



Understory vegetation in old-growth and second-growth *Tsuga canadensis* forests in western Massachusetts

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ABSTRACT

We compared the understory communities (herbs, shrubs, and tree seedlings and saplings) of old-growth and second-growth eastern hemlock forests (*Tsuga canadensis*) in western Massachusetts, USA. Second-growth hemlock forests originated following clear-cut logging in the late 1800s and were 108–136 years old at the time of sampling. Old-growth hemlock forests contained total ground cover of herbaceous and shrub species that was approximately 4 times greater than in second-growth forests ($4.02 \pm 0.41\%/m^2$ versus $1.06 \pm 0.47\%/m^2$) and supported greater overall species richness and diversity. In addition, seedling and sapling densities were greater in old-growth stands compared to second-growth stands and the composition of these layers was positively correlated with overstory species composition (Mantel tests, $r > 0.26$, $P < 0.05$) highlighting the strong positive neighborhood effects in these systems. Ordination of study site understory species composition identified a strong gradient in community composition from second-growth to old-growth stands. Vector overlays of environmental and forest structural variables indicated that these gradients were related to differences in overstory tree density, nitrogen availability, and coarse woody debris characteristics among hemlock stands. These relationships suggest that differences in resource availability (e.g., light, moisture, and nutrients) and microhabitat heterogeneity between old-growth and second-growth stands were likely driving these compositional patterns. Interestingly, several common forest understory plants, including *Aralia nudicaulis*, *Dryopteris intermedia*, and *Viburnum alnifolium*, were significant indicator species for old-growth hemlock stands, highlighting the lasting legacy of past land use on the reestablishment and growth of these common species within second-growth areas. The return of old-growth understory conditions to these second-growth areas will largely be dependent on disturbance and self-thinning mediated changes in overstory structure, resource availability, and microhabitat heterogeneity.

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1. Introduction

The understory layer is a critical component of forest ecosystems typically supporting the vast majority of total ecosystem floristic diversity (Halpern and Spies, 1995; Gilliam and Roberts, 2003) and providing habitat elements to associated wildlife species (Carey and Johnson, 1995). These communities also play a central role in the dynamics and functioning of forest ecosystems by influencing long-term successional patterns (Phillips and Murdy, 1985; Abrams and Downs, 1990; Oliver and Larson, 1996; McCarthy et al., 2001; Royo and Carson, 2005;

Nyland et al., 2006) and contributing to forest nutrient cycles (Chapin, 1983; Zak et al., 1990; Anderson and Eickmeier, 2000; Chastain et al., 2006). Due to the recognized ecological importance of forest understory plants, considerable effort has been devoted to determining the impacts of land-use practices on the structure and diversity of these communities (Whitney and Foster, 1988; Matlack, 1994; Motzkin et al., 1996; Bellemare et al., 2002; Eberhardt et al., 2003; Goslee et al., 2005; Fraterrigo et al., 2006, see also *Ecological Applications* Special Feature vol. 5, 1995). This work has demonstrated the importance of past land use in shaping contemporary patterns of understory vegetation and has indicated that distinct community assemblages may characterize various stages of forest succession.

Understory communities in old-growth forest ecosystems are often quite distinct relative to forests originating following agricultural clearing or forest harvesting (Whitney and Foster, 1988; Matlack, 1994; Qian et al., 1997; Goebel et al., 1999).

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Although the diversity of understory plants may be low in some old-growth systems (Metzger and Schultz, 1984; Scheller and Mladenoff, 2002), other studies have indicated that certain taxa may be more abundant or restricted to these forests (Whitney and Foster, 1988; Matlack, 1994; Halpern and Spies, 1995; Moola and Vasseur, 2004). The affinity of certain species to old-growth forests has been attributed to several factors, including reproductive characteristics of the plants (Peterken and Game, 1984; Matlack, 1994; Meier et al., 1995), and characteristics of the environment in old-growth forests, including favorable substrates (e.g., coarse woody debris, pit and mound topography) and microclimatic conditions (e.g., deeply shaded microsites), that are typically less common or absent from second-growth systems (Harmon and Franklin, 1989; Peterson and Campbell, 1993; Chen et al., 1995; McGee and Kimmerer, 2002). As a result of the reproductive limitations and unique microhabitat requirements of some old-growth plant species, the conservation of old-growth forest ecosystems may be of critical importance for the maintenance of viable populations of certain plant species, particularly in landscapes highly fragmented by a history of intensive land use (Meier et al., 1995). In addition, the maintenance of late-successional understory plant communities is becoming an increasingly common forest management objective creating a greater need for an understanding of the environmental conditions promoting the abundance of these species (Alaback, 1984; Bailey et al., 1998; Lindh and Muir, 2004).

Old-growth forests are extremely scarce on the landscapes of southern New England constituting roughly 0.1% of the forested land base of states such as Massachusetts (D'Amato et al., 2006). Numerous studies in this region have demonstrated differences in understory community composition between secondary and primary forests (i.e., forests originating following agricultural clearing versus logging exclusively, Motzkin et al., 1996; Donohue et al., 2000; Bellemare et al., 2002); however, our understanding of the compositional differences that may exist between old-growth and primary forests is fairly limited (but see Whitney and Foster, 1988; Cooper-Ellis, 1998). This study compares the understory vegetation of the few remaining old-growth forests in western

