

Burial of downed deadwood is strongly affected by log attributes, forest ground vegetation, edaphic conditions, and climate zones¹

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Abstract: Deadwood can represent a substantial portion of forest ecosystem carbon stocks and is often reported following good practice guidance associated with national greenhouse gas inventories. In high-latitude forest ecosystems, a substantial proportion of downed deadwood is overgrown by ground vegetation and buried in the humus layer. Such burial obfuscates the important process of deadwood carbon transfer to other pools (e.g., litter and soil) and emission to the atmosphere (i.e., rates of decay). Using data from the Swedish National Forest Inventory, we found that the proportion of downed logs that is buried increased from temperate to boreal forests. Several factors affect the probability of burial, including log attributes (e.g., decay class), ground vegetation (e.g., moss dominance, type of moss cover), and edaphic conditions (e.g., soil type, depth of organic layer). Combined assessments suggest that about 24% of the carbon in the aboveground downed deadwood pool was found to be buried in boreal forests. Deadwood burial has important implications for forest carbon dynamics and associated monitoring (e.g., United Nations Framework Convention on Climate Change reporting) as such a pool typically decomposes much slower compared with aboveground deadwood.

Key words: buried wood, coarse woody debris, greenhouse gas accounting, wood decomposition, soil carbon.

Résumé : Le bois mort peut constituer une portion importante des stocks de carbone de l'écosystème forestier et on le rapporte souvent en suivant le guide de bonne pratique associé aux inventaires nationaux des gaz à effet de serre. Dans les écosystèmes forestiers situés à des latitudes élevées, une portion importante du bois mort au sol est envahie par la végétation et enterrée dans la couche d'humus. Cet enterrement occulte l'important processus de transfert du carbone du bois mort vers d'autres réservoirs (p. ex. la litière et le sol) et l'émission dans l'atmosphère (c.-à-d. le taux de décomposition). En utilisant des données de l'inventaire forestier national suédois, nous avons trouvé que la proportion de billes au sol enterrées augmente en passant des forêts tempérées aux forêts boréales. Plusieurs facteurs influencent la probabilité que les billes soient enterrées, incluant les caractéristiques des billes (p. ex. la classe de décomposition), la végétation au sol (p. ex. la dominance des mousses, le type de couverture muscinale) et les conditions édaphiques (p. ex. le type de sol, la profondeur de la couche organique). Des évaluations combinées indiquent qu'environ 24 % du carbone dans le réservoir de bois mort aérien tombé au sol est enterré dans les forêts boréales. L'enterrement du bois mort a d'importantes répercussions sur la dynamique du carbone forestier et son suivi (p. ex. la Convention cadre des Nations Unies concernant les rapports sur le changement climatique) étant donné qu'un tel réservoir se décompose typiquement beaucoup plus lentement comparativement au bois mort aérien. [Traduit par la Rédaction]

Mots-clés : bois enterré, débris ligneux grossiers, comptabilité des gaz à effet de serre, décomposition du bois, carbone du sol.

Introduction

Buried wood is defined as downed deadwood that is more than 50% covered by soil, litter, or ground vegetation (Moroni et al. 2015). Until recently, it has been assumed that all downed wood is completely decomposed above the ground with associated rates of wood decomposition and carbon (C) dynamics being modelled using wood decay functions parameterized with decay rate constants (Laiho and Prescott 2004; Rock et al. 2008). Recently, it has become evident that burial of downed deadwood is widespread in boreal forests (Moroni et al. 2015) where the amount of buried wood can equal or even exceed the amount of aboveground deadwood (Harvey et al. 1981; Hagemann et al. 2009, 2010).

Deadwood can represent a substantial portion of the total C stock in forest ecosystems. It has been found that downed dead-

wood can account for approximately 20% of total ecosystem C in old-growth (Harmon et al. 1990) and secondary (Bradford et al. 2009; Woodall et al. 2013) forests. Despite this, numerous aspects of deadwood dynamics remain as substantial knowledge gaps (Russell et al. 2015) of which the phenomena of buried deadwood looms large. There is no evidence to suggest that buried deadwood is included in forest C stock estimates despite the inherent effect that it has on detrital decomposition rates and C temporal dynamics. It has been documented that the climatic conditions affect the rate of wood decomposition (Russell et al. 2014), but the process of burial would certainly alter this rate for any given piece of deadwood. In cool and moist environments, burial can slow down decomposition (Jomura et al. 2007; Hagemann et al. 2010), effectively preserving the wood (see also Eckstein et al. (2009) and

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Edvardsson et al. (2012) documenting wood preservation for millennia in peat deposits). Furthermore, deadwood is an obligatory C pool for reporting in international greenhouse gas accounting following the Intergovernmental Panel on Climate Change (IPCC) recommendations (IPCC 2006).

