed similar changes in community properties as in this study.

For example, after 30 years or more of forest regeneration following the decline of the American chestnut, Keever (1953) and Stephenson (1986) observed increases in richness associated with the chestnut decline. Additionally, modeling the effect of beech bark disease on trees co-occurring with beech showed increased hemlock density at the end of the initial 25 year period of the model (LeGuerrier et al. 2003). The long-term changes in community properties observed in other studies are consistent with the patterns observed following the mortality of hemlock.

In summary, the relative dominance and decline of eastern hemlock caused short-term decreases in basal area and density, and increases in diversity and equitability. This study is the first to indicate that impacts of the HWA varied depending on the relative dominance of hemlock. The impact of HWA also caused the selective mortality of hemlock, and is likely one of the main factors that influenced community change. Because patterns were not consistent across all time intervals, hemlock decline may also be regulated by other factors, such as water availability, that were not examined in this study. The short-term changes observed in this study may foreshadow long-term changes in the community structure, because changes immediately following disturbances may dictate the future composition and successional processes (Egler 1954). The decline of a dominant tree, such as hemlock, will also affect ecosystem properties by altering resource availability and because of the specific site conditions associated with hemlock (Rogers 1980, Rooney and Dress 1997).

While studies on disturbance or decline caused by other biotic or abiotic factors have shown changes to communities and ecosystems over the long-term (Bormann and Likens. 1979, Clark 1990, Foster and Zebryk 1993, Fain et al. 1994, Johnson 1995, Abrams and Orwig 1996), this study revealed short-term effects on basal area, density, and diversity in response to hemlock decline associated with an invasive non-native insect. These short-term effects on hemlock communities in turn may influence

ecosystem services, particularly water quality and nutrient availability, and also displace organisms that utilize hemlock as their primary habitat or resource.

Chapter 3

Impacts of Hemlock Decline and Dominance on Changes in Net Primary Production and Biomass

Introduction

Invasive insects may alter net primary production (NPP) and standing biomass by increasing plant mortality rates and altering plant community composition (Keever 1973, Brown and Schroeder 1999). Unlike other disturbances, which often affect a wide range of plant species, invasive insects often directly affect only one or a few species (McClure 1991b, Byington et al. 1994). As a result, invasive insects (native or non-native) negatively influence ecosystem processes, such as NPP. These negative effects may differ greatly from the other types of disturbances (Vose et al. 1999, Li et al. 2003). In addition, the impacts of invasive insects on NPP are likely to vary with the relative dominance of the host species (Runkle 1990). Although some studies have assessed the influence of native insect outbreaks on production (Romme et al. 1986, Piene et al. 2003), few studies have assessed the effect of non-native invasive insects on NPP and standing biomass, or how other factors, such as relative host dominance and related community properties, may influence the impacts of invasive insects on NPP and biomass.

Net primary production and biomass differ in their response during the recovery and development of forests following a disturbance (Bormann and Likens 1979). After a disturbance event, the rapid growth of seedlings and greater growth rates of established trees increase the annual accumulation of organic matter (NPP; Hibbs 1982, Romme et al. 1986). In contrast, total community biomass, the amount of living matter at a point in time (Whittaker 1961, Newbould 1970), recovers more slowly (Odum 1969), requiring many years of tree growth to compensate for lost biomass. Thus, in early stages of forest

development, biomass accumulates relatively rapidly, though total biomass is relatively low. As ecosystems mature, NPP decreases while total biomass is at its maximum (Odum 1969, Mattson and Addy 1975). This pattern reflects increasing competition between plants and decomposers in mature ecosystems (Loreau 1998). However, the inclusion of biotic events, such as herbivory, may alter interactions between biomass and NPP during ecosystem development (Odum 1969). Because of the temporal variability in the growth and establishment of forests following defoliation, understanding both the short-term and long-term responses of forests is critical for predicting the impacts of invasive insects on NPP and standing biomass.

The negative effect of invasive insects on NPP and standing biomass may vary with the relative amount of host decline. Defoliation caused by invasive insects initially reduces production of host trees because of the removal of leaf components. If mortality is limited, short-term effects of defoliation may subsequently increase production by stimulating an increased photosynthetic rate and growth of new tissue (Mattson and Addy 1975, Turner et al. 1995, Schlesinger 1997). Such patterns have been observed during episodic outbreaks of several native invasive insects (Romme et al. 1986, Piene et al. 2003). For example, foliage weight increased in trees affected by spruce budworm (Piene et al. 2003) and mountain pine beetle (Romme et al. 1986). Growth increment was greater in infested trees that survived than in protected trees (Romme et al. 1986). Thus, insect-related defoliation and mortality may increase ecosystem-level NPP depending on the degree of disturbance and the response of the affected host species.

Currently, an invasive non-native insect, the hemlock woolly adelgid (HWA; *Adelgis tsugae* Annand.) is causing widespread mortality and defoliation of eastern hemlock (*Tsuga canadensis* (L.) Carr.). Because eastern hemlock is a widespread tree species in the eastern US (Braun 1950), the decline of hemlock is expected to have extensive effects on biomass and NPP. One key factor likely to influence the response of NPP and biomass is hemlock dominance because in areas of high relative dominance

there will probably be a greater reduction in tree density. Further, the impact on NPP may also be greater in areas of high hemlock dominance because of the potential response of co-occurring trees to the decline of hemlock. The greater resource availability associated with the defoliation and mortality of hemlock is likely to increase the growth rates of co-occurring trees and also stimulate the production of understory seedlings and saplings. If hemlock decline is offset by increased growth rates of co-occurring trees, the HWA may lead to a net increase in NPP in hemlock-dominated stands. The loss of a dominant tree species on NPP and standing biomass will likely have cascading effects on understory microclimate (Jenkins et al. 1999), soil community structure (Turner 2003), and higher trophic level organisms that utilize hemlock as a resource (Rooney and Dress 1997).

In this study, I examined short-term (< 5 years) and long-term (≈ 15 years) effects of hemlock decline and dominance on NPP and biomass. Hemlock decline and dominance are expected to affect biomass and NPP by shifting resources to unaffected co-occurring species (Matson and Addy 1975) or by altering species recruitment and growth (Canham 1989, Foster et al. 1997). Because the impact of hemlock decline is likely to vary depending on species composition, I assessed ecosystem responses in areas of high, intermediate and low hemlock composition. The objectives of this study were to: (1) assess the effect of hemlock dominance and decline on short-term growth response in three regional forests; (2) assess the effect of hemlock dominance and decline on short-term changes in biomass increment, leaf litterfall, and the sum of biomass and litterfall (NPP) in one of these forests; and (3) compare short-term and long-term (15 years) changes in growth between stand-types and species in order to contrast growth rates of hemlock and co-occurring tree species over different time periods. I hypothesized that there would be a short-term increase in NPP and a short-term decrease in standing biomass, with the greatest change occurring in hemlock-dominated stands. In addition, I hypothesized that basal area would decrease significantly more in hemlock-dominated

stands compared to mixed or hardwood-dominated stands over a 15 year period, unless the growth or establishment of co-occurring or new individuals compensated for hemlock decline.

Methods

Changes in NPP and biomass were examined in three regional forests in southern New York and northwestern New Jersey/northeastern Pennsylvania. Plots in Black Rock Forest (BRF), Ward Pound Ridge Reservation (WPR) and Delaware Water Gap National Recreation Area (DWG) were studied to assess the effects of hemlock dominance and decline on biomass and NPP. At the time of the study, the three regional forests had similar compositions, but different levels of HWA-related mortality (Chapter 2). In addition to the measurements conducted at all forests, leaf litterfall was collected at BRF in order to assess the effect of hemlock decline and dominance on changes in leaf litterfall. BRF was also used to assess long-term changes in basal area prior to and during hemlock decline.

In each of the three forests, three plots were established in each of three stand-types, hemlock-dominated, mixed, and hardwood-dominated, for a total of 27 plots (Table 4, Chapter 2, Page 25). Stand-types were defined using an index of hemlock relative importance (RI; the average of relative density and relative basal area) calculated from initial measurements of all trees > 1 cm diameter at breast height (DBH; 1.37 m above ground level) in 1999 at BRF, in 2000 at WPR, and in 2001 at DWG. Plots were considered hemlock-dominated if hemlock RI was ≥ 50% (Chapter 2). Mixed plots ranged from 6 to 49% hemlock RI, and hardwood-dominated plots were < 6% hemlock RI. Detailed descriptions of all three forests and community properties are provided in Chapter 2 (Table 5, Page 26). Biomass change was measured on live trees > 15 cm DBH from 1999 to 2002 at BRF, 2000 to 2002 at WPR, and 2001 to 2002 at DWG (Table 1).

Table 1. Plot biomass, basal area and relative importance by species in hemlock-dominated (E), mixed (M), and hardwood-dominated (A) stands from Black Rock Forest (B), Ward Pound Ridge (W), and Delaware Water Gap (D). Relative importance was measured on live trees > 15 DBH at the onset of measurements at each forest. Described species were present in > 30% of the study plots (Chapter 2, Table 1, Page 16).

Plot	Biomass (Mg ha^{-1})	Basal Area (m^2 ha^{-1})	Relative Importance† by species					
			ACRU	ACSA	BELE	QUPR	QURU	TSCA
B1E	189.1	33.5	1.9	-	2.2	15.8	8.9	59.9
B2E	157.0	26.0	9.2	1.0	5.8	7.1	10.7	36.6
B3E	179.9	25.6	0.0	12.7	0.0	9.8	17.8	20.0
B4M	187.5	24.4	2.9	4.3	3.7	28.2	36.6	13.8
B5M	150.9	23.0	-	-	1.6	35.2	16.9	33.7
B6M	251.3	32.9	2.3	1.2	6.0	23.1	42.7	23.7
B7A	94.0	14.4	-	-	-	81.5	17.7	4.0
B8A	212.7	23.6	1.7	9.4	5.3	22.8	29.7	-
B9A	163.2	19.9	1.3	4.4	11.0	60.3	2.3	-
W1E	153.5	19.6	-	15.0	41.8	-	-	15.7
W2E	63.9	12.5	-	21.5	29.8	-	-	35.7
W3E	62.3	13.4	-	-	24.2	-	-	60.8
W1M	197.6	29.6	14.4	-	13.7	-	-	38.1
W2M	200.8	26.9	-	59.0	4.6	10.7	-	25.1
W3M	141.6	24.1	-	9.3	4.5	17.8	25.3	29.2
W1A	165.3	21.4	7.5	6.4	15.6	33.5	19.0	6.3
W2A	269.6	30.4	-	50.0	6.9	-	18.2	-
W3A	253.3	35.3	-	17.7	5.1	3.8	18.2	0.0
D1E	273.9	67.3	-	3.2	-	2.9	-	59.6
D2E	358.8	63.9	4.3	-	-	3.7	-	64.6
D4E	278.4	56.8	11.1	0.0	5.0	-	-	84.0
D1M	118.1	23.7	-	5.4	-	6.5	0.0	40.5
D2M	270.6	50.1	-	-	13.7	-	11.0	39.1
D4M	189.3	31.6	-	24.1	21.8	5.8	-	7.7
D1A	125.0	18.7	-	-	-	7.8	-	-
D2A	312.6	33.6	4.7	-	-	12.9	-	-
D4A	241.3	29.2	11.8	0.0	-	0.0	-	-

ACRU, *Acer rubrum* L.; ACSA, *Acer saccharum* Marsh.; BELE, *Betula lenta* L.; QUPR, *Quercus prinus* L.; QURU, *Quercus rubra* L.; TSCA, *Tsuga canadensis* (L.) Carr.
† Relative Importance = average of relative basal area and relative density displayed as a percent.
- species were not present in these plots.

Measuring trees within or near the canopy is common in many other studies (Romme et al. 1986, Agrawal and Stephenson 1995, Keever 1973, Dunn 1986, Abrams and Orwig 1996) and trees > 15 cm DBH accounted for approximately 90% of the basal area in the watersheds.

Stem biomass was calculated from regression equations that directly relate biomass to DBH (Ter-Mikaelian and Korzukhin 1997). Although studies have developed regression equations to calculate stem biomass using other variables in addition to DBH (e.g. height), adding additional variables did not substantially increase the correlation coefficient (Freedman et al. 1982, Ter-Mikaelian and Korzukhin 1997). The basic formula used for calculating biomass was:

$$\mathbf{M = aD^b} \qquad \text{EQ. 1}$$

where M is oven-dry weight (kg), D is the DBH (cm), *a* is the slope, and *b* is a species-specific parameter that defines the allometric regression equation. For the majority of the forest species, specifically, American beech (*Fagus grandifolia* Ehrh.), American basswood (*Tilia americana* L.), black birch (*Betula lenta* L.), yellow birch (*Betula alleghaniensis* Britt.), eastern hemlock, hickory (*Carya spp.*), red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.), chestnut oak (*Quercus prinus* L.), red oak (*Quercus rubra* L.), white oak (*Quercus alba* L.), and yellow poplar (*Liriodendron tulipifera* L.), values used for *a* and *b* were from Brenneman et al. (1978). Parameter values from Bridge (1979, as cited in Ter-Mikaelian and Korzukhin 1997) were used to calculate biomass of black oak (*Quercus velutina* Lam.); values from Perala and Alban (1994) were used to calculate biomass of American elm (*Ulmus americana* L.); and values from Ker (1980) were used to calculate biomass of eastern white pine (*Pinus strobus* L.).