Massachusetts with adjacent second-growth forests that originated following logging in the late 19th Century, but were never cleared for agricultural purposes. Many of the old-growth forests in western Massachusetts are surrounded by compositionally similar second-growth stands providing the opportunity to investigate the influence of differing past land-use on the understory communities of forests with similar overstory species composition and edaphic and landscape settings. In addition, the majority of these old-growth forests are dominated by eastern hemlock (*Tsuga canadensis*), a species currently threatened by the introduced hemlock woolly adelgid (*Adelges tsugae*, HWA, Orwig and Foster, 1998). Although none of these forests are currently infested by HWA, this introduced pest is within 3 km of several old-growth stands (C. Burnham, unpublished data). As a result, studies characterizing the floristic composition of the understory layer prior to HWA infestation will serve as an important baseline for monitoring the response of these ecosystems to this novel disturbance (Small et al., 2005; Eschtruth et al., 2006; Cleavitt et al., 2008). Similarly, the regeneration dynamics and floristic diversity of hemlock-dominated old-growth stands throughout the range of this species have been dramatically influenced by herbivory stemming from overabundant white-tail deer (*Odocoileus virginianus*) populations (Anderson and Loucks, 1979; Frelich and Lorimer, 1985; Alverson et al., 1988; Mladenoff and Stearns, 1993; Rooney and Dress, 1997; Long et al., 1998; Weckel et al., 2006). The lack of similar high populations within our study region provides an important opportunity to assess the structure and composition of systems currently unaffected by this conservation and management issue facing hemlock forests in many other regions of North America (Rooney et al., 2000).

2. Materials and methods

2.1. Study area

Sampling was conducted in 16 old-growth and 8 second-growth hemlock forests in the Berkshire Hills and Taconic Mountains of western Massachusetts (Table 1). This area has a

Table 1
Physiographic and general stand characteristics of eastern hemlock study sites in western Massachusetts, USA. Canopy tree age and compositional data were collected as part of a larger study examining the disturbance dynamics of these systems (see D'Amato and Orwig, 2008 for detailed methods).

Study site	Status ^a	Percent hemlock ^b	Average canopy tree age ^c (year)	Elevation (m)	Slope (°)	Aspect (°)
Bash Bish Falls	OG	76.9	226 (277)	370–450	26–46	353–4
Black Brook	OG	79.4	210 (328)	470–520	23–38	350–10
Cold River A1	OG	52.7	229 (374)	390–480	36–40	336–340
Cold River A2	OG	61.6	246 (488)	400–490	33–41	296–320
Cold River B	OG	76.5	188 (333)	330–490	40–42	332–340
Cold River D	OG	71.2	216 (441)	350–390	20–31	272–321
Deer Hill	OG	81.4	182 (282)	550–580	33–38	270–336
Grinder Brook	OG	88.1	236 (333)	360–450	38–43	27–50
Hopper A	OG	63.8	196 (414)	580–700	26–40	225–270
Hopper B	OG	42.4	198 (329)	600–680	31–35	280–321
Manning Brook	OG	75.1	219 (352)	360–420	29–35	45–77
Mt. Everett	OG	67.0	237 (325)	470–530	31–45	35–50
Money Brook	OG	77.9	206 (302)	600–660	24–32	33–308
Tower Brook	OG	50.0	177 (244)	450–470	33–42	70–88
Todd Mt.	OG	76.8	209 (377)	450–470	28–35	315–358
Wheeler Brook	OG	73.1	206 (300)	330–370	19–28	107–143
Bash Bish Falls	2G	70.0	115 (171)	380–430	26–34	325–350
Cold River A	2G	60.0	132 (182)	430–510	29–36	290–303
Cold River B	2G	69.8	108 (270)	340–380	31–35	255–290
Deer Hill	2G	52.5	113 (216)	500–540	35–38	350–0
Dunbar Brook	2G	72.6	136 (204)	380–410	27–36	45–68
Grinder Brook	2G	57.3	128 (151)	400–460	25–46	40–70
Money Brook	2G	70.5	133 (201)	590–620	26–34	260–290
Trout Brook	2G	63.0	136 (323)	320–370	29–32	330–340

^a OG: old-growth; 2G: second-growth.

^b Importance value calculated as ((relative basal area) + (relative density))/2.

^c Value in parentheses represents age of oldest tree with complete increment core sample.

humid, continental climate with average annual levels of precipitation ranging from 116.2 to 129.5 cm and mean monthly temperatures from -7.7°C in January to 22.2°C in July (NCDC, 2006). Study areas were located on steep slopes (range: $25\text{--}41^{\circ}$) and ranged in elevation from 305 to 685 m a.s.l. Soils in these areas are predominantly well-drained sandy loam soils formed from weathered gneiss, schist, and phyllite (Zen et al., 1983; Scanu, 1988).

Old-growth and second-growth status was assigned based on extensive analysis of historical and dendroecological evidence collected from these areas (D'Amato et al., 2006). Based on these analyses, old-growth areas were classified as sites lacking any evidence of past land-use and containing at least five old (>225 years old) canopy trees per hectare (cf. McGee et al., 1999). In contrast, early state documents indicated that several second-growth areas adjacent to old-growth areas were clear-cut harvested in the 1870s–1900s (Avery and Slack, 1926; D'Amato and Orwig, 2008). In addition, dendroecological analyses of second-growth areas confirmed that all second-growth sites were clear-cut harvested between the 1870s and 1900s as dramatic release and recruitment pulses were observed in these stands during these decades (D'Amato, 2007). In contrast to second-growth stands found in other mountainous regions of New England, there was little evidence that these areas were burned following clear-cut harvesting (cf. Goodale and Aber, 2001). Care was taken in the selection of second-growth sites to ensure that the environmental settings (e.g., elevation, topographic position, slope steepness, and aspect) were as similar to those of the old-growth hemlock stands as possible.

