Understory Vegetation in Old-Growth and Second-Growth Tsuga Canadensis Forests in Western Massachusetts

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1   **RUNNING HEAD:** Old-growth forest understories

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4   Western Massachusetts

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1 **ABSTRACT**

2 We compared the understory communities (herbs, shrubs, and tree seedlings and saplings) of

3 old-growth and second-growth eastern hemlock forests (*Tsuga canadensis*) in western

4 Massachusetts, USA. Second-growth hemlock forests originated following clearcut logging in

5 the late 1800s and were 108 to 136 years old at the time of sampling. Old-growth hemlock

6 forests contained total ground cover of herbaceous and shrub species that was approximately 4

7 times greater than in second growth forests (4.02 ± 0.41 versus 1.06 ± 0.47 %/m^2) and supported

8 greater overall species richness and diversity. In addition, seedling and sapling densities were

9 greater in old-growth stands compared to second-growth stands and the composition of these

10 layers was positively correlated with overstory species composition (Mantel tests, $r > 0.26$, $P <$

11 0.05) highlighting the strong positive neighborhood effects in these systems. Ordination of study

12 site understory species composition identified a strong gradient in community composition from

13 second-growth to old-growth stands. Vector overlays of environmental and forest structural

14 variables indicated that these gradients were related to differences in overstory tree density,

15 nitrogen availability, and coarse woody debris characteristics among hemlock stands. These

16 relationships suggest that differences in resource availability (e.g., light, moisture, and nutrients)

17 and microhabitat heterogeneity between old-growth and second-growth stands were likely

18 driving these compositional patterns. Interestingly, several common forest understory plants,

19 including *Aralia nudicaulis*, *Dryopteris intermedia,* and *Viburnum alnifolium*, were significant

20 indicator species for old-growth hemlock stands, highlighting the lasting legacy of past land use

21 on the reestablishment and growth of these common species within second-growth areas. The

22 return of old-growth understory conditions to these second-growth areas will largely be

1 dependent on disturbance and self-thinning mediated changes in overstory structure, resource

2 availability, and microhabitat heterogeneity.

3 **KEYWORDS:** *Tsuga canadensis,* understory vegetation, old-growth, Massachusetts,

4 neighborhood effects, species diversity

5

6 **1. Introduction**

7   The understory layer is a critical component of forest ecosystems typically supporting the

8 vast majority of total ecosystem floristic diversity (Halpern and Spies 1995, Gilliam and Roberts

9 2003) and providing habitat elements to associated wildlife species (Carey and Johnson 1995).

10 These communities also play a central role in the dynamics and functioning of forest ecosystems

11 by influencing long-term successional patterns (Philips and Murdy 1995, Abrams and Downs

12 1990, Oliver and Larson 1996, McCarthy et al. 2001, Royo and Carson 2005, Nyland et al. 2006)

13 and contributing to forest nutrient cycles (Chapin 1983, Zak et al. 1990, Anderson and Eickmeier

14 2000, Chastain et al. 2006). Due to the recognized ecological importance of forest understory

15 plants, considerable effort has been devoted to determining the impacts of land-use practices on

16 the structure and diversity of these communities (Whitney and Foster 1988, Matlack 1994,

17 Motzkin et al. 1996, Bellemare et al. 2002, Eberhardt et al. 2003, Goslee et al. 2005; Fraterringo

18 et al. 2006, see also *Ecological Applications* Special Feature Vol. 5, 1995). This work has

19 demonstrated the importance of past land use in shaping contemporary patterns of understory

20 vegetation and has indicated that distinct community assemblages may characterize various

21 stages of forest succession.

22   Understory communities in old-growth forest ecosystems are often quite distinct relative

23 to forests originating following agricultural clearing or forest harvesting (Whitney and Foster

1988, Matlack 1994, Qian et al 1997, Goebel et al. 1999). Although the diversity of understory

plants may be low in some old-growth systems (Metzger and Shultz 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

4

1 following agricultural clearing versus logging exclusively, Motzkin et al. 1996, Donahue et al.

2 2000, Bellemare et al. 2002); however, our understanding of the compositional differences that

3 may exist between old-growth and primary forests is fairly limited (but see Whitney and Foster

4 1988, Cooper-Ellis 1998). This study compares the understory vegetation of the few remaining

5 old-growth forests in western Massachusetts with adjacent second-growth forests that originated

6 following logging in the late 19th Century, but were never cleared for agricultural purposes.

7 Many of the old-growth forests in western Massachusetts are surrounded by compositionally

8 similar second-growth stands providing the opportunity to investigate the influence of differing

9 past land-use on the understory communities of forests with similar overstory species

10 composition and edaphic and landscape settings. In addition, the majority of these old-growth

11 forests are dominated by eastern hemlock (*Tsuga canadensis*), a species currently threatened by

12 the introduced hemlock woolly adelgid (*Adelges tsugae,* HWA, Orwig and Foster 1998).