At BRF, above-ground NPP was calculated by summing biomass change (stem growth) and plant losses (leaf litter) using the following formula (Newbould 1970)

$$\mathbf{ANPP = \Delta B + L} \qquad \text{EQ. 2}$$

where ΔB is the change in above-ground biomass from t_1 to t_2 and L is the leaf loss due to leaf litterfall. Although the original equation included a parameter to incorporate leaf loss due to herbivory or consumption, this parameter was not included in this study because sap-feeding insects do not significantly affect leaf area through consumption (Meyer 1993, Carson and Root 1999). The impact of sap-feeding insects, like the HWA, is measured by the increased loss of leaves by the host plant, captured through litterfall collection (Meyer 1993, Carson and Root 1999). The estimate of ANPP at BRF is conservative, or perhaps an underestimate, as other herbivores may impact leaf loss, and therefore ANPP, in these forests. Other studies have quantified leaf loss due to herbivores at < 10% of the total NPP (Aber and Melillo 1991).

To examine leaf litterfall patterns, 12 collection baskets, each with an area of 2.25 m^2, were placed randomly within the central 20 x 20 m area of each plot at BRF. Baskets were lined with 1 mm mesh and set in a fixed position using a 12" nail in order to prevent basket movement and to maintain a consistent collection area. However, events such as wind, rain and animal disturbance caused some movement or destruction of litter baskets. Approximately 4% of the 108 baskets were affected by disturbance. Disturbed baskets were eliminated from analyses. Litter was collected 24 times from August 1999 to November 2001. The most intensive sampling (every 1 – 2 weeks) occurred in autumn, when the majority of leaf loss occurred. Sampling occurred every other month from the end of the winter throughout the rest of the year. Immediately upon returning from the forest, leaves were dried to a constant mass at 50°C. After drying, leaves were sorted by species and weighed. For 1999, leaves from all baskets were sorted and weighed. For

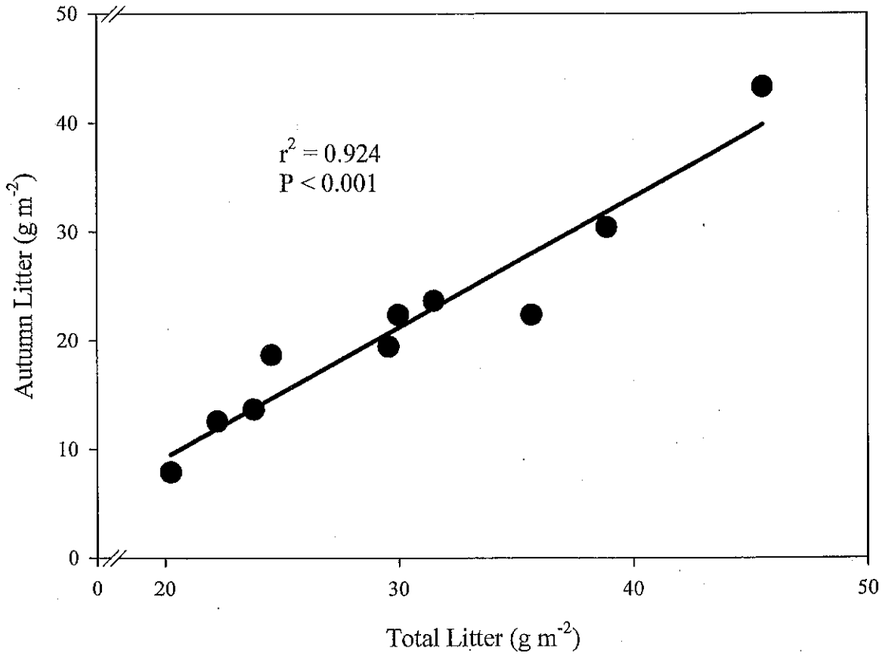
2000 and 2001, leaf material from six of the baskets in each plot were sorted and weighed from collections occurring during peak litterfall (approximately September 15 to November 5) because in general, the greatest amount of leaf litterfall occurred during this time interval (data not shown). In order to obtain a better estimate of total leaf litterfall during 2000 and 2001 for NPP calculations, a linear equation relating peak autumn litterfall to total litterfall (August to December) was calculated using the data from 1999 (Figure 1). The total litterfall amounts for each plot during 2000 and 2001 were separately extrapolated using this regression equation and the average basket contents during the autumn.

To examine long-term patterns of species growth between 1985 and 2000, DBH was re-measured on all trees within 33 long-term plots at BRF. These plots were established in 1985 using procedures outlined in Chapter 2 (Page 21). The three stand-types were equally represented in the 33 plots. Nine of the 33 plots were the same plots used for short-term analyses at BRF.

Data Analysis

To assess differences between stand-types in short-term changes in biomass, repeated measures analysis of variance (ANOVA; SYSTAT v.10, SPSS Inc., Chicago, IL) was used. When analyses included data collected from more than one forest, stand-types were nested as a random variable within forest to account for variation between forests (Sokal and Rohlf 1995). Separate analyses were conducted to account for the different forest sampling intervals (Table 3, Chapter 2, Page 23). In addition, data from WPR and DWG were analyzed separately from data from all three forests in 2001 to 2002 to assess any influence of missing data from BRF in 2001. I verified the assumption of normality visually by using density displays, and of homogeneity of variances by using Bartlett's Test. Effects were considered significant if $\alpha < 0.05$.

Figure 1. Relationship between autumn leaf litterfall (October 1999) and total leaf litterfall (August to December 1999) per plot. The corresponding equation is, October 1999 litterfall = -14.74 + 1.199x. Note axis break on the x-axis.



Regression analyses were used to assess the effect of mortality or community properties on biomass change. To assess the effects and/or interactions between forest and the specified independent variable, the GLM function in SYSTAT was used. Because not all forests were measured during all measurement intervals, separate analyses were conducted for the following time intervals: BRF from 1999 to 2002; BRF and WPR from 2000 to 2002; WPR and DWG from 2001 to 2002; and all three forests from 2001 to 2002. Studentized Residuals was used to test for statistical outliers. Detected outliers ($P < 0.05$) were removed and the regression was reanalyzed. Effects were considered significant if $\alpha < 0.05$. Non-parametric correlations between CDC and biomass change were tested using Kendall's Tau statistic.

Stand-type differences in NPP at BRF were tested using single factor ANOVA. In addition, stand-type differences in the two components of NPP, biomass change and leaf litterfall, were tested individually using ANOVA. Because litter collection baskets in two plots were re-located after the 1999 litter collection, litterfall was only compared between 2000 and 2001. The effects and interactions of stand-type and species on standing biomass and leaf litterfall were analyzed using two-way repeated measures ANOVA. In order to assess the pattern of hemlock needlefall over time, repeated measures ANOVA was used to assess interactions between stand-type and time on hemlock needlefall from August to December 1999. Finally, repeated measures ANOVA was used to test the separate and interactive effects of stand-type and species on basal area growth between 1985 and 2000.

Results

Effects on Biomass

Effects of stand-type on changes in biomass were examined to assess whether decline in hemlock dominance altered the response of biomass accumulation.

Specifically, a significant stand-type x time interaction (within subject effect) would indicate that the biomass change varied between stand-types. Significant stand-type effects alone (between subject effects) would indicate that stand-types differed in their standing biomass, but the rate of change did not differ between stand-types. There were significant stand-type x time interactions on the change in biomass between 2001 and 2002 at WPR and DWG, and at all three forests (Table 2). Data from WPR (Figure 2) illustrate the general pattern across forests that biomass increased an average of 3.2 Mg ha^{-1} in hemlock-dominated stands, 2.5 Mg ha^{-1} in mixed stands and 4.1 Mg ha^{-1} in hardwood-dominated stands. In addition, there was a significant stand-type effect on biomass at BRF and WPR in both 2000 and 2002, with the smallest standing biomass occurring in hemlock-dominated stands (Figure 3). There were also significant forest effects on mean biomass between 2001 and 2002 at WPR and DWG (WPR = 167.5 Mg ha^{-1}; DWG = 240.9 Mg ha^{-1}; P = 0.043). There were no other significant effects of stand-type and forest or interactions between stand-type or forest and time on biomass during the other time intervals.

Significant effects of hemlock decline on biomass change were assessed in this study to establish the potential impact of HWA on biomass change. Additional indirect effects of the HWA, for example, the effects of the HWA on community properties, may also alter the accumulation of biomass in these forests. There were significant interactions between richness and forest on changes in biomass at all three forests between 2001 and 2002, and at BRF and WPR between 2000 and 2002 (P = 0.004 and 0.005, respectively; Figure 4). As richness increased, there was a significant increase in biomass change at WPR across both time intervals. However, the slopes were not significantly different from zero at BRF and DWG. There was a significant interaction between diversity and forest on biomass change from 2001 to 2002 at all three forests (P = 0.010). As diversity increased there was a significant increase in biomass change at

Table 2. Repeated measures ANOVA of the effects of stand-type and forest on changes in biomass over time at Black Rock Forest (B), Ward Pound Ridge (W), and Delaware Water Gap (D). Significant interactions with time indicate a within subject effect in the RM ANOVA. Significant treatment effects and interactions are denoted by bold typeface. Treatment effects were considered significant if $P < 0.05$. df = degrees of freedom, F = F ratio, P = probability.

	Biomass				
Effect	**Forest**	**Year**	**df**	**F**	**P**
Stand-type	B	1999-2002	2	0.58	0.587
Stand-type x time			4	0.57	0.687
Forest	B, W	2000-2002	1	0.23	0.639
Stand-type (Forest)			4	3.54	**0.039**
Forest x time			1	2.06	0.177
Stand-type (Forest) x time			4	0.84	0.524
Forest	W, D	2001-2002	1	5.11	**0.043**
Stand-type (Forest)			4	3.05	0.060
Forest x time			1	4.29	0.060
Stand-type (Forest) x time			4	3.93	**0.029**
Forest	B†, W, D	2001-2002	2	3.68	0.050
Stand-type (Forest)			6	2.25	0.095
Forest x time			2	2.61	0.106
Stand-type (Forest) x time			6	2.95	**0.041**

†Three plots were not included in analysis due to missing data.

Figure 2. Mean (±1 SE) biomass in hemlock-dominated, mixed, and hardwood-dominated stand-types from 2001 and 2002. There was a significant stand-type x time interaction observed in the nested-repeated measures ANOVA (Table 2). Representative data from Ward Pound Ridge are shown; the general pattern was consistent across forests. Note axis break on the *y*-axis. F: Forest; S(F): Stand-type(Forest); *: $P < 0.05$; NS: Not significant.

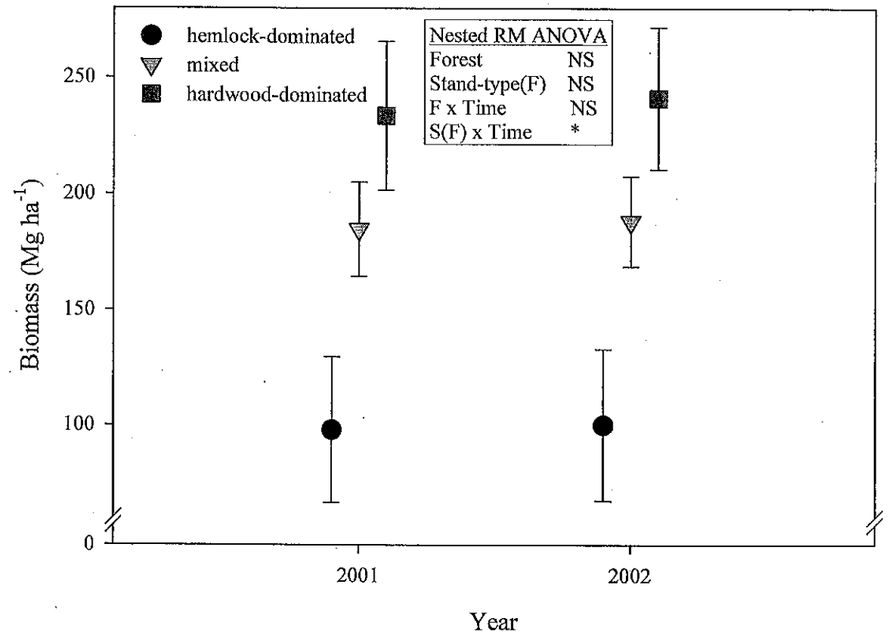


Figure 3. Mean (+ 1 SE) biomass in hemlock-dominated, mixed and hardwood-dominated stand-types at WPR. There was a significant stand-type effect observed in the nested-repeated measures ANOVA between 2000 and 2002 (Table 2). The stand-type effect was consistent over the study interval, as the stand-type x time interaction was not significant. Representative data from WPR are shown; the general pattern was consistent across BRF and WPR. F: Forest; S(F): Stand-type(Forest); *: $P < 0.05$; NS: Not significant.

