Assessing and modeling standing deadwood attributes under alternative silvicultural regimes in the Acadian Forest region of Maine, USA

Matthew B. Russell, Laura S. Kenefic, Aaron R. Weiskittel, Joshua J. Puhlick, and John C. Brissette

Abstract: Estimating the amount of standing deadwood in forests is crucial for assessing wildlife habitat and determining carbon stocks. In this analysis, snags (standing dead trees) in various stages of decay were inventoried across eight silvicultural treatments in eastern spruce–fir forests in central Maine nearly 60 years after treatments were initiated. Several modeling strategies were developed to estimate number of snags per hectare in various stages of decay. An unmanaged reference area displayed the highest basal area and volume of snags (5.4 ± 3.1 m^2·ha^{-1} and 29.4 ± 23.6 m^3·ha^{-1}, respectively, (mean ± standard deviation)), while the lowest basal area and volume (0.9 ± 1.0 m^2·ha^{-1} and 3.1 ± 5.2 m^3·ha^{-1}) were observed in selection system with a 5-year cutting cycle. Models indicated that snag abundance was related to stand density, depth to water table, and the average harvest interval of the treatment. At a fixed stand density, approximately 140% more snags were predicted to occur in treatments with an average harvest interval of 55 compared with 5 years. An index of error reflecting the number of snags found in certain decay classes was reduced by 40% when predictions from count regression models fit with a mixed modeling strategy were used over ordinal regression. Results from these analyses can help to reduce the disparities between observed and modeled snag stocking levels and further our understanding of the relationships between live and standing dead trees inherent to eastern spruce–fir forests.

Résumé : Il est essentiel d'estimer la quantité de bois mort debout dans les forêts pour évaluer l'habitat faunique et déterminer les stocks de carbone. Dans cette étude, les chicots (arbres morts debout) à différents stades de décomposition ont été inventoriés dans huit traitements sylvicoles dans des peuplements mélangés d'épicéa et de sapin situés dans le centre du Maine, presque 60 ans après le début des traitements. Plusieurs stratégies de modélisation ont été développées pour estimer le nombre de chicots à l'hectare rendus à différents stades de décomposition. Une zone témoin non aménagée avait la surface terrière et le volume les plus élevés de chicots, soit respectivement (moyenne ± écart type) 5,4 ± 3,1 m^2·ha^{-1} et 29,4 ± 23,6 m^3·ha^{-1}, tandis que la surface terrière et le volume les plus faibles (0,9 ± 1,0 m^2·ha^{-1} et 3,1 ± 5,2 m^3·ha^{-1}) ont été observés dans la coupe de jardinage avec une rotation de cinq ans. Les modèles indiquaient que l'abondance de chicots était reliée à la densité du peuplement, à la profondeur de la nappe phréatique et à la l'intervalle moyen entre les récoltes. Avec une densité de peuplement fixe, les modèles prédisaient approximativement 140% plus de chicots dans les traitements dont l'intervalle entre les récoltes était de 55 ans comparativement à cinq ans. Un indice d'erreur reflétant le nombre de chicots observés dans certaines classes de décomposition a été réduit de 40% lorsqu'on utilisait les prédictions des modèles de régression de variables explicatives de dénombrement ajustés avec une stratégie de modélisation mixte plutôt que la régression ordinale. Les résultats de ces analyses peuvent contribuer à réduire les écarts entre les niveaux observés de densité relative des chicots et ceux qui sont prédits par les modèles et améliorer notre compréhension des relations entre les arbres vivants et les arbres morts sur pied propres aux forêts mélangées d'épicéa et de sapin.

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Introduction

Snags (standing dead trees) play an important role in forest carbon dynamics (Harmon et al. 2011) and are key elements for maintaining forest biodiversity and providing a heterogeneous forest structure (Harmon et al. 1986). As a consequence, managing for snags is required by many forest certification programs (Sustainable Forestry Initiative 2004). In the northeastern United Staes and eastern Canada, site-specific management guidelines have been established with the goal of

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maintaining sufficient levels of snags (Woodley 2005; Elliot 2008; Benjamin 2010). Despite the ecological importance of snags and requirement that they be included in forest management planning, snags are rarely the focus of traditional forest inventories (Kenning et al. 2005). Quantifying and predicting the amount and characteristics of snags is critical to determining forest structure and composition.

Predicting the number of snags per unit area is often difficult given that snags are less abundant than live trees and display high spatial (Raphael and Morrison 1987) and temporal (Ganey and Vojta 2005; Morrison and Raphael 1993) variability. The shortfalls of models predicting standing dead trees were recently highlighted by Woodall et al. (2012), who found that standing dead tree carbon stocks were overestimated by 100% at the national level when compared with field measurements across the United States. This had tremendous influence on overall carbon stocks — predicted carbon across the United States was overestimated by 4%, principally resulting from inadequacies in predicting attributes of snags (Woodall et al. 2012).

Despite these difficulties, researchers have had some success in quantifying and predicting snag abundance. Relationships between the number, basal area, and volume of snags and live trees have been observed in multiple forest types (e.g., Temesgen et al. 2008; Woodall and Westfall 2009). Using a national forest inventory in the United States, Woodall and Westfall (2009) found that relative density of live trees could be an effective measure of deadwood biomass, but deadwood stocking levels might only be high in stands where relative density is very high or low. The authors term the "deadwood stocking conundrum zone" as the area where much less is known about deadwood stocking levels in these stand types (Woodall and Westfall 2009). The minimal influence of stand density in predicting deadwood abundance in this zone encourages researchers to investigate additional stand and site factors that relate specifically to snag abundance. These factors might include soil conditions, site physiographic features, disturbances (e.g., insects, disease, and wind), and forest management activities such as method of silviculture.

Forest management may reduce snag abundance and recruitment by removing low-vigor trees. Large snags are most likely to be found in unharvested stands (Garber et al. 2005; Marcot et al. 2010) and snag density has been found to be lower in stands that receive intensive management (Wisdom and Bate 2008). On average, over 40 snags·ha^{-1} >30 cm diameter at breast height (DBH) were observed in old-growth northern hardwood stands compared with an average of 12 snags·ha^{-1} >30 cm DBH in selection stands (Goodburn and Lorimer 1998). Pulses of snags can occur during self-thinning and immediately after catastrophic weather events (Jones et al. 2009), while inputs of snags may be continuous in an old-growth stage (Jonsson 2000).