13 Although none of these forests are currently infested by HWA, this introduced pest is within 3

14 km of several old-growth stands (C. Burnham, unpublished data). As a result, studies

15 characterizing the floristic composition of the understory layer prior to HWA infestation will

16 serve as an important baseline for monitoring the response of these ecosystems to this novel

17 disturbance (Small et al. 2005; Eschtruth et al. 2006, Cleavitt et al. 2008). Similarly, the

18 regeneration dynamics and floristic diversity of hemlock-dominated old-growth stands

19 throughout the range of this species have been dramatically influenced by herbivory stemming

20 from overabundant white-tail deer (*Odocoileus virginianus*) populations (Anderson and Loucks

21 1979, Frelich and Lorimer 1985, Alverson et al. 1988, Mladenoff and Stearns 1993, Rooney and

22 Dress 1997, Long et al. 1998, Weckel et al. 2006). The lack of similar high populations within

23 our study region provides an important opportunity to assess the structure and composition of

1   systems currently unaffected by this conservation and management issue facing hemlock forests

2   in many other regions of North America (Rooney et al. 2000).

3

4   **2. Materials and Methods**

5   *2.1. Study area*

6   Sampling was conducted in 16 old-growth and 8 second-growth hemlock forests in the

7   Berkshire Hills and Taconic Mountains of western Massachusetts (Table 1). This area has a

8   humid, continental climate with average annual levels of precipitation ranging from 116.2 to

9   129.5 cm and mean monthly temperatures from $-7.7°$ C in January to $22.2°$ C in July (NCDC

10   2006). Study areas were located on steep slopes (range: $25-41°$) and ranged in elevation from

11   305-685 m.a.s.l. Soils in these areas are predominantly well-drained sandy loam soils formed

12   from weathered gneiss, schist, and phyllite (Zen et al. 1983, Scanu 1988).

13   Old-growth and second-growth status was assigned based on extensive analysis of

14   historical and dendroecological evidence collected from these areas (D'Amato et al. 2006).

15   Based on these analyses, old-growth areas were classified as sites lacking any evidence of past

16   land-use and containing at least five old (> 225 years old) canopy trees per hectare (cf. McGee et

17   al. 1999). In contrast, early state documents indicated that several second-growth areas adjacent

18   to old-growth areas were clear-cut harvested in the 1870s-1900s (Avery and Slack 1926;

19   D'Amato and Orwig 2008). In addition, dendroecological analyses of second-growth areas

20   confirmed that all second-growth sites were clear-cut harvested between the 1870s-1900s as

21   dramatic release and recruitment pulses were observed in these stands during these decades

22   (D'Amato 2007). In contrast to second-growth stands found in other mountainous regions of

23   New England, there was little evidence that these areas were burned following clear-cut

1 harvesting (c.f. Goodale and Aber 2001) Care was taken in the selection of second-growth sites

2 to ensure that the environmental settings (e.g., elevation, topographic position, slope steepness,

3 and aspect) were as similar to those of the old-growth hemlock stands as possible.

4

5 *2.2. Vegetation sampling*

6   Vegetation sampling plots were part of a larger study examining the structure and

7 disturbance dynamics of old-growth and second-growth forests in western Massachusetts

8 (D'Amato and Orwig 2008, D'Amato et al. 2008). Depending on stand size, 3-5 0.04-ha plots

9 were established along transects orientated through the central portion of each study area and

10 permanently marked. Percent cover of all vascular herbaceous plants, shrubs, and tree seedlings

11 were estimated by species in eight 1-m^2 sub-plots randomly located within each 0.04-ha

12 sampling plot during May and June 2004. Seedling densities were also determined in these sub-

13 plots. A complete census of herbaceous and shrub species was made in each 0.04-ha sampling

14 plot to generate master species lists. This census was repeated in the late summer to ensure

15 species emerging following the initial vegetation sampling were accounted for. No additional

16 species were identified during these late summer censuses. Species and diameter at breast height

17 (DBH) was recorded for every tree (stems $\geq$ 1.37 m tall and $\geq$ 10 cm DBH) rooted within the

18 0.04-ha plots. In addition, all saplings (stems $\geq$ 1.37 m tall and $\leq$ 10 cm DBH) were tallied by

19 species. Measurements of forest floor environmental characteristics, including coarse woody

20 debris abundance, soil pH, and nitrogen availability determined from mixed-bed cation and anion

21 resin bags were also made within each 0.04 ha plot. Methods used for sampling CWD and soil

22 characteristics are summarized in D'Amato et al. (2008) and D'Amato (2007). Species

23 nomenclature follows Gleason and Cronquist (1990).

1   *2.3. Statistical analyses*

2   Percent cover of herbs and shrubs and seedling and sapling densities were averaged for

3   each study area and compared between old-growth and second-growth forests using Wilcoxon

4   rank-sum tests. In addition, average species richness (number of species in study area, S),

5   diversity (Shannon-Wiener index, *H'*), and evenness (*E*, Pielou 1969) of understory herbs and

6   shrubs were compared between old-growth and second-growth forests using the same procedure.