Although wood burial has been documented as a widespread phenomenon, it is not ubiquitous across global forest ecosystems. In their review, Moroni et al. (2015) documented that the amount of buried wood differs substantially across forest ecosystems and hypothesized several factors that may influence wood burial, including wood properties (e.g., decay class, log dimension, tree species), stand attributes (e.g., ground vegetation — especially moss cover, tree species composition, well-drained versus paludified ground), and disturbance factors (e.g., forest fires, forest management). As their review summarized data across rather heterogeneous data sources, they were unable to rank the importance of these factors, although they strongly emphasized the importance of paludified (i.e., waterlogged or swamp) forests as a hotspot for large quantities of buried wood.

In this study, using data from the Swedish National Forest Inventory (Swedish NFI), which documents nearly all of the potential factors hypothesized as important for wood burial, we present the first comprehensive dataset to document the frequency of buried wood across a wide range of forest conditions in temperate and boreal forests. Using this information, we assess their relative importance and quantify the amount of C in buried and above-ground wood, which refines our understanding of the proportion of C transferred to other forest C pools (e.g., soil) across varying forest types and climate zones.

Material and methods

Sampling protocol

Sweden has 28.1 million hectares of productive forest (average growth $> 1 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$) spanning the following climate zones roughly from south to north: temperate (2% of the area, also labeled nemoral zone), hemiboreal (24%), south boreal (12%), mid boreal (43%, including 2% in north-south boreal), and north boreal (19%, including 5% in the alpine zone). The Swedish NFI is a stratified systematic cluster-sampling inventory of concentric sample plots (Fridman et al. 2014). The sample plots are clustered into permanent and temporary tracts. Permanent tracts are re-measured every 5th year and temporary tracts are measured only once. A complete inventory of deadwood with stems diameters (i.e., diameter at breast height, DBH) of at least 100 mm was introduced in 1994 (Fridman and Walheim 2000). The deadwood inventory plots had a radius of 10 m. Downed logs were recorded if (i) the point of inclusion (thickest end of the log) was inside the plot and (ii) minimum 1.3 m of the log length had a diameter $> 100 \text{ mm}$ (corresponding to a minimum DBH of 100 mm for standing dead trees). Logs covered by vegetation were recorded when the trunk outline was clearly visible below the ground vegetation, but no vegetation was removed to seek additional logs. The whole log was considered when recording vegetation cover, even if the log was partially outside the plot. Log volume was calculated from the log length and mid diameter inside the plot. The deadwood data used in this study are from permanent plots surveyed during 2004–2008.

For each sample plot, several tree, stand, and site variables are recorded. The variables from the Swedish NFI used in this study are listed in Table 1.

Data preparation

The field data from the Swedish NFI database comprised a combination of continuous, semiquantitative, and categorical variables. Some of the variables were recoded prior to the statistical analysis (Table 1).

Table 1. Wood attributes and environmental factors recorded for downed dead wood in the Swedish National Forest Inventory.

Variable	Value range, field data	Value range, analyzed data
Wood attribute		
Vegetation cover (%), buried	0–100	0 or 1 (0–49% or 50–100% vegetation cover)
Trunk diameter (mm)	100–920 ^a	100–350 ^b
Decay class	5 classes	5 classes ^c
Tree species	23 classes	4 classes ^d
Stand attributes		
Stand age (years)	0–350	0–200 ^b
Surface vegetation (cryptogams)	5 classes	5 classes ^e
Vascular plant vegetation	12 classes	12 classes ^f
Edaphic conditions		
Soil type	5 classes	3 classes ^g
Peat depth (cm)	30–510	3 classes ^h
Climate zone		
Vegetation zone	7 classes	4 classes ⁱ

^aMaximum diameter of focal species: *Picea*, 670 mm; *Pinus*, 669 mm; *Betula*, 820 mm.

^bTruncated range to avoid misleading effects in partial dependence plots.

^cDecay classes: D0, D1, D2, D3, D4; see main text for explanation.

^dTree species: pine, spruce, birch, other tree species.

^eSurface vegetation (cryptogams): lichen dominance, lichens frequent, fresh mosses, minerotrophic peat mosses, ombrotrophic peat mosses.

^fVascular plant vegetation: bilberry, calluna, fern dominance, broad grass, thin grass, lingonberry, low herbs, low sedges, no vegetation, poor dwarf bush, tall herbs, tall sedges.

^gSoil types: moraine soil, peat soil, rock ground.

^hPeat depth class: 0–29 cm, 30–100 cm, 101–510 cm.

ⁱVegetation zones: temperate and hemiboreal, south boreal, mid boreal, north boreal.

The principal response variable in this study, “buried”, was derived from primary data on log length cover by vegetation. The primary data were recoded from a continuous scale of 0%–100% to 0 (less than 50% cover) or 1 (minimum 50% cover) to conform to a definition of buried wood proposed by Moroni et al. (2015).

