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Quantifying understorey vegetation in the US Lake States: a proposed framework to inform regional forest carbon stocks

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The contribution of understorey vegetation (UVEG) to forest ecosystem biomass and carbon (C) across diverse forest types has, to date, eluded quantification at regional and national scales. Efforts to quantify UVEG C have been limited to field-intensive studies or broad-scale modelling approaches lacking field measurements. Although large-scale inventories of UVEG C are not common, species- and community-level inventories of vegetation structure are available and may prove useful in quantifying UVEG C stocks. This analysis developed a general framework for estimating UVEG C stocks by employing per cent cover estimates of UVEG from a region-wide forest inventory coupled with an estimate of maximum UVEG C across the US Lake States (i.e. Michigan, Minnesota and Wisconsin). Estimates of UVEG C stocks from this approach reasonably align with expected C stocks in the study region, ranging from 0.86 ± 0.06 Mg ha^{-1} in red pine-dominated to 1.59 ± 0.06 Mg ha^{-1} for aspen/birch-dominated forest types. Although the data employed here were originally collected to assess broad-scale forest structure and diversity, this study proposes a framework for using UVEG inventories as a foundation for estimating C stocks in an often overlooked, yet important ecosystem C pool.

Introduction

Understorey vegetation (UVEG) in forest ecosystems is typically defined as all forest vegetation growing under an overstorey (Helms 1998), including herbaceous and woody plants in addition to trees that may eventually grow into the overstorey. UVEG plays a central role in contributing to forest ecosystem structure and composition: its presence and abundance provide key elements for biodiversity (Halpern and Spies, 1995), nutrient cycling (Gilliam, 2007) and forest fuel loads (Arno, 2000) and shape future overstorey tree structure and diversity (Legare *et al*., 2002). The presence, abundance and diversity of UVEG can serve as indicators of forest ecosystem health (Schulz *et al*., 2009; Suchar and Crookston, 2010), allowing assessments of forest fuel components, wildlife habitat, degree of anthropogenic disturbance (Dale *et al*., 2008) and presence of non-native species (Glasgow and Matlack, 2007; Schulz and Gray, 2013). Although models that estimate UVEG biomass are inherently difficult to construct, parameterize and validate (Suchar and Crookston, 2010; Eskelson *et al*., 2011), such models remain a critical need across a range of disciplines (e.g. fuel monitoring and C stock assessments) over broad spatial scales (e.g. National Greenhouse Gas Inventory). From a national perspective in the US, estimates of UVEG C stocks are reported to the United Nations Framework Convention on Climate Change (Muukkonen and Mäkipää, 2006; USEPA, 2011; Smith *et al*., 2013) as a component of aboveground live tree C.

In an effort to improve our understanding of total forest ecosystem C, both forest C measurement and accounting have been highlighted as a research need for informing management of forest C stocks (Birdsey *et al*., 2006). The need to base C models on empirical data from annual monitoring efforts is essential for assessing forest C stocks in the context of global change (Woodall, 2012). In the case of UVEG, little attention has been given to quantifying their C stocks likely because of the small proportion of total ecosystem biomass that UVEG represents (Zavitkovski, 1976; Tremblay and Larocque, 2001) coupled with the inherent compositional and seasonal variability of this ecosystem component (González-Hernández *et al*., 1998; Tremblay and Larocque, 2001; Gilliam, 2007). In addition, destructive sampling methods for determining UVEG C stocks (e.g. clipping and weighing), albeit highly accurate, are associated with high costs and can suffer reduced accuracy when scaled to represent large geographic regions (Catchpole and Wheeler, 1992). Fortunately, nondestructive estimates of UVEG biomass obtained using per cent cover estimates fall within the 95 per cent confidence limits using destructive sampling (Yarie and Mead, 1989; Muukkonen *et al*., 2006). Several studies have attempted to circumvent these challenges using a combination of destructive sampling and allometric scaling. For example, Porté *et al*. (2009) estimated UVEG biomass by first using destructive sampling to establish UVEG biomass stocks and then related these stocks to a volumetric index that incorporated per cent cover of UVEG by height. Suchar and Crookston (2010) used a two-stage approach in which maximum UVEG biomass for a given site was determined and then modified based on factors that limit understorey biomass, such as competition, climate and presence/absence of disturbance. The influence of canopy cover of overstorey trees – a promising predictor variable to relate overstorey structure with understorey attributes – has (González-Hernández *et al*., 1998; McKenzie *et al*., 2000; Muukkonen *et al*., 2006) and has not (Porté *et al*., 2009; Suchar and Crookston, 2010) been correlated with UVEG cover and/or biomass. However, the majority of investigations quantifying UVEG attributes have been limited to individual forest types and/or focused on a particular plant functional group (e.g. shrubs or herbs). As a result, these studies may not contain sufficient variability across multiple forest structures and spatial scales necessary for establishing relationships between UVEG C, overstorey structure and climate information.

The Forest Inventory and Analysis (FIA) program of the USDA Forest Service conducts a systematic inventory of forest ecosystem attributes across the US (Bechtold and Patterson, 2005). Although destructive sampling of UVEG is not carried out in FIA inventories, field observations of vegetation cover and species composition are routinely collected on a subset of plots in the national forest inventory (Schulz *et al*., 2009; USDA Forest Service, 2012, 2013a). The inventory has a variety of plot protocols each region may adopt, ranging from identification of UVEG species' cover individually or by growth form and height class. If the most parsimonious approach to determining a forest's UVEG structure results in UVEG C population estimates that are not statistically different from more detailed (i.e. expensive) surveys, then perhaps more robust monitoring of UVEG C pools could be conducted across large scales. These cover estimates could potentially be used to describe UVEG C by relating them to detailed studies that have clipped and weighed understorey plants within a given region and forest type. Hence, regional inventories of UVEG cover and species composition (such as conducted by the FIA program) could be used to 'leverage' the information gathered on a limited number of destructively sampled UVEG study sites to potentially refine the monitoring of plant biomass and C in the UVEG pool.