7   Multivariate tests for differences in the composition of understory vegetation (herbs, shrubs, and

8   seedlings) between old-growth and second-growth forests were conducted using multi-response

9   permutation procedures (MRPP) in PC-ORD version 4.28 (McCune and Mefford 1999). MRPP

10   is a non-parametric, randomization-based multivariate test of differences between groups that

11   compares the plots within *a priori* groups to a random allocation of plots (McCune and Grace

12   2002). Sørensen distances were used to calculate average within-group distances for MRPP.

13   Indicator species analysis (Dufrene and Legendre 1997) was used to describe how well certain

14   understory species differentiated between old-growth and second-growth forests.

15   Non-metric multidimensional scaling (NMS; McCune and Grace 2002) was used to

16   examine patterns in understory community composition within and among old-growth and

17   second-growth forests. As was the case for MRPP, NMS used Sørensen distances to calculate a

18   distance matrix for the 24 study areas. To reduce noise in the data set, species with fewer than 3

19   occurrences were removed from the data matrices (McCune and Grace 2002). The "slow-and-

20   thorough" autopilot mode of NMS in PC-ORD was used to generate solutions. This procedure

21   determines the optimal ordination solution by stepping down in dimensionality from a six-axis to

22   one-axis solution using 40 runs performed on real data followed by 50 Monte Carlo runs using

23   random data (McCune and Mefford 1999). Optimal dimensionality was based on the number of

1   dimensions with the lowest stress (i.e., smallest departure from monotonicity in the relationship

2   between distance in the original space and distance in the reduced ordination space, McCune and

3   Grace 2002). For this study, the minimum stress configuration included 3 axes; however, the

4   two axes accounting for the most variability in the original data set are presented. The

5   relationship between understory community composition and environmental and forest structural

6   characteristics, including inorganic N availability, forest floor C:N ratio, abundance of coarse

7   woody debris, and overstory tree density, were explored using the bi-plot function in PC-ORD

8   (McCune and Mefford 1999). Ordinations were rigidly rotated to place the environmental or

9   forest structural variable with the highest correlation with understory community composition on

10 the first axis. Average percent cover of herbs, shrubs, and seedlings were used for MRPP and

11 NMS. Relationships between species abundance and NMS axis scores were explored using

12 Kendall's tau statistic (SAS version 9.1, SAS Institute Inc. 2004).

13   Matrix correlation was used to evaluate the degree of association between various strata

14 (e.g., herbs and shrubs, seedlings, saplings, overstory trees) within hemlock stands using Mantel

15 tests in PC-ORD (McCune and Mefford 1999). These tests calculate the correlation between two

16 dissimilarity matrices, which were derived using Sørensen distances in this study. We were

17 particularly interested in the influence of the overstory tree community on the composition of the

18 understory, seedling and sapling layers (i.e., neighborhood effects sensu Frelich and Reich

19 1995). Therefore, an overstory tree community dissimilarity matrix was correlated against the

20 understory, seedling, and sapling layer matrices. Similarly, the seedling and sapling dissimilarity

21 matrices were correlated against each other to examine the degree of association between these

22 two strata. Probability levels for the Mantel tests were calculated using 1000 Monte Carlo

23 randomizations (McCune and Mefford 1999) and the overstory matrix was based on importance

1   values for overstory species in each stand. Significance levels were set at $\alpha = 0.05$ for all

2   analyses and experiment-wide probability levels were protected by a sequential Bonferroni

3   procedure (Rice 1989).

4

5   **3. Results**

6   *3.1. Diversity and cover of understory herbs and shrubs*

7   A total of 47 understory herb and shrub species was identified across the 24 hemlock

8   stands examined in this study (Table 2). Of the species identified, 29 occurred only in old-

9   growth hemlock stands; no species were restricted to second-growth hemlock stands (Table 2).

10   No non-native species were found in either old-growth or second-growth stands (Table 2).

11   Importantly, the greater number of species found within old-growth forests may be an artifact of

12   the sampling design, as there were twice as many old-growth study areas as second-growth.

13   Nonetheless, compared with second-growth stands, old-growth forests had approximately 4

14   times the amount of total ground cover of herbaceous and shrub species (4.02 ± 0.41 versus 1.06

15   ± 0.47 %/m^2) and supported greater overall species richness and diversity (Table 3). In contrast,

16   evenness of herb and shrub species was greater in second-growth stands due in large part to the

17   lower species richness in these systems (Table 3).

18

19   *3.2. Tree seedlings and saplings*

20   Densities of seedlings and saplings were greater in old-growth stands compared to

21   second-growth stands (Table 4). *Acer pensylvanicum*, *Tsuga canadensis*, and *Betula spp.* (*B.*

22   *lenta* and *B. alleghaniensis* combined) generally had the highest seedling densities in both old-

23   growth and second-growth forests , and *A. pensylvanicum* was the only species that occurred in

1   all stands (Table 4). Most seedling species were found in both old-growth and second-growth

2   forests; however, *Pinus strobus* and *Acer saccharum* only occurred as seedlings in old-growth

3   stands. Seedling densities varied considerably between old-growth and second-growth forests as

4   *T. canadensis, Picea rubens,* and *Betula* spp. had higher densities in old-growth stands while

5   *Acer rubrum* had higher densities in second-growth stands (Table 4). Overall, the composition

6   of the seedling layer was positively associated with the composition of the overstory layer

7   (Mantel test, $r = 0.27$, $P < 0.05$), suggesting the successful establishment of overstory species

8   within the understory layer of these stands.