A system with five decay classes (D0–D4) is based on the proportion of the length of the deadwood objects consisting of decomposed soft wood (within parentheses): recently dead (D0; no decomposed wood), little decayed wood (D1; 1%–9%), little to medium decayed wood (D2; 10%–25%), medium decayed wood (D3; 26%–75%), very decayed wood (D4; 76%–100%). In the field, a section is considered to have “soft wood” if a sharp instrument, e.g., a knife or similar object, easily penetrates the surface when pushed into the wood. The D4, the final stage, is further characterized by the wood being soft through the whole cross section, i.e., a sharp instrument can be pushed through the log.

For most variables we kept the field data unchanged. We pooled similar categories for variables with few observations in certain categories to improve the balance of observations across the categories (e.g., for peat cover, the two intermediate classes were pooled: 15 100 logs on plots with 0% peat cover, 543 logs on plots with less than 50% peat cover, 427 logs on plots with more than 50% peat cover, and 1175 logs on plots with 100% peat cover). For the variable “tree species”, we recoded the field data by keeping only the tree species *Pinus sylvestris* ($n = 5577$ logs), *Picea abies* ($n = 5783$ logs), and *Betula* spp. ($n = 3806$ logs) and pooled the remaining 20 tree species categories ($n = 2079$ logs). Before this recoding, we assessed the effect of full tree species resolution in logistic regression analysis and found that the effect of individual tree species was either nonsignificant (18 tree species categories) or weakly significant (p values ≈ 0.05 level; 4 tree species categories). We also assessed the effect of reduced tree species resolution in cross-validation tests and found that the predictive ability of the model

with 4 tree species categories was almost identical to that of the model with 23 tree species categories.

Prior to analysis using boosted regression trees (BRT; R package *gbm*, <https://cran.r-project.org/web/packages/gbm/index.html>) (see below), we adjusted high values for trunk diameter (all diameters > 350 mm were set to 350 mm) and stand age (all stand ages > 200 years were set to 200) to avoid misleading partial dependence plots due to weak empirical support from few observations.

Data analysis

We analyzed the data using two methods. First, we used BRT to assess the quantitative effects of different log properties, stand attributes, and climate zones on the burial probability. This is an exploratory machine-learning method that builds up a predictive model based on regression trees (Elith et al. 2008). This method has gained popularity because it scores among the best in predictive performance tests, easily handles a mixture of categorical and quantitative predictors, and assumes no specific functional response of the phenomenon to be modelled. The partial dependence plots from BRT models display the effect of each predictor on the response (i.e., probability of wood burial). The measurement unit in the partial dependence plots is the marginal effect of the predictor on $\text{logit}(p)$ of the response, after accounting for the average effects of all other predictors in the model. Thus, effect values close to 0 have negligible marginal effect on the response (a burial probability of 0.5). An effect value of -1.5 roughly corresponds to a probability of 0.2, while 1.5 roughly corresponds to a probability of 0.8. Similarly, effect values of -0.5 and 0.5 roughly correspond to probabilities of 0.4 and 0.6, respectively.

We also used logistic regression to assess the effect of the same log properties, stand attributes, and climate zones that were analyzed using the BRT method. We found very strong agreement between the two methods as the coefficients from the logistic regression varied in the same manner as the response levels from the BRT analysis. Because the two methods produced similar results, we chose to present only results from the BRT analysis as they are more illustrative than those from the logistic regression.

We calculated the C content of wood in different decay classes based on Sandström et al. (2007) that provide C content for decay stages being used in this study. We adopted their values and assigned C content to decay classes D0 to D4 using tree species specific values for pine, spruce, and birch. Next, we quantified the amount of C in all buried and all exposed logs (i.e., not buried) separately and calculated the proportion of C that was buried as a percentage of the C in all exposed plus buried logs.

Results

Using a definition of buried wood being 50% or more covered by ground vegetation, our analysis of 17 245 logs across Sweden using BRT revealed significant drivers of deadwood burial with serious implications for C monitoring and associated C dynamics.

Log attributes

A log's decay class was the factor that most strongly affected the probability of burial. This is indicated by the widest effect range of this factor (Fig. 1, upper left panel) as compared with the effect range of the factors in the other partial dependence plots (Fig. 1). These effect levels correspond to a probability range between 0.2 and 0.8 due to this factor alone (for interpretation of the effect values, see Materials and methods).

There was no difference in burial probability between pine and spruce logs. The birch logs had slightly lower burial probability compared with the conifer logs (Fig. 1, upper central panel). The tree category "other" had a significantly higher burial probability, but this was likely an artifact due to the censoring effects of unidentified trees biasing results towards moderate to very decayed logs. In two alternative analyses (not included) with moderate or

full tree species resolution, there was no consistent and significant effect of identified tree species, except for aspen, which had slightly reduced burial probability.