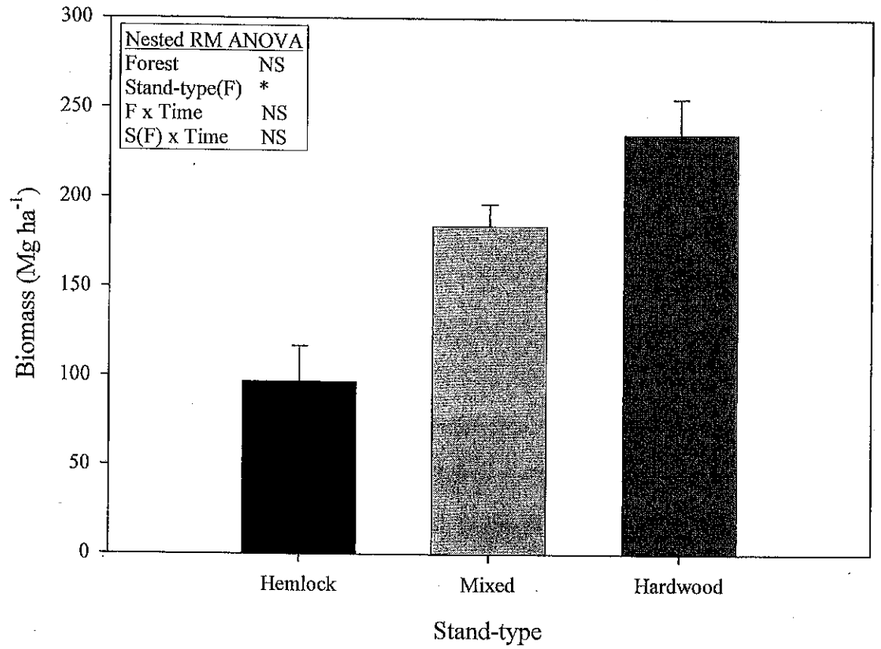
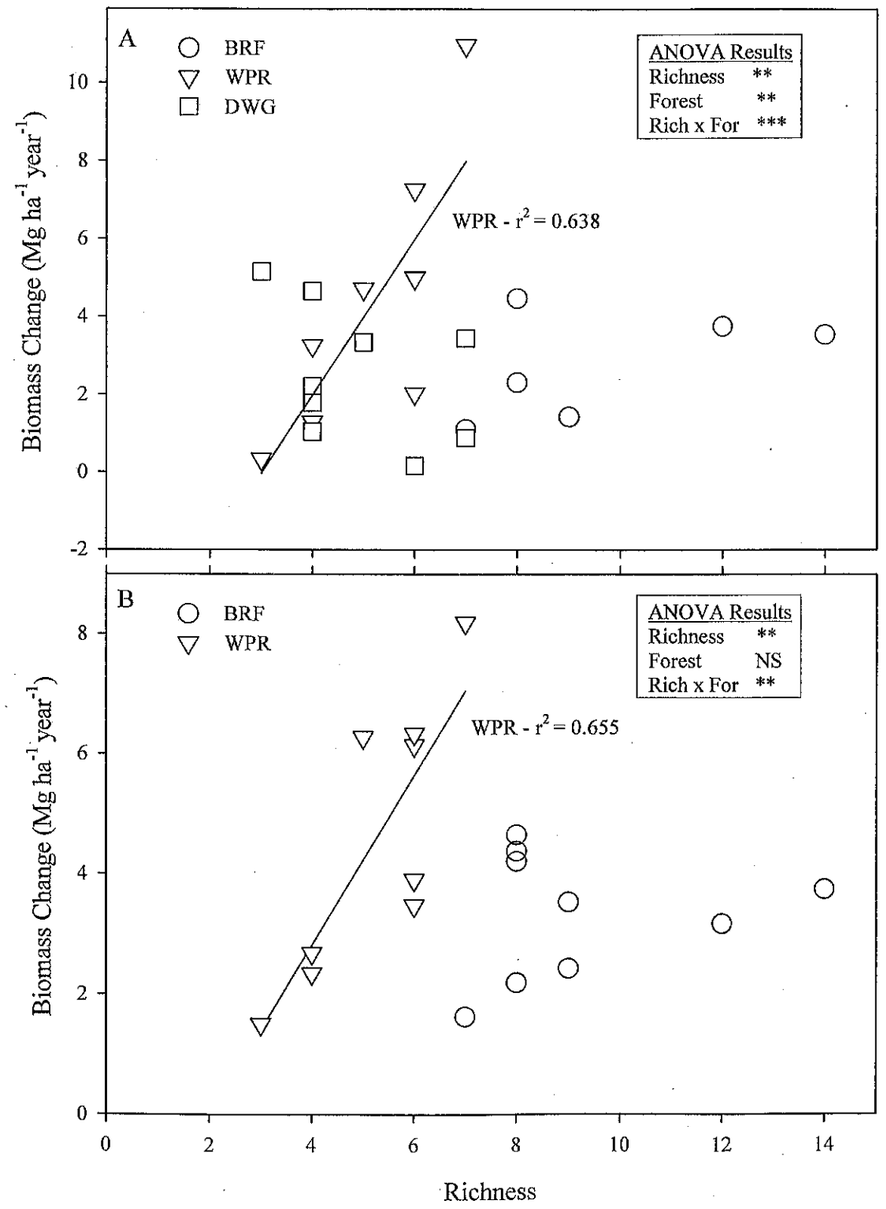


Figure 4. Effects of richness on biomass change at (A) Black Rock Forest (BRF), Ward Pound Ridge (WPR), and Delaware Water Gap (DWG) between 2001 and 2002 and (B) BRF and WPR between 2000 and 2002. Lines with slopes significantly different from zero at $P < 0.05$ are shown. The corresponding equations for WPR were, biomass change $_{2001\text{-}2002} = 2.00 + 6.03x$ and biomass change $_{2000\text{-}2002} = -2.84 + 1.41x$. **: $P < 0.01$; ***: $P < 0.001$; NS: Not significant.



BRF and WPR (Figure 5A), with a steeper slope occurring at WPR. The slope of diversity and biomass change at DWG was not significantly different from zero. Between 2000 and 2002, there was a significant effect of diversity on biomass change at BRF and WPR ($P < 0.001$). As diversity increased there was a significant increase in biomass change (Figure 5B). There were no significant effects or interactions between mortality and forest or between density and forest on biomass change. There was no significant correlation between CDC and biomass change from 2001 to 2002 ($P > 0.05$).

Effects on NPP

Changes in production were expected based on the direct effects of the HWA on hemlock growth and the indirect effects on the growth of trees co-occurring with hemlock. Mean above-ground NPP at BRF ranged from 2.7 to 5.9 Mg ha^{-1} $year^{-1}$ during the interval 2000 to 2001 (Table 3), but NPP did not significantly vary across stand-types (Table 4). In addition, there were no significant effects of stand-type on biomass change over all measurement periods. There was a significant interaction between stand-type and time on litterfall (Table 4, Figure 6). Between 2000 and 2001, litterfall decreased 6.7% and 26.2% in hemlock-dominated and mixed stands, respectively, and increased 9.8% in hardwood-dominated stands. In addition, there were significant interactions between species and time on biomass and litterfall at BRF (Table 5). All species except red oak had small increases in biomass and litterfall (Figure 7). Red oak had a large decrease in litterfall from 2000-2001.

The short-term patterns of hemlock needlefall were assessed from August 1, 1999 to December 15, 1999. Examining potential changes in the timing and extent of hemlock needlefall is important for understanding the impact of the HWA, because these factors influence the availability of resources for the growth or establishment of other species. Hemlock needlefall was significantly greater in hemlock stands compared to mixed or

Figure 5. Effects of diversity on biomass change at (A) Black Rock Forest (BRF), Ward Pound Ridge (WPR), and Delaware Water Gap (DWG) between 2001 and 2002, and at (B) BRF and WPR between 2000 and 2002. Lines with slopes significantly different from zero at $P < 0.05$ are shown. The corresponding equations are: BRF, biomass change = $-0.23 + 2.32x$; WPR, biomass change = $-4.34 + 6.37x$. The equation for the BRF and WPR (2000-2002) is: biomass change = $-0.68 + 3.44x$. Note axis breaks on the x-axes. **: $P < 0.01$; NS: Not significant.

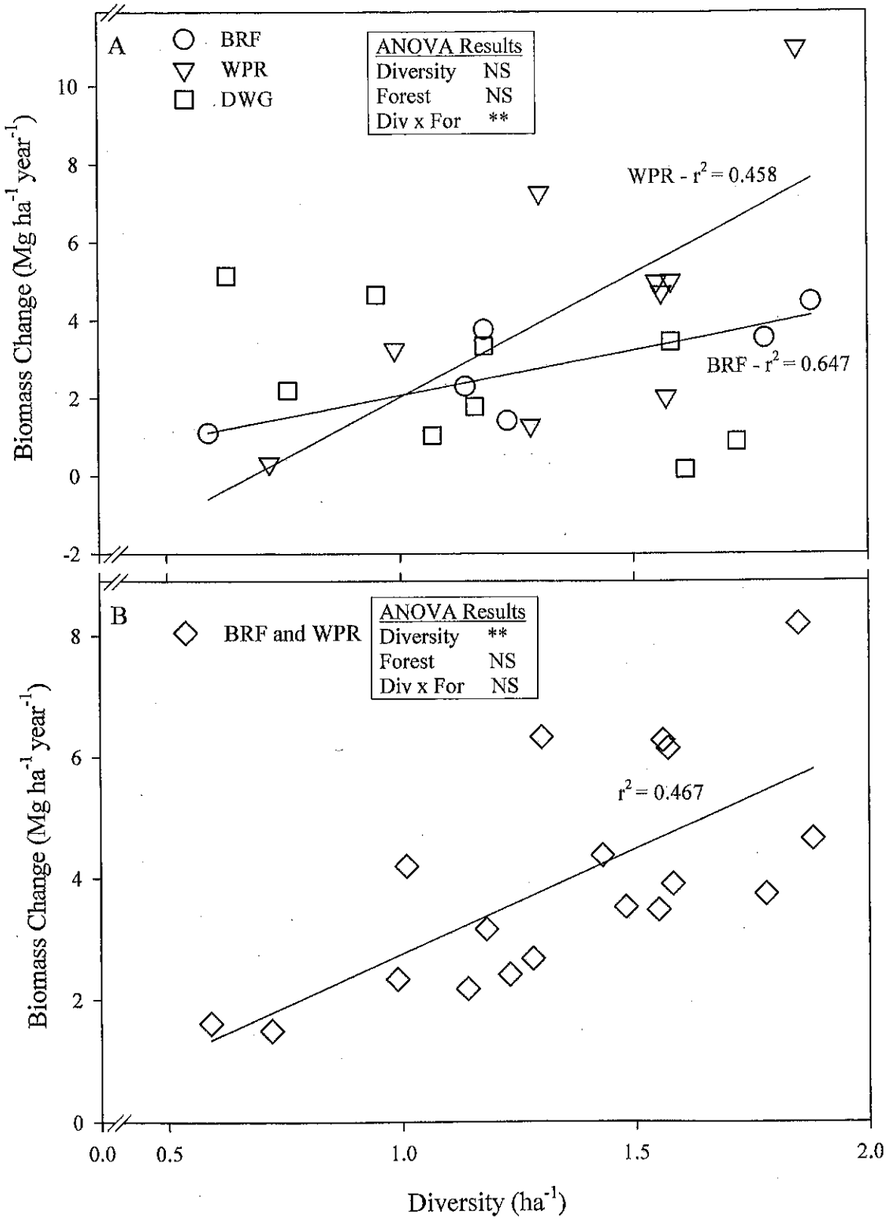


Table 3. Mean (1 SE) biomass, total leaf litterfall and NPP in hemlock-dominated, mixed and hardwood-dominated stand-types at BRF from 2000 to 2001 (n = 9). Total litterfall values are from the extrapolation of the 2000 and 2001 autumn litterfall amounts calculated using the equation from Figure 1.