The primary goal of this study was to combine destructively sampled vegetation data with extensively sampled cover and species composition information to inform UVEG C stocks for two common forest types in the Lake States region (Michigan, Minnesota and Wisconsin) of the US. Specific objectives were to (1) develop a framework for quantifying UVEG C using per cent cover estimates collected by a region-wide forest inventory in red pine-dominated (*Pinus resinosa* Ait.) and aspen (*Populus* spp.)/birch (*Betula* spp.)-dominated stands combined with destructively sampled UVEG plots and (2) assess alternative estimates of UVEG C using varying field protocols associated with the region-wide forest inventory which might inform future monitoring efforts.

Methods

UVEG data

Clipped and weighed data

Measurements of understorey vegetation C ($UVEG_C$) were collected from stands located in red pine-dominated and aspen/birch-dominated forest types in Minnesota (Bradford and Kastendick, 2010). In Minnesota, quaking aspen (*Populus tremuloides* Michx.), red pine and paper birch (*Betula papyrifera* Marsh.) are three of the most common species as measured by total live tree volume, representing over 135 million m^3 of growing stock in the state (Miles and VanderSchaaf, 2012). Similarly, red pine and aspen/birch species represent 148 and 67 million m^3 of live tree volume in Michigan (Pugh, 2013) and Wisconsin (Perry, 2013), respectively. Thirty stands dominated by red pine (~81 per cent of stand basal area) on low-fertility outwash soils were sampled across a range of ages from 7 to 160 years. Twenty-eight aspen/birch stands found on moraine and till and/or outwash soils were sampled across a range of ages from 6 to 133 years. The aspen/birch stands were dominated by quaking and bigtooth (*Populus grandidentata* Michx.) aspen (~67 per cent of stand basal area) with lesser amounts of paper birch. Overstorey tree measurements were conducted on all woody stems ≥2.5 cm diameter at breast height (d.b.h.) on three 0.02-ha sample plots within each stand. The total basal area ranged from 0.1 to 78.7 m^2 ha^{-1} across these forests.

The UVEG stocks comprised herbaceous material (defined as all herbs, graminoids and club mosses collected on 0.25 m^2 plots (one for each 0.02-ha main plot, totaling 87 and 84 plots in the red pine and aspen/birch stands, respectively) that were clipped, dried to a constant mass, weighed and multiplied by the per cent C in the sample (obtained by grinding herbaceous material and analysing total C) and woody stems <2.5 cm d.b.h., where biomass was estimated using species-specific regional models and C was assumed to be 50 per cent of biomass (Bradford and Kastendick, 2010). The UVEG C stocks were scaled to per hectare values and were analysed with the corresponding overstorey tree information for each plot (i.e. basal area).

FIA data

The FIA program is responsible for inventorying forests of the US, including vegetation on permanent sample plots established across the US using a three-phase inventory (Bechtold and Patterson, 2005). During the inventory's first phase (P1), sample plot locations are established at an intensity of approximately one plot per 2400 ha. If the plot lies partially or wholly within a forested area, field personnel visit the site and establish a phase two (P2) inventory plot. Standard forest inventory plots (i.e. P2) consist of four 7.32-m (24.0-ft) fixed radius subplots for a total plot area of approximately 0.07 ha, where standing tree and site attributes are measured. During FIA's third phase (P3), a subset of P2 plots (sample intensity of one plot per 38 849 ha) are sampled for additional variables related to forest ecosystem health, including detailed UVEG characteristics (e.g. species, per cent cover of UVEG in various height layers and ground variables including lichen, litter/duff and moss).

UVEG measurements collected at the P3 sample intensity were used throughout this analysis. Field observations of UVEG attributes in the Lake States were obtained from the publically available FIA database (Figure 1; Forest Inventory and Analysis, 2013). Plot data were queried according to the FIA forest type classification (USDA Forest Service, 2013a). Data were collected from June to mid-September between 2001 and 2010. All electronically available data were used in this analysis; however, only forested subplots that were accessible by field crews were analysed. Within these data, a variety of forest condition information was assessed, including stand size class and the presence/absence of stand treatments and/or disturbance within a plot. Ocular canopy cover estimates for UVEG were recorded by field crews using a standard cover protocol (Daubenmire, 1959) with measurement error tolerances to mimic Braun-Blanquet (1932) cover classes.

Several general assessments were made for UVEG on each subplot (dataset hereafter termed SUBP) and more specifically by measurements of each individual species found within a subplot (termed SUBP-SPP). Together, these two sets of measurements comprise the FIA's Vegetation Diversity and Structure Indicator (Schulz *et al*., 2009). For the SUBP data, vegetation cover was measured ocularly through an assessment of all plants present on a subplot, in 1-per cent intervals located in four height layers (Figure 2). For the SUBP-SPP data, canopy cover assessments were

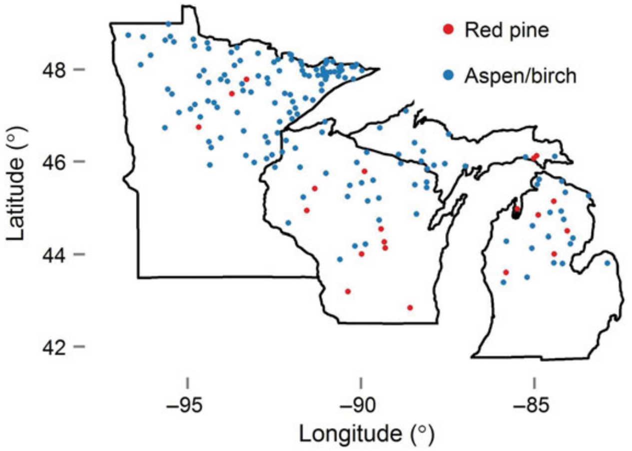

Figure 1 Approximate location of UVEG plots collected across the US Lake States, 2001–2010.