We found a surprising increase of burial probability from the smallest to the largest logs. This factor was of minor importance, however, as the partial dependence effect was slightly below zero for log diameters below 15 cm and slightly above zero for log diameters above 30 cm (Fig. 1, upper right panel).

Stand attributes

The surface vegetation (i.e., cryptogams comprising lichens and mosses) was the most important stand attribute affecting wood burial. The burial probability increased from lichen-dominated ground, to fresh feathermoss type (e.g., *Hylocomium splendens*, *Pleurozium schreberi*, *Ptilium crista-castrensis*) dominance, and further to minerotrophic and ombrotrophic peat mosses (Fig. 1, mid row, left panel).

The field layer vegetation (i.e., the vascular plants) had almost no effect on wood burial probability. Most vegetation types had effects close to zero, indicating neutral effect on wood burial (Fig. 1, mid row, central panel). Only two vegetation types ("no vegetation" and "poor dwarf bush") exhibited slightly reduced burial probability and two vegetation types (tall herbs, tall sedges) had slightly increased burial probability.

The edaphic conditions also influenced the burial probability. We found a large difference between logs resting on moraine or peat soil compared with those on rocky ground with strongly reduced burial probability (Fig. 1, mid row, right panel). In addition, we found that peat depth > 1 m increased burial probability compared with shallower peat depths (Fig. 1, bottom row, central panel).

Stand age had a minimal effect on wood burial. There was a slightly reduced burial probability during the first 0–20 years after stand replacement (typically clear-felling), while the burial probability was more or less constant at a neutral level in young, typically managed forests, as well as old unmanaged forests (Fig. 1, bottom row, left panel).

Climate zones

We coarsely examined the effect of climate on downed deadwood burial through assuming broad vegetation zones representing general climate zones. We observed a weak effect of vegetation zone on wood burial with slightly increasing probability from the temperate and hemiboreal zones, through the south boreal zone, to the mid and north boreal zones (Fig. 1, bottom row, right panel).

Soil carbon input from deadwood

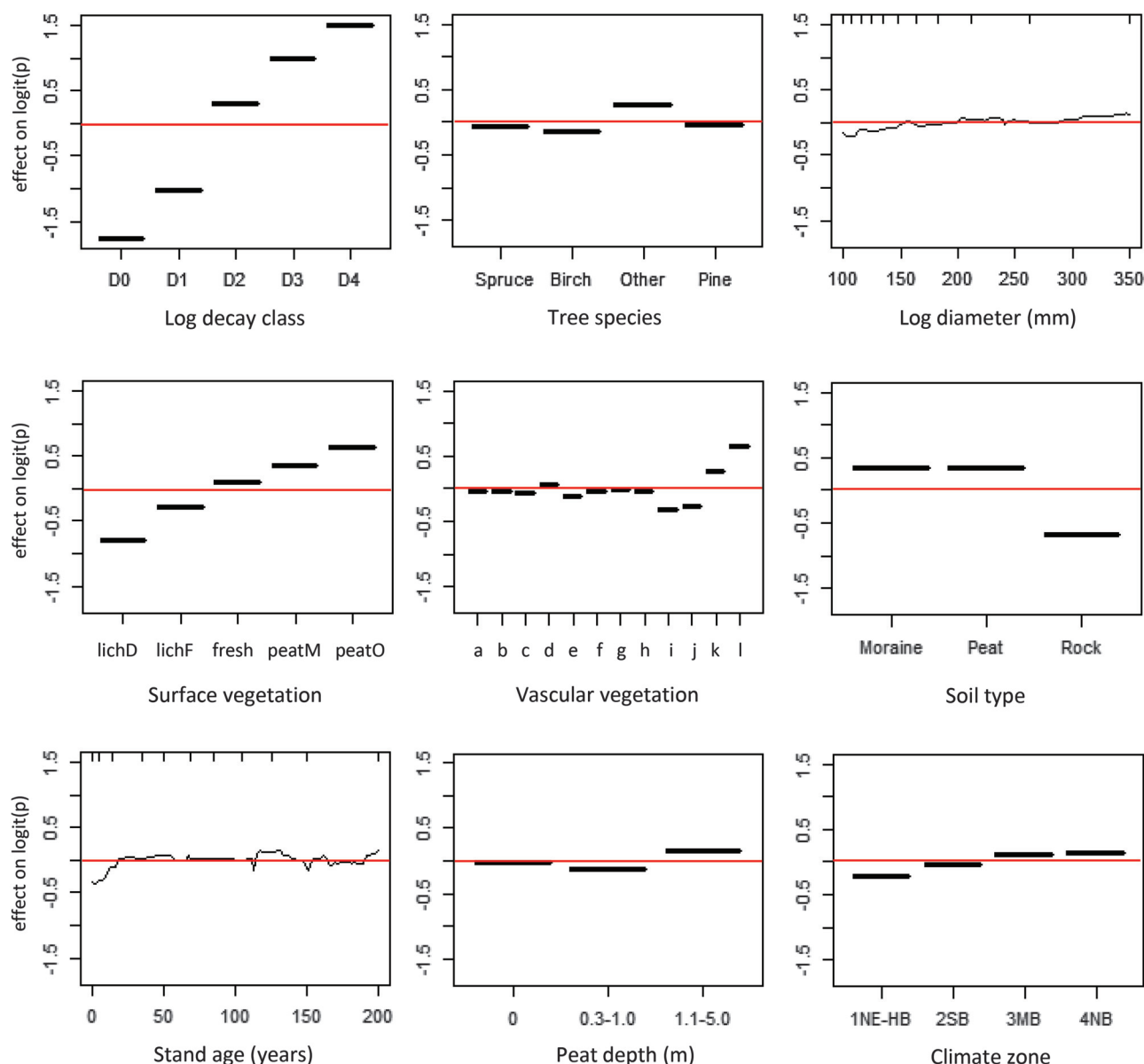
A significant portion of aboveground deadwood is buried, thereby contributing to the forest soil C pool over long time scales. Using the C content of logs in different stages of decay, we quantified the remaining C in the buried logs to determine the amount of C from the logs that entered the soil.