9   *Tsuga canadensis* had the highest sapling density across old-growth and second-growth

10   stands and was the only species found in the sapling layer of all hemlock stands investigated

11   (Table 4). *A. penslyvanicum* and *Fagus grandifolia* were generally more abundant in old-growth

12   versus second-growth stands (Table 4). Several species occurring as seedlings within a given

13   forest type were not observed as saplings (Table 4). For example, *Pinus strobus* and *Betula*

14   *papyrifera* saplings were not observed in old-growth stands despite the presence of these species

15   in the seedling layer and in the overstory (Table 4). Likewise, saplings of *B. papyrifera* and

16   *Quercus rubra* were not found in second-growth stands despite their presence in the seedling

17   layer of these systems. Nonetheless, composition of the sapling layer among hemlock stands was

18   positively correlated with the composition of the seedling layer (Mantel test, $r = 0.29$, $P < 0.05$).

19   In addition, there was a positive correlation between the composition of the sapling layer and the

20   composition of the overstory layer (Mantel test, $r = 0.30$, respectively, $P < 0.05$). Conversely,

21   sapling densities were negatively correlated with density of overstory trees (Kendall's tau = -

22   0.53, $P < 0.05$).

23

1   *3.3. Understory layer composition*

2   Understory communities differed between old-growth and second-growth stands (Multi-

3   response permutation procedures {MRPP}; A=0.03, *P* < 0.05); however, the small effect size

4   (A=0.03) derived from MRPP suggested that there was also a wide range of variation in

5   understory community composition within old-growth and second-growth stands, respectively

6   (McCune and Grace 2002). This was illustrated by the broad distribution of points for each of

7   these stand types in the ordination of understory vegetation (Figure 1), which explained 65.2 %

8   of the variation in the raw data (NMS ordination, final stress = 12.35, final instability = 0.00001).

9   Most of the variation in understory vegetation among stands was explained by Axis 1 (30.4%),

10   which represented a gradient from sites with low overstory tree densities and high NH_4-N

11   availability in the negative portion of Axis 1 to higher density sites with lower levels of available

12   NH_4-N in the positive portion (Figure 1). Correlations of species with this axis indicated that

13   there was greater abundance of the fern species, *Polypodium virginianum* (τ = -0.55) and

14   *Dryopteris intermedia* (τ = -0.52), within old-growth study sites located in the negative portion

15   of Axis 1 (Figure 1, Table 5).

16   The distribution of study areas along Axis 2, which explained 27.8 % of the variation,

17   generally ranged from sites with a smaller proportion of the total downed coarse woody debris

18   (CWD) pools in decay class IV (highly decayed, cf. Fraver et al. 2002) to sites with higher

19   proportions of this deadwood type (Figure 1). Study sites with downed woody debris pools

20   containing a higher proportion of wood in advanced stages of decay tended to have greater

21   amounts of *Kalmia latifolia* and *Tsuga candensis* in the understory as there was a significant

22   positive correlation between the abundance of these species and Axis 2 (Table 5). Importantly,

23   average volumes of decay class IV downed CWD were more than 9 times greater in old-growth

1   stands compared to second-growth stands (21.3 ± 7.7 vs. 2.2 ± 0.9 m^3/ha in old-growth and

2   second-growth stands, respectively). Furthermore, total volumes of downed CWD were four

3   times as high in the old-growth stands examined in this study (D'Amato et al. 2008).

4   Despite the wide range of variation in understory community composition within both

5   old-growth and second-growth stands (based on MRPP), Indicator Species Analysis identified

6   four species indicative of the understory layer in old-growth hemlock forests relative to second-

7   growth stands: *Dryopteris intermedia*, *Viburnum alnifolium*, *Aralia nudicaulis*, and *Tsuga*

8   *canadensis* (Figure 2). Several other species, including *Lycopodium lucidulum, Polypodium*

9   *virginianum*, and *Polystichum acrostichoides,* were also more common in old-growth stands

10   (Figure 2). In contrast, only *Acer rubrum* seedlings were more common in second-growth stands

11   (Figure 2). There was no significant relationship between the composition of understory herbs

12   and shrubs and the composition of overstory trees among hemlock stands (Mantel test, $r = 0.02$,

13   $P = 0.37$).

14

15   **4. Discussion**

16   This study indicates that, despite compositional similarities in overstory trees, differences

17   exist between the understory communities characterizing old-growth and second-growth

18   hemlock forests in western Massachusetts. In particular, old-growth forests had higher species

19   richness and diversity, as well as a greater abundance of understory herbs and shrubs, and tree

20   seedlings and saplings compared to second-growth forests. The observed importance of

21   overstory tree density, nitrogen availability, and coarse woody debris characteristics in

22   explaining the variation in understory composition among hemlock stands suggests that

1 differences in resource availability (e.g., light, moisture, and nutrients) and microhabitat

2 heterogeneity between old-growth and second-growth stands were likely driving these patterns.