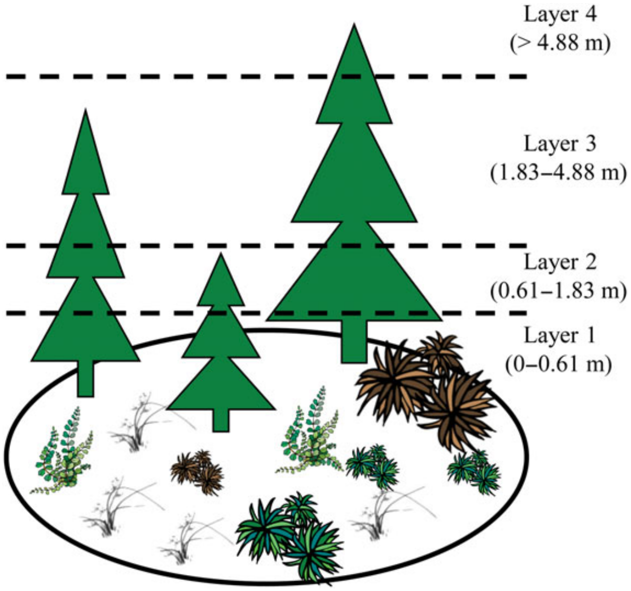

Figure 2 Canopy height layers for assigning per cent cover estimates by subplots or individual species in the forest vegetation plots.

made individually for all vascular plant species with live stems within or foliage hanging over forested portions of the subplots. The per cent canopy cover was measured similarly as in the SUBP data in 1-per cent intervals, although species were recorded in three height layers: (1) 0–1.83, (2) 1.83–4.88 and (3) >4.88 m. Species were identified and are described in this analysis according to their listing in the PLANTS database (USDA NRCS, 2010). Additional information on the FIA's data collection protocols can be found in Schulz *et al.* (2009) and Woodall *et al.* (2010).

Subplot-level metrics representing a variety of stand structural characteristics were computed for overstorey trees using the associated overstorey tree data (i.e. P2 measurements). These included the number of trees per hectare (TPH; trees ha^{-1}), basal area per hectare (BAPH; $\text{m}^2\ \text{ha}^{-1}$), quadratic mean diameter (QMD; cm) and relative density (RD; the ratio between a plot's stand density index and a maximum value dependent on species composition of the plot; Woodall *et al.*, 2005). To represent overstorey per cent canopy cover (CC_{OVER}), tree crown widths were estimated using d.b.h. and other predictor variables using static models (Bragg, 2001; Bechtold, 2003). Using these estimates of crown width, CC_{OVER} was evaluated for each plot and subplot and was corrected for crown overlap (Crookston and Stage, 1999).

A framework for quantifying C in UVEG

In this analysis, overstorey conditions were based on all woody stems ≥2.5 cm d.b.h.. Because trees <2.5 cm d.b.h. are not accounted for in the FIA program in terms of biomass/C and these seedlings are almost surely shorter in height than the defined 4.88 m UVEG threshold, the understorey was defined as all vascular plants (including trees, shrubs/subshrubs/woody vines, forbs and graminoids) growing <4.88 m in height from the forest floor. Given direct measurements of UVEG biomass were not conducted in the FIA subplot data (i.e. not clipped and weighed), we sought a framework upon which we could use the clipped and weighed data from Bradford and Kastendick (2010) and per cent cover estimates of UVEG from the FIA data to estimate their UVEG C. Using this framework, we assumed that a higher per cent cover in an FIA subplot would be closer to the maximum amount of UVEG C than we might expect for a given forest type under specific stand conditions.

Biomass residing in UVEG may be expressed as a function of maximum UVEG biomass for a specific forest type under a given set of stand conditions (Suchar and Crookston, 2010). To approximate this maximum value, we developed a modelling framework that used the UVEG_C data that were destructively sampled and then weighed. We employed two modelling strategies in assessing this maximum value: nonlinear mixed-effects (NLME) models and nonlinear quantile regression (NLQR). An NLME modelling strategy is appealing given it accounts for the hierarchical nature of these data (i.e. clipped and weighed sample plots nested within stands) and incorporates both fixed and random effects (Pinheiro and Bates, 2000). As a surrogate for the maximum amount of C found in UVEG on a subplot (hereafter termed $\text{UVEG}_{\text{C-MAX}}$), the BAPH was used as a fixed effect given its strong correlation with clipped and weighed UVEG_C (Pearson correlation of −0.56 and −0.58 for red pine and aspen/birch forest types, respectively)

$$\text{UVEG}_{\text{C-MAX}} = \exp(\alpha_0 + a_i + a_{ij} + \alpha_1 \text{BAPH}) \tag{1}$$

where the α_0 and α_1 values were fixed effects estimated for each forest type, a_i is a random effect term for each stand i and a_{ij} is a random effect term for each plot j nested within each stand i. Model parameters were estimated using the nonlinear mixed-effects models (nlme) function available in the 'nlme' package in R (Pinheiro *et al.*, 2013).

When considering a regression framework, NLME regression may result in estimating our response variable (i.e. UVEG_C obtained from the clipped and weighed data) conditioned solely on the statistical mean. To circumvent this assumption, we employed quantile regression techniques (Cade and Noon, 2003). Given that we were interested in the maximum estimate of C found in UVEG on a subplot (hereafter termed $\text{UVEG}_{\text{C-MAX}}$) and not the mean (i.e. a least-squares approach), the 50th, 75th, 90th and 99th quantiles were fit to represent the maximum potential UVEG C for each stand

$$\text{UVEG}_{\text{C-MAX}} = \exp(\alpha_0 + \alpha_1 \text{BAPH}) \tag{2}$$

where the α_i values were coefficients estimated for each forest type from the various percentiles using the nonlinear quantile regression (nlrq) function available in the 'quantreg' package in R (Koenker, 2013). We evaluated the NLME and NLQR models by comparing the slope and intercept terms for each model, contrasting each of their predictions (e.g. NLME *vs* NLQR 0.99) with values reported for the same forest types as presented in the literature, and examining the models in representing extreme values present in the data (e.g. large UVEG_C predictions).