For all logs combined, the remaining proportion of C that entered the soil was 20.7%. When we restricted the sample to the logs in the boreal zone ($n = 11\,388$ logs), this proportion increased to 24.7%, whereas it was 14.6% for the logs in the temperate and hemiboreal zones ($n = 5857$ logs).

When we grouped the logs in different soil classes, it turned out that only 4% of the C became buried in forest on rocky ground, while the proportion increased to 20% on moraine soil, and 27% on peat soil (Fig. 2). The corresponding proportions in boreal forests were 1%, 24%, and 31% for rocky ground, moraine soil, and peat soil, respectively (Fig. 2).

Also, the ground vegetation significantly affected the burial of downed logs. When we grouped the logs according to the surface vegetation, it turned out that 11% and 20% of the C were buried in lichen-dominated and lichen-rich vegetation, respectively. In fresh "feathermoss type" vegetation, the proportion of buried C

Fig. 1. Partial dependence plots from BRT models of downed wood burial probability. Each panel displays the marginal effect of the predictor (on $\logit(p)$ of the probability of burial) after accounting for the average effect of all other predictors. See Materials and methods for interpretation of the effect response scale. The mid line in each panel represents no effect of the predictor. Surface vegetation: lichD, lichen dominance; lichF, lichens frequent; fresh, fresh mosses; peatM, minerotrophic peat; peatO, ombrotrophic peat. Vascular vegetation: a, bilberry; b, calluna; c, fern dominance; d, broad grass; e, thin grass; f, lingonberry; g, low herbs; h, low sedges; i, no vegetation; j, poor dwarf bush; k, tall herbs; l, tall sedges.



was 20%, while the proportions increased to 23% and 32% in minerotrophic brown moss vegetation and ombrotrophic *Sphagnum* moss vegetation, respectively (Fig. 3). All of these proportions of buried C were somewhat higher in the boreal zone. For the lichen-rich and feathermoss types in particular, there was a pronounced difference in C burial between the temperate and boreal zones (Fig. 3). For the *Sphagnum* moss vegetation, we found an additional effect of peat depth, as the proportion of buried C was 31% from logs on peat deposits 0.3–1.0 m deep, while the corresponding proportion was 36% buried C from logs on peat deposits more than 1.0 m deep (Fig. 3). In this swamp forest vegetation, the differences between temperate and boreal zones were much smaller (Fig. 3).

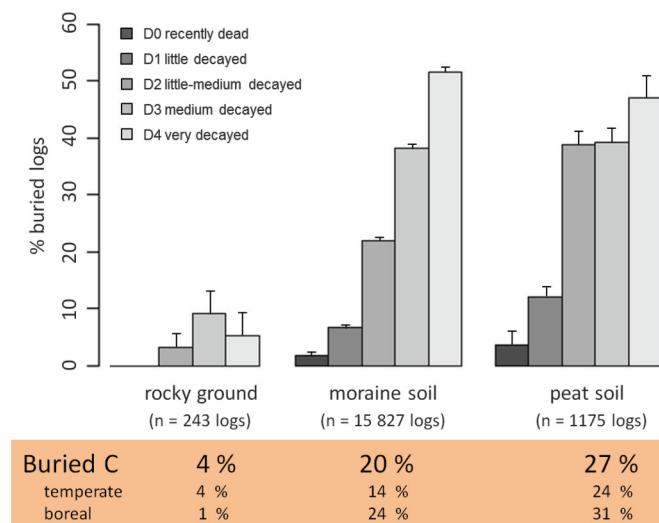
A closer inspection of Figs. 2 and 3 suggests that the burial probability of decay class D1 and especially decay class D2 is a key

factor in determining the proportion of C that is buried in different forest types. In lichen-dominated vegetation, no logs in decay class D1 and only 9% of the logs in decay class D2 were buried. In contrast, for logs in *Sphagnum* moss vegetation on deep peat deposits, about 20% of the D1 logs and close to 50% of the D2 logs were buried. Thus, in lichen-dominated vegetation, nearly all wood was decomposed above the ground, while a substantial proportion of medium-decayed logs became buried in peat soils with *Sphagnum* vegetation. In other forest types, the situation is intermediate between these two situations.