	Biomass (Mg ha^{-1})		Litter (Mg ha^{-1} year^{-1})		NPP (Mg ha^{-1} year^{-1})	
Stand-type	2000	2001	2000	2001	2000	2001
Hemlock	180.5 (6.8)	120.2 (60.4)	0.79 (0.03)	0.76 (0.07)	5.9 (3.5)	4.0 (0.6)
Mixed	199.5 (31.1)	51.4 (51.4)	0.88 (0.08)	0.75 (0.04)	3.8 (1.9)	2.7 (N/A)
Hardwood	158.6 (32.6)	162.1 (33.3)	0.90 (0.09)	0.95 (0.09)	2.8 (2.7)	4.3 (0.8)

Table 4. Summary of ANOVA and repeated measures ANOVA on the effects of stand-type on NPP, biomass change, and litterfall at BRF. Data are pooled across tree species. Significant interactions with time denote a within subject effect in the RM ANOVA.

ANOVA						
			NPP		Biomass Change	
Effect	**Year**	**df**	**F**	**P**	**F**	**P**
Stand-type	2000	2	0.321	0.737	0.349	0.719
Stand-type	2001[†]	2	0.583	0.611	0.487	0.656
Stand-type	2000-2002	2	-	-	0.373	0.703
REPEATED MEASURES ANOVA						
			Leaf Litterfall			
Stand-type	2000-2001	2	1.210	0.362		
Stand-type x time		2	7.512	**0.023**		

[†] Three plots were not included in the analysis due to missing data.

Figure 6. Mean (± 1 SE) autumn leaf litterfall (Mg ha^{-1}) from Black Rock Forest in 2000 and 2001. Litterfall per area was calculated as the total amount summed across six collection baskets from the autumn of 2000 and 2001. There was a significant stand-type x time interaction observed in the repeated measures ANOVA (Table 4). Note axis break on the *y*-axis. *: $P < 0.05$; NS: Not significant.

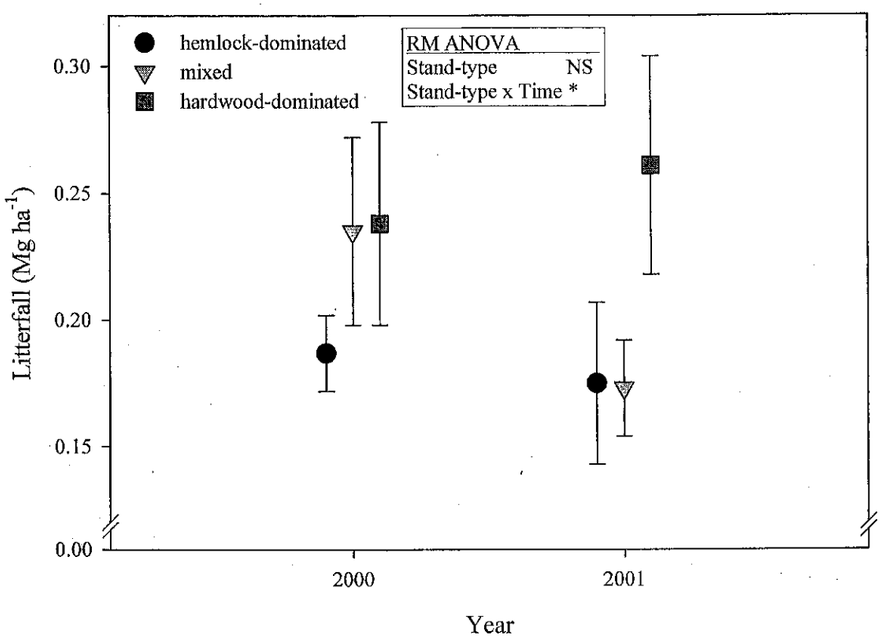
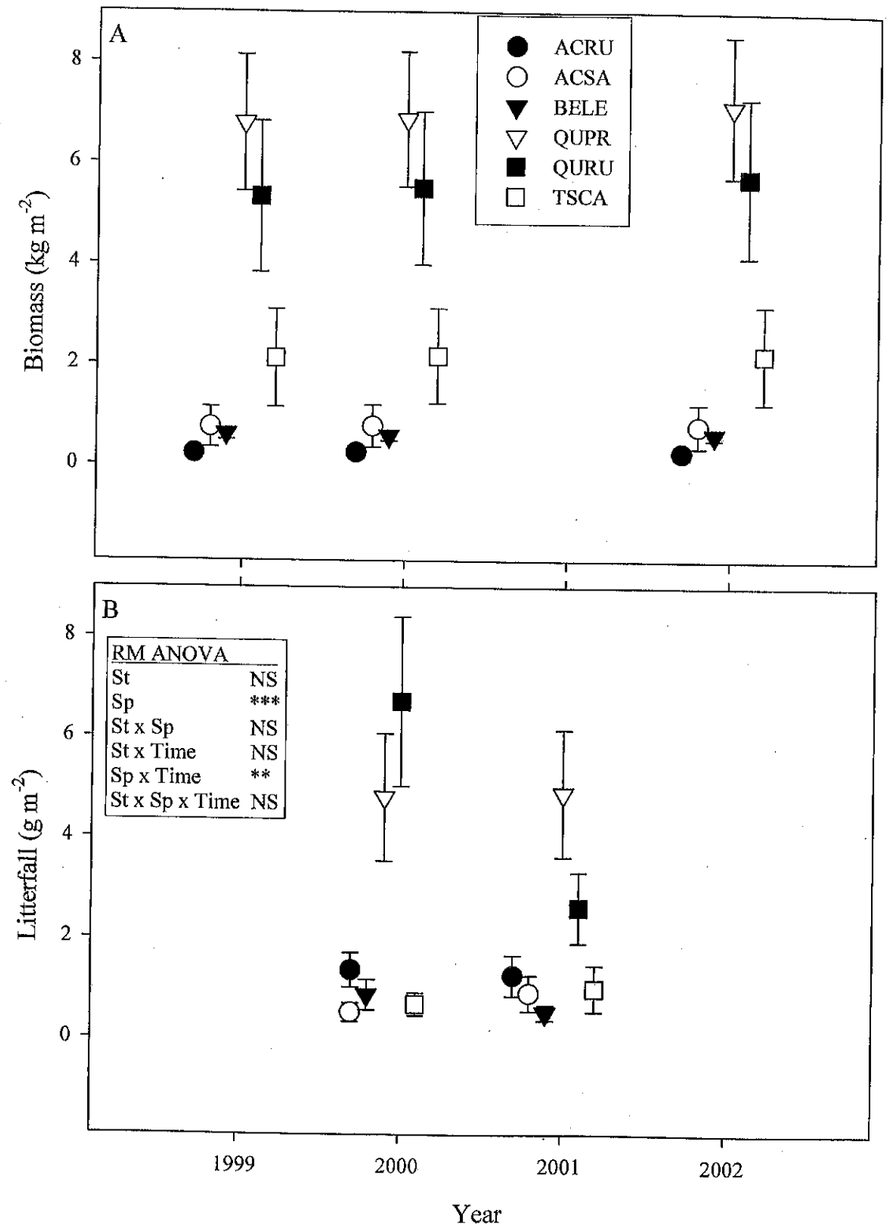


Table 5. Repeated measures ANOVA of the effects of stand-type, species, and stand-type by species on biomass and litterfall at BRF (n = 54).

		Biomass 1999 - 2002†		Litterfall 2000 - 2001	
Effect	**df**	**F**	**P**	**F**	**P**
Stand-type	2	0.552	0.582	1.134	0.333
Species	5	7.026	**< 0.001**	6.929	**< 0.001**
Stand-type x Species	10	1.136	0.375	0.655	0.757
Stand-type x time	4	0.047	0.996	1.166	0.323
Species x time	10	3.561	**0.001**	4.702	**0.002**
Stand-type x Species x time	20	0.485	0.961	1.467	0.192

†RM ANOVA excludes 2001 because of missing plot data.

Figure 7. (A) Mean (± 1 SE) biomass and (B) litterfall by species (Sp) at BRF. Data are pooled across stand-type (St) because there were no significant stand-type effects or significant interactions between species and stand-type on biomass or litterfall (Table 5). Species abbreviations are defined in Table 1. RM ANOVA results apply to both figures A and B. **: $P < 0.01$; ***: $P < 0.001$; NS: Not significant.



hardwood-dominated stands (P = 0.008; Figure 8). There was no significant effect of time on hemlock needlefall over the specified time interval (P = 0.104).

Long-term Patterns of Growth

The effects of stand-type on long-term changes in basal area demonstrate the growth rates of hemlock and trees co-occurring with hemlock prior to and during the introduction of the HWA. Plot basal area at BRF increased 19%, 17% and 31% in hemlock-dominated, mixed and hardwood-dominated stand-types, respectively, from 1985 to 2000 (Table 6), but stand-types did not significantly vary in standing basal area or in change in basal area over time (Table 7). In addition, there were no significant effects or interactions between stand-types, species or time on species growth rates between 1985 and 2000.

Discussion

Biomass increased between 2001 and 2002 in all stands, with the greatest change in hardwood-dominated stands (Figure 2). There were no significant effects of stand-type on biomass between 1999 and 2001. These results are counter to my hypothesis that the greatest biomass increase would occur in hemlock-dominated stands. Although I predicted that increased growth rates of co-occurring trees in hemlock-dominated and mixed stands would offset hemlock mortality (Chapter 2), these results suggest that hemlock mortality may have exceeded the compensatory response of co-occurring trees between 2001 and 2002. The lack of significant stand-type effects between 1999 and 2001 followed by significant stand-type effects between 2001 and 2002 infer that hemlock decline may negatively effect biomass change in hemlock-dominated stands. On the other hand, the high variability across stand-types, forests, and time may account for the lack of significant differences between stand-types in biomass change during the

Figure 8. Stand-type affected mean (+ 1 SE) hemlock needlefall from August 1, 1999 to December 16, 1999 at Black Rock Forest. There was a significant stand-type effect observed in the repeated measures ANOVA (P = 0.008). The stand-type effect was consistent over the study interval, as the stand-type x time interaction was not significant (P = 0.104). Note that to set needlefall amounts to constant units, values were adjusted to account for the different collection durations. *: P < 0.05; NS: Not significant.

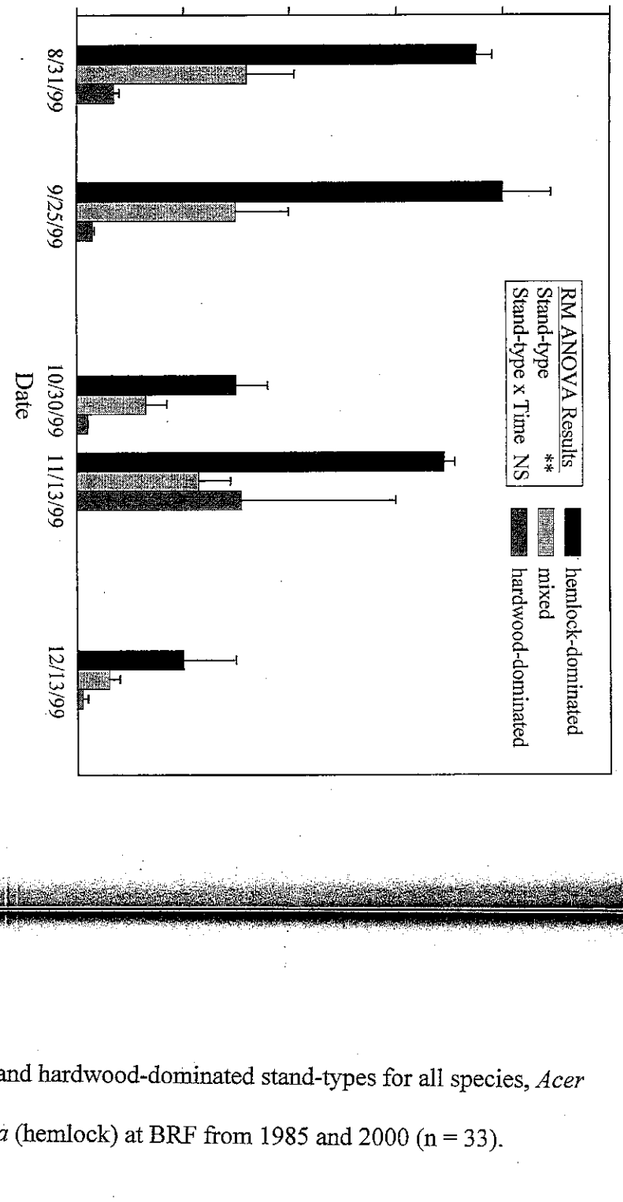


Table 6. Mean (1 SE) basal area in hemlock-dominated, mixed, and hardwood-dominated stand-types for all species, *Acer* (red and sugar maple), *Quercus* (chestnut and red oak), and *Tsuga* (hemlock) at BRF from 1985 and 2000 (n = 33).