It was unrealistic to assume that all forest stands in the FIA data displayed UVEG_C equal to $\text{UVEG}_{\text{C-MAX}}$. For determining UVEG_C stocks for the

FIA data, field observations of understorey canopy cover (CC_{UVEG}; expressed as a proportion) for height layers <4.88 m were employed to 'scale down' $UVEG_{C\text{-}MAX}$ using a volumetric approach. Understorey vegetation C ($UVEG_C$; Mg ha^{-1}) was defined as all aboveground C for vascular plants (including trees, shrubs/subshrubs/woody vines, forbs and graminoids) growing <4.88 m on a forested subplot.

The estimation strategy used to quantify $UVEG_C$ for the FIA subplots was accomplished in four stages. First, $UVEG_{C\text{-}MAX}$ was estimated in each subplot using equations (1) and (2). Second, $UVEG_{C\text{-}MAX}$ was reduced by taking into account field observations of CC_{UVEG} and the height layer in which CC_{UVEG} was assessed. In doing this, three values were multiplied: (1) $UVEG_{C\text{-}MAX}$ obtained from the clipped and weighed data, (2) CC_{UVEG} assessed for each subplot or species within subplot in a given height layer located on a subplot and (3) the midpoint of a specific height layer divided by the maximum height threshold for which UVEG is defined (in the case of the FIA data, 4.88 m). The third stage involved repeating the first and second steps for each of the remaining height layers for which CC_{UVEG} was assessed. The fourth stage summed all of the $UVEG_C$ estimates (Mg ha^{-1}) by height layer to arrive at a final estimate of $UVEG_C$ for a subplot. Written more generally, the framework for estimating $UVEG_C$ can be described as

$$UVEG_{C_i} = \sum_{1}^{j} \{UVEG_{C\text{-}MAX_i} \times CC_{UVEG_{ij}} \times (Midpt_{ij}/MaxHt_i)\} \qquad (3)$$

where $UVEG_{C_i}$ is the C found in UVEG <4.88 m on subplot i, $UVEG_{C-MAX_i}$ is the maximum C in UVEG for subplot i estimated from equation (1), $CC_{UVEG_{ij}}$ is the canopy cover expressed as a proportion for a subplot or species within subplot for height layer j found in subplot i, $Midpt_{ij}$ is the midpoint of height layer j (m) and $MaxHt_i$ is the maximum height threshold (m) for subplot i used in determining $UVEG_{C_i}$ (i.e. 4.88 m for the FIA data). A graphical display of this proposed framework is summarized in Figure 3. We examined the top three species by height layer that contributed the largest values of $UVEG_C$, as measured by the mean $UVEG_C$ estimated for each forest type.

Results

UVEG attributes

For the clipped and weighed data, $UVEG_C$ stocks ranged from 0.03 to 4.70 Mg ha^{-1} and from 0.16 to 18.65 Mg ha^{-1} for the red pine ($n = 87$) and aspen/birch forest types ($n = 84$), respectively. The NLME and NLQR regressions indicated a decreasing slope related to $UVEG_C$ as overstorey basal area increased (Table 1; Supplementary data, Appendix 1). Likelihood ratio tests indicated that the random effects a_i and a_{ij} were significant ($P < 0.001$) for both forest types. Random effects for the stand/plot terms in the NLME models were centred around zero (Figure 4). Fit indices (analogous to R^2 values) for predictions of UVEG using fixed plus random effects (0.582 and 0.654 for red pine and aspen/birch, respectively) outperformed fit indices for predictions using fixed effects alone (0.236 and 0.211 for red pine and aspen/birch, respectively). Employing these various modelling strategies provided