Previous research found that site index was negatively associated with number (Eskelson et al. 2009) and basal area (Temesgen et al. 2008) of snags in Oregon and Washington, USA. Conversely, higher site productivity was associated with higher volumes of snags in boreal forests of Finland (Siitonen et al. 2000) and the southern United States (Spetich and Guldin 1999). Slope and aspect have been shown to be significantly positively correlated with number of snags (Eskelson et al. 2009), but showed no relationship with snag basal area (Temesgen et al. 2008). Only recently have researchers begun to model snag quality attributes such as decay class (Bater et al. 2009; Eskelson et al. 2012). Generally, count regression models have been used to estimate the frequency of snags within a stand (Temesgen et al. 2008; Eskelson et al. 2009), while predictions of snag abundance within decay classes have followed a probability-based approach. Ordinal regression techniques, for example, have been used to partition the number of dead trees in a stand into decay classes (Bater et al. 2009; Eskelson et al. 2012).

Predictions of snag abundance have previously required detailed knowledge of physiographic variables including slope, aspect, and elevation (Temesgen et al. 2008; Eskelson et al. 2009) or use of remote sensing technologies (Bater et al. 2009; Eskelson et al. 2012). Yet, forest managers may have limited information of this type. However, they often have a clear understanding of the methods of silviculture applied and a tree list of live trees obtained through a forest inventory. Modeling techniques that relate snag attributes to traditional forest inventory data would be advantageous and expedient for direct use by forest and wildlife habitat managers.

The goal of this study was to relate snag attributes to site and stand characteristics and silvicultural treatment on the Penobscot Experimental Forest (PEF) in central Maine. The PEF is representative of forests found throughout the Acadian Forest region and is comprised of naturally regenerated, mixed-species stands under both even- and uneven-aged silvicultural regimes. The silvicultural experiment on the PEF has well-established prescriptions of over 60 years, data on live tree attributes, and detailed soils and site information, together which provide an excellent data set to analyze the relationships between live tree attributes, site conditions, and snag abundance. The specific objectives of this study were to (1) evaluate snag abundance, basal area, and volume across eight silvicultural treatments ranging from unharvested reference to commercial clearcut, (2) develop models comparing two methods that estimate total snag abundance and snag abundance within four decay classes as a function of stand characteristics and average harvest interval, and (3) assess the performance of the developed models for predicting abundance and attributes of snags under various silvicultural regimes.

Methods

Study area

This study was conducted on the 1619 ha PEF located in the towns of Bradley and Eddington, Maine (44°52′N, 68°38′W; mean elevation of 43 m). At the PEF, climate estimates indicate that mean annual temperature and precipitation are 6.2 °C and 110 cm, respectively (Rehfeldt 2006). Soils are primarily derived from glacial till and range from well-drained loams and sandy loams on glacial till ridges to poorly and very poorly drained silt loams in flatter areas between ridges (Sendak et al. 2003).

Located within the Acadian Forest, the PEF is characterized by a mixture of northern conifer and hardwood species that dominate its forest cover. Conifer species include red (*Picea rubens* Sarg.), white (*Picea glauca* (Moench) Voss), and black spruce (*Picea mariana* (Mill.) BSP), balsam fir (*Abies balsamea* (L.) Mill.), eastern hemlock (*Tsuga canadensis* (L.) Carr.), eastern white pine (*Pinus strobus* L.), and northern

Table 1. Descriptions of silvicultural treatments at the Penobscot Experimental Forest, Bradley and Eddington, Maine.

Treatment	Code	Average harvest interval (years)	Description
Unharvested reference	REF	55	Control treatment without harvesting since the 1800s
Commercial clearcut	CC	30	Removal of all merchantable trees
Selection with 5-year cutting cycle	SC05	5	Single-tree selection with a 5-year cutting cycle
Selection with 10-year cutting cycle	SC10	10	Single-tree selection with a 10-year cutting cycle
Selection with 20-year cutting cycle	SC20	20	Single-tree selection with a 20-year cutting cycle
Shelterwood	SW	55	Shelterwood with a regeneration harvest and a final harvest
Fixed diameter limit	FDL	22	Removal of all merchantable trees above species-specific fixed diameters at variable time intervals
Modified diameter limit	MDL	22	Removal of all merchantable trees above species-specific flexible diameters at fixed time intervals

white cedar (*Thuja occidentalis* L.). Hardwood species include red maple (*Acer rubrum* L.), paper (*Betula papyrifera* Marsh.) and gray birch (*Betula populifolia* Marsh.), and quaking (*Populus tremuloides* Michx.) and bigtooth aspen (*Populus grandidentata* Michx.).

An operational-scale experiment to compare 10 silvicultural treatments was established by US Forest Service (USFS) researchers on the PEF between 1952 and 1957. The experiment was designed to investigate the influence of silviculture on the growth, yield, and economics of eastern spruce–fir (northern conifer) stands. In the 1990s, a number of ecological variables were added to broaden the focus from traditional timber management to how silviculture impacts forest ecosystems.

The experiment was laid out in a completely randomized design in a conifer-dominated portion of the PEF, primarily in red spruce – balsam fir – eastern hemlock cover types (Frank and Blum 1978). Treatments include uneven-aged, even-aged, and exploitive cutting regimes and an unharvested reference as an experimental control (Table 1; Sendak et al. 2003). The uneven-aged treatments include selection cutting with 5-, 10-, and 20-year cutting cycles with target residual diameter distributions (q = 1.96 on 5 cm DBH classes) and basal areas (for trees ≥1.3 cm DBH: 26.4, 23.0, and 18.4 $m^2 \cdot ha^{-1}$, respectively). These treatments included some cultural treatments, such as pruning and cleaning; spruce species were favored. Marking guidelines were used to prioritize removals in the merchantable size classes. Even-aged treatments include a two-stage shelterwood treatment in which the initial (establishment) cut occurred in the mid-1950s with overstory removal approximately 10 years later, leaving a residual basal area of submerchantable and unmerchantable trees amounting to approximately 7.0 $m^2 \cdot ha^{-1}$.

Exploitive cutting is represented in the experiment by fixed and modified (flexible) diameter-limit treatments as well as commercial clearcutting. In the diameter-limit treatments, all merchantable trees of desired species were removed above fixed or flexible species-specific diameter limits, while unmerchantable trees and those below the diameter limits were retained. Harvests were conducted in the fixed diameter limit when the initial volume regrew (this occurred every 20 to 25 years) and every 20 years in the modified diameter limit. Residual basal area averaged 16.8 and 22.9 $m^2 \cdot ha^{-1}$ in the fixed and modified treatments, respectively, following three harvests. All merchantable trees were removed in the commercial clearcut treatment and undesirable species and cull trees were left scattered or in small patches. Two harvests occurred in this treatment, where the most recent in the 1980s removed a greater volume than the first due to changes in merchantability standards (Sendak et al. 2003). An unharvested reference area was also established that serves as the experiment's control. The treatments, each with two stand-level replicates, were randomly assigned to experimental units averaging 10 ha in size. Sixteen experimental units were analyzed in this analysis.