	Basal Area (m^2 ha^{-1})							
	All Species		*Acer*		*Quercus*		*Tsuga*	
Stand-type	**1985**	**2000**	**1985**	**2000**	**1985**	**2000**	**1985**	**2000**
Hemlock	34.51 (5.33)	41.01 (5.95)	1.18 (1.15)	1.46 (1.41)	18.03 (4.32)	21.35 (5.23)	11.19 (3.88)	13.35 (3.99)
Mixed	34.32 (3.64)	40.04 (4.06)	2.36 (0.79)	2.90 (0.96)	17.33 (2.95)	20.45 (3.57)	9.81 (2.65)	10.39 (2.73)
Hardwood	20.92 (4.25)	27.25 (4.75)	0.42 (0.92)	0.54 (1.12)	17.13 (3.45)	22.68 (4.17)	0.42 (3.09)	0.56 (3.18)

Table 7. Repeated measures ANOVA of the effects of stand-type on basal area change between 1985 and 2000. Results reflect analyses conducted on data from all species, *Acer*, *Quercus*, and *Tsuga*.

		Basal Area 1985 - 2000							
		All Species		*Acer*		*Quercus*		*Tsuga*	
Effect	**df**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**
Stand-type	2	2.97	0.067	2.27	0.140	0.16	0.853	0.54	0.595
Stand-type x time	2	0.94	0.910	0.91	0.426	2.91	0.696	0.21	0.810

interval 1999 to 2001. In order to resolve these two opposing ideas, additional analysis of long-term growth rates of individual trees may help explain the different patterns observed between time intervals. Other studies have shown lower growth rates in hemlock trees as well as that biomass may take five to 50 years to respond to species decline or disturbance (Keever 1953, Reich et al. 1997).

In order to further resolve the inconsistent patterns observed over different time intervals, the results from the short-term analysis of biomass change were compared with NPP and the long-term changes in basal area measured at BRF. There were no significant stand-types effects on NPP or the long-term growth patterns. This long-term pattern, along with the short-term pattern at the beginning of this study (1999-2001) bolsters the argument that there were no differences in species growth rates in hemlock-dominated, mixed or hardwood-dominated stands. However, at the end of the study period, there were significant differences between stand-types suggesting commencement of the impact of the HWA on biomass change. The pattern observed at the end of the study period is consistent with other studies that observed greater growth rates of hardwood compared to hemlock trees (Reich et al. 1997), but inconsistent with lack of significant differences from 1985 to 2000 and from 1999 to 2001. Short- and long-term patterns of biomass accumulation suggest that hardwood stands began to have significantly greater growth rates relative to mixed and hemlock-dominated stands beginning in 2001. The greater growth rate occurred after 15 years of no significant differences between stand-types (based on both long- and short-term data) suggesting that the slower growth rate of hemlock trees or the increased growth rates of hardwood trees are commencing in these forests.

Hemlock decline may have an indirect effect on biomass change through the HWA effects on community properties (Chapter 2, Figure 6, Page 47). In my study, the relationship between diversity and biomass change at BRF and WPR between 2001 and 2002 showed a positive linear response (Figure 5), consistent with the general pattern

observed in other studies; there is greater production at sites with high diversity (Chapin et al. 2002). The relationship was not as clear for richness and biomass change where there was only a significant positive relationship at WPR (Figure 4). The community type, abiotic factors, and the scale of the study may alter the relationship between diversity and productivity (Tilman and Downing 1994). The significant interactions between richness and forests (Figure 4) and between diversity and forest (Figure 5) on biomass change show that forests differ in their responses to richness and to diversity. Nonetheless, the significant effects of community properties on production further influence biomass accumulation by altering the influence of hemlock on other species and subsequently increasing growth rates of trees associated with hemlock.

Litterfall significantly increased in hardwood-dominated plots and decreased in hemlock-dominated and mixed plots (Figure 6). This was not consistent with my hypothesis. I expected litterfall to be highest in hemlock-dominated stands, associated with increased production of trees co-occurring with hemlock or an increase in hemlock needlefall because of hemlock defoliation. As stated above, the effects of the HWA may have begun to occur in 2001 and 2002 and in fact caused a negative response in biomass change compared to hardwood-dominated stands. Therefore, the greater litterfall increase in hardwood-dominated stands was consistent with the biomass change observed in hardwood-dominated stands from 2001 to 2002. But the temporal pattern of hemlock litterfall (Figures 7 and 8) was relatively consistent across time suggesting the expected pulse of hemlock needlefall with hemlock mortality either occurred prior to the start of this study or had yet to occur in some plots. Thus, there was an impact of hemlock dominance and decline on litterfall, however the response was not expected based on the hypothesis that trees would increase production following defoliation or mortality.

For most species, biomass significantly increased over time, though the relative amount of change was small (Figure 7). Increases in biomass and litterfall were not consistent across all species. While tree biomass increased, leaf litterfall decreased in red

oak and red maple. These differences between biomass and litterfall may be attributed to the differential distribution of resources by individual trees to overcome environmental stress (Foster and Zebryk 1993, Rutkowski and Stottlemyer 1993, Spetich and Parker 1998), such as the severe drought conditions that occurred in 1999 (Heim and Changery, 1999; W. Schuster – Black Rock Forest, personal communication). Environmental stress may increase the amount of resources allocated to stem growth as opposed to leaves (Foster and Zebryk 1993). Although all components of production did not increase in all species, the redistribution of nutrients from less productive or dead individuals should increase the production of living trees following hemlock decline. However there were only species and no stand-type effects on biomass or litterfall from 2000 to 2001. Even so, the different amounts of litterfall contributed by different species across the forests will likely influence forest nutrient dynamics by contributing different amounts of resources to the forest floor. The role of hemlock dominance and decline on the amount of nitrogen in the leaves, litter, and soil will be discussed in Chapter 4.

In summary, there were significant short-term effects of stand-type on biomass change between 2001 and 2002 as hemlock dominance influenced the greater growth rates in hardwood-dominated stands compared to mixed or hemlock-dominated stands. The greater biomass change in hardwood-dominated stands may be a result of the decreased hemlock growth because of the HWA which caused lower biomass change in hemlock-dominated and mixed stands. The amount of hemlock mortality or the decrease in hemlock growth rates was greater than the proposed greater growth rate of co-occurring trees in hemlock-dominated and mixed stands. The effects of diversity and richness on biomass change correspond to the expected pattern; there was greater biomass change in plots with higher diversity and richness, but this pattern varied across forests. The variation in responses of biomass change and production to HWA impacts infer that production was likely moderated by other factors, including composition and abiotic factors that influence the growth rates of forest species following disturbances.

Chapter 4

Impacts of Hemlock Decline and Dominance on Nitrogen Pools and Fluxes

Introduction

Invasive organisms, hurricanes, and fires substantially alter nutrient cycling in forests (Bormann and Likens 1979, Lovett et al. 2002). Considerable attention has been devoted to the impacts of hurricanes and fires on nutrient cycling (e.g. Clark 1990, Fahey et al. 1991, Neill et al. 1997), while comparatively little is known about the impacts of invasive non-native insects (Jenkins et al. 1999, Lovett et al. 2002). More research on invasive insects is critical because ecosystem responses to abiotic disturbances may not accurately predict the impacts of invasive insects. Unlike abiotic disturbances, invasive insects often cause selective mortality of only one or a few tree species within a forest (Keever 1953, Parker and Leopold 1983, Runkle 1990, Lovett et al. 2002). Therefore, ecosystem responses to disturbances may reflect the type of disturbance, as well as the relative dominance of the imperiled tree species (Liebhold et al. 1995, Orwig 2002).

Another key factor in the response of forest ecosystems to disturbance is the amount and availability of nitrogen (N; Bormann et al. 1977) because N often regulates the growth and development of forests (Pastor et al. 1984, Nadelhoffer et al. 1985, Zak et al. 1989, Reich et al. 1997, Chapin et al. 2002, Jackson et al. 2002, Joshi et al. 2003). Accordingly, forest responses to disturbances may vary spatially with variation in soil nitrogen content (Reich et al. 1997; Lovett et al. 2002). Further, disturbances may alter the amount of internally cycled N (Lovett et al. 2004). Because external inputs of N are relatively small compared to internally cycled N (Schlesinger 1997), the alteration of N pools or fluxes may have an adverse effect on plant and microbial communities (Reich et

al. 1997), and forest recovery may be delayed until internal N cycling is re-established (Lovett et al. 2004). Therefore the recovering forest ecosystems from invasive insects may depend on the amount of available N.

The impact of invasive insects on nitrogen cycling is likely to vary with the extent of decline of affected trees. Specifically, mortality and defoliation add additional litter and increase light availability to the forest floor. Increased leaf litter to the forest floor influences the nitrogen cycle by adding organic matter for decomposition by the microbial community (Harris and Riha 1991). Increased light availability (Canham 1989) and warmer soil temperatures (Zak et al. 1989) increase microbial activity, which, in turn, increases available soil N (Schlesinger 1997). Therefore, with increasing tree defoliation and mortality, nitrogen availability will likely increase depending on the amount of leaf litter on the forest floor (Ferrari 1999) and changes in light availability (Canham 1989).

An ecosystem experiencing extensive tree mortality is the eastern hemlock forest (*Tsuga canadensis* (L.) Carr.) in the northeastern US. The decline of eastern hemlock, a dominant late-successional species (Braun 1950), is associated with the introduction of the hemlock woolly adelgid (HWA; *Adelgis tsugae* Annand.) into this region (Orwig and Foster 1998). In laboratory experiments, the HWA leads to mortality of eastern hemlock in approximately four years (McClure 1990), but may take shorter (Orwig and Foster 1998) or longer (W. Schuster – Black Rock Forest, personal communication) periods of time in natural habitats depending on the density of the HWA, abiotic factors (McClure 1991a, McClure 1991b), and perhaps genetic variation in HWA and hemlock. Hemlock decline is likely to have wide-ranging community and ecosystem effects because there is no other tree species in the eastern US that provides a similar deep shade and moist soils (Rogers 1978). As hemlock mortality continues, changes to community structure and ecosystem function will reflect the composition of species that replace hemlock in areas formerly dominated by hemlock (Orwig and Foster 1998). Accordingly, both the relative

impact of the HWA on hemlock decline and the relative dominance of hemlock may be important factors affecting the internal cycling of nitrogen and the amount of nitrogen available in forest communities during and following hemlock decline.

The primary objective of this study was to assess changes in nitrogen fluxes and pools at different levels of hemlock dominance and decline. Two specific objectives were to assess changes in net nitrogen mineralization and nitrification, and changes in the pools of nitrogen in three main forest components: live leaves, leaf litter, and soil. I also assessed changes in carbon pools in these three compartments because changes in nitrogen cycling are often linked to changes in carbon pools (Schlesinger 1997, Lovett et al. 2004). I hypothesized that net N mineralization, net N nitrification, and the pools of C and N in the soil would be greater in hemlock-dominated stands than in mixed or hardwood-dominated stands. I also hypothesized that soil N pools and fluxes would increase with increasing hemlock decline (measured as mortality and crown defoliation). Additionally, I hypothesized that nitrogen concentration in leaf and litter pools would be greater in hemlock-dominated stands than in mixed and hardwood-dominated stands.

Methods

Soil N mineralization and nitrification rates, and total C and N were examined at Black Rock Forest (BRF), Ward Pound Ridge Reservation (WPR), and Delaware Water Gap National Recreation Area (DWG). Soils at BRF are primarily spodsols in areas dominated by eastern hemlock, while the hardwood-dominated areas primarily consist of alfisols (Scholz 1931). WPR, approximately 30 miles east of the BRF, is in the same physiographic region as BRF and has similar soils (B. Herr – Ward Pound Ridge, personal communication). DWG is approximately 50 miles west of BRF on the border of the Appalachian Plateau. DWG has highly organic spodsols in hemlock-dominated areas and alfisols in hardwood-dominated areas (Battles et al. 2000). These forests are

characterized by very high rock content (e.g. Barringer and Clemants 2003), a characteristic typical of soils across the distribution of eastern hemlock (Godman and Lancaster 1990).

To examine the impacts of hemlock dominance and decline on soil carbon and soil nitrogen, three plots were established in each of three stand-types (hemlock-dominated, mixed, and hardwood-dominated) within each forest, for a total of 27 plots. Stand-type classifications and forest descriptions can be found in Chapter 2 (Tables 4 and 5, Pages 15-26).