3

4 *4.1. Diversity and Abundance of Understory Herbs and Shrubs*

5   Overstory tree density strongly influences patterns of understory species richness and

6 abundance (Alaback 1982, Peet and Christensen 1988, Oliver and Larson 1996). Several studies

7 have demonstrated that lower levels of species richness and abundance characterize dense,

8 closed canopy forests within the stem exclusion phase of development (sensu Oliver 1981,

9 Alaback 1982, Halpern 1988, Schoonmaker and McKee 1988, Eycott et al. 2006, Jules et al.

10 2008), whereas richness and abundance often increase as forests mature and self-thinning and

11 gap-scale disturbances create and maintain canopy openings (Davison and Forman 1982,

12 Alaback and Hermain 1988 Eycott et al. 2006). In this study, the second-growth stands we

13 examined were primarily in the stem exclusion phase of development, and the low sapling

14 densities and understory plant abundance and richness observed in these systems were likely a

15 reflection of the lower levels of resource availability (e.g., light, nutrients) in the understory layer

16 during this stage of stand development (Klinka et al. 1996, Oliver and Larson 1996). In contrast,

17 the structure of the old-growth areas had been primarily influenced by more than three centuries

18 of small to moderate gap-scale disturbances (D'Amato and Orwig 2008) resulting in stands

19 characterized by lower tree densities, larger trees, multi-layered canopies, and an abundance of

20 downed coarse woody debris and canopy gaps (D'Amato et al. 2008). Presumably, the diversity

21 of microhabitats and greater levels of resource availability associated with these structural

22 attributes (Alaback 1982, Oian et al. 1997, D'Amato 2007) and disturbance processes (Beatty

23 1984, Moore and Vankat 1986, Peterson et al. 1990, Reader and Bricker 1992) resulted in a

1   greater abundance and richness of understory plants within old-growth stands compared to dense

2   second-growth stands.

3   Overall, the composition and abundance of understory plants among hemlock stands in

4   this study were similar to those reported elsewhere for second-growth (Rogers 1980, Eschtruth et

5   al. 2006) and old-growth hemlock forests (Whitney and Foster 1988). While the old-growth

6   stands in this study had a greater abundance of understory herb and shrubs compared to second-

7   growth, these values were much lower than those reported for other forest types in the region

8   (e.g., Rogers 1980, Gilliam et al. 1995). The sparse nature of understory vegetation within these

9   systems is likely a reflection of the low levels of nutrient and light availability, as well as higher

10   forest floor and soil acidity levels typically characterizing hemlock-dominated forests relative to

11   other forest types such as northern hardwood forests (Rogers 1980, Mladenoff 1987, Canham et

12   al. 1994, Lovett et al. 2004). Although these understory conditions limit the abundance of

13   understory herbs and shrubs, they tend to favor the establishment of conspecific regeneration

14   within hemlock-dominated stands (i.e., positive overstory-understory neighborhood effects,

15   Frelich and Reich 1995). These positive neighborhood effects between overstory trees and

16   understory regeneration were illustrated by the strong, positive associations in Mantel tests

17   conducted between overstory composition and the composition of the seedling and sapling layers

18   within the hemlock stands examined in this study. Correspondingly, management approaches

19   aimed at restoring old-growth characteristics to existing second-growth hemlock systems should

20   rely on selection systems that not only emulate the gap-scale disturbance regimes historically

21   characterizing these systems (c.f. D'Amato and Orwig 2008) but also maintain the understory

22   conditions favoring long-term hemlock establishment and recruitment (Brissette and Kenefic

23   2000).

1   Several species were more abundant in old-growth than second-growth hemlock

2   understories, including *Aralia nudicaulis, Dryopteris intermedia,* and *Viburnum alnifolium*.

3   Several other studies examining the composition of old-growth, primary, and secondary forests

4   in the northeastern United States have also indicated that these species were more abundant in

5   old-growth and primary forest ecosystems (Nichols 1913, Egler 1940, Whitney and Foster 1988,

6   Motzkin et al. 1999, Singleton et al. 2001). For example, the occurrence of *A. nudicaulis* and *V.*

7   *alnifolium* was much greater in old-growth white pine-hemlock forests as compared to secondary

8   white pine-hemlock forests in central New England (Whitney and Foster 1988). These patterns

9   were attributed to the sensitivity of these species to competitive displacement and microclimatic

10   changes following forest harvesting, as well as to the dispersal and colonization limitations of *V.*

11   *alnifolium* (Whitney and Foster 1988, Motzkin et al. 1999). In contrast, the lack of suitable

12   microhabitats in secondary forests was suggested as a possible explanation for the greater

13   frequency of *Dryopteris intermedia* in primary forests compared to post-agricultural forests in

14   central New York (Singleton et al. 2001). Although we did not directly examine dispersal rates