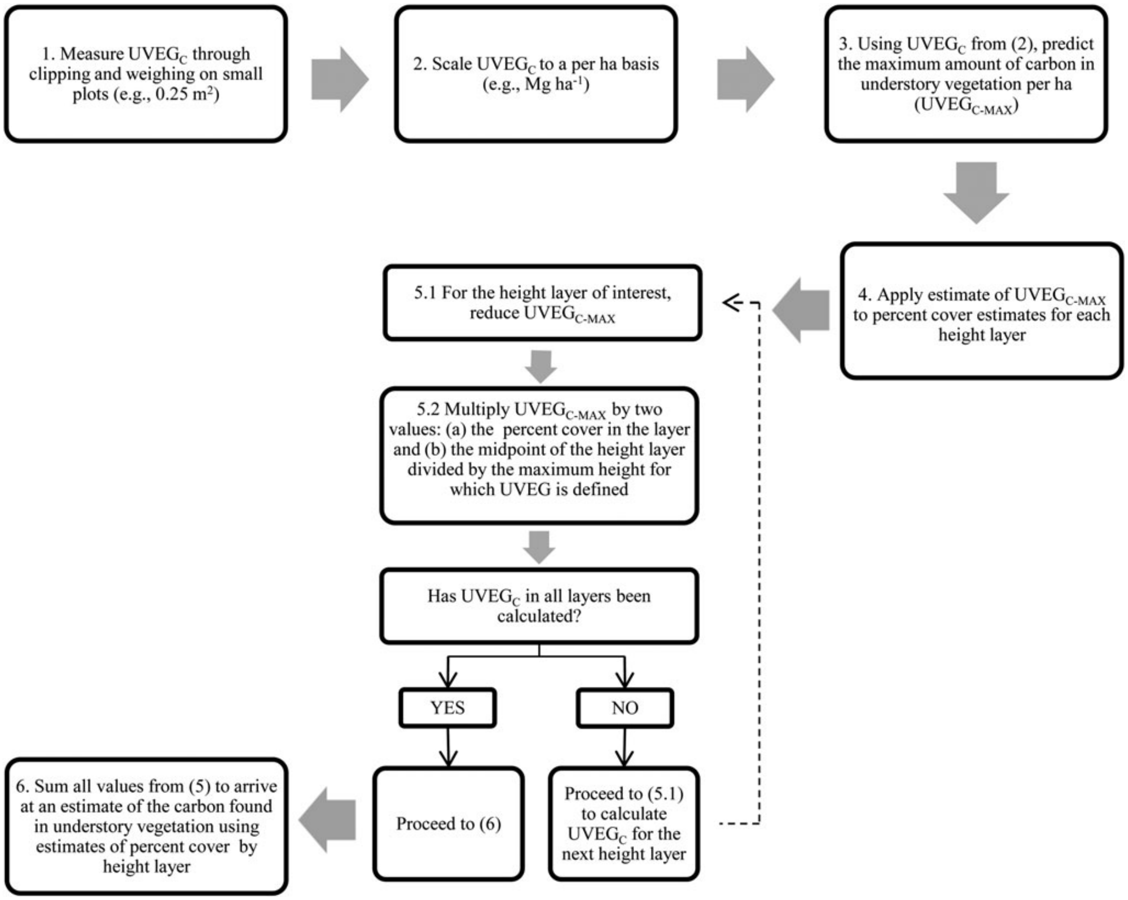

Figure 3 Proposed framework for quantifying C found in UVEG employing clipped-and-weighed data (steps 1–3) to estimate C using operational forest inventories of vegetation cover by height layer (steps 4–6).

Table 1 Parameters for estimating the maximum amount of carbon found in UVEG ($UVEG_{C\text{-}MAX}$) using NLME (equation (1)) and NLQR (equation (2)) models[1,2,3]

Parameter	Quantile	Estimate	SE	*P* value
Forest type = red pine				
α_0	NLQR 0.99	2.16263	0.24246	0.00000
	NLQR 0.90	1.66976	0.14465	0.00000
	NLQR 0.75	1.51484	0.20489	0.00000
	NLQR 0.50	1.02065	0.40712	0.01408
	NLME	0.85732	0.30467	0.00670
α_1	NLQR 0.99	−0.02301	0.00562	0.00010
	NLQR 0.90	−0.02089	0.00435	0.00001
	NLQR 0.75	−0.02639	0.00510	0.00000
	NLQR 0.50	−0.02726	0.00998	0.00763
	NLME	−0.02700	0.00672	0.00020
Forest type = aspen/birch				
α_0	NLQR 0.99	3.21606	0.25613	0.00000
	NLQR 0.90	2.69050	0.34228	0.00000
	NLQR 0.75	2.39960	0.26098	0.00000
	NLQR 0.50	2.30790	0.25516	0.00000
	NLME	1.20438	0.23179	0.00000
α_1	NLQR 0.99	−0.05683	0.01731	0.00151
	NLQR 0.90	−0.05785	0.01057	0.00000
	NLQR 0.75	−0.06188	0.00943	0.00000
	NLQR 0.50	−0.07875	0.01022	0.00000
	NLME	−0.03316	0.00743	0.00000

[1] Models for NLQR is $UVEG_{C\text{-}MAX} = \exp(\alpha_0 + \alpha_1 BAPH)$.
[2] Model for NLME is $UVEG_{C\text{-}MAX} = \exp(\alpha_0 + a_i + a_{ij} + \alpha_1 BAPH)$.
[3] Variables: basal area per hectare (BAPH; $m^2\ ha^{-1}$), α_js are parameters to be estimated, a_i is a random effect term for each stand *i*, a_{ij} is a random effect term for each plot *j* nested within each stand *i*.

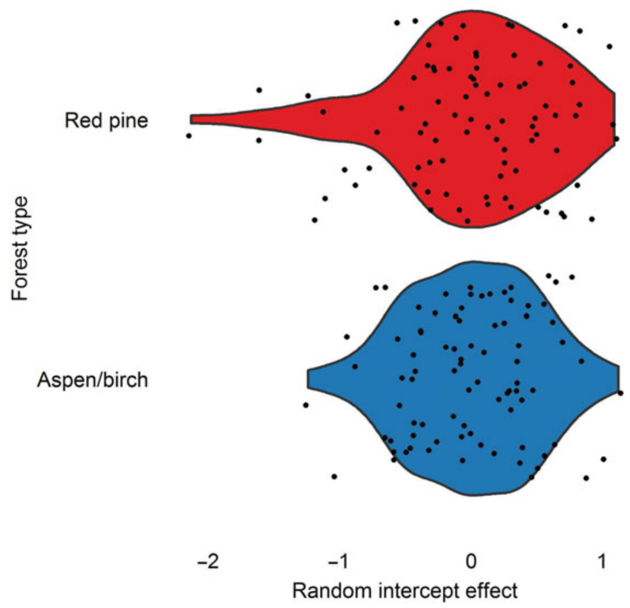

Figure 4 Violin plot of the distribution of random effects (points) associated with the intercept term for NLME models for plots nested within stands for the clipped and weighed data.

a unique set of coefficients for each forest type, which ultimately resulted in different predictions of $UVEG_C$ when scaled using the FIA per cent cover data (Table 2). Confidence intervals (95 per cent level) associated with the NLQR slope parameters in both forest types generally overlapped, while intercept terms for both NLME and NLQR models were more variable (e.g. the intercept term for aspen birch for NLME and NLQR models; Figure 5).

Ultimately, the NLRQ model fit at the 90th quantile was selected to represent $UVEG_{C\text{-}MAX}$. While representing the maximum potential UVEG C for both forest types, the 0.90 quantile was preferred because higher quantiles (e.g. the 99th) were sensitive to extreme values present in the clipped and weighed data (e.g. large values of $UVEG_C$ at low BAPH; Supplementary data, Appendix 1). Slope parameters were similar for both NLRQ models fitted at the 90th and 99th percentiles and intercept parameters overlapped (Figure 5). Hence, the final models chosen to represent $UVEG_{C\text{-}MAX}$ were

$$\begin{aligned} UVEG_{C\text{-}MAX} &= \exp(1.66976 - 0.02089 \times BAPH); \\ &\quad \text{for red pine forest types, and} \\ UVEG_{C\text{-}MAX} &= \exp(2.69050 - 0.05785 \times BAPH); \\ &\quad \text{for aspen/birch forest types.} \end{aligned} \tag{4}$$

Employing the NLRQ predictions from the 90th quantile resulted in the mean values of 0.86 ± 0.05 and 1.59 ± 0.06 Mg ha^{-1} for the red pine and aspen/birch plots (respectively) located across the region. The selection of other model forms in representing $UVEG_{C\text{-}MAX}$, such as the NLME model form, was avoided as they did not represent a true maximum value of $UVEG_C$ and resulted in small values of $UVEG_{C\text{-}MAX}$ (e.g. Table 2) when compared with the literature.