In order to address changes in mineralization and nitrification over time, cylindrical, 10 cm diameter (785 cm^3) soil cores were excavated to 10 cm depth or bedrock at approximately 14 m intervals along a diagonal transect (28 m long) across each plot. Paired cores were collected every other month from May 2001 to November 2001 at BRF and WPR, and every other month from April 2002 to December 2002 at all three forests. One of the two cores was removed from the field immediately (initial) and one core was incubated in the field for two months (final). The final core was immediately covered by clear plastic to prevent influx of water and reduce the potential for leaching, and the bottom was covered with 1 mm mesh to keep the core intact while allowing for microbial movement (Eno 1960). Some final cores (0-3 cores per sampling period) were lost or destroyed by animals during the two-month incubation period. Lost or destroyed samples were eliminated from the analyses. For each two month interval, a new set of cores was taken adjacent to the original cores. Due to weather at BRF, the December 2002 soil cores were not collected. Preliminary analyses (Mates-Muchin unpublished data) and other studies (Nadelhoffer et al. 1983, Pastor et al. 1984, Ferrari 1999, Joshi et al. 2003) showed little nitrogen mobilization during the winter; therefore samples were not incubated from November 2000 to May 2001 or from December 2001 to April 2002.

Soil samples were sieved through a 4-mm screen to remove rocks and large roots. Two 10 g (± 0.05 g) samples were weighed; one for extraction of available nitrogen, and the other for dry mass (50°C to a constant mass; Norris et al. 2001) and total C and N analyses (see below). Available N was extracted using 50 mL of 1 M KCl in a 125 mL high density polyethylene bottle. After agitating the soil and KCl mixture at 300 rpm for 1 hour, the extract was filtered through a 2.5 cm diameter glass fiber syringe filter (Type A/E, Pall Life Sciences, East Hills, NY). When large particles prevented samples from being filtered through the syringe, samples were gravity filtered using a 7.6 cm diameter glass fiber filter (Type A/E, Pall Life Sciences, East Hills, NY). Extracted samples were stored frozen (-20°C) in 8 mL scintillation vials. Samples were then thawed and analyzed for available N with an autoanalyzer (TRAACS 800, Bran & Lubbe, Buffalo Grove, IL) following the manufacturer's instructions. Ammonium was determined using Berthelot reaction chemistry (Searle 1975) and nitrate was determined using hydrazine sulfate (Kamphake et al. 1967). Results were initially converted to mg kg^{-1} based on the amount of KCl used for extraction (50 mL) and the dry mass of the samples. Net N mineralization was calculated as the difference between the sum of ammonium plus nitrate in the final and initial samples. Net N nitrification was the difference between the nitrate in the final and initial samples. Net N mineralization and nitrification were standardized based on the bulk density of the soil (L. Watt – personal communication) and expressed as kg ha^{-1} $year^{-1}$.

The dry soil samples described above were also analyzed for total C and N using a CHN analyzer (2400 series II CHNS/O, PerkinElmer, Wellesley, MA). In order to determine the total amount of C and N in the tree pools, a subset of litter samples collected at BRF (see Chapter 3) from October 2000 and October 2001 that had > 1 g of leaf tissue were ground using a Wiley Mill (Thomas Scientific, Swedesboro, NJ) with size 40 delivery tube (0.425 mm mesh). The ground leaf tissue was then analyzed for total C and N. In July 2000 and July 2001, a sling shot was used to collect live leaf

samples from crowns of the five main species at BRF: hemlock, red oak (*Quercus rubra* L.), chestnut oak (*Quercus prinus* L.), red maple (*Acer rubrum* L.), and black birch (*Betula lenta* L.). These samples were dried at 50°C to a constant mass, ground, and analyzed for total C and N using the CHN analyzer.

Data analysis

In order to address the hypotheses that gradients in hemlock dominance affected net N mineralization and nitrification, separate analyses were performed on seasonal and annual variation of net N mineralization and nitrification. For data collected from all three forests in 2002, nested ANOVA was used to examine annual variation in net N mineralization and nitrification. For inter-annual and seasonal variation between stand-types at BRF and WPR from 2001 to 2002, nested-repeated measures ANOVA was used. A nested design, with stand-type nested within forest, was used to account for ecological variability associated with sampling across forests, because stand-type is considered a random effect in this experimental design (Sokal and Rohlf 1995). All analyses were conducted using SYSTAT 10 (SPSS Inc., Chicago, IL). I verified the assumption of normality visually by using density displays, and of homogeneity of variances by using Bartlett's Test.

Regression analyses were used to assess the effects of hemlock mortality on net N mineralization and nitrification. The separate and interactive effects of mortality and forest on net N mineralization and nitrification were analyzed using the GLM function in SYSTAT. Data were examined for outliers using Studentized Residuals. If outliers were detected ($P < 0.05$), all outliers were removed and the regression was reanalyzed. For all analyses, treatments were considered significant if $\alpha < 0.05$. Non-parametric correlations between CDC and net N mineralization or nitrification were tested using Kendall's Tau statistic.

In order to test the hypothesis that soil nitrogen pools were greater in hemlock-dominated stands, the effects of stand-type on total soil N were tested using nested ANOVA. Because soil carbon may have a mediating effect on total soil N (Schlesinger 1997), stand-type effects on total soil C and carbon:nitrogen (C:N) were also examined. To assess whether there were significant forest or stand-type effects on total C and N, or significant interactions with time, nested-repeated measures ANOVA was used for soil data collected from 2001 and 2002 at BRF and WPR.

Regression analyses were conducted to examine the effect of hemlock mortality on total C, N and C:N within and across forests. Non-parametric correlations between CDC and soil C and N were tested using Kendall's Tau statistic. In addition, correlations between net N mineralization, net N nitrification, total soil N and total soil C were examined because nitrogen is a key factor in decomposition by microbial communities. The Pearson correlation coefficient was used to assess relationships between soil fluxes (net N mineralization and net N nitrification) and pools (total C and N) from BRF and WPR in 2001 and from all three forests in 2002.

Leaf and litter samples, collected only at BRF, were analyzed to test the hypotheses that these C and N pools varied with hemlock dominance. The effects of stand-type, species and time on leaf and litter components were tested using repeated measures ANOVA. Because total C and N are often linked in forests, and because total C and N cycle between forest compartments, correlation analysis was used to test for associations between total C and N pools in leaf, litter and soil at BRF.

Results

Effects on Soil Fluxes and Pools

Effects of stand-type on changes in nitrogen fluxes or pools were examined to assess whether gradients in hemlock dominance altered ecosystem processes. Significant

interactions between stand-type and time on net N mineralization or nitrification (within subject effects) would indicate that annual or seasonal patterns of N fluxes varied with hemlock dominance. However, a significant stand-type effect alone (between subject effects) would indicate that stand-types only differ in the relative amount of net N mineralization or nitrification. There was a significant effect of stand-type on annual net N nitrification in 2002 (Table 1). In general, the greatest rate of net N nitrification occurred in hemlock-dominated stands (Figure 1). There were significant stand-type effects on seasonal net N nitrification, but there were no significant interactions with time (Table 2). Therefore, stand-types differed in the total amount of net N nitrification in 2002, but not in the seasonal patterns of net N nitrification; hence, the stand-type effect on the total amount of net N nitrification in 2002 is reflected in the effect of stand-type on annual net N nitrification. There was a significant stand-type x time interaction on net N mineralization measured every other month at BRF and WPR (Table 2). The rate of change of N mineralization varied seasonally across stand-types from 2001 to 2002 (Figure 2).

Rates of N nitrification and mineralization varied significantly between forests across the study period. There were significant forest x time interaction effects on seasonal and annual patterns of net N mineralization from 2001 to 2002, and on seasonal net N nitrification in 2002 (Tables 2 and 3). There were significant forest effects on total soil C and N and C:N at BRF and WPR in 2001 and 2002 ($P = 0.010$, $P < 0.001$, and $P < 0.001$, respectively). Total soil C also significantly varied across forests in 2002 when analyzing data from all three forests (Tables 1 and 3). There were no other significant effects of forest on total soil N or C:N.

Regression analyses were used to test the effects of hemlock mortality on soil pools and fluxes. There was a significant effect of hemlock mortality on the annual rate of N nitrification in 2001 at BRF and WPR ($P = 0.008$). The amount of available nitrate

Table 1. Nested ANOVA for the effects of forest and stand-type on annual net N mineralization, net N nitrification, total soil N and C, and C:N at Black Rock Forest, Ward Pound Ridge and Delaware Water Gap. df = degrees of freedom, F = F ratio, P = probability. Treatment effects were considered significant if $P < 0.05$.

NESTED ANOVA												
			Net N Nitrification		Net N Mineralization		Total Soil N		Total Soil C		C:N	
Effect	**Year**	**df**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**
Forest	2002	2	7.09	**0.005**	1.08	0.362	3.26	0.062	7.33	**0.005**	2.11	0.151
Stand-type (Forest)		6	4.22	**0.008**	1.07	0.416	0.39	0.878	0.84	0.555	0.78	0.596

Figure 1. Mean (+ 1 SE) net N nitrification in 2002 in hemlock-dominated, mixed, and hardwood-dominated stands at Black Rock Forest. There was a significant stand-type effect observed in the nested ANOVA (Table 1). Representative data from Black Rock Forest are shown; the general pattern was consistent across forests. **: $P < 0.01$.

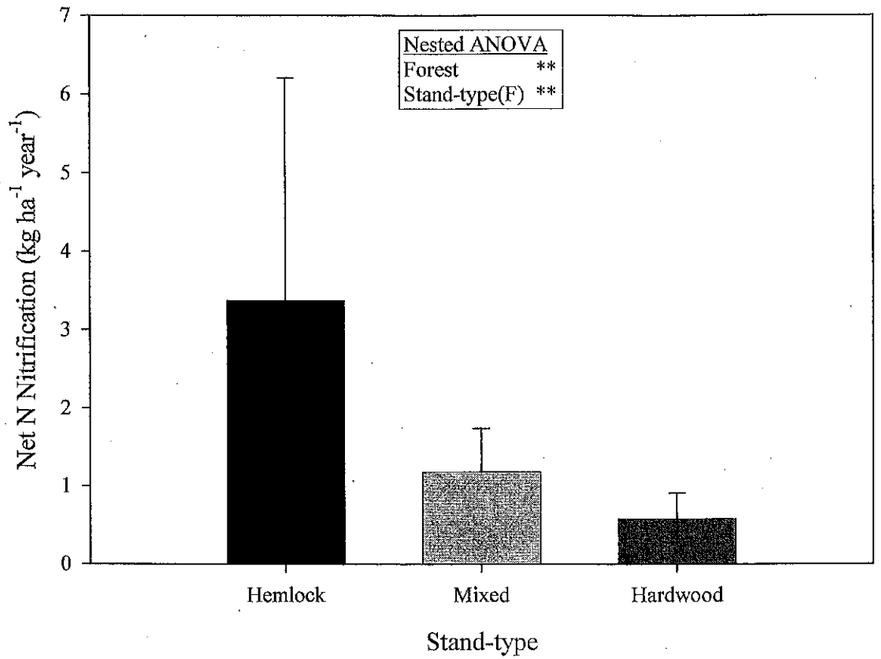


Table 2. Nested-repeated measures ANOVA of the seasonal variation in net N mineralization and net N nitrification from Black Rock Forest (BRF) and Ward Pound Ridge (WPR) between 2001 and 2002, and from all three forests in 2002. Significant treatment effects and interactions are denoted by bold typeface. Treatment effects were considered significant if $P < 0.05$

				Net N Nitrification		Net N Mineralization	
Effect	**Forest**	**Year**	**df**	**F**	**P**	**F**	**P**
Forest	BRF, WPR	2001-2002	1	4.15	0.064	0.13	0.722
Stand-type (Forest)			4	0.11	0.978	0.72	0.592
Forest x time			5	1.42	0.229	5.53	**< 0.001**
Stand-type (Forest) x time			20	0.90	0.593	2.97	**0.006**
Forest	BRF, WPR, DWG	2002	2	7.12	**0.005**	1.01	0.384
Stand-type (Forest)			6	4.68	**0.005**	0.44	0.845
Forest x time			4	0.76	0.556	1.22	0.319
Stand-type (Forest) x time			12	0.94	0.521	0.94	0.524

Figure 2. Mean (± 1 SE) net N mineralization measured seasonally from May 2001 to October 2002 in hemlock-dominated, mixed, and hardwood-dominated stands. There was a significant stand-type x time interaction observed in the nested-repeated measures ANOVA (Table 2). Representative data from BRF are shown; the general pattern was consistent across forests. **: $P < 0.01$; ***: $P < 0.001$; NS: Not significant.