15   or microhabitat associations in this study, it is likely that these mechanisms (e.g., dispersal

16   limitations, lack of suitable microhabitats, Meier et al. 1995) were influencing the differences in

17   abundance of these species between old-growth and second-growth hemlock forests. In

18   particular, *A. nudicaulis* and *V. alnifolium* spread primarily by vegetative means (Edwards 1984,

19   Nyland et al. 2006) and this reliance on clonal spread may have limited their ability to re-

20   colonize second-growth areas following harvesting (cf. Meier et al. 1995). Likewise, the lower

21   abundance of suitable microhabitats observed among second-growth hemlock stands (e.g.,

22   decayed logs, McGee 2001, D'Amato et al. 2008) may have contributed to the lower abundance

23   of *D. intermedia* in these systems. An additional possible explanation for the absence or lower

1   abundance of these species in second-growth areas is that these species were never present in

2   these stands prior to harvesting. Despite this consideration, the historical ubiquity of these plant

3   species throughout these landscapes makes this explanation highly unlikely (Egler 1940). Due to

4   affinity of these species to old-growth and primary forests found in this and other studies in the

5   region, the abundance of these species might serve as useful indicators for evaluating the success

6   of management strategies aimed at restoring old-growth characteristics to second-growth

7   hemlock systems.

8

9   *4.2. Composition and Abundance of Tree seedlings and Saplings*

10   The high densities of *Tsuga canadensis* and *Acer pensylvanicum* seedlings observed in

11   old-growth and second-growth stands in this study were consistent with the findings of other

12   studies quantifying seedling densities in hemlock-dominated forests (e.g., Rogers 1980, Yorks et

13   al. 2000, Kizlinski et al. 2002) and was likely due to the ability of both these species to survive in

14   the low light levels and acidic soils characterizing these ecosystems (Hibbs 1979, Burns and

15   Honkala 1990, Lei and Lechowicz 1990, Kobe et al. 1995). In contrast, the prolific seed

16   production and seed banking abilities of the mid-tolerant species, *Betula lenta* and *B.*

17   *alleghaniensis*, likely contributed to the abundance of these seedlings among hemlock study

18   areas as these species often dominate the seed banks of hemlock-dominated forests (Castovsky

19   and Bazzaz 2000, Yorks et al. 2000, Sullivan and Ellison 2006). While these species may

20   germinate under low light conditions, their survival in these stands is dependent on canopy gaps

21   that increase light availability in the forest understory (Carlton and Bazzaz 1998, Orwig and

22   Foster 1998, Webster and Lorimer 2005). This was demonstrated by the affinity of *B.*

23   *alleghaniensis* and *B. lenta* saplings to recent canopy gaps within the hemlock stands we

1   sampled (A. W. D'Amato, personal observation), as well as by the tremendous increase of these

2   species observed in the sapling layer of hemlock forests defoliated by hemlock woolly adelgid

3   (Orwig and Foster 1998, Kizlinski et al. 2002, Stadler et al. 2005). Based on these findings from

4   infested stands in the region and the characteristics of the seedling layers in the present study, it

5   is highly likely that a similar increase in *B. alleghaniensis* and *B. lenta* will occur on these sites

6   when hemlock woolly adelgid reaches these areas.

7   Although there were compositional similarities in the seedling and sapling layers between

8   old-growth and second-growth hemlock stands (Table 4), densities of seedlings and saplings

9   were much greater in old-growth stands. The factors described as influencing the patterns for

10   understory herb and shrub abundance between old-growth and second-growth stands (e.g.,

11   greater diversity of microhabitats and resource availability in old-growth stands) also likely

12   contributed to the patterns in seedling and sapling densities. In particular, several studies have

13   demonstrated the importance of decaying logs on the forest floor as microhabitats for certain tree

14   species (Christy and Mack 1984, Harmon and Franklin 1989, Beach and Halpern 2001),

15   including *T. canadensis* and *B. alleghaniensis* (Mladenoff and Stearns 1993, Corinth 1995,

16   McGee 2001, Marx and Walters 2008). In this study, the abundance of highly decayed downed

17   wood (decay class III and IV combined, after Fraver et al. 2002) was almost five times greater in

18   old-growth forests compared to second-growth forests (56.2 vs. 11.6 m^3/ha). While we did not

19   specifically sample downed logs for seedling and sapling abundance, seedlings of *T. canadensis*

20   and *Betula* spp. were commonly observed on these substrates within our study areas (A.W.

21   D'Amato, personal observation, Figure 3). In addition, the association of *T. canadensis* with this

22   microhabitat was demonstrated by the positive correlation between proportion of highly decayed

23   downed coarse woody debris and *T. canadensis* abundance in the ordination of understory

18

1   community composition (Figure 1). Due to the importance of deadwood substrates in these

2   systems, the deliberate felling and retention of canopy trees in harvest gaps should be integrated

3   into management strategies aimed at restoring old-growth conditions to second-growth hemlock

4   stands. Importantly, including these provisions for CWD creation at each harvest entry will be

5   critical for ensuring that a diversity of decay classes are present in these stands over time (cf.