2.2. Vegetation sampling

Vegetation sampling plots were part of a larger study examining the structure and disturbance dynamics of old-growth and second-growth forests in western Massachusetts (D'Amato and Orwig, 2008; D'Amato et al., 2008). Depending on stand size, 3–5 0.04-ha plots were established along transects orientated through the central portion of each study area and permanently marked. Percent cover of all vascular herbaceous plants, shrubs, and tree seedlings were estimated by species in eight 1-m^2 sub-plots randomly located within each 0.04-ha sampling plot during May and June 2004. Seedling densities were also determined in these sub-plots. A complete census of herbaceous and shrub species was made in each 0.04-ha sampling plot to generate master species lists. This census was repeated in the late summer to ensure species emerging following the initial vegetation sampling were accounted for. No additional species were identified during these late summer censuses. Species and diameter at breast height (DBH) was recorded for every tree (stems ≥ 1.37 m tall and ≥ 10 cm DBH) rooted within the 0.04-ha plots. In addition, all saplings (stems ≥ 1.37 m tall and ≤ 10 cm DBH) were tallied by species. Measurements of forest floor environmental characteristics, including coarse woody debris abundance, soil pH, and nitrogen availability determined from mixed-bed cation and anion resin bags were also made within each 0.04-ha plot. Methods used for sampling CWD and soil characteristics are summarized in D'Amato et al. (2008) and D'Amato (2007). Species nomenclature follows Gleason and Cronquist (1991).

2.3. Statistical analyses

Percent cover of herbs and shrubs and seedling and sapling densities were averaged for each study area and compared between old-growth and second-growth forests using Wilcoxon rank-sum tests. In addition, average species richness (number of species in study area, S), diversity (Shannon–Wiener index, H'), and

evenness (E , Pielou, 1969) of understory herbs and shrubs were compared between old-growth and second-growth forests using the same procedure. Multivariate tests for differences in the composition of understory vegetation (herbs, shrubs, and seedlings) between old-growth and second-growth forests were conducted using multi-response permutation procedures (MRPP) in PC-ORD version 4.28 (McCune and Mefford, 1999). MRPP is a non-parametric, randomization-based multivariate test of differences between groups that compares the plots within a *priori* groups to a random allocation of plots (McCune and Grace, 2002). Sørensen distances were used to calculate average within-group distances for MRPP. Indicator species analysis (Dufendre and Legendre, 1997) was used to describe how well certain understory species differentiated between old-growth and second-growth forests.

Non-metric multidimensional scaling (NMS; McCune and Grace, 2002) was used to examine patterns in understory community composition within and among old-growth and second-growth forests. As was the case for MRPP, NMS used Sørensen distances to calculate a distance matrix for the 24 study areas. To reduce noise in the data set, species with fewer than three occurrences were removed from the data matrices (McCune and Grace, 2002). The “slow-and-thorough” autopilot mode of NMS in PC-ORD was used to generate solutions. This procedure determines the optimal ordination solution by stepping down in dimensionality from a six-axis to one-axis solution using 40 runs performed on real data followed by 50 Monte Carlo runs using random data (McCune and Mefford, 1999). Optimal dimensionality was based on the number of dimensions with the lowest stress (i.e., smallest departure from monotonicity in the relationship between distance in the original space and distance in the reduced ordination space, McCune and Grace, 2002). For this study, the minimum stress configuration included three axes; however, the two axes accounting for the most variability in the original data set are presented. The relationship between understory community composition and environmental and forest structural characteristics, including inorganic N availability, forest floor C:N ratio, abundance of coarse woody debris, and overstory tree density, were explored using the bi-plot function in PC-ORD (McCune and Mefford, 1999). Ordinations were rigidly rotated to place the environmental or forest structural variable with the highest correlation with understory community composition on the first axis. Average percent cover of herbs, shrubs, and seedlings were used for MRPP and NMS. Relationships between species abundance and NMS axis scores were explored using Kendall's τ statistic (SAS version 9.1, SAS Institute Inc., 2004).

Matrix correlation was used to evaluate the degree of association between various strata (e.g., herbs and shrubs, seedlings, saplings, overstory trees) within hemlock stands using Mantel tests in PC-ORD (McCune and Mefford, 1999). These tests calculate the correlation between two dissimilarity matrices, which were derived using Sørensen distances in this study. We were particularly interested in the influence of the overstory tree community on the composition of the understory, seedling and sapling layers (i.e., neighborhood effects sensu Frelich and Reich, 1995). Therefore, an overstory tree community dissimilarity matrix was correlated against the understory, seedling, and sapling layer matrices. Similarly, the seedling and sapling dissimilarity matrices were correlated against each other to examine the degree of association between these two strata. Probability levels for the Mantel tests were calculated using 1000 Monte Carlo randomizations (McCune and Mefford, 1999) and the overstory matrix was based on importance values for overstory species in each stand. Significance levels were set at $\alpha = 0.05$ for all analyses and experiment-wide probability levels were protected by a sequential Bonferroni procedure (Rice, 1989).

3. Results

3.1. Diversity and cover of understory herbs and shrubs

A total of 47 understory herb and shrub species was identified across the 24 hemlock stands examined in this study (Table 2). Of the species identified, 29 occurred only in old-growth hemlock stands; no species were restricted to second-growth hemlock stands (Table 2). No non-native species were found in either old-growth or second-growth stands (Table 2). Importantly, the greater number of species found within old-growth forests may be an artifact of the sampling design, as there were twice as many old-growth study areas as second-growth. Nonetheless, compared with second-growth stands, old-growth forests had approximately 4 times the amount of total ground cover of herbaceous and shrub species ($4.02 \pm 0.41\%/m^2$ versus $1.06 \pm 0.47\%/m^2$) and supported greater overall species richness and diversity (Table 3). In contrast, evenness of herb and shrub species was greater in second-growth stands due in large part to the lower species richness in these systems (Table 3).

3.2. Tree seedlings and saplings

Densities of seedlings and saplings were greater in old-growth stands compared to second-growth stands (Table 4). *Acer pensylvanicum*, *T. canadensis*, and *Betula* spp. (*B. lenta* and *B. alleghaniensis* combined) generally had the highest seedling densities in both old-growth and second-growth forests, and *A. pensylvanicum* was the only species that occurred in all stands (Table 4). Most seedling species were found in both old-growth and second-growth forests; however, *Pinus strobus* and *Acer saccharum* only occurred as seedlings in old-growth stands. Seedling densities varied considerably between old-growth and second-growth forests as *T. canadensis*, *Picea rubens*, and *Betula* spp. had higher densities in old-growth stands while *Acer rubrum* had higher densities in second-growth stands (Table 4). Overall, the composition of the seedling layer was positively associated with the composition of the overstory layer (Mantel test, $r = 0.27$, $P < 0.05$), suggesting the successful establishment of overstory species within the understory layer of these stands.