Discussion

Wood burial has recently been documented as a common and widespread phenomenon, especially in boreal forests (Moroni

Fig. 2. Percentage of buried logs in each decay class across different soil types. Uncertainty bars represent 95% confidence intervals of the estimated percentages. Buried carbon is calculated as the amount of carbon in buried logs as the proportion of the carbon in aboveground plus buried logs. For each soil type, buried carbon is calculated for all logs combined and separated into subsets of logs in the temperate and boreal zones.



et al. 2015). In this study, we present the first analysis quantifying the probability of burial across different environmental conditions based on a comprehensive national forest inventory of Swedish boreal forests. We found that 24.9% of all logs were buried (defined as a log with more than half of its length covered by ground vegetation). The C in buried logs comprised 20.7% of the C in all logs (i.e., buried and exposed logs combined). Behind these aggregated values, we found large differences in the burial probability and buried C across forest types.

Factors affecting burial

Decay class emerged as the single most important factor that affected wood burial. The decay relationship is rather obvious, as logs sink to the ground when they lose their structural integrity as a result of the decay (Fraver et al. 2013). Furthermore, the cross section collapses to an ellipsoid and finally the log is fragmented into small pieces. During this process, logs become increasingly prone to overgrowth by the ground vegetation. Thus, for all logs combined and for different subsets, we found a consistent pattern of increasing probability of wood burial with advanced degree of decay. The same pattern was reported by Moroni et al. (2015) and can be postulated as perhaps a universal relationship.

We found a weak relationship of increasing probability of burial with increasing log diameter. This relationship was quite surprising and in conflict with the results from Dynesius et al. (2010), who found that increasing trunk diameter reduced vegetation cover and the probability of wood burial. In the study by Dynesius and co-authors, all logs were experimentally felled and placed in known positions 5 years prior to the re-inventory. Thus, we consider their documented effect to represent the real relationship between log diameter and overgrowth. It is worth noting that many logs in the Dynesius study were positioned in swamp forest with *Sphagnum* moss vegetation on deep peat deposits causing rapid burial (see growth rates of *Sphagnum* mosses below).

In our study, we interpret the positive relationship between log diameter and burial probability to be, at least to some extent, an artifact due to reduced detection probability of smaller partially overgrown logs with implication regarding the monitoring of deadwood resources. Often the top section of small-diameter logs

is overgrown and becomes almost invisible during inventory activities. Small logs can easily go unnoticed, especially if the exposed part is outside the inventory plot. Large-diameter logs are often visible when overgrown as one can still see their outline beneath the ground vegetation. Thus, we assume that the real relationship is more likely to be the opposite in accordance with the findings of Dynesius et al. (2010). There is, however, a possibility of increased probability of burial of large logs due to larger logs taking longer to decay and thus having longer residence times with more chance of being covered by the surface vegetation. Unfortunately, we cannot sort out the relative importance of these opposing effects of log size from the current dataset, which suggests a need for continued research.