6   D'Amato and Catanzaro 2007).

7   Beyond differences in microhabitat and resource availability, it is likely that the greater

8   sapling densities in old-growth stands were also related to the differences in the nature of

9   disturbance in these systems as compared to second-growth stands. Both of these systems have

10   experienced small to moderate canopy disturbances over the past century (D'Amato and Orwig

11   2008); however, the size of canopy gaps created in old-growth stands is generally greater due to

12   the larger overstory trees in these stands (cf. Dahir and Lorimer 1996). As a result, these stands

13   contain understory light conditions more favorable for the recruitment of mid-tolerant and

14   tolerant species into the sapling layer. Moreover, the extreme shade tolerance of *T. canadensis*

15   allows it to persist under low light levels in the forest understory for extended periods of time,

16   often exceeding a century (Godman and Lancaster 1990, A.W. D'Amato, personal observation).

17   Therefore, some of the hemlock saplings within old-growth stands likely recruited prior to the

18   establishment of the second-growth areas examined, thus contributing to the greater abundance

19   of this species within old-growth areas. These patterns reinforce the suitability of selection

20   systems for increasing hemlock regeneration in second-growth systems and restoring canopy

21   complexity through the creation of well-developed sapling layers.

22   Interestingly, several compositional and structural components extirpated from the

23   understory layer of hemlock stands in other regions of the northeastern United States due to

1   overbrowsing by white-tail deer, including *Taxus canadensis* and abundant *T. canadensis*

2   saplings (Frelich and Lorimer 1985, Alverson et al. 1988, Rooney and Dress 1997, Long et al.

3   1998, Weckel et al. 2006), were commonly documented in the old-growth and second-growth

4   stands observed in this study. Due to the comparatively low deer densities in our study region

5   (~10 per square mile, MassWildlife 2008), these results serve as an illustration of the dramatic

6   effect white-tail deer is having on the structure and dynamics of eastern hemlock forests in other

7   portions of this species' range and represent a baseline for assessing how future increases in deer

8   densities within western Massachusetts affect the conservation and management of these

9   systems. Moreover, recent results highlighting the positive interactive effects of canopy

10   disturbance due to hemlock woolly adelgid infestation and severity of deer browsing underscore

11   the importance of simultaneously monitoring the impacts of these and other disturbance agents

12   on the future plant community dynamics of these currently unaffected systems (Eschtruth and

13   Battles 2008).

14

15   **5. Conclusions**

16   The understory communities in the old-growth hemlock stands examined in this study are

17   distinctive from those in hemlock dominated stands originating following logging in the late 19th

18   century. Understory vegetation characteristics within these old-growth stands, including species

19   richness, herb and shrub cover, and seedling and sapling densities, are much greater than those

20   observed within the understories of second-growth areas due in large part to the greater resource

21   availability and microhabitat heterogeneity characterizing these systems. Notably, differences in

22   composition, richness, and diversity between old-growth and second-growth hemlock stands

23   resulted from either the absence or lower abundance of several common forest herbs and shrubs

1   within second-growth stands and were not due to the presence of rare species in old-growth.

2   Despite the lack of old-growth obligate understory species in these stands, the understory

3   communities of these old-growth systems represent important habitat features on the landscape

4   providing greater levels of forage and cover for a variety of wildlife relative to second-growth

5   hemlock stands. The return of old-growth understory conditions to these second-growth areas

6   will be largely dependent on disturbance and self-thinning mediated changes in overstory

7   structure, resource availability, and microhabitat heterogeneity within these systems. As such,

8   management strategies, including the use of gap-based silvicultural systems and the creation and

9   retention of CWD, may serve as effective approaches for actively restoring these understory

10   conditions to second-growth stands. Although hemlock woolly adelgid is not present at any

11   hemlock stands examined in this study, our results suggest that the loss of hemlock from these

12   areas will lead to the tremendous increases in *B. lenta* and *B. alleghaniensis* observed in infested

13   hemlock forests in this region (Orwig and Foster 1998). More importantly, infestation of these

14   areas will irreversibly alter the composition and structure of the few remaining old-growth

15   forests in southern New England.

16

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Study site	Status[1]	Percent hemlock[2]	Average canopy tree age[3] (yr)	Elevation (m)	Slope (°)	Aspect (°)

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		Average Percent	canopy tree	Elevation	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°

1 Table 1. Physiographic and general stand characteristics of eastern hemlock study sites in

2 western Massachusetts, USA. Canopy tree age and compositional data were collected as part of

3 a larger study examining the disturbance dynamics of these systems (see D'Amato and Orwig

4 2008 for detailed methods).

5 **Table 1. (continued)**

Study site	Status[1]	hemlock[2]	age[3] (yr)	(m)	(°)	(°)
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°

1   [1]OG = old growth, 2G = second-growth

2   [2]Importance value calculated as: ((Relative basal area) + (Relative Density))/2

3   [3]Value in parentheses represents age of oldest tree with complete increment core sample
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13   **Table 2.** Herb, graminoid, shrub, fern, and club moss species identified in the understory of old-

14   growth (OG) and second-growth (2G) hemlock forests in western Massachusetts. Species

1   occurrences are based on complete censuses of 0.04-ha plots within each study area (3-5 plots

2   per site). Nomenclature follows Gleason and Cronquist (1991).