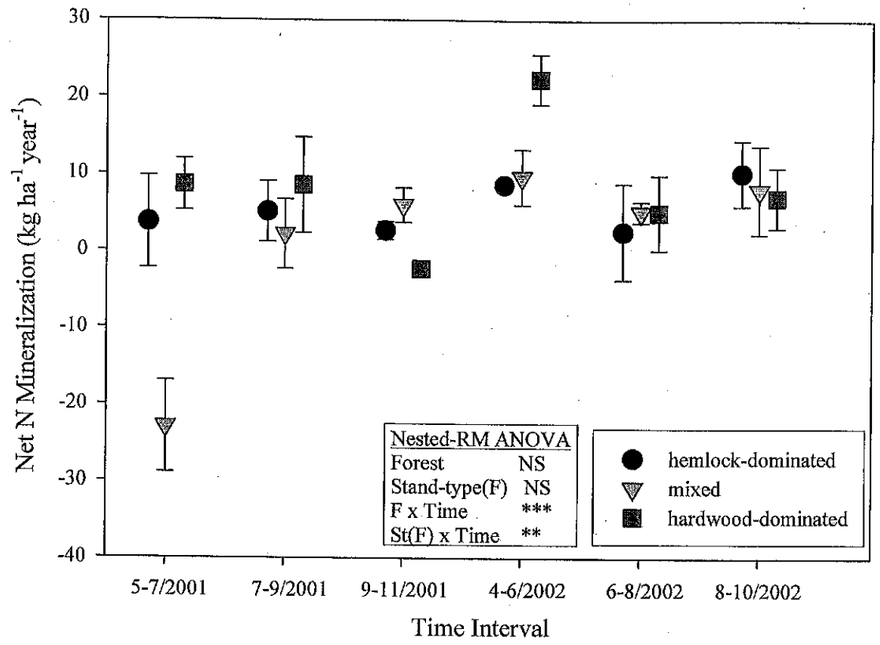


Table 3. Mean (1 SE) net N mineralization, net N nitrification, total soil C, and total soil N from Black Rock Forest (BRF), Ward Pound Ridge (WPR), and Delaware Water Gap (DWG) in 2001 and 2002. P values of significant effects or interactions are also found in Tables 1 and 2.

Forest	Net N Mineralization 2001†						Net N Mineralization 2002†						Annual Net Mineralization††			
	May-July		July-Sept.		Sept.-Nov.		April-June		June-August		August-Oct.		2001		2002	
BRF	-3.51	(5.56)	5.30	(2.66)	2.14	(1.43)	13.60	(2.61)	4.32	(2.36)	8.41	(2.40)	3.93	(6.09)	26.33	(4.99)
WPR	10.01	(4.00)	2.45	(0.92)	2.81	(1.30)	7.32	(1.67)	5.35	(2.05)	5.73	(2.13)	15.27	(5.02)	18.40	(4.24)
DWG							7.09	(1.43)	9.38	(3.71)	7.64	(3.00)			25.93	(3.69)

	Net N Nitrification 2001						Net N Nitrification 2002**						Annual Net Nitrification			
	May-July		July-Sept.		Sept.-Nov.		April-June		June-August		August-Oct.		2001		2002**	
BRF	0.51	(0.94)	-0.65	(0.31)	0.53	(0.21)	1.29	(0.48)	0.23	(0.29)	0.20	(0.21)	0.39	(1.13)	1.71	(0.94)
WPR	5.72	(2.66)	3.23	(2.25)	0.79	(0.29)	2.78	(1.31)	0.76	(0.89)	0.67	(0.74)	9.74	(4.43)	4.22	(1.88)
DWG							0.66	(0.16)	0.06	(0.13)	-1.53	(0.53)			-0.76	(0.57)

	Soil C 2001***		Soil N 2001		Soil C 2002**		Soil N 2002	
BRF	33.17	(2.67)	1.42	(0.13)	27.45	(2.87)	1.24	(0.13)
WPR	13.88	(2.27)	0.98	(0.13)	14.75	(2.17)	0.79	(0.09)
DWG					27.92	(2.99)	1.10	(0.13)

Net N mineralization and net N nitrification values are in kg ha^{-1} $year^{-1}$.
Significant forest effects ** = $P < 0.01$; *** = $P < 0.001$.
† = significant seasonal forest x time interaction from 2001-2002 at BRF and WPR only ($P = 0.005$).
†† = significant annual forest x time interaction from 2001-2002 at BRF and WPR only ($P = 0.025$).

in the soil decreased with increasing hemlock mortality (Figure 3). There were no other significant effects of hemlock mortality or interactions between hemlock mortality and forest on net N mineralization or nitrification ($P > 0.05$ in all cases). Crown defoliation was positively correlated with net N nitrification from 2002 ($\tau = 0.502$, $P < 0.01$). There were no other correlations between CDC and net N mineralization, net N nitrification, total soil C and total soil N ($P > 0.05$ in all cases).

Correlation analysis was also used to examine relationships between soil C and N (Table 4). Total soil C was correlated with total soil N from BRF and WPR in 2001 (Figure 4). In 2002, there were significant correlations between net N mineralization and total soil N, as well as between total soil C and total soil N. There were no other significant correlations among soil C and N parameters (Table 4).

Effects on Leaf and Litter Pools

The effects of stand-type on the amount of C and N in the leaf and litter pools were assessed to determine if these factors varied with hemlock dominance. In the leaf, litter and soil compartments between 2000 and 2001 at BRF, there were no significant effects or interactions between stand-types and time on total C or N or C:N (Table 5). However, there were significant effects of stand-type on leaf and litter C and N for individual species (Table 6). Red oak leaves had the highest C:N ($P = 0.015$) and the lowest N concentration ($P = 0.006$) in hardwood-dominated plots compared to mixed and hemlock-dominated plots. Red maple leaves had the highest C:N in hardwood-dominated plots as well ($P = 0.030$). Finally, chestnut oak litter C:N was greatest in hardwood-dominated plots compared to hemlock-dominated and mixed plots ($P = 0.016$). There were no significant interactions between stand-type x time or species x time on total C and N in the leaf and litter compartments. Also, there were no correlations between leaf, litter, and soil compartments in 2000 and 2001 ($P > 0.05$ in all cases).

Figure 3. The effect of hemlock mortality on net N nitrification in 2001 at BRF and WPR. The corresponding equation is Net N nitrification = 6.12 - 53.21*x*.

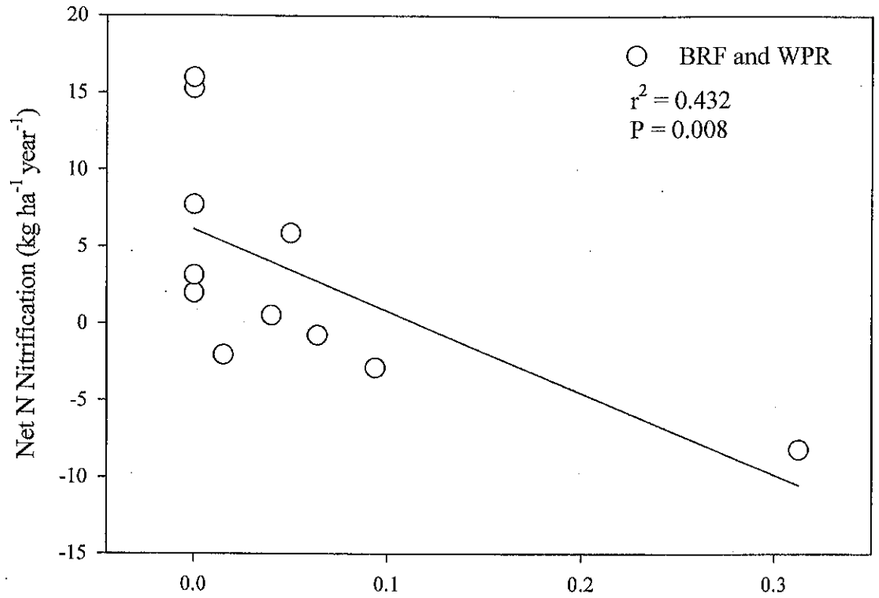


Table 4. Pearson correlation matrix comparing net N mineralization, net N nitrification, total soil C, and total soil N from BRF and WPR in 2001 and from all forest in 2002.

2001				
	Net N Mineralization	Net N Nitrification	Total Soil C	Total Soil N
Net N Mineralization	1			
Net N Nitrification	0.58	1		
Total Soil C	-0.32	-0.31	1	
Total Soil N	-0.23	-0.16	0.89 **	1

2002				
	Net N Mineralization	Net N Nitrification	Total Soil C	Total Soil N
Net N Mineralization	1			
Net N Nitrification	0.10	1		
Total Soil C	0.35	-0.14	1	
Total Soil N	0.57 *	0	0.85 **	1

* = P < 0.05; ** = P < 0.01.

Figure 4. Correlations between total soil C and total soil N in (A) 2001 at Black Rock Forest and Ward Pound Ridge, and (B) 2002 at all forests. (C) Correlation between total soil N and net N mineralization in 2002 at all forests.

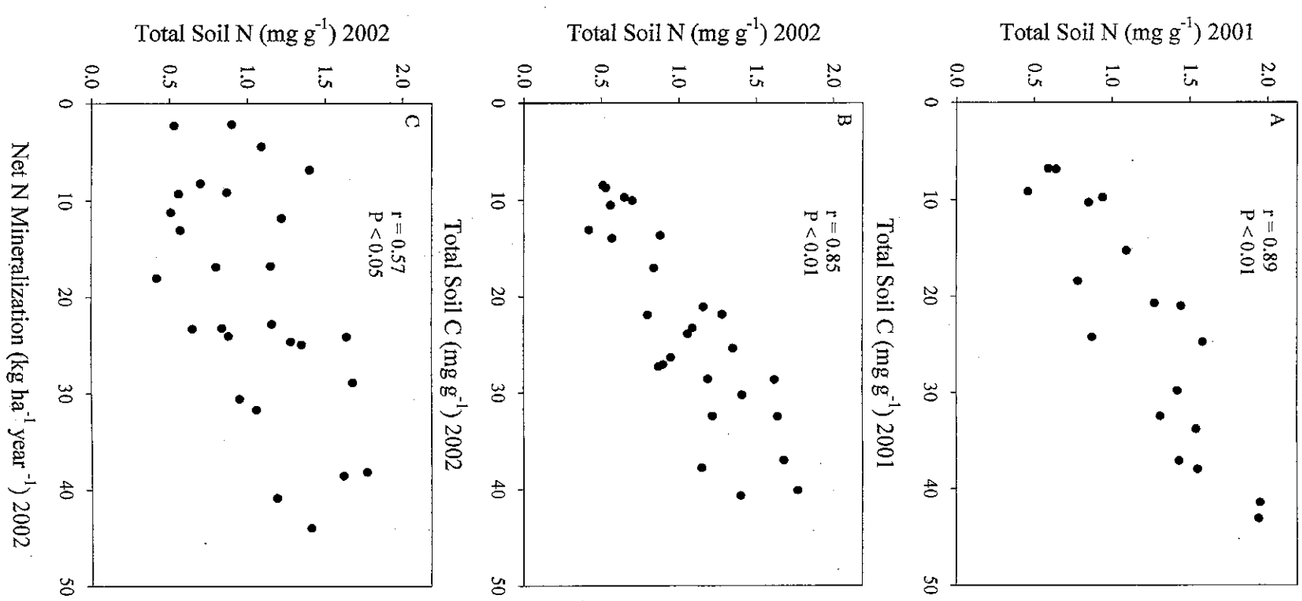


Table 5. Mean (1 SE) total C (mg g^{-1}), total N (mg g^{-1}), and C:N in leaf, litter and soil samples from BRF in 2000 and 2001. There were no significant effects of stand-type or interactions between stand-type and time on total C, total N, and C:N in leaf, litter and soil ($P > 0.05$ in all cases)

Stand-type	Total C 2000	Total C 2001	Total N 2000	Total N 2001	C:N 2000	C:N 2001
			Leaf			
Hemlock	49.74 (0.23)	48.86 (0.34)	2.15 (0.08)	2.07 (0.09)	23.16 (0.78)	23.72 (1.02)
Mixed	49.52 (0.96)	49.19 (0.35)	1.96 (0.13)	1.89 (0.10)	25.46 (1.77)	26.12 (1.43)
Hardwood	48.87 (0.15)	49.12 (0.53)	1.90 (0.04)	1.93 (0.08)	25.70 (0.59)	25.58 (1.33)
			Litter			
Hemlock	49.47 (1.08)	51.12 (0.21)	0.84 (0.09)	0.99 (0.03)	59.86 (5.58)	51.91 (1.73)
Mixed	49.39 (0.45)	49.25 (0.89)	0.86 (0.03)	0.80 (0.88)	57.53 (1.82)	63.11 (6.28)
Hardwood	49.44 (0.95)	50.32 (0.24)	0.73 (0.04)	0.74 (0.23)	68.43 (4.96)	68.75 (4.37)
			Soil			
Hemlock	19.50 (5.33)	36.42 (3.44)	0.72 (0.22)	1.64 (0.16)	27.66 (1.74)	22.26 (1.13)
Mixed	22.62 (5.22)	38.02 (2.72)	1.13 (0.32)	1.64 (0.15)	22.51 (5.28)	23.38 (1.29)
Hardwood	18.22 (4.83)	25.07 (4.07)	0.73 (0.19)	1.22 (0.23)	25.02 (0.92)	21.27 (2.97)

Table 6. Mean (1 SE) leaf N (mg g^{-1}), leaf C:N, and litter C:N for red maple (ACRU), red oak (QURU), and chestnut oak (QUPR) in hemlock-dominated, mixed, and hardwood-dominated stands at Black Rock Forest. Repeated measures ANOVA indicated significant effects of stand-type on N and C:N, but there were no significant interactions between stand-type and time.