For the red pine and aspen/birch forest types sampled under the FIA program, 55 and 317 subplots were assessed for UVEG characteristics, respectively. All subplots contained positive $UVEG_C$ stocks (i.e. zero CC_{UVEG} was never assessed). In total, 313 and 714 unique species growing <4.88 m were observed in the red pine and aspen/birch forest types, respectively. In terms of overall $UVEG_C$ stocks, subcanopy trees and to a lesser extent shrubs contributed the most to $UVEG_C$ stocks for plants occurring in the 1.83–4.88 m height layer (mean ranged from 0.07 to 0.40 Mg ha^{-1} provided the

Table 2 Summary of modelled predictions of UVEG C (Mg ha^{-1}) using per cent cover estimates from forest inventory and analysis subplots (Schulz *et al.*, 2009; USDA Forest Service, 2012, 2013a) for red pine (*n* = 55) and aspen/birch (*n* = 317) forest types in the US Lake States

Forest type	Source[1]	Mean	SE	Minimum	Maximum
Red pine	NLME	0.32	0.02	0.08	0.76
	NLRQ 0.50	0.37	0.02	0.09	0.89
	NLRQ 0.75	0.63	0.04	0.15	1.49
	NLRQ 0.90	0.86	0.05	0.19	1.93
	NLRQ 0.99	1.32	0.08	0.31	3.03
Aspen/birch	NLME	0.53	0.02	0.06	1.79
	NLRQ 0.50	0.82	0.04	0.02	4.95
	NLRQ 0.75	1.13	0.05	0.06	5.60
	NLRQ 0.90	1.59	0.06	0.10	7.55
	NLRQ 0.99	2.74	0.11	0.18	12.8

[1] Model types are NLME and NLRQ.

species occurred on the subplot). Species contributing to UVEG$_C$ were more diverse in the 0–1.83 m height layer. Considering the top six species as measured by their mean UVEG$_C$ in the 0–1.83 m layer, these were represented by forbs/herbs ($n = 4$), shrubs ($n = 1$) and graminoids ($n = 1$). The mean UVEG$_C$ in this shortest height layer ranged from 0.11 to 0.14 Mg ha^{-1}, provided the species occurred on the subplot (Table 3). The Pearson correlation coefficients (r) between UVEG$_C$ computed from the 90th percentile NLRQ estimate and overstorey tree canopy cover at the subplot level was significant ($P < 0.001$) when using a model-based estimate of CC$_{OVER}$ derived from the overstorey tree crown width equations ($r = -0.26$) but not for field observations of total canopy cover assessed from an aerial view ($r = -0.06$; $P = 0.219$). The r values between UVEG$_C$ computed from the NLME estimate and overstorey tree canopy cover at the subplot level were not significant both for the model-based estimate of CC$_{OVER}$ derived from the overstorey tree crown width equations ($r = -0.06$; $P = 0.083$) and for field observations of total canopy cover assessed from an aerial view ($r = -0.80$; $P = 0.131$). The per cent cover of mosses in both forest types averaged less than 1 per cent across the FIA subplots, likely representing a lower total amount of C in these ecosystems when compared with other growth forms (e.g. forbs and shrubs).

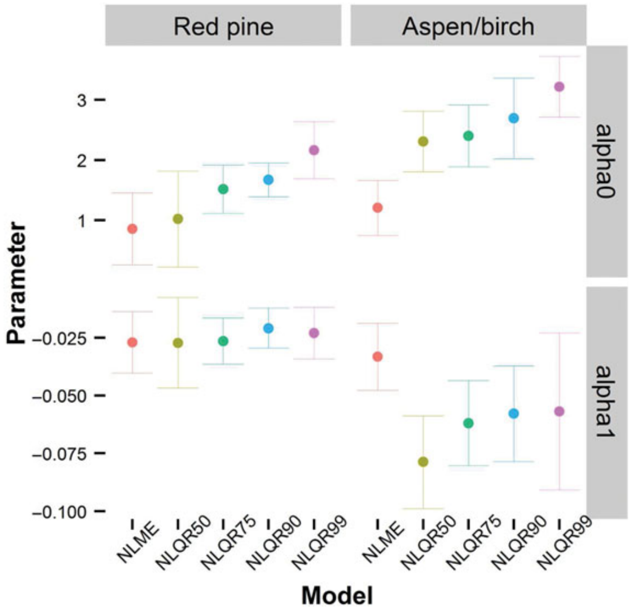

Figure 5 Intercept (α_0) and slope parameters (α_1; error bars indicate 95per cent confidence intervals) for NLQR and NLME models estimating C found in UVEG for two common forest types located in the US Lake States.

A framework for quantifying C in UVEG

The combination of scaling UVEG$_{C\text{-}MAX}$ using field observations of CC$_{UVEG}$ and employing the volumetric approach produced similar distributions whether analysing UVEG cover assessed at the subplot (i.e. SUBP) or species within subplot (i.e. SUBP-SPP) levels (Supplementary data, Appendix 2). The mean estimated UVEG$_C$ (SUBP method) was 0.86 ± 0.05 and 1.59 ± 0.06 Mg ha^{-1} for the red pine and aspen/birch forest types, respectively. The mean difference between the two methods (SUBP minus SUBP-SPP) for assessing CC$_{UVEG}$ was −0.06 and −0.90 Mg ha^{-1} for the red pine and aspen/birch forest types, respectively. The Pearson correlation coefficient of 0.73 ($P < 0.0001$) indicated a significant positive correlation and was close to one when comparing methods that used field observations of CC$_{UVEG}$ through either approach.