Species	OG	2G	Species	OG	2G
Herbs			Herbs (cont.)		
Actaea alba	X		*Monotropa uniflora*	X	X
Aralia nudicaulis.	X	X	*Oxalis acetosella*	X	
Arisaema triphyllum.	X		*Polygonatum pubescens*	X	
Aster acuminatus.	X	X	*Solidago flexicaulis*	X	
Aster dumosus	X		*Tiarella cordifolia*	X	
Aster divericatus	X		*Trientalis borealis*	X	X
Chimaphila maculate.	X	X	*Trillium erectum*	X	
Circaea alpina	X	X	*Trillium undulatum*	X	X
Clintonia borealis	X		*Viola rotundifolia*	X	
Cypripedium acaule	X		Graminoids		
Epigaea repens	X	X	*Carex pensylvanica*	X	X
Galium spp.	X	X	Ferns		
Gaultheria procumbens	X	X	*Adiantum pedatum*	X	
Laportea canadensis	X		*Dryopertis intermedia*	X	X
Maianthemum canadense	X		*Dryopteris marginalis*	X	
Medeola virginiana	X		*Polypodium virginianum*	X	
Mitchella repens	X	X	*Thelypteris phegopteris*	X	

3   **Table 2. (continued)**

Species	OG	2G	Species	OG	2G

Shrubs			Club mosses		
Cornus alternifolia	X		*Lycopodium annotinum*	X	
Hamamelis virginiana	X	X	*Lycopodium lucidulum*	X	X
Kalmia latifolia	X	X	*Polystichum acrostichoides*	X	X
Rhododendron canescens	X				
Rubus allegheniensis	X				
Rubus idaeus	X				
Sambucus racemosa	X				
Solidago flexicaulis	X				
Taxus canadensis	X				
Vaccinium angustifolium	X	X			
Viburnum acerifolium	X				
Viburnum alnifolium	X	X			

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9 **Table 3.** Mean cover and site-level species richness (*S*), diversity (*H'*), and evenness (*E*) of all

10 herbaceous (herbs, ferns, graminoids, and club mosses) and shrub species in old-growth and

1 second-growth hemlock stands. Values are based on average cover and frequency of herb and

2 shrub species across understory subplots within each study area (1 m^2, 24-40 per site) Standard

3 errors are in parentheses and means with different letters are significantly different ($P < 0.05$,

4 Wilcoxon rank-sum test).

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

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

1 **Table 4.** Average seedling and sapling densities (#/ha) in old-growth and second-growth

2 hemlock forests. Ranges appear in parentheses for each species and standard errors are depicted

3 for totals. Totals with different letters indicate significant differences between old-growth and

4 second-growth stands ($P < 0.05$, Wilcoxon Rank-Sum test). Species-level values represent site-

5 level averages, whereas totals represent averages across old-growth and second-growth stands,

6 respectively.

7 [1]Seedlings of *Betula alleghaniensis* and *B. lenta* were combined for estimates of seedling

8 density.

1   ²Includes less common species not listed in table, *Fraxinus americana, Ostrya virginiana, Pinus*

2   *resinosa, Sorbus americana,* and *Tilia americana.*

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4   **Table 5.** Correlations (Kendall's τ) between the average percent cover of understory herbs,

5   shrubs, and tree seedlings within each study area (%/m^2) and non-metric multidimensional

6   scaling Axis 1 and 2. Species in bold have significant correlations with axes scores ($P < 0.05$

7   (Bonferroni-protected).

Species	Axis 1	Axis 2	Species	Axis 1	Axis 2
Acer pensylvanicum	-0.17	0.07	*Mitchella repens*	0.04	-0.27
Acer rubrum	0.45	0.34	*Monotropa uniflora*	0.20	0.29
Acer saccharum	-0.42	-0.08	*Oxalis acetosella*	-0.44	0.10
Acer spicatum	-0.39	-0.02	*Picea rubens*	-0.30	0.17
Aralia nudicaulis	-0.41	0.13	*Polystichum acrostichoides*	-0.27	0.03
Aster acuminatis	-0.48	0.12	***Polypodium virginianum***	**-0.55**	0.12
Betula spp.	-0.33	0.41	*Quercus rubra*	0.40	0.21
Dryopteris intermedia	**-0.52**	-0.17	*Taxus canadensis*	-0.42	0.01
Fagus grandifolia	0.19	-0.23	*Trientalis borealis*	-0.37	0.13
Kalmia latifolia	0.18	**0.56**	*Trillium undulatum*	0.05	0.32
Lycopodium lucidulum	-0.39	-0.11	***Tsuga canadensis***	-0.37	**0.50**
Maianthemum canadense	-0.18	0.14	*Viburnum alnifolium*	-0.35	0.15

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