	Leaf					Litter	
Stand-type	ACRU C:N *		QURU N**		QURU C:N*	QUPR C:N*	
Hemlock-Dominated	26.20	(0.4)	0.05	(0.003)	22.18 (0.6)	65.48	(3.4)
Mixed	30.64	(0.9)	0.05	(0.004)	21.12 (1.1)	61.91	(2.1)
Hardwood-Dominated	33.79	(1.4)	0.04	(0.002)	23.89 (0.9)	71.75	(2.5)

* = $P < 0.05$; ** = $P < 0.01$.

Discussion

Annual net N nitrification was significantly greater in hemlock-dominated plots in 2002 (Figure 1), consistent with my hypothesis. Net N nitrification was also positively correlated with CDC, suggesting that differences between stand-types may be a function of differences in hemlock defoliation. Further, a study that compared HWA infested and un-infested sites similarly observed greater N nitrification rates associated with greater HWA infestation (Jenkins et al. 1999). Other studies on the impacts of tree defoliation or mortality on nitrogen cycling have observed increases in nitrogen in stream or soil water, an indicator of increasing nitrification rates (Swank et al. 1981, Yorks et al. 2003). The impact of hemlock decline on nitrogen cycling resulted in greater net N nitrification in areas with greater hemlock decline. The greater N nitrification rates may have resulted from greater amounts of unutilized, available N by co-occurring trees, or increasing microbial activity, which expedite the transfer of ammonium to nitrate (Johnson 1995, Jenkins et al. 1999, Lovett et al. 2002).

The variability in available N was expected based on the different levels of hemlock dominance, as well as the variation in water availability and photosynthetic activity in the spring, summer, and fall (Ferrari 1999, Schlesinger 1997). While annual net N mineralization did not significantly vary across stand-types, stand-types significantly varied in seasonal net N mineralization from 2001 to 2002 at BRF and WPR (Figure 2). Although I expected highest N mineralization rates in hemlock-dominated stands, there were no significant stand-type effects. However, the variation in net N mineralization over time was consistent with seasonal patterns expected in the stand-types. The high net N mineralization in hardwood-dominated stands may reflect the high litter turnover rates associated with hardwood trees (Reich et al. 1997). Net N mineralization in hardwood-dominated and mixed stands may be more dependent on abiotic factors that control litter turnover rates. Conversely, in hemlock-dominated

stands, net N mineralization was more constant across time because hemlock needles generally have higher C:N and therefore slower turnover rates (Nadelhoffer et al. 1983). The greater variability observed in mixed stands may be due to the combination of hardwood trees and hemlock decline that cause greater variability depending on abiotic factors, absorption by co-occurring species, and the availability or type of litter being decomposed.

The high N nitrification rate observed in hemlock-dominated stands may also be associated with N mineralization rates in hemlock-dominated stands because the amount of ammonium available should influence the microbial conversion of ammonium to nitrate. However, there were no correlations between net N mineralization and net N nitrification across the study period. This lack of correlation may be due to high seasonal variability in N mineralization and N nitrification rates, or differences between stand-types. The transfer of ammonium to nitrite is influenced by the ability of plants and microbes to immobilize nitrogen throughout the growing season (Ollinger et al. 2002). The amount of available ammonium absorbed by plants and microbes decreases the potential for the oxidation of ammonium to nitrate (Day and Monk 1977, Lovett et al. 2004).

Hemlock decline was expected to have the greatest effect on the rates of N mineralization and N nitrification in areas with the greatest amount of hemlock mortality because increased defoliation and mortality should increase microbial activity and light availability, both contributing factors to N mineralization and nitrification rates. But, as hemlock mortality increased, net N nitrification decreased. Although this is contrary to my hypothesis, it may be due to the decrease in hemlock density, which reduces the number of plants available to absorb excess nitrogen (Bernhardt et al. 2003). It is therefore possible that increased nitrate generally associated with increased mortality was either taken up by co-occurring trees and microbes or was removed from the available soil pool via leaching (Swank et al. 1981). If leaching occurred, the future ecosystems

will be deficient of available nitrogen for re-growth. Thus, the decline of a dominant tree will alter forest nitrogen cycling, although the fate of the nitrate observed in this study is not known.

The extent of crown defoliation was positively correlated with net N nitrification in 2002. This correlation suggests that there was greater nitrate available at the end of the study period in plots with greater hemlock defoliation. Factors potentially causing this result include increased resource availability resulting from needle or leaf litterfall (Lovett et al. 2004). But CDC was not correlated with other response variables, mainly net N mineralization and total soil N. Contrasting results from the correlation of CDC and mortality with net N nitrification may be attributed to the difference in the time intervals measured and the impact of crown defoliation versus mortality on ecosystem processes. For example, increases in defoliation may cause reduced tree vigor, and coupled with tree mortality, there may be fewer pathways for nitrogen uptake.

The amount of available inorganic and organic N in the soil is expected to be correlated based on the decomposition of organic matter. However, there were few correlations between net N mineralization, net N nitrification, total soil N, and total soil C. Other studies also hypothesized a feedback loop linking nutrient uptake, litterfall and net N mineralization, but they only observed these linkages in stable ecosystems (Pastor et al. 1984). The lack of correlations in this disturbed system may be because disturbances disrupt the nitrogen cycle (Bormann and Likens 1979) and change the relationship between the elemental cycles and productivity (Pastor et al. 1984).

The amount of C and N in the soil may depend on the amount of organic matter being transferred from leaf pool to the soil, the rate of decomposition of litter, and the amount of organic C or N in the microbial pool (Lovett et al. 2004). I predicted that there would be greater soil N in hemlock-dominated plots because of the increase in N being transferred from the aboveground to the belowground pools. In addition, species composition should influence the amount of soil N because of the variability in the

amount of N in the leaves of different species and because of the different species' leaf turnover rates (Lovett et al. 2004). However, there were no significant effects of stand-type on soil C or N. The lack of significant stand-type effects may be attributed to the high variability in the forest soils. Further, the high variability may be due to compositional differences within stand-types and differences between the soil properties that influence the decomposition of organic matter from the leaf to the soil pools.

The transfer of C and N from the leaves to the forest floor creates a chemical link between leaves, litter, and soil. Additionally, these elements should be correlated based on the cellular relationship between C and N (Schlesinger 1997), and the necessity of C and N for metabolic processes in both the plant and microbial community (Bormann and Likens 1967, Ollinger et al. 2002, Lovett et al. 2004). Across species, there were no significant differences between stand-types in leaf or litter C, N, and C:N. The lack of significant difference is likely due to the variability of species composition within and across stand-types as well as the difference in species cellular structure. However, there were significant effects of stand-type on N and C:N in leaves and litter of individual species. Although the amount of C and N in hemlock needles did not vary across stand-type, red oak and red maple leaves, and chestnut oak litter varied across stand-type in N and C:N at BRF. The significant difference in the C and N of individual species suggest these species may affect the pools of C and N in the soil by contributing different levels of C and N from the leaves to the soil. Additionally, the amount of N in the leaves of hardwood trees was greater in hemlock-dominated stands. This result suggests that there may be greater N available for trees in hemlock-dominated stands compared to hardwood-dominated stands. Greater N in hardwood leaves in hemlock-dominated stands is contrary to the general pattern expected in healthy hemlock-dominated stands, because hemlock is a strong competitor for resources (Godman and Lancaster 1990).

Soil, leaf and litter compartments were not correlated in 2000 and 2001. I expected that soil and litter, and leaf and litter C and N would be correlated based on the

transfer of material from one compartment to the next. As leaves are transferred from the tree compartment to the soil compartment, much of the C and N are transferred to the soil for decomposition (Schlesinger 1997). These variables may not have been linked in my study because of high variability of C and N in the leaves, litter and soil within plots.

In summary, the dominance and decline of hemlock affected the N nitrification rates, suggesting that ecosystem processes are changing as a result of the impact of the HWA on eastern hemlock forests. The lack of significant stand-type effects on net N mineralization and total C and N suggest that either: (1) these parameters have not yet been affected by hemlock decline and dominance, (2) these parameters have been affected by hemlock decline and dominance prior to the start of this study, or (3) there is high variability in forest soils within watersheds due to the impact of other abiotic and biotic factors that influence these parameters. The variation in the response of net N nitrification and net N mineralization, and the lack of correlation between these variables (and soil, leaf, and litter), suggests a decoupling of the N cycle due to the impact of the disturbance (Pastor et al. 1984). The contrasting directions of the relationships between net N nitrification and hemlock decline (mortality and CDC) suggest that the impact of hemlock defoliation in 2002 may increase available nitrogen because of the greater amount of resources being transferred to the forest floor or due to decreased capacity of trees to utilize excess nitrogen, whereas the effect of mortality in 2001 may reduce the amount of available nitrogen due to the increased microbial activity, greater uptake by co-occurring trees, or nitrate leaching. The significantly greater hardwood tree C and N in hemlock-dominated stand-types suggest that hardwood leaves may be contributing greater amounts of nutrients to the forest floor and hardwood trees utilizing the excess nutrients associated with hemlock decline. The ultimate impact of the HWA on eastern hemlock forests was observed in the significant effects of hemlock dominance and decline on net N nitrification. The loss of a dominant tree species caused widespread

changes to forest communities and ecosystems by altering nitrogen, light, and other abiotic factors that influence forest development and recovery following disturbance.

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Changes in Forest Productivity and Nitrogen Cycling Associated with Decline of Eastern Hemlock

Dissertation directed by James D. Lewis, Ph.D.

The impact of invasive insects threatens communities and ecosystems. In northeastern forests, the hemlock woolly adelgid (HWA; *Adelgis tsugae* Annand.) has influenced the decline of the eastern hemlock (*Tsuga canadensis* L. Carr.). However, the effect of the HWA on community and ecosystem change has been understudied, especially across varying levels of hemlock mortality and dominance. To address community and ecosystem change, I measured the effects of hemlock mortality and dominance on forest community composition, net primary production (NPP), net N mineralization, and net N nitrification. Twenty-seven plots were established in three regional forests. Plots were categorized into hemlock-dominated, mixed, and hardwood-dominated stand-types based on hemlock relative importance. Nested-repeated measures ANOVA and regression analyses were used to assess the effects of stand-type and mortality on communities and ecosystems. There were significant effects of stand-type on basal area, density, diversity and equitability, with the greatest decreases (basal area, density) and increases (diversity, equitability) occurring in hemlock-dominated plots. Also, as hemlock mortality increased, the change in basal area and density decreased, and the change in diversity increased. Between 2001 and 2002, there was a significant change over time of live tree biomass with the greatest change occurring in hardwood-dominated stands. This was contrary to my hypothesis that there would be greater NPP in stand-types with greater hemlock dominance or decline. Species litterfall significantly varied across stand-types with the greatest litterfall increase occurring in hardwood-dominated stands. NPP and biomass did not vary across stand-types over any other time interval. The lack of significant stand-type effects except from 2001 to 2002 was perhaps because of a delayed growth response of trees co-occurring with hemlock. There was a significant effect of stand-type on net N nitrification. Mortality also significantly affected net N nitrification with the greater rate occurring in plots with greater hemlock mortality. Thus, the significant effects of hemlock dominance and mortality on communities and ecosystems indicated that forests are changing with the loss of eastern hemlock. Community and ecosystem level experiments must continue assess short- and long-term effects of invasive insects, because the impacts of invasive insects will continue to influence forest dynamics.

VITA

Jonathan Todd Mates-Muchin, son of Carol and Jerome Muchin, was born on March 18, 1974, in Milwaukee, WI. Shortly after birth, his family moved to Los Angeles, CA, where he graduated from University High School in 1992. In 1996, he received his Bachelor of Science degree in Biology from the University of California, Santa Barbara.

Following a year abroad in Israel, studying in the Negev Desert, he entered Fordham University in 1998. During his time at Fordham, he was awarded a Presidential Scholarship and taught biology at Fordham's Lincoln Center Campus. In 2003, he earned a Masters of Science in Biology. After moving to Buffalo, NY in 2002, he has continued his pursuit under the direction of Dr. James D. Lewis. He currently lives in Oakland, CA with his family.