T. canadensis had the highest sapling density across old-growth and second-growth stands and was the only species found in the sapling layer of all hemlock stands investigated (Table 4). *A. pensylvanicum* and *Fagus grandifolia* were generally more abundant in old-growth versus second-growth stands (Table 4). Several species occurring as seedlings within a given forest type were not observed as saplings (Table 4). For example, *P. strobus* and *Betula papyrifera* saplings were not observed in old-growth stands despite the presence of these species in the seedling layer and in the overstory (Table 4). Likewise, saplings of *B. papyrifera* and *Quercus rubra* were not found in second-growth stands despite their presence in the seedling layer of these systems. Nonetheless, composition of the sapling layer among hemlock stands was positively correlated with the composition of the seedling layer (Mantel test, $r = 0.29$, $P < 0.05$). In addition, there was a positive correlation between the composition of the sapling layer and the composition of the overstory layer (Mantel test, $r = 0.30$, respectively, $P < 0.05$). Conversely, sapling densities were negatively correlated with density of overstory trees (Kendall's $\tau = -0.53$, $P < 0.05$).

3.3. Understory layer composition

Understory communities differed between old-growth and second-growth stands (multi-response permutation procedures [MRPP]; $P < 0.05$); however, the small effect size ($A = 0.03$) derived

Table 2

Herb, graminoid, shrub, fern, and club moss species identified in the understory of old-growth (OG) and second-growth (2G) hemlock forests in western Massachusetts. Species occurrences are based on complete censuses of 0.04-ha plots within each study area (3–5 plots per site). Nomenclature follows Gleason and Cronquist (1991).

Species	OG	2G
Herbs		
<i>Actaea alba</i>	X	
<i>Aralia nudicaulis</i>	X	X
<i>Arisaema triphyllum</i>	X	
<i>Aster acuminatus</i>	X	X
<i>Aster dumosus</i>	X	
<i>Aster divericatus</i>	X	
<i>Chimaphila maculata</i>	X	X
<i>Circaea alpina</i>	X	X
<i>Clintonia borealis</i>	X	
<i>Cypripedium acaule</i>	X	
<i>Epigaea repens</i>	X	X
<i>Galium</i> spp.	X	X
<i>Gaultheria procumbens</i>	X	X
<i>Laportea canadensis</i>	X	
<i>Maianthemum canadense</i>	X	
<i>Medeola virginiana</i>	X	
<i>Mitchella repens</i>	X	X
<i>Monotropa uniflora</i>	X	X
<i>Oxalis acetosella</i>	X	
<i>Polygonatum pubescens</i>	X	
<i>Solidago flexicaulis</i>	X	
<i>Tiarella cordifolia</i>	X	
<i>Trientalis borealis</i>	X	X
<i>Trillium erectum</i>	X	
<i>Trillium undulatum</i>	X	X
<i>Viola rotundifolia</i>	X	
Graminoids		
<i>Carex pensylvanica</i>	X	X
Ferns		
<i>Adiantum pedatum</i>	X	
<i>Dryopteris intermedia</i>	X	X
<i>Dryopteris marginalis</i>	X	
<i>Polypodium virginianum</i>	X	
<i>Thelypteris phegopteris</i>	X	
Shrubs		
<i>Cornus alternifolia</i>	X	
<i>Hamamelis virginiana</i>	X	X
<i>Kalmia latifolia</i>	X	X
<i>Rhododendron prinophyllum</i>	X	
<i>Rubus allegheniensis</i>	X	
<i>Rubus idaeus</i>	X	
<i>Sambucus racemosa</i>	X	
<i>Solidago flexicaulis</i>	X	
<i>Taxus canadensis</i>	X	
<i>Vaccinium angustifolium</i>	X	X
<i>Viburnum acerifolium</i>	X	
<i>Viburnum alnifolium</i>	X	X
Club mosses		
<i>Lycopodium annotinum</i>	X	
<i>Lycopodium lucidulum</i>	X	X
<i>Polystichum acrostichoides</i>	X	X

from MRPP suggested that there was also a wide range of variation in understory community composition within old-growth and second-growth stands, respectively (McCune and Grace, 2002). This was illustrated by the broad distribution of points for each of these stand types in the ordination of understory vegetation (Fig. 1), which explained 65.2% of the variation in the raw data (NMS ordination, final stress = 12.35, final instability = 0.00001). Most of the variation in understory vegetation among stands was explained by Axis 1 (30.4%), which represented a gradient from sites with low overstory tree densities and high NH_4-N availability in the negative portion of Axis 1 to higher density sites with lower levels of available NH_4-N in the positive portion (Fig. 1).

Table 3

Mean cover and site-level species richness (*S*), diversity (*H'*), and evenness (*E*) of all herbaceous (herbs, ferns, graminoids, and club mosses) and shrub species in old-growth and second-growth hemlock stands. Values are based on average cover and frequency of herb and shrub species across understory subplots within each study area (1 m², 24–40 per site). Standard errors are in parentheses and means with different letters (a and b) are significantly different ($P < 0.05$, Wilcoxon rank-sum test).

	Old-growth (<i>n</i> = 16)	Second-growth (<i>n</i> = 8)
Plant cover (%/m ²)	4.02 (0.41)a	1.06 (0.47)b
Richness (<i>S</i>)	13.56 (1.11)a	6.88 (0.83)b
Diversity (<i>H'</i>)	2.12 (0.08)a	1.64 (0.11)b
Evenness (<i>E</i>)	0.83 (0.01)a	0.88 (0.02)b

Correlations of species with this axis indicated that there was greater abundance of the fern species, *Polypodium virginianum* ($\tau = -0.55$) and *Dryopteris intermedia* ($\tau = -0.52$), within old-growth study sites located in the negative portion of Axis 1 (Fig. 1, Table 5).