Data collection

A network of permanent sample plots (PSPs) was established along transects nested within each experimental unit, averaging 18 plots per unit. The PSPs consisted of a nested design with 0.08, 0.02, and 0.008 ha circular plots sharing the same plot center. The USFS routinely inventories these PSPs: all pole- and sawtimber-sized trees ≥11.4 cm DBH) are measured on the 0.08 ha plot, large saplings (6.4 cm ≤ DBH < 11.4 cm) are measured on the 0.02 ha plot, and small saplings (1.3 cm ≤ DBH < 6.4 cm) are measured on the 0.008 ha plot. PSPs have been remeasured by USFS every 10 years, and if harvesting is scheduled, immediately pre- and post-harvest. Live trees are uniquely numbered in these plots and experimental unit, plot and tree number, species, DBH, and status (e.g., live tree versus snag) are recorded.

In 2010 and 2011, for each PSP all snags ≥11.4 cm DBH were measured on the 0.08 ha plot, and snags ≥2.5 cm DBH were measured on the 0.02 ha plot. Snag species, DBH, height, and decay class were recorded. A four-class system was used to designate the stage of decay of snags (Heath and Chojnacky 2001): (1) structurally sound, bark intact, (2) sound but somewhat rotten, branch stubs attached, partially soft texture, (3) rotten, branch stubs mostly pulled out, heavy bark peeling, soft texture, and (4) no structural integrity, bark detached or absent.

Soils and physiographic data used for this study were collected by Bryce (2009) on or adjacent to the PSPs. Soil variables included thickness of organic and eluvial horizons, depth to redoximorphic features, and Briggs (1994) soil drainage class. Slope and aspect of the PSPs were also recorded.

Depth to water table was obtained from a GIS raster layer based on the algorithm of Murphy et al. (2011) and was defined as the distance from soil surface to the normal high level of the water table.

For each experimental unit, stand conditions in 2010 and 2011 were estimated by projecting the DBH measurements of live trees obtained from the most recent USFS inventory using a species-specific annualized DBH increment model (fixed-effects) parameterized with PEF data (Russell et al. 2011; eq. 2). Predicted DBH increment to the snag inventory year (2010 or 2011) was added to the most recently measured DBH. Projections ranged from 0 to 9 years (mean of 4.5) depending on the experimental unit.

Plot-level metrics representing a variety of stand structural characteristics were computed for live trees. These included number of trees (TPH) (4475 ± 2908 trees·ha^{-1}), basal area (34.4 ± 12.4 m^2·ha^{-1}), stand density index (956.1 ± 358.3) (Ducey and Larson 2003; a measure of density based on the number of trees per hecatare and the diameter of the average tree), relative density (0.38 ± 0.16) (Woodall et al. 2005; the ratio between a plot's value and a maximum stand density index dependent on species composition), and crown competition factor (CCF) (884.6 ± 436.6). CCF was calculated using the maximum crown width equations presented in Russell and Weiskittel (2011). Here, CCF was defined as the ratio between the average crown area available to a tree and the maximum crown area that an open-grown tree could display. The average harvest interval (AHI) was calculated for uneven-aged and exploitive treatments, while the number of years since the initiation of the USFS experiment in the 1950s was used in the unharvested reference and shelterwood treatments (Table 1). Volumes for snags and live trees were estimated using volume integrals of the species-specific taper equations of Li et al. (2012). Using integrals allowed us to account for volume reduction in snags that experienced breakage, without requiring a measurement of diameter at breakage (Aakala et al. 2008).

Estimating live tree and snag density

Two methods were used to compare models estimating the number of live trees and snags in various stages of decay. In the first method, a count regression model (COUNTREG) was used to predict the number of stems in a specific tree status class (k = 5 classes are described below). In the second method, ordinal regression (ORDREG) techniques were used to estimate the proportion of stems in a specific tree status class.

For both the COUNTREG and ORDREG methods, the total number of live trees plus snags per hectare (TSPH) was first estimated:

$$\text{[1]} \qquad \mathrm{TSPH} = \mathrm{TPH} + \mathrm{SPH}$$

where TPH and SPH are live trees and snags per hectare, respectively, and SPH = SPH.d1 + SPH.d2 + SPH.d3 + SPH.d4 where SPH.d1, SPH.d2, SPH.d3, and SPH.d4 are snags per hectare in decay classes 1 through 4, respectively. For the COUNTREG method, the number of stems in each of the five classes was predicted separately. For the ORDREG method, the proportion of stems in each of the five classes was estimated similar to Eskelson et al. (2012).

For the COUNTREG method, Poisson and negative binomial models were employed to test their effectiveness in accounting for the variability observed in the data. Count regression models are useful in describing the nonnegative integer values for estimating the number of snags found in a fixed area of land (Temesgen et al. 2008; Eskelson et al. 2009). The Poisson regression model is the benchmark model for count data and can be applied to data whether the response variable is a count or continuous, but becomes restrictive when estimating attributes other than the mean (Winkelmann 2008). Negative binomial regression models are count models that include an overdispersion parameter, making them more flexible than Poisson models (Eskelson et al. 2009). The mean number of snags per hectare was 407 with a standard deviation of 621, indicating tremendous overdispersion of the data (see supplementary material (Table S1) for experiment means).[1] Assumptions of the Poisson method were that the number of snags in a given class was distributed with mean equal to variance. Assumptions of the negative binomial method were that snags were distributed with parameters reflecting the mean and overdispersion of data separately.

Comparing the two models becomes an evaluation of the degree of overdispersion in the data, unobserved heterogeneity, and excess zero values (Winkelmann 2008, p. 174). A preliminary hypothesis was that negative binomial methods would be most effective for characterizing snag abundance in these data because snags were absent in 5% of the plots and data were overdispersed.