Table 3 The top three species that contribute the most to UVEG C (as measured by mean subplot C) when they occur by height layer for two common forest types in the US Lake States

Forest type	Height layer (m)	Species				Mean subplot C ± SE (Mg C ha^{-1})[1]	Subplots observed (%)
		Scientific	Common	USDA PLANTS ID	Growth form		
Red pine	0–1.83	*Linaria vulgaris*	Yellow toadflax	LIVU2	Forb/herb	0.12 ± 0.12	11
		Oryzopsis asperifolia	Roughleaf ricegrass	ORAS	Graminoid	0.11 ± 0.06	16
		Pteridium aquilinum	Western brackenfern	PTAQ	Forb/herb	0.11 ± 0.02	47
	1.83–4.88	*Pinus banksiana*	Jack pine	PIBA2	Tree	0.26 ± 0.06	18
		Pinus resinosa	Red pine	PIRE	Tree	0.21 ± 0.04	89
		Quercus velutina	Black oak	QUVE	Tree	0.07 ± 0.04	27
Aspen/birch	0–1.83	*Pteridium aquilinum*	Western brackenfern	PTAQ	Forb/herb	0.13 ± 0.02	52
		Alnus incana ssp. *rugosa*	Speckled alder	ALINR	Shrub	0.14 ± 0.04	15
		Eurybia macrophylla	Bigleaf aster	EUMA27	Forb/herb	0.12 ± 0.01	59
	1.83–4.88	*Populus tremuloides*	Quaking aspen	POTR5	Tree	0.40 ± 0.05	76
		Populus grandidentata	Bigtooth aspen	POGR4	Tree	0.28 ± 0.11	18
		Alnus incana ssp. *rugosa*	Speckled alder	ALINR	Shrub	0.34 ± 0.12	15

[1] Means are presented conditioned that a species was observed on a minimum of 10% of all subplots within a forest type. Values presented are calculated using the NLQR model estimated at the 0.90 quantile.

Discussion

Using field observations of UVEG cover found in various height layers sampled at varying spatial intensities across the US Lake States coupled with a limited number of destructively sampled sites, a framework was developed to estimate UVEG C stocks in forest subcanopies. Although the vegetation data employed here were collected with the original purpose of forest structure/diversity assessments, these data served as a useful tool in developing an approach for determining UVEG C stocks. Through evaluation of our study's results, future development could focus on applying the proposed framework at broader scales than considered in this study (i.e. the National Greenhouse Gas Inventory). Given that detailed examinations of UVEG have occurred in most regions (Zavitkovski, 1976; Alaback, 1982; Phillips and Shure, 1990; Tremblay and Larocque, 2001; Bisbing *et al*., 2010) and ocular estimates of understorey plant communities are common components of forest inventories, this framework can be applied to increase our understanding of UVEG C stocks in other temperate and boreal forest ecosystems. For example, if UVEG measurements by height class are collected, $UVEG_C$ could be estimated by scaling from a maximum $UVEG_C$, as in equations (1) and (2).

The observation that subcanopy tree and shrub species contributed the most to $UVEG_C$ did not come as a surprise. These trees and shrubs were abundant within the 1.83- to 4.88-m height layer. Although the contribution of other plant growth forms to $UVEG_C$ was much less, the approach presented here detected the presence of a diversity of plant growth forms found in lower height layers (i.e. the 0–1.83 m height layer). In addition to trees and shrubs, species that contributed the most to $UVEG_C$ in this height layer (including forbs/herbs and graminoids) contributed less to the mean $UVEG_C$ (<0.14 Mg C ha^{-1}). This finding agrees with that of Porté *et al.* (2009) who found that woody species generally displayed greater UVEG biomass stocks than herbaceous species, albeit stand differences were present. These findings suggest that the proposed framework can provide an assessment of UVEG C stocks for various growth forms occurring under a variety of forest conditions that are often not individually measured during forest inventories.

Given that most studies seek to quantify $UVEG_C$ at a specific spatial scale of interest (e.g. McKenzie *et al*., 2000; Suchar and Crookston, 2010), this study is unique by combining the detailed clipped and weighed data with a strategic forest inventory. A direct determination of $UVEG_C$ was not feasible considering the available data in the extensive FIA dataset; hence, we obtained $UVEG_C$ by first estimating a $UVEG_{C\text{-}MAX}$ at a given site and modifying these estimates using field observations of canopy cover in various height layers. In doing this, detailed data collected at the experimental level aided in determining $UVEG_C$ throughout the region of interest. Drawing on the relationships between maximum biomass and UVEG characteristics (McKenzie *et al*., 2000; Suchar and Crookston, 2010), estimating this value is essential under this framework as future $UVEG_C$ stocks will be dependent on it. If the current framework were to be implemented, a similar approach employing clipped and weighed UVEG data could be used to determine $UVEG_C$ stocks. Immediate gains could be attained using this framework by assessing alternative implementations of this maximum value. For example, if a user seeks to quantify UVEG C stocks in a specific forest type, this maximum value could be quantified using information from typical forest conditions (i.e. model-based approach) or from direct field measurements assuming 100 per cent cover of a subplot or key species found within a subplot (i.e. field-based approach). Regardless of the method used in determining $UVEG_{C\text{-}MAX}$, using per cent cover and height has long been applied to estimate UVEG volume and/or biomass loadings (Crafts, 1938; Olsen and Martin, 1981). Predictions of $UVEG_C$ presented here using NLRQ 0.90 (Table 2) appear to be within the bounds of what has been observed in these forest types across the region. The mean values for red pine forests (0.86 Mg ha^{-1}) generally agree with the range of 0.2–1.3 Mg ha^{-1} of $UVEG_C$ presented in Bradford *et al.* (2012) for sub-boreal *Pinus* forests with a range of stand disturbances. Similarly for the aspen/birch forest types, our ranges obtained from employing the 90th percentile maximum and then scaling using per cent cover estimates (0.10–7.55 Mg ha^{-1}) were similar to $UVEG_C$ sampled in aspen (3.39 Mg ha^{-1}) and birch (2.02 Mg ha^{-1}) stands by Zavitkovski (1976) in northern Wisconsin. Similarly, our mean prediction for aspen/birch forests (1.59 Mg ha^{-1}) was consistent with the 1.04–1.50 Mg ha^{-1} range reported by Klockow *et al.* (2013) in aspen stands in northern Minnesota. The results of these comparisons provide confidence for refining and applying the methodologies herein to approximate $UVEG_C$ in a variety of forest types.