The distribution of study areas along Axis 2, which explained 27.8% of the variation, generally ranged from sites with a smaller proportion of the total downed coarse woody debris (CWD) pools in decay class IV (highly decayed, cf. Fraver et al., 2002) to sites with higher proportions of this deadwood type (Fig. 1). Study sites with downed woody debris pools containing a higher proportion of wood in advanced stages of decay tended to have greater amounts of *Kalmia latifolia* and *T. canadensis* in the understory as there was a significant positive correlation between the abundance of these species and Axis 2 (Table 5). Importantly, average volumes of decay class IV downed CWD were more than 9 times greater in old-growth stands compared to second-growth stands (21.3 ± 7.7 m³/ha versus 2.2 ± 0.9 m³/ha in old-growth and second-growth stands, respectively). Furthermore, total volumes of downed CWD were four times as high in the old-growth stands examined in this study (D'Amato et al., 2008).

Despite the wide range of variation in understory community composition within both old-growth and second-growth stands (based on MRPP), Indicator Species Analysis identified four species indicative of the understory layer in old-growth hemlock forests relative to second-growth stands: *D. intermedia*, *Viburnum alnifolium*, *Aralia nudicaulis*, and *T. canadensis* (Fig. 2). Several other species, including *Lycopodium lucidulum*, *P. virginianum*, and *Polystichum acrostichoides*, were also more common in old-growth stands (Fig. 2). In contrast, only *A. rubrum* seedlings were more common in second-growth stands (Fig. 2). There was no significant

Table 4

Average seedling and sapling densities (#/ha) in old-growth and second-growth hemlock forests. Ranges appear in parentheses for each species and standard errors are depicted for totals. Totals with different letters indicate significant differences between old-growth and second-growth stands ($P < 0.05$, Wilcoxon rank-sum test). Species-level values represent site-level averages, whereas totals represent averages across old-growth and second-growth stands, respectively.

Species	Old-growth (<i>n</i> = 16)		Second-growth (<i>n</i> = 8)	
	Seedlings (#/ha)	Saplings (#/ha)	Seedlings (#/ha)	Saplings (#/ha)
<i>Acer pensylvanicum</i>	13747 (417–7917)	165 (0–383)	4688 (417–13750)	8 (0–25)
<i>Acer rubrum</i>	1371 (0–7917)	2 (0–25)	3177 (0–12083)	10 (0–25)
<i>Acer saccharum</i>	677 (0–9167)	18 (0–300)	–	1 (0–8)
<i>Betula alleghaniensis</i>	–	41 (0–169)	–	3 (0–17)
<i>Betula lenta</i>	–	74 (0–442)	–	20 (0–67)
<i>Betula spp.</i> ^a	5722 (0–27083)	–	2500 (417–9167)	–
<i>Betula papyrifera</i>	15 (0–250)	–	185 (0–1667)	–
<i>Fagus grandifolia</i>	820 (0–3125)	119 (0–363)	990 (0–2917)	66 (0–200)
<i>Picea rubens</i>	1169 (0–5313)	36 (0–275)	52 (0–417)	9 (0–75)
<i>Pinus strobus</i>	83 (0–500)	–	–	–
<i>Quercus rubra</i>	133 (0–1250)	1 (0–8)	313 (0–1250)	–
<i>Tsuga canadensis</i>	13760 (1250–51250)	354 (31–942)	3958 (0–15833)	189 (75–400)
Total ^b	38104 (5927)a	847 (83)a	14948 (4113)b	306 (34)b

^a Seedlings of *B. alleghaniensis* and *B. lenta* were combined for estimates of seedling density.

^b Includes less common species not listed in table, *Fraxinus americana*, *Ostrya virginiana*, *Pinus resinosa*, *Sorbus americana*, and *Tilia americana*.

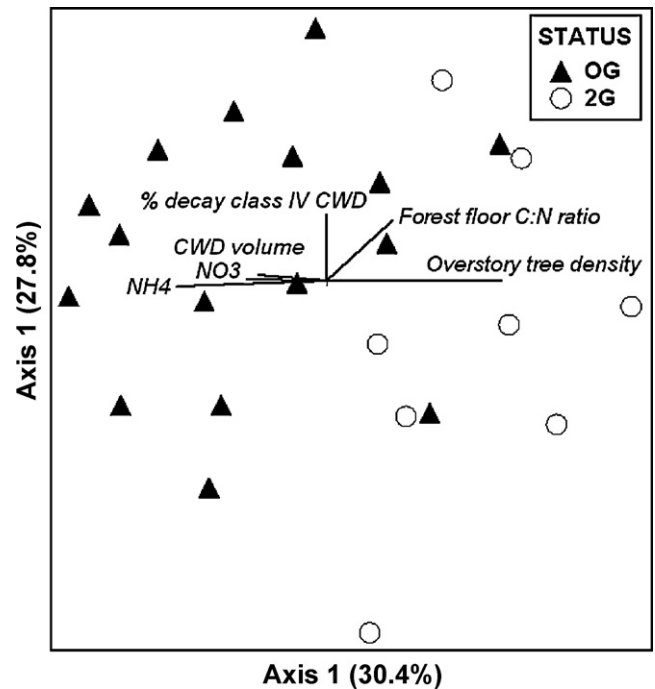


Fig. 1. Non-metric multidimensional scaling (NMS) ordination of understory vegetation composition in old-growth (black triangles) and second-growth (open circles) eastern hemlock forests. Vector length represents the explanatory power of the environmental and stand structural variables. This ordination diagram was rigidly rotated to place the variable “overstory tree density” parallel with NMS axis 1 as this variable had the highest correlation with understory composition. See Table 5 for species correlations with NMS axes 1 and 2.

relationship between the composition of understory herbs and shrubs and the composition of overstory trees among hemlock stands (Mantel test, $r = 0.02$, $P = 0.37$).