Stand density measures for live trees, soils information, and AHI were used to estimate the mean number of stems in each tree status class, denoted hereafter as μ_k. For both methods, μ_{TSPH} was first estimated. For the COUNTREG method, μ_k was then estimated for the remaining tree status classes. The general model for estimating μ_k was

$$\text{[2]} \qquad \mu_k = \exp(\beta_0 + \beta_1 X_{1k} + \ldots + \beta_p X_{pk})$$

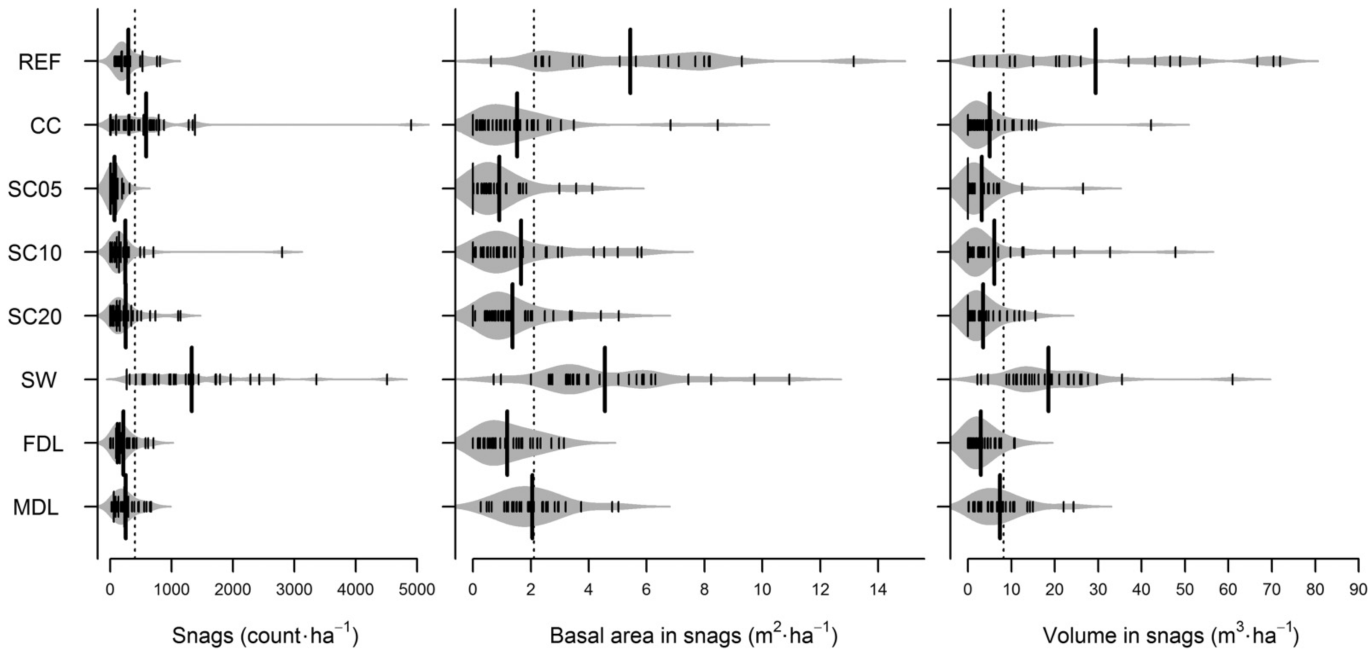
where p represents the number of predictor variables and the β_i parameters were estimated via the Poisson and negative binomial models. Parameters were estimated using forward variable selection (R Development Core Team 2011) and models were compared using Akaike's information criteria (AIC) and log-likelihoods when additional predictor variables were added.

For the ORDREG method, TPH, SPH.d1, ..., SPH.d4 were modeled as ordinal data (Bater et al. 2009; Eskelson et al. 2012). The proportions of stems within each of the k tree status classes (i.e., live, d1, d2, d3, or d4) were modeled as cumulative probabilities, such that

$$\text{[3]} \qquad \begin{aligned} &P(k = \text{live}) = \pi_{\text{live}} = \gamma_1 \\ &P(k = \text{live or d1}) = \pi_{\text{live}} + \pi_{\text{d1}} = \gamma_2 \\ &P(k = \text{live or d1 or d2}) = \pi_{\text{live}} + \pi_{\text{d1}} + \pi_{\text{d2}} = \gamma_3 \\ &P(k = \text{live or d1 or d2 or d3}) = \pi_{\text{live}} + \pi_{\text{d1}} + \pi_{\text{d2}} + \pi_{\text{d3}} = \gamma_4 \\ &P(k = \text{live or d1 or d2 or d3 or d4}) = \pi_{\text{live}} + \pi_{\text{d1}} + \pi_{\text{d2}} + \pi_{\text{d3}} + \pi_{\text{d4}} = \gamma_5 \end{aligned}$$

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/x2012-131.

Fig. 1. Count, basal area, and volume of snags within silvicultural treatment and unit for sample plots measured at the Penobscot Experimental Forest, Bradley and Eddington, Maine. Short lines indicate plot observations, grey shading denotes distribution of values, long lines indicate means within unit, and broken lines represent overall population mean.



Cumulative probabilities were then estimated by

$$[4] \qquad \gamma_k = 1 - \exp\{-\exp[\theta_k - (\alpha_0 + \alpha_1 X_{1k} + ... + \alpha_p X_{pk})]\}$$

where θ_k is the intercept term for tree status class k and the α_i parameters were estimated in the proportional odds model. As the ORDREG method predicts cumulative probabilities as opposed to snag abundance, we used the predicted number of trees plus snags per hectare (μ_{TSPH}) calculated from eq. 2 using the count regression model. Then, to estimate the number of live trees and snags within each of the k status classes for each plot, μ_{TSPH} was multiplied by the predicted π_k for that plot.

Because of similarities in snag attributes (Fig. 1) and the relatively large values produced for standard errors in using eight silvicultural treatments as indicator variables, the treatments were grouped into $j = 5$ more generalized treatments for the ORDREG method. Estimates were made for the unharvested reference (REF), commercial clearcut (CC), selection cutting with 5-, 10-, and 20-year cycles (SC05, SC10, and SC20, respectively), shelterwood (SW), and modified and fixed diameter-limit cutting (MDL and FDL, respectively). These condensed treatment groupings are referred to as REF, CC, SC, SW, and DL, respectively. Incorporating silviculture into models was accomplished by using AHI and considering the treatment grouping as an indicator variable (1 if plot was found in a given silvicultural treatment; 0 if not). Models were parameterized as

$$[5] \qquad \mu_k = \exp(a_0 + a_1\mathrm{CCF} + a_2\mathrm{DWT} + a_3\mathrm{AHI} + a_4\mathrm{CC} + a_5\mathrm{SC} + a_6\mathrm{SW} + a_7\mathrm{DL})$$

Upon incorporating silvicultural treatment in the ORDREG model, subsequent model forms including CCF and depth to water table did not reduce AIC. The final ORDREG model chosen was

$$[6] \qquad \gamma_k = 1 - \exp\{-\exp[\theta_k - (\alpha_0 + \alpha_1\mathrm{AHI} + \alpha_2\mathrm{CC}_{\mathrm{jk}} + \alpha_3\mathrm{SC}_{jk} + \alpha_4\mathrm{SW}_{jk} + \alpha_5\mathrm{DL}_{jk})]\}$$

For the COUNTREG method, indicator variables for type of silviculture were not significant in predicting the number of snags in multiple decay classes. Instead, a mixed modeling strategy was used with experimental unit as a random effect. The final COUNTREG model chosen was

$$[7] \qquad \mu_k = \exp(\beta_0 + b_i + \beta_1\mathrm{CCF} + \beta_2\mathrm{DWT} + \beta_3\mathrm{AHI})$$

where β_i's are fixed-effects parameters estimated using either Poisson or negative binomial regression and b_i is a random intercept term for the ith experimental unit ~$N(0, \sigma^2 b_i)$.