The similarities in $UVEG_C$ estimates made at either the subplot levels or species within subplot levels (e.g. SUBP *vs* SUBP-SPP) was unexpected given the varying degrees of fieldwork needed to make such assessments. This could likely arise because a minimal amount of species overlap may be present when species-level assessments are conducted within a specific height layer. Hence, considerable agreement would ultimately result when comparing subplot-level assessments to those conducted at the species level when cover estimates are summed to represent the subplot. In terms of monitoring UVEG for the sole objective of determining its contributions to forest C, this ultimately means that the time and costs associated with identifying individual species may be reduced by assessing UVEG cover at scales greater than the individual (e.g. subplot). However, sustained monitoring of UVEG at the species level will continue to be needed to understand the role of UVEG in ecosystem processes (e.g. energy flow and nutrient cycling) and as an indicator of forest health (e.g. monitoring the presence and abundance of non-native species; Schulz and Gray, 2013). Future sampling protocols across the US will employ a design that quantifies UVEG cover by specific growth habit forms (USDA Forest Service, 2013b), providing a bridge between detailed species-level estimates and coarser assessments made at each subplot. Hence, UVEG data will likely continue to be available in the near future to assess C stocks found in forest understories across the US potentially using frameworks such as the one examined in this study.

Stand structural variables will be particularly useful in regions that display both younger, developing forests that are approaching the stem exclusion stage of stand development and stands at older developmental stages with complex, stratified canopy conditions (sensu Oliver and Larson, 1996). Suchar and Crookston (2010) tested the hypothesis that CC_{OVER} would serve as a surrogate for representing these overstorey–understorey interactions, but their data neither refuted nor supported that hypothesis. The minimal contribution of class variables such as stand disturbance type and presence/absence of treatment could support the idea of high resiliency of the forest understorey to these agents (Suchar and Crookston, 2010). The property of zero inflation has been cited as a potential problem when modelling UVEG data (Eskelson *et al.*, 2011), but zero inflation was not a characteristic of the data analysed here. If managers are interested in quantifying the presence and abundance of a select number of species (e.g. invasive or keystone species), it may be worthwhile to consider zero-inflated modelling strategies when characterizing UVEG attributes. Although nonvascular species (i.e. mosses) comprised a very small amount in these forest types, their contribution to UVEG$_C$ may be more prevalent in other ecosystems such as boreal forests.

The development of a UVEG modelling framework for the Lake States highlighted several knowledge gaps with regard to forest C in subcanopy layers. One research unknown is determining how well scaling from maximum estimates represents the biomass for species displaying uniquely different growth habit forms (e.g. shrubs *vs* forbs *vs* graminoids), or the properties of species within a growth habit (e.g. wood density of shrub species). From a modelling perspective, trade-offs may exist between mixed-effects models through their ability to account for hierarchical error structures (a common property of UVEG data) and quantile regression approaches that contain the ability to estimate a maximum amount of UVEG for a given set of stand conditions. Future work could seek to employ adjustment factors by growth habit group when scaling across these species and/or incorporate information of plant functional traits into estimates of UVEG C. Sources such as the TRY plants database (www.try-db.org) will likely aid in such a scaling effort. A second knowledge gap is determining how best to estimate the maximum UVEG biomass at a given site, which could be accomplished through using either a model-based or field-based approach or some combination thereof (Wilson *et al.*, 2013). A third area of potential research is determining how novel data sources can be used in determining plant biomass. For example, recent advances have been made in estimating UVEG characteristics using remote sensing technologies (Martinuzzi *et al.*, 2009; Wing *et al.*, 2012). As LiDAR-derived estimates of per cent cover and height become commonplace in vegetation surveys, the framework developed here could seemingly be adapted to determine UVEG C using remotely sensed data (e.g. Sherrill *et al.*, 2008).

Conclusions

Robust estimates of UVEG C across the diverse forest ecosystems may only be possible through systematic destructive sampling of UVEG across a multitude of forest types and stand conditions. Barring substantial funding for such a time-consuming effort, novel frameworks for leveraging currently available datasets to estimate UVEG C should be explored as an intermediate and efficient next step. Through a combination of common stand attributes (e.g. climate and forest structure) and UVEG biodiversity metrics (e.g. cover by plant form) consistently sampled across the US Lake States, estimates of UVEG C stocks were determined that reasonably align with what is expected in red pine and aspen/birch forests. An important difference is that our study's framework allows incorporation of data from strategic field-based inventories with UVEG C (e.g. species presence and abundance). Within the context of monitoring UVEG C stocks for global change, the incorporation of annual field-based data is optimal. Continued validation of this approach could involve comparing our framework with alternative approaches for determining UVEG biomass, such as ones that clip and weigh plant material. Unfortunately, efforts in conducting such comparisons (especially at a national scale) would be associated with high costs and a tremendous emphasis in field experiments. In the interim, cover assessments made within a few height layers provide a potential source of data upon which to design UVEG C predictive models. Future research that focuses on methods used to scale biomass estimates across species groups in addition to improving estimates to accurately determine maximum UVEG biomass at specific sites are further options that can advance the proposed framework. Collectively, these steps should improve our knowledge of C dynamics in this difficult-to-quantify component of forest ecosystems.

Supplementary data

Supplementary data are available at *Forestry* online.

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Conflict of interest statement

None declared.

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