4. Discussion

This study indicates that, despite compositional similarities in overstory trees, differences exist between the understory communities characterizing old-growth and second-growth hemlock forests in western Massachusetts. In particular, old-growth forests had higher species richness and diversity, as well as a greater abundance of understory herbs and shrubs, and tree seedlings and saplings compared to second-growth forests. The observed

Table 5
Correlations (Kendall's τ) between the average percent cover of understory herbs, shrubs, and tree seedlings within each study area (%/m²) and non-metric multidimensional scaling Axes 1 and 2. Species in bold have significant correlations with axes scores ($P < 0.05$ (Bonferroni-protected)).

Species	Axis 1	Axis 2	Species	Axis 1	Axis 2
<i>A. pensylvanicum</i>	-0.17	0.07	<i>Mitchella repens</i>	0.04	-0.27
<i>A. rubrum</i>	0.45	0.34	<i>Monotropa uniflora</i>	0.20	0.29
<i>A. saccharum</i>	-0.42	-0.08	<i>Oxalis acetosella</i>	-0.44	0.10
<i>Acer spicatum</i>	-0.39	-0.02	<i>P. rubens</i>	-0.30	0.17
<i>A. nudicaulis</i>	-0.41	0.13	<i>P. acrostichoides</i>	-0.27	0.03
<i>Aster acuminatis</i>	-0.48	0.12	<i>P. virginianum</i>	-0.55	0.12
<i>Betula</i> spp.	-0.33	0.41	<i>Q. rubra</i>	0.40	0.21
<i>Dryopteris intermedia</i>	-0.52	-0.17	<i>Taxus canadensis</i>	-0.42	0.01
<i>F. grandifolia</i>	0.19	-0.23	<i>Trientalis borealis</i>	-0.37	0.13
<i>K. latifolia</i>	0.18	0.56	<i>Trillium undulatum</i>	0.05	0.32
<i>L. lucidulum</i>	-0.39	-0.11	<i>T. canadensis</i>	-0.37	0.50
<i>Maianthemum canadense</i>	-0.18	0.14	<i>V. alnifolium</i>	-0.35	0.15

importance of overstory tree density, nitrogen availability, and coarse woody debris characteristics in explaining the variation in understory composition among hemlock stands suggests that differences in resource availability (e.g., light, moisture, and nutrients) and microhabitat heterogeneity between old-growth and second-growth stands were likely driving these patterns.

4.1. Diversity and abundance of understory herbs and shrubs

Overstory tree density strongly influences patterns of understory species richness and abundance (Alaback, 1982; Peet and Christensen, 1988; Oliver and Larson, 1996). Several studies have demonstrated that lower levels of species richness and abundance characterize dense, closed canopy forests within the stem exclusion phase of development (sensu Oliver, 1981; Alaback, 1982; Halpern, 1988; Schoonmaker and McKee, 1988; Eycott et al., 2006; Jules et al., 2008), whereas richness and abundance often increase as forests mature and self-thinning and gap-scale disturbances create and maintain canopy openings (Davison and Forman, 1982; Alaback and Herman, 1988; Eycott et al., 2006). In this study, the second-growth stands we examined were primarily in the stem exclusion phase of development, and the low sapling densities and understory plant abundance and richness observed in these systems were likely a reflection of the lower levels of resource availability (e.g., light, nutrients) in the understory layer during this stage of stand development (Klinka et al., 1996; Oliver

and Larson, 1996). In contrast, the structure of the old-growth areas had been primarily influenced by more than three centuries of small to moderate gap-scale disturbances (D'Amato and Orwig, 2008) resulting in stands characterized by lower tree densities, larger trees, multi-layered canopies, and an abundance of downed coarse woody debris and canopy gaps (D'Amato et al., 2008). Presumably, the diversity of microhabitats and greater levels of resource availability associated with these structural attributes (Alaback, 1982; Qian et al., 1997; D'Amato, 2007) and disturbance processes (Beatty, 1984; Moore and Vankat, 1986; Peterson and Campbell, 1993; Reader and Bricker, 1992) resulted in a greater abundance and richness of understory plants within old-growth stands compared to dense second-growth stands.

Overall, the composition and abundance of understory plants among hemlock stands in this study were similar to those reported elsewhere for second-growth (Rogers, 1980; Eschtruth et al., 2006) and old-growth hemlock forests (Whitney and Foster, 1988). While the old-growth stands in this study had a greater abundance of understory herbs and shrubs compared to second-growth, these values were much lower than those reported for other forest types in the region (e.g., Rogers, 1980; Gilliam et al., 1995). The sparse nature of understory vegetation within these systems is likely a reflection of the low levels of nutrient and light availability, as well as higher forest floor and soil acidity levels typically characterizing hemlock-dominated forests relative to other forest types such as northern hardwood forests (Rogers, 1980; Mladenoff, 1987;