Model validation

Validation of the developed models was assessed on 82 plots (approximately 30%) that were randomly withheld from model parameterization. The Reynolds et al. (1988) error index (EI) was employed as an evaluation measure to compare ORDREG and COUNTREG models because of its ability to measure goodness-of-fit with data that are summarized in classes, such as the data found in various stages of decay in this analysis:

$$[8a] \qquad \mathrm{EI} = \sum_{k=1}^{k_i} \left| n_{ik} - \hat{n}_{\mathrm{ik}} \right|$$

where n_{ik} and $\hat{n}_{ik}$ are the observed and predicted number of trees and snags per hectare in the kth status class found on the ith plot, respectively. To assess the performance of the Poisson versus negative binomial COUNTREG models, the root mean square error (RMSE) and mean absolute bias (MAB) were computed within each tree status class:

$$[8b] \qquad \mathrm{RMSE} = \sqrt{\sum_{i=1}^{n} (\mathrm{obs} - \mathrm{pred})^2/n}$$

$$[8c] \qquad \mathrm{MAB} = \sum_{i=1}^{n} \left|\mathrm{obs} - \mathrm{pred}\right|/n$$

where obs and pred are observed and predicted number of stems, respectively, and n is the number of plots.

Results

Standing deadwood attributes

The data collected in 2010–2011 contained 2751 snags comprised of 8 conifer and 13 hardwood species across 260 PSPs. Species could not be identified for 21 (<1%) of these snags. Snag abundance was positively correlated with slope and stand structural characteristics. Snag basal area was negatively correlated with depth to water table and positively correlated with stand structural characteristics. Live tree abundance averaged 4475 ± 2908 trees·ha^{-1}, while snag abundance averaged 407 ± 621 snags·ha^{-1}. Live tree basal area averaged 34.4 ± 12.4 m^2·ha^{-1}, but varied within treatment. For example, live tree basal area ranged from 27.3 to 63.9 m^2·ha^{-1} in the reference treatment. Snag basal area averaged 2.1 ± 2.2 m^2·ha^{-1} and varied with silvicultural treatment (Fig. 1). There was a general positive relationship between live tree and snag basal area (Fig. 2). Live tree volume averaged 299.7 ± 134.9 m^3·ha^{-1}, while snag volume averaged 8.7 ± 12.4 m^3·ha^{-1} (see supplementary material (Table S1) for means presented by silvicultural treatment).

Across the eight different silvicultural treatments, mean snag diameter ranged from 5.7 cm in commercial clearcut to 16.6 cm in reference treatments and mean snag height ranged from 4.4 m in the 20-year selection to 7.2 m in reference treatments (Fig. 3). Mean basal area and volume in snags were highest in reference (5.4 m^2·ha^{-1} and 29.4 m^3·ha^{-1}) and shelterwood treatments (4.6 m^2·ha^{-1} and 18.5 m^3·ha^{-1}). Mean snag density was highest in shelterwood (1329 snags·ha^{-1}) and commercial clearcut treatments (583 snags·ha^{-1}). Mean basal area, volume, and snag density were lowest in 5-year selection and fixed diameter limit. Basal area, volume, and abundance of snags varied across PSPs within silvicultural treatments. There was a large amount of within-treatment variability for the reference and shelterwood treatments (Fig. 1).

Mean volume of snags in various decay classes generally decreased as stage of decay increased (Fig. 4). Seventy-nine percent of observed snags across all PSPs were in decay classes 1 and 2. The mean percentage of snag volume in soft stages of decay (classes 3 and 4) was highest (27%) in reference and lowest (6%) in the modified diameter limit. Soft snags were absent in 107 (41%) of the PSPs. The absence of soft snags was noted primarily in the selection (5-, 10-, and 20-year) and diameter-limit (fixed and modified) treatments.

Fig. 2. Observed plot basal area in live trees and snags with loess regression line for 260 plots in eight silvicultural treatments at Penobscot Experimental Forest, Bradley and Eddington, Maine.

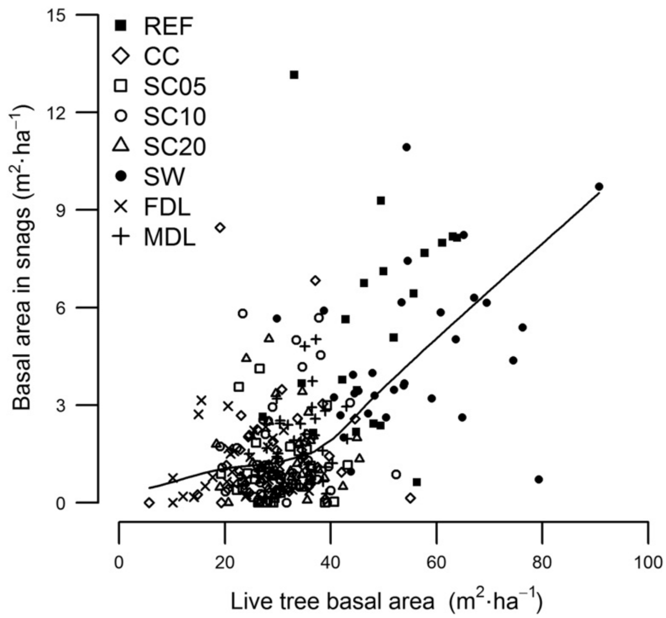
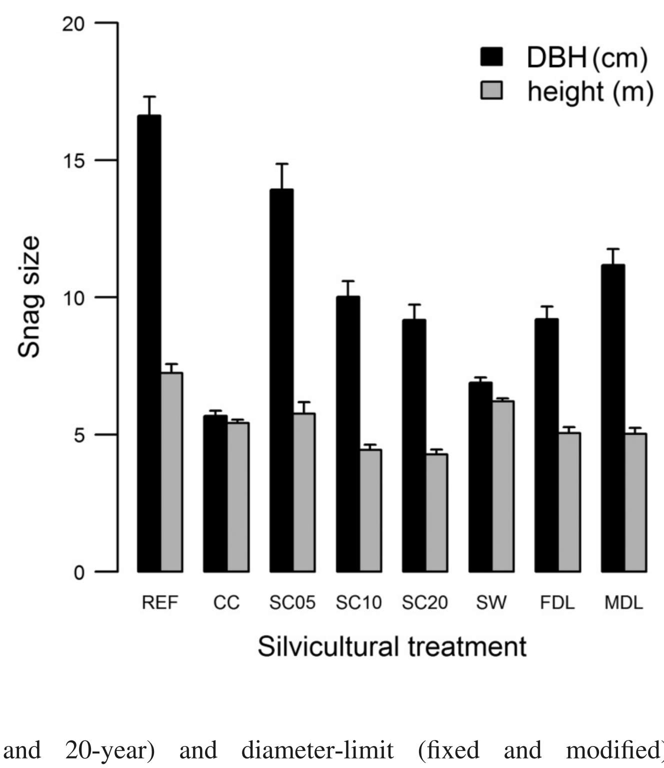