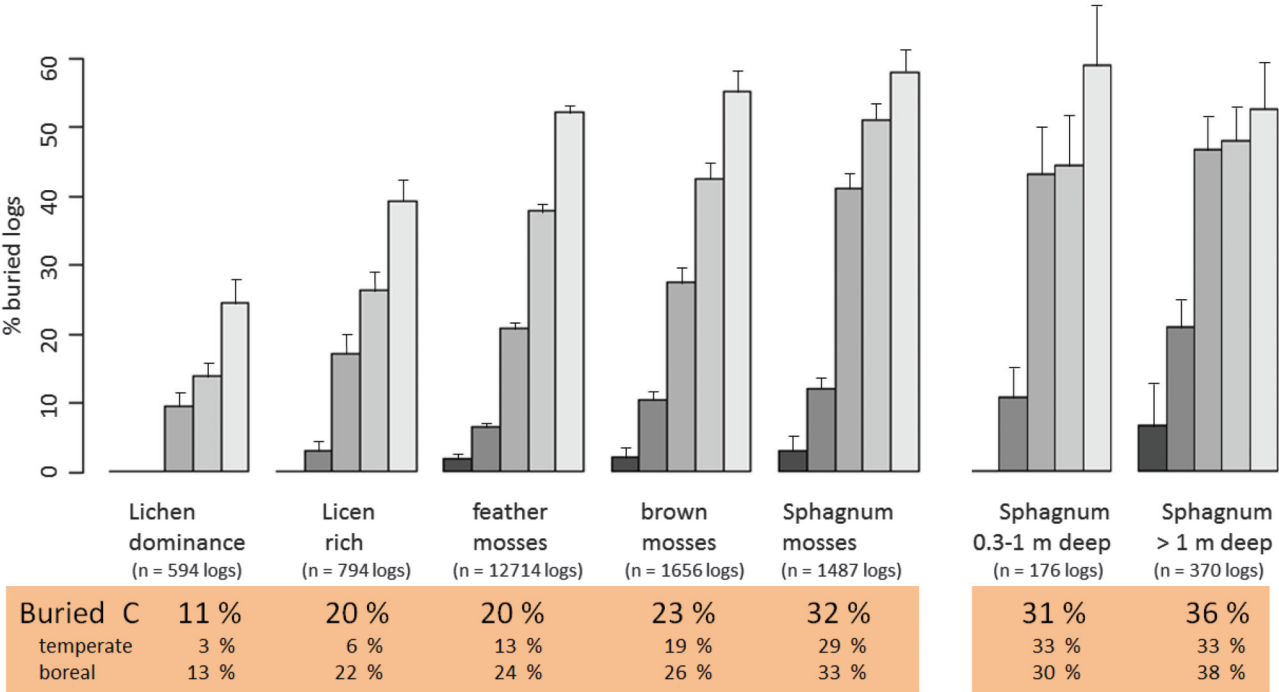
The surface vegetation of cryptogams (lichens and mosses) had a strong effect on wood burial. The lowest probability of burial occurred in lichen-dominated vegetation; it gradually increased across types with lichens frequently present (but not dominating) and feathermoss types, to vegetation with peat-forming mosses in which *Sphagnum* mosses facilitated the highest probability of burial. In the Swedish NFI, vascular vegetation was characterized separately from surface vegetation. The majority of these types had no effect on wood burial. Only one of the vascular vegetation types (tall herbs) was rather common and also exhibited an effect on wood burial. It should be noted that this particular vegetation type “buries” downed logs through the accumulation of dead plant material from the previous growing seasons. Such dead plant material decomposes completely during the summer, with the logs becoming exposed again in the late summer to early fall.

These findings clearly suggest that it is the surface layer component of lichens and mosses that drives the wood burial process rather than the vascular plants. Thus, our results strongly support the hypothesis by Moroni et al. (2015) that suggested that mosses are more important than vascular plants for wood burial. The vertical growth of *Sphagnum* mosses is typically 3–6 cm·year⁻¹ (Asada et al. 2003; Breeuwer et al. 2008). This growth rate fully accounts for the burial of some logs during a 5-year period, as observed by Dynesius et al. (2010).

Edaphic conditions also affected the burial probability, and the decisive factor is most likely the compactness of the ground. Rocky ground strongly decreased wood burial in contrast to moraine and peat soils. It should be noted that the operational criterion for separating between moraine or peat soils in the Swedish NFI is whether the peat thickness is shallower or thicker than 30 cm. Thus, in many sites, the moraine soil type is overlaid by a thin peat layer. We found an additional effect that deeper peat deposits increased the probability of burial. The underlying mechanism is most likely how soon the trunk achieves ground contact. Dynesius et al. (2010) found that the proportion of log with ground contact was the single most important factor facilitating burial. Thus, when a tree falls on rocky ground, moraine soils, or on soils with a shallow peat layer, the branches act as stilts and delay ground contact, as well as overgrowth by the vegetation. On deep peat deposits, fallen trees are rapidly absorbed by the loose ground and *Sphagnum* moss growth.

We found an increasing probability of wood burial from the south to the north (i.e., latitudinal gradient). The increase was most pronounced from the temperate–hemiboreal to south boreal zones, and only a weak increase occurred further to mid and north boreal zones (Fig. 1). We attribute this increased probability towards the north at least partly to slower wood decomposition and longer residence time in the colder boreal climate (e.g., Russell et al. 2014). There were, however, different changes in the probability of burial between edaphic conditions and bottom vegetation types (Figs. 2 and 3). In the Swedish NFI, the mosses are not identified to species, but coarsely divided into “fresh” soil mosses (corresponding to feathermosses in the boreal zone) and peat mosses (which are further separated into *Sphagnum* mosses and other peat-forming mosses). When moving southwards from the

Fig. 3. Percentage of buried logs in each decay class across different ground vegetation types for all logs ($n = 17\,245$ logs) and for the subset of logs on *Sphagnum* ground vegetation on peat soil (two rightmost panels, $n = 176$ and 370 logs). Uncertainty bars represent 95% confidence intervals of the estimated percentages. Buried carbon is calculated as the amount of carbon in buried logs as the proportion of the carbon in aboveground plus buried logs. For each ground vegetation type, buried carbon is calculated for all logs combined and separated into subsets of logs in the temperate and boreal zones.



boreal zone, the moss cover changes to other species with sparser surface cover due to stronger competition from grasses and herbs. In addition, there is also a change from thick humus layers in the boreal zone to other soil types towards the south. Therefore, although the surface vegetation class remains the same across the climate zones, the actual vegetation may be quite different.