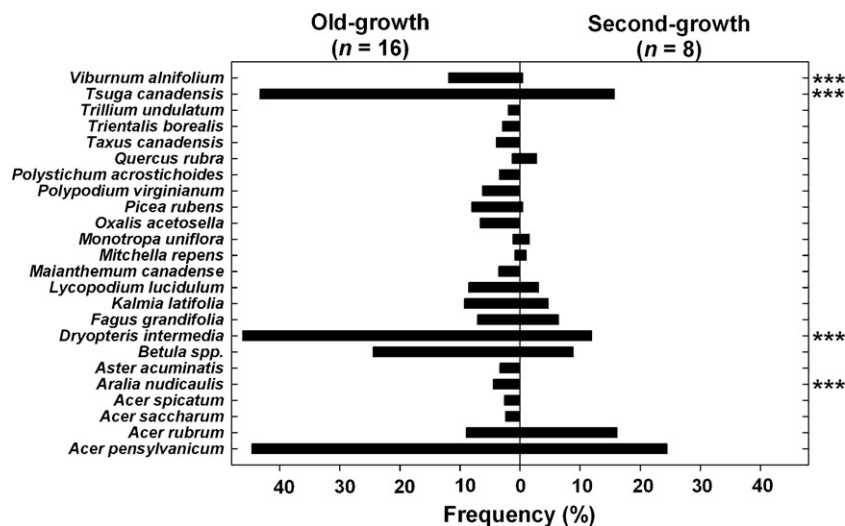


Fig. 2. Average frequency of occurrence (%) of common plant species within old-growth and second-growth eastern hemlock forests in western Massachusetts. Frequency is based on occurrence within understory sampling plots (1 m², 24–40 per stand) and only species occurring within at least three study areas (12.5% of total) are shown. Asterisks indicate significant indicator species for old-growth forests based on Indicator Species Analysis (Dufendre and Legendre, 1997, $P < 0.05$ based on Monte Carlo randomization tests using 1000 runs). There were no significant indicator species for second-growth stands.

Canham et al., 1994; Lovett et al., 2004). Although these understory conditions limit the abundance of understory herbs and shrubs, they tend to favor the establishment of conspecific regeneration within hemlock-dominated stands (i.e., positive overstory-understory neighborhood effects, Frelich and Reich, 1995). These positive neighborhood effects between overstory trees and understory regeneration were illustrated by the strong, positive associations in Mantel tests conducted between overstory composition and the composition of the seedling and sapling layers within the hemlock stands examined in this study. Correspondingly, management approaches aimed at restoring old-growth characteristics to existing second-growth hemlock systems should rely on selection systems that not only emulate the gap-scale disturbance regimes historically characterizing these systems (cf. D'Amato and Orwig, 2008) but also maintain the understory conditions favoring long-term hemlock establishment and recruitment (Brissette and Kenefic, 2000).

Several species were more abundant in old-growth than second-growth hemlock understories, including *A. nudicaulis*, *D. intermedia*, and *V. alnifolium*. Several other studies examining the composition of old-growth, primary, and secondary forests in the northeastern United States have also indicated that these species were more abundant in old-growth and primary forest ecosystems (Nichols, 1913; Egler, 1940; Whitney and Foster, 1988; Motzkin et al., 1999; Singleton et al., 2001). For example, the occurrence of *A. nudicaulis* and *V. alnifolium* was much greater in old-growth white pine-hemlock forests as compared to secondary white pine-hemlock forests in central New England (Whitney and Foster, 1988). These patterns were attributed to the sensitivity of these species to competitive displacement and microclimatic changes following forest harvesting, as well as to the dispersal and colonization limitations of *V. alnifolium* (Whitney and Foster, 1988; Motzkin et al., 1999). In contrast, the lack of suitable microhabitats in secondary forests was suggested as a possible explanation for the greater frequency of *D. intermedia* in primary forests compared to post-agricultural forests in central New York (Singleton et al., 2001). Although we did not directly examine dispersal rates or microhabitat associations in this study, it is likely that these mechanisms (e.g., dispersal limitations, lack of suitable microhabitats, Meier et al., 1995) were influencing the differences in abundance of these species between old-growth and second-growth hemlock forests. In particular, *A. nudicaulis* and *V. alnifolium* spread primarily by vegetative means (Edwards, 1984; Nyland et al., 2006) and this reliance on clonal spread may have limited their ability to re-colonize second-growth areas following harvesting (cf. Meier et al., 1995). Likewise, the lower abundance of suitable microhabitats observed among second-growth hemlock stands (e.g., decayed logs, McGee, 2001; D'Amato et al., 2008) may have contributed to the lower abundance of *D. intermedia* in these systems. An additional possible explanation for the absence or lower abundance of these species in second-growth areas is that these species were never present in these stands prior to harvesting. Despite this consideration, the historical ubiquity of these plant species throughout these landscapes makes this explanation highly unlikely (Egler, 1940). Due to affinity of these species to old-growth and primary forests found in this and other studies in the region, the abundance of these species might serve as useful indicators for evaluating the success of management strategies aimed at restoring old-growth characteristics to second-growth hemlock systems.

4.2. Composition and abundance of tree seedlings and saplings

The high densities of *T. canadensis* and *A. pensylvanicum* seedlings observed in old-growth and second-growth stands in this study were consistent with the findings of other studies

quantifying seedling densities in hemlock-dominated forests (e.g., Rogers, 1980; Yorks et al., 2000; Kizlinski et al., 2002) and was likely due to the ability of both these species to survive in the low light levels and acidic soils characterizing these ecosystems (Hibbs, 1979; Burns and Honkala, 1990; Lei and Lechowicz, 1990; Kobe et al., 1995). In contrast, the prolific seed production and seed banking abilities of the mid-tolerant species, *Betula lenta* and *B. alleghaniensis*, likely contributed to the abundance of these seedlings among hemlock study areas as these species often dominate the seed banks of hemlock-dominated forests (Catovsky and Bazzaz, 2000; Yorks et al., 2000; Sullivan and Ellison, 2006). While these species may germinate under low light conditions, their survival in these stands is dependent on canopy gaps that increase light availability in the forest understory (Carlton and Bazzaz, 1998; Orwig and Foster, 1998; Webster and Lorimer, 2005). This was demonstrated by the affinity of *B. alleghaniensis* and *B. lenta* saplings to recent canopy gaps within the hemlock stands we sampled (A.W. D'Amato, personal observation), as well as by the tremendous increase of these species observed in the sapling layer of hemlock forests defoliated by hemlock woolly adelgid (Orwig and Foster, 1998; Kizlinski et al., 2002; Stadler et al., 2005). Based on these findings from infested stands in the region and the characteristics of the seedling layers in the present study, it is highly likely that a similar increase in *B. alleghaniensis* and *B. lenta* will occur on these sites when hemlock woolly adelgid reaches these areas.