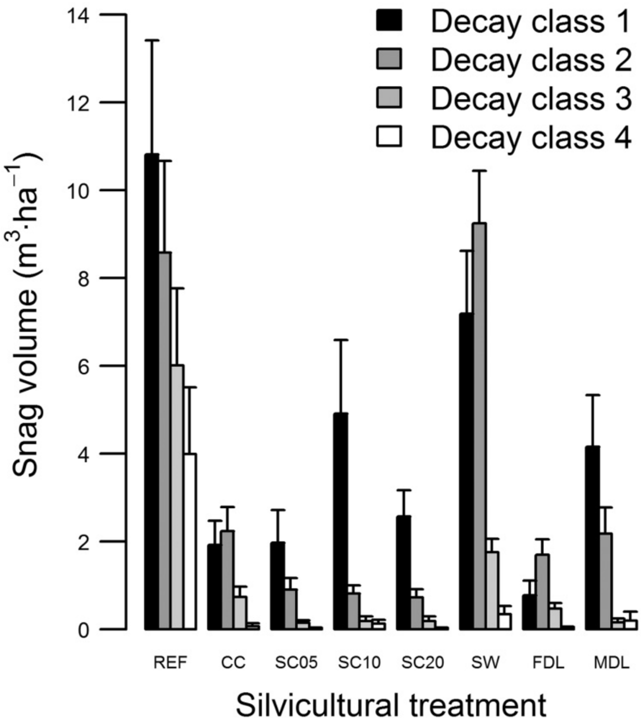
Fig. 3. Mean snag diameter at breast height (DBH) and height with standard errors by silvicultural treatment from data collected at the Penobscot Experimental Forest, Bradley and Eddington, Maine.



Modeling standing deadwood

Across nearly all snag decay classes, COUNTREG predictions outperformed ORDREG methodologies. EI (eq. 8a) was

Fig. 4. Mean snag volume with standard errors in various decay classes by silvicultural treatment at the Penobscot Experimental Forest, Bradley and Eddington, Maine.



1.76×10^5 for the ORDREG method and 1.13×10^5 and 9.90×10^4 for COUNTREG predictions that employed fixed effects solely for the Poisson and negative binomial regression models, respectively. For the Poisson and negative binomial models that incorporated experimental unit as a random effect, EI was 9.04×10^4 and 9.25×10^4, respectively. EI was reduced by 40% when fixed-effect COUNTREG was used over ORDREG models.

Model evaluation statistics comparing Poisson and negative binomial count regression models were similar when predicting TPH and SPH in various decay classes (Table 2). When only comparing fixed-effects equations, RMSE and MAB were lower for negative binomial models, except for snags in advanced decay stages (SPH.d3 and SPH.d4). However, Poisson regression predictions generally resulted in slightly lower RMSE and MAB values compared with negative binomial predictions when the random effect of experimental unit was taken into account.

Model predictions indicated a strong positive relationship between live tree and snag densities. Model predictions followed observations in the data, i.e., the highest densities and basal area of snags were predicted to occur in stands with a long AHI. At a CCF of 400%, approximately 140% more snags were predicted to occur in stands with an AHI of 55 compared with 5 years (Fig. 5). Depth to water table was an influential variable that captured the proportional dynamics between hard (decay classes 1 and 2) and soft (decay classes 3 and 4) snags. As depth to water table increased, models indicate a greater proportion of snags in the soft decay stage (Fig. 6). For the AHI of the unharvested reference treatment, eq. 7 was fit using multiple years: this included 0 (assuming no

Table 2. Root mean square error (RMSE) and mean absolute bias (MAB) for predicting trees (TPH) and snags per hectare (SPH) in decay classes 1 (d1) through 4 (d4) using Poisson and negative binomial count regression models.

		Fit statistic			
		Fixed		Fixed plus random	
Method	Metric	RMSE	MAB	RMSE	MAB
Poisson	TPH	1888.1	1396.3	1398.9	1040.0
	SPH.d1	264.1	153.3	250.4	152.5
	SPH.d2	344.9	134.8	331.4	136.0
	SPH.d3	188.9	61.5	173.2	54.2
	SPH.d4	19.5	7.6	17.6	7.4
Negative binomial	TPH	1617.2	1169.1	1527.2	1073.1
	SPH.d1	238.8	147.0	239.0	150.2
	SPH.d2	340.5	136.7	333.5	134.2
	SPH.d3	186.4	61.8	180.1	58.4
	SPH.d4	19.7	7.6	17.5	7.4

harvest) and 120 (assuming last harvest occurred sometime in the late 1800s). We found all values to produce consistent predictions to the interval initially used (55, assuming no harvesting since the beginning of the experiment). Either the AHI was not significant in predicting the number of snags in a given decay class or it showed a significant positive term for predicting snags in decay classes 2 and 3 (Table 3).

Discussion

Standing deadwood attributes

Standing deadwood basal area and volume were generally greater in silvicultural treatments with less frequent harvests, or in which harvesting has not occurred during the course of the experiment. This supports previous research that found that snag density is lower in intensively managed stands (Wisdom and Bate 2008) and that attributes of individual snags such as height and DBH are greater in unmanaged stands (Garber et al. 2005). This was evident in the reference (not harvested during the experiment) and shelterwood treatments (last harvested in the 1960s). Here, plot- (e.g., snag abundance and basal area) and snag-level attributes (e.g., height) were consistently larger than in the remaining treatments.