Soil carbon input

The changing probability of burial across edaphic conditions and ground vegetation types strongly influenced the amount of C that entered the soil. The most common combination of edaphic condition and ground vegetation was moraine soil with feathermoss-type bottom vegetation (70% of all logs occurred in this situation). In such situations, we found that about 24% of the C in the wood was buried in the boreal forest. On rocky ground, the amount of buried C was only 1% in the boreal zone, whereas it was 31% on boreal peat soils. On peat soils, both moss type and peat depth affected the amount of buried C, with highest input rates in deep *Sphagnum* peat layers (38% of C buried in the boreal zone). These quantitative effects of the edaphic conditions and vegetation types upon burial have not been documented before and show that it is instrumental to relate wood burial and C dynamics of deadwood to these forest conditions.

We want to stress that the proportion of buried C that is reported in our study is a static assessment and does not represent the proportion of buried C relative to the original input of C from natural mortality of trees. The amount of C in the logs was higher when the trees died, which makes the amount of buried C smaller relative to that reference. On the other hand, the actual amount of buried wood is higher because deeply buried logs were not recorded in this study. Thus, it is the relative differences in C burial across forest conditions that are noteworthy from our study and not the quantitative values as such.

Until recently, it has been assumed that all deadwood (except roots) is decomposed above the ground. Very little information

exists about the effects of burial on wood decomposition rates. In Canada, Moroni et al. (2010) documented that the residence time of buried wood in well-drained humus layers was 2–4 times longer than wood in aboveground positions in the same forests. From peat excavation sites in Sweden and Germany, it has been documented that buried wood has been well preserved for 5000–7000 years in permanently waterlogged peat soil (Eckstein et al. 2009; Edvardsson et al. 2012). These observations suggest that wood burial slows down the decomposition significantly under conditions typically found in boreal forests (both in humus on well-drained moraine soils and in peat layers in swamp forests). The elevated probability of burial and long-term preservation of buried wood in peatland forests give strong support to the notion by Moroni et al. (2015) that paludified forests are particularly important sites for wood burial.

Monitoring and research challenges

In this study, we have focused on differences in probability of burial across forest conditions and the implications for C dynamics in the forests. Several research challenges and knowledge gaps remain to be filled before we have a complete quantification of the prevalence of wood burial and its implications for forest C dynamics at a global scale.

First, we recommend that all national forest inventories include the attribute “overgrown by vegetation” in their field forms when monitoring deadwood. It is instrumental to have a clear definition of burial separating coverage by live ground vegetation and dead vegetation and litter that seals the log from free air circulation, thereby being more influenced by the edaphic conditions than the aerial conditions. It is also instrumental to record key wood attributes (especially decay class) and stand attributes (especially edaphic conditions and ground vegetation types with special attention to dominance of lichens and different moss types). Such data from countries representing different climate zones and forest biomes will provide excellent data to demon-

strate the frequency and importance of wood burial in different forest systems.

Second, there is a need to analyze the amount of C in wood at burial relative to that of the live tree and not to only other downed wood in various stages of decay. This should, however, be part of a larger scope addressing transition rates from live trees to standing dead trees to downed logs in different decay classes and finally to buried wood, the transition time or transition probability per time unit, the effects of different environmental factors as demonstrated in our study, and finally, the associated C loss through decomposition between these transitions.

Third, it is important to document the effects of different edaphic conditions on the decomposition of buried wood. Soil moisture is most likely a key factor for subterranean decomposition, and separating between well-drained soil, periodically inundated soil, and permanent waterlogged soil is a logical first distinction. Ideally, this should be done using hydrological instrumentation, but indirect soil moisture classification using vegetation types will probably give significant response effects. A possible way to compare subterranean wood decomposition across different edaphic conditions is to measure decay rates of roots attached to stumps with known year of logging.

Conclusions

We have documented that wood burial and soil C input from deadwood is common and important across nearly all boreal forest types. Wood burial seems to be equally frequent in young and old forests. The probability of burial varies, however, with ground vegetation and edaphic conditions. Thus, it is important to distinguish between different forest types both in C accounting and in modelling frameworks targeting forest C dynamics and trajectories of forest C accumulation in the context of climate change. As deadwood is a C pool central to the direction of C flow from living biomass to either the atmosphere as an emission or to other C pools (e.g., soils) as a transfer, accurately estimating associated C stocks and dynamics in C dense forests (e.g., boreal) should be a focal point of future research given humanity's desire to mitigate atmospheric CO₂.

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