Although there were compositional similarities in the seedling and sapling layers between old-growth and second-growth hemlock stands (Table 4), densities of seedlings and saplings were much greater in old-growth stands. The factors described as influencing the patterns for understory herb and shrub abundance between old-growth and second-growth stands (e.g., greater diversity of microhabitats and resource availability in old-growth stands) also likely contributed to the patterns in seedling and sapling densities. In particular, several studies have demonstrated the importance of decaying logs on the forest floor as microhabitats for certain tree species (Christy and Mack, 1984; Harmon and Franklin, 1989; Beach and Halpern, 2001), including *T. canadensis* and *B. alleghaniensis* (Mladenoff and Stearns, 1993; Corinth, 1995; McGee, 2001; Marx and Walters, 2008). In this study, the abundance of highly decayed downed wood (decay classes III and IV combined, after Fraver et al., 2002) was almost five times greater in old-growth forests compared to second-growth forests (56.2 m³/ha versus 11.6 m³/ha). While we did not specifically sample downed logs for seedling and sapling abundance, seedlings



Fig. 3. Downed hemlock log within an old-growth hemlock stand on Mt. Everett, MA. Note the abundant *Tsuga canadensis* and *Betula alleghaniensis* seedlings.

of *T. canadensis* and *Betula* spp. were commonly observed on these substrates within our study areas (A.W. D'Amato, personal observation, Fig. 3). In addition, the association of *T. canadensis* with this microhabitat was demonstrated by the positive correlation between proportion of highly decayed downed coarse woody debris and *T. canadensis* abundance in the ordination of understory community composition (Fig. 1). Due to the importance of deadwood substrates in these systems, the deliberate felling and retention of canopy trees in harvest gaps should be integrated into management strategies aimed at restoring old-growth conditions to second-growth hemlock stands. Importantly, including these provisions for CWD creation at each harvest entry will be critical for ensuring that a diversity of decay classes are present in these stands over time (cf. D'Amato and Catanzaro, 2007).

Beyond differences in microhabitat and resource availability, it is likely that the greater sapling densities in old-growth stands were also related to the differences in the nature of disturbance in these systems as compared to second-growth stands. Both of these systems have experienced small to moderate canopy disturbances over the past century (D'Amato and Orwig, 2008); however, the size of canopy gaps created in old-growth stands is generally greater due to the larger overstory trees in these stands (cf. Dahir and Lorimer, 1996). As a result, these stands contain understory light conditions more favorable for the recruitment of mid-tolerant and tolerant species into the sapling layer. Moreover, the extreme shade tolerance of *T. canadensis* allows it to persist under low light levels in the forest understory for extended periods of time, often exceeding a century (Godman and Lancaster, 1990, A.W. D'Amato, personal observation). Therefore, some of the hemlock saplings within old-growth stands likely recruited prior to the establishment of the second-growth areas examined, thus contributing to the greater abundance of this species within old-growth areas. These patterns reinforce the suitability of selection systems for increasing hemlock regeneration in second-growth systems and restoring canopy complexity through the creation of well-developed sapling layers.

Interestingly, several compositional and structural components extirpated from the understory layer of hemlock stands in other regions of the northeastern United States due to overbrowsing by white-tail deer, including *Taxus canadensis* and abundant *T. canadensis* saplings (Frelich and Lorimer, 1985; Alverson et al., 1988; Rooney and Dress, 1997; Long et al., 1998; Weckel et al., 2006), were commonly documented in the old-growth and second-growth stands observed in this study. Due to the comparatively low deer densities in our study region (~10 per square mile, MassWildlife, 2008), these results serve as an illustration of the dramatic effect white-tail deer is having on the structure and dynamics of eastern hemlock forests in other portions of this species' range and represent a baseline for assessing how future increases in deer densities within western Massachusetts affect the conservation and management of these systems. Moreover, recent results highlighting the positive interactive effects of canopy disturbance due to hemlock woolly adelgid infestation and severity of deer browsing underscore the importance of simultaneously monitoring the impacts of these and other disturbance agents on the future plant community dynamics of these currently unaffected systems (Eschtruth and Battles, 2008).

5. Conclusions

The understory communities in the old-growth hemlock stands examined in this study are distinctive from those in hemlock dominated stands originating following logging in the late 19th century. Understory vegetation characteristics within these old-growth stands, including species richness, herb and shrub cover, and seedling and sapling densities, are much greater than those

observed within the understories of second-growth areas due in large part to the greater resource availability and microhabitat heterogeneity characterizing these systems. Notably, differences in composition, richness, and diversity between old-growth and second-growth hemlock stands resulted from either the absence or lower abundance of several common forest herbs and shrubs within second-growth stands and were not due to the presence of rare species in old-growth. Despite the lack of old-growth obligate understory species in these stands, the understory communities of these old-growth systems represent important habitat features on the landscape providing greater levels of forage and cover for a variety of wildlife relative to second-growth hemlock stands. The return of old-growth understory conditions to these second-growth areas will be largely dependent on disturbance and self-thinning mediated changes in overstory structure, resource availability, and microhabitat heterogeneity within these systems. As such, management strategies, including the use of gap-based silvicultural systems and the creation and retention of CWD, may serve as effective approaches for actively restoring these understory conditions to second-growth stands. Although hemlock woolly adelgid is not present at any hemlock stands examined in this study, our results suggest that the loss of hemlock from these areas will lead to the tremendous increases in *B. lenta* and *B. alleghaniensis* observed in infested hemlock forests in this region (Orwig and Foster, 1998). More importantly, infestation of these areas will irreversibly alter the composition and structure of the few remaining old-growth forests in southern New England.

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