The average volume of 9 $m^3 \cdot ha^{-1}$ (>2.5 cm DBH) of standing deadwood observed across all PSPs in this study is less than the 39 to 50 $m^3 \cdot ha^{-1}$ range (>9 cm DBH) reported by Taylor and MacLean (2007) in balsam fir – spruce stands in New Brunswick and the 15 to 41 $m^3 \cdot ha^{-1}$ range (>9 cm DBH) reported by Aakala et al. (2008) in balsam fir – black spruce stands in Quebec. However, both of these studies were conducted in unharvested stands, while the stands on the PEF encompass multiple silvicultural and harvesting regimes. The mean of 29.4 $m^3 \cdot ha^{-1}$ of snags found in the PEF's reference treatment is more similar to the values observed in these previous studies (Taylor and MacLean 2007; Aakala et al. 2008).

There are few estimates of snag densities specific to the state of Maine, but coarse estimates suggest 2.7 $snags \cdot ha^{-1}$ greater than 38.1 cm DBH across the state's forests (McWilliams et al. 2005) and 195 to 217 $snags \cdot ha^{-1}$

Fig. 5. Predictions of total snag abundance and snag abundance within four decay classes for a range of crown competition factors (CCF) and average harvest intervals.

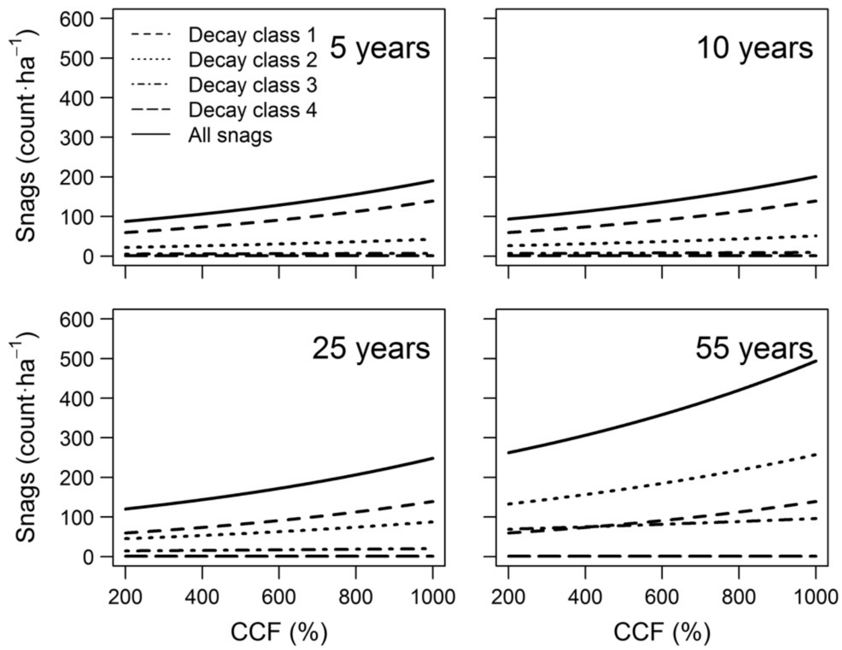
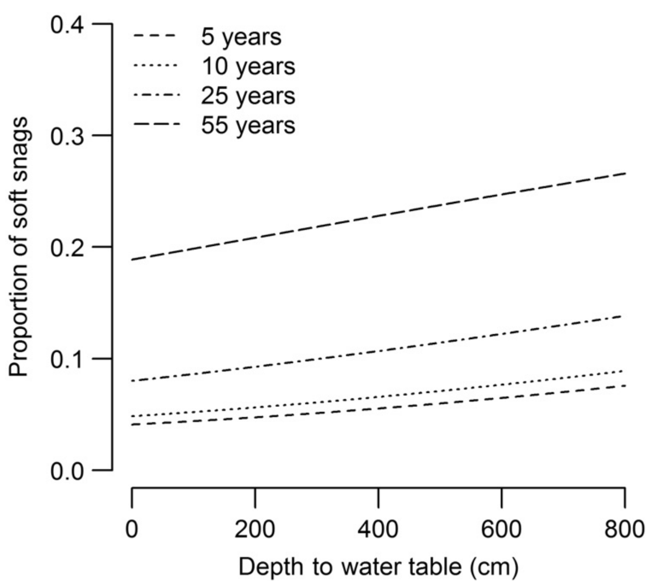


Fig. 6. Predictions of proportion of snags in soft decay stage (decay classes 3 and 4) across a range of values for depth to water table for various average harvest intervals.



greater than 7.5 cm DBH in eastern white pine – oak – hemlock stands in southern Maine (Kenning et al. 2005). This study observed an average of 407 snags·ha^{-1} greater than 2.5 cm DBH across all PSPs, but showed considerable variability across and within treatments (Fig. 1). The stark differences observed in snag abundance at the PEF is likely due to the fact that a much smaller minimum DBH (2.5 cm) was used for data collection, whereas other studies commonly employ a minimum DBH of 9 cm (Cline et al. 1980; Taylor and MacLean 2007; Aakala et al. 2008) and may additionally establish a minimum height requirement that is much higher than DBH (e.g., Cline et al. 1980). We favored this smaller size limit so that the number of snags and live trees per hectare could be compared using the same DBH threshold. Upon querying the data, analyses suggested that if a minimum DBH of 9 cm was used, standing dead trees would have averaged 70 snags·ha^{-1}. Similarly, snags would have been absent in 17% of all plots compared with the 5% that was observed.

The large number of small-diameter snags observed in the experimental units where the shelterwood treatment was applied can be attributed to the fact that both units of the treatment were undergoing self-thinning. Measurement of these plots during this stage of stand development captured the pulse of snags that was introduced following crown closure in the stand. Additionally in the shelterwood treatment, some submerchantable and unmerchantable trees were left following the final overstory removal, which may have contributed to the snag population. From the perspective of maintaining habitat suitability or biodiversity features, these smaller-diameter snags are less likely to be as important as larger-diameter snags. This finding encourages researchers to incorporate stand development stage in addition to silvicultural treatment to adequately describe the amount of standing deadwood on a given site. Silvicultural practices that maintain large-diameter reserve trees are important for future ecosystem dynamics — as these reserve trees senesce, they can provide important ecological functions as legacy trees.

Large-scale disturbances have been absent at the PEF over the last 60 years, but the last major disturbance was likely a 1913–1919 eastern spruce budworm outbreak (Seymour 1992). There has been little research in Maine on the degree to which this outbreak influenced the amount of standing dead-

Table 3. Parameter estimates (standard errors in parentheses) for predicting trees plus snags (TSPH), trees (TPH), and snags per hectare (SPH) in decay classes 1 (d1) through 4 (d4) using Poisson count regression models.

