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# „Remnant old-growth trees enhance large woody debris loading in low-order streams of northern hardwood forests“

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## ABSTRACT

New England's landscapes are characterized by secondary hardwood forests that are recovering from $19^{th}$ century clearing and land use. It remains poorly understood how forest-stream dynamics and associated ecosystem services change as these forests develop towards a late-successional condition. This study addresses this knowledge gap by investigating the effects of riparian forest structure on wood loading of 13 low-order streams draining mature northern hardwood forests at the Hubbard Brook Experimental Forest (HBEF) in New Hampshire. We assessed in-stream large woody debris (LWD) along 300 m longitudinal transects within 13 stream reaches using the line-intercept method (LIM) and a total wood census (TWC). We sampled in-stream habitat features, such as pools and debris dams, and measured attributes of riparian forest structure. We applied multi-hierarchical Bayesian models to investigate the effects of forest structure on LWD loading and the effects of LWD loading on pool- and debris dam frequency. We used a paired-t-test to compare estimates of the LIM to the TWC. Forest structure affected LWD loading, indicating strong effects of big tree density and dead tree density among other structural attributes. Debris dam frequency strongly depended on LWD frequency, while pool frequency depended on stream geomorphology. The LIM and the TWC delivered significantly different results when comparing 50 m stream sections. Our findings highlight the importance of evaluation of adequate transect lengths for further applications of the LIM. We conclude that biological legacies like remnant old-growth trees are important structural attributes which promote LWD in low-order streams.

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### About this thesis

This thesis is composed of two chapters. Chapter 1, “Riparian forests influence low-order streams in northern hardwood forests” is a literature review and introduces the state of the art. Chapter 2, “Remnant old-growth trees enhance large woody debris loading in low-order streams of northern hardwood forests” contains a short introduction, research questions and hypothesis, methodology, results of my study, discussion, conclusion, and references. Figures and Tables can be found at the end of the document. The appendix includes an abstract in English Language and a “Zusammenfassung” in German language.

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# CHAPTER 1: RIPARIAN FORESTS INFLUENCE LOW-ORDER STREAM SYSTEMS IN NORTHERN HARDWOOD FORESTS

## Land use history of the Hubbard Brook Valley

The majority of forests in the northeastern United States are still recovering from 19th century clearing and exhibit less structural complexity than they did pre-European settlement (Foster, Motzkin, et al., 1998). Holmes and Likens, (2016) provide a comprehensive review of history, ecology and research at Hubbard Brook Experimental Forest in their Book “Hubbard Brook. The Story of a Forest Ecosystem”. They state that the analysis of sediment cores from Mirror Lake revealed that the vegetation and plant communities in the Hubbard Brook region have changed dramatically multiple times since the last glaciation period 14,000 years ago. Once forests became established, their composition was dynamic, with fluctuating species compositions and disturbances of many kinds, including outbreaks of pests, diseases, and pollutants from humans. The most dominant tree species in the pre-settlement forest, roughly 300 years ago, were American beech (*Fagus grandifolia*), sugar maple (*Acer saccarum*), eastern hemlock (*Tsuga Canadensis*), and red spruce (*Picea rubra*), a mix very similar to that occurring today (M. B. Davis, 1985). Based on witness tree records it can be surmised that the tree composition at HBEF in the pre-settlement period (circa 1500 to 1750) was different from the tree composition of today, with ten times more red spruce (*Picea rubra*), especially at middle and high elevations, and with American beech as the dominant hardwood species. However, maples and birches, especially paper birch (*Betula papyrifera*) were much less frequent than in present-day forests (Chittenden, 1905; Vadeboncoeur et al., 2012). Based on forest structure and composition in the Bowl, a Research Natural Area with remnant old-growth stands about 28 km east of HBEF, it can be assumed that the pre-settlement forest in the region contained more larger trees, more frequent openings in the canopy because of tree falls, and a greater mix of different age classes. Although humans have been present in the White Mountains region for at least 10,000 years, human impact on the forest seems low until 300 to 350 years ago. European settlers arrived in the region in the late 18th century. In the early 1800s trees, mostly red spruce and eastern hemlock, were harvested in the upper and middle parts of the Hubbard Brook Valley.

Extensive selective logging took place in the early 1900s. Four logging camps were located in the Hubbard Brook Valley. Initially, harvesting was directed towards merchantable spruce, along with some hemlock (*Tsuga canadensis*) and balsam fir (*Abies balsamea*). Later, hardwoods were harvested as well. It has been estimated that by 1920, 166 million board feet of logs had been harvested from Hubbard Brook Valley (Cogbill 1989, unpublished manuscript as cited in Holmes & Likens, 2016). Trees were cut with handsaws and axes. Logs were dragged out across the snow by horses and oxen, which limited the disturbance of the ground. After having removed much of the economically valuable timber the logging companies sold their forest landholdings in the valley to the federal government in 1920. In 1921 the land was transferred to the U.S. Forest Service and incorporated into the White Mountain National Forest (Hornbeck, 2001). Since 1920, the vegetation has largely remained undisturbed, apart from some salvage logging following a hurricane in 1938, and the experimental harvesting between the mid-1960s and the 1980s.

The forest of today can be described as a multi-aged, unmanaged, second-growth northern hardwood forest. Most trees range from 60 to 120 years in age. There are some older trees that must have escaped cutting because they were too young, in poor condition or in case of yellow birch (*Betula alleghaniensis*), of undesirable wood quality (Holmes & Likens, 2016). A study by Bormann et al. 1970 revealed that seven tree species account for 90 % of the basal area: yellow birch (*Betula alleghaniensis*) accounts for 9.0 $m^2*ha^{-1}$, followed by red spruce (*Picea rubra*) with 3.5 $m^2*ha^{-1}$, sugar maple (*Acer saccarum*) with 3.3 $m^2*ha^{-1}$, , American beech (*Fagus grandifolia*) with 3.3 $m^2*ha^{-1}$, red maple (*Acer rubrum*) with 2.1 $m^2*ha^{-1}$, paper birch (*Betula papyrifera*) with 2.1 $m^2*ha^{-1}$, balsam fir (*Abies balsamea*) with 1.5 $m^2*ha^{-1}$ and all other species with 2.8 $m^2*ha^{-1}$.

## The Hubbard Brook Ecosystem Study

The Hubbard Brook Experimental Forest in the White Mountains of New Hampshire is one of the most comprehensively studied landscapes on Earth (Holmes & Likens, 2016). Forest- stream interactions have been studied at HBEF for more than 50 years. The Hubbard Brook Ecosystem Study was initiated in the early 1960s as a collaborative project of several ecologists, hydrologists, and ecosystem scientists and started out with a solid base of studies on nutrient-hydrological interactions (Likens et al., 1977, 1996, 1998). As the study evolved, questions began to arise about other components of the ecosystem and a wide range of subsequent studies followed.

Studies at HBEF are focused on watershed-ecosystems. Watersheds are defined as water catchment basins or discrete drainage areas (Holmes & Likens, 2016). The small-watershed system approach offers the opportunity to understand how water, nutrients and organisms interact ecologically in topographically defined watershed ecosystems. This approach is applied in many long-term studies at HBEF. Whole watershed manipulation experiments were conducted to test the effects of common forest management practices like deforestation, whole three harvest, strip cut harvest, and other disturbances on stream water yield and chemistry (F. H. Bormann et al., 2010; Burton & Likens, 1