Parameter	Metric TSPH	TPH	SPH.d1	SPH.d2	SPH.d3	SPH.d4
β_0	7.42 (0.11)	7.34 (0.11)	3.83 (0.17)	2.51 (0.32)	1.01 (0.52)	−0.198 (0.64)
β_1	9.24×10^{-4} (2.1×10^{-6})	9.34×10^{-4} (2.3×10^{-6})	1.06×10^{-3} (1.0×10^{-5})	8.27×10^{-4} (1.1×10^{-5})	4.12×10^{-4} (2.0×10^{-5})	4.37×10^{-4} (6.8×10^{-5})
β_2	1.56×10^{-4} (5.6×10^{-6})	0.820×10^{-5} (5.8×10^{-6})	2.54×10^{-4} (3.0×10^{-5})	1.34×10^{-3} (2.8×10^{-5})	1.59×10^{-3} (4.3×10^{-5})	-4.60×10^{-4} (2.2×10^{-4})
β_3	—	—	—	3.59×10^{-2} (9.6×10^{-3})	5.20×10^{-2} (1.6×10^{-2})	—
$\sigma^2 b_i$	0.161	0.177	0.394	0.444	1.17	5.30

Note: Model: $\mu_k = \exp(\beta_0 + b_i + \beta_1\text{CCF} + \beta_2\text{DWT} + \beta_3\text{AHI})$.

wood. Insight from nearby New Brunswick suggests that half of all snags observed in spruce – fir stands experiencing repeated budworm attacks were either broken or uprooted (Taylor and MacLean 2007), indicating that natural disturbances may influence snag dynamics in substantially different patterns than the harvest disturbances studied here.

Measurements of individual snags were consistent with those observed elsewhere for the species examined. The mean snag height of 4.9 m observed in second-growth northern hardwood stands in New Hampshire (Yamasaki and Leak 2006) was similar to the mean of 5.6 m observed in this study. The findings of Garber et al. (2005) using a standing deadwood inventory of the PEF in 1997 remain true for snags inventoried in 2011: snag heights are approximately one third greater in unharvested stands than in managed stands. The similarities between these two measurements highlight the importance of furthering our knowledge concerning the temporal elements of snag dynamics, which would require collecting repeated measurements on individual snags. Monitoring the temporal aspects of snag attributes is essential for understanding snag longevity and quantifying decay dynamics.

The volume of snags in various decay classes generally followed a negative exponential trend as they moved towards more advanced decay stages. This is similar to the findings of Goodburn and Lorimer (1998) who observed that 80% of snags in northern hardwood and hemlock–hardwood stands under a range of forest management regimes were slightly and moderately decayed, as we observed 79% of snags in decay classes 1 and 2. Coupled with knowledge of individual snag attributes such as DBH and height, results can be used for evaluating how stands managed under a specific silviculture treatment can provide suitable wildlife habitat for a given species. For example, habitat management guidelines have been suggested for several bird species in Maine, such as establishing a minimum diameter of 55.9 and 30.5 cm for pileated woodpeckers (*Dryocopus pileatus*) and yellow-bellied sapsuckers (*Sphyrapicus varius*), respectively (Elliot 2008).

Modeling standing deadwood

The robustness of the Poisson model predictions came as somewhat of a surprise given that the negative binomial model contains an additional parameter that directly reflects the overdispersion of the data. This could be due to the fact that the proportion of plots measured that contained no snags was quite low (5%), whereas in other studies the problem of excess zeros was quite high (e.g., Eskelson et al. 2009, their fig. 1).

The fact that COUNTREG outperformed ORDREG methods showed that snag density can be quantified if one treats the snags observed within each decay class as the dependent variables, as opposed to considering snags across the entire sample as ordinal data. The inability of the ORDREG method to capture the variability observed across all decay classes could be because few explanatory variables were related to predicting the cumulative probabilities of snags found in each decay class. This is similar to the results of Bater et al. (2009), who used only one LiDAR-derived variable to predict stem density in different wildlife tree classes, and by Eskelson et al. (2012), who found that stand age, a surrogate for stand development stage in even-aged stands, was the only significant predictor for estimating snag density across three decay classes. Characterizing stand development stage would be difficult in the forests of Maine, as traditional metrics such as stand age are ineffective for use in stands treated with silvicultural systems that create and maintain uneven-aged structures.

For the Poisson regression models, CCF was an effective stand density measure (based on live trees) for predicting snag abundance in these mixed-species stands. As CCF is a species-specific measure of stand density that relates the maximum area available to a live tree of a given species to the maximum area that it could occupy if it were open-grown, CCF takes into account the contribution that species differences play in estimating stand density. CCF could theoretically capture the vertical heterogeneity of the stand, whereas other measures of density such as basal area are solely measured at breast height and are often confounded with stand age and site quality. As stand structures become more diverse with snag presence, we hypothesize CCF to be a useful predictor of live tree stand density in these mixed-species stands. Results highlight the ability to use live tree attributes to predict those of snags (Woodall and Westfall 2009).

No relationships were found between soils variables and overall snag abundance and basal area, but the models indicated that the proportion of soft snags increased as depth to water table increased, (i.e., as soil drainage improved). This relationship could be due to the high number of snags observed in decay classes 1 and 2 in the shelterwood treatments that are primarily on poorly or very poorly drained soils (Bryce 2009). The low proportion of total snags in a soft decay stage is likely due to the fact that snags found on poorly drained soils are likely to have poor mechanical stability. This was hypothesized by Garber et al. (2005), who suggested that differences in snag longevity, and hence the increased probability that a standing snag could reach an advanced decay stage, could be attributed to microsite conditions and the interactions between microsite and species. The degree that soil drainage can be used to quantify downed deadwood pools merits further exploration, as snags can be considered at the interim stage between live trees and downed deadwood.

The primary benefit of employing explanatory variables such as live tree density, site characteristics, and AHI is that estimates of snag density can be made using routine forest inventory information from live trees. As snags are not usually the focus of traditional inventories, models that accurately predict snag density and snag density within certain decay stages can play a role in estimating forest carbon stocks under alternative forest management regimes or assessing habitat suitability for a specific wildlife species. Testing the performance of models that predict snags across various forest management regimes can help to reduce the disparities between model predictions and field observations as noted by Woodall et al. (2012). Explanatory variables described herein are common to most forest inventories and can bridge the gap between the timber-focused output provided by forest growth models and the nontimber characteristics inherent in these forests.

Conclusions

Employing snag data gathered across eight silvicultural treatments in central Maine, this analysis found that snag density and snag quality attributes were related to stand density, soil drainage, and silviculture. An unmanaged reference and shelterwood treatment displayed the largest observed basal areas and volumes in snags nearly 60 years after treatments were initiated. Poisson regression models outperformed competing modeling strategies in characterizing the variability observed in the data collected across the sample plots and in describing snag density within specific stages of decay. Results showcase the importance of incorporating silvicultural treatment into models that estimate snags and relating snags to variables commonly collected as part of routine forest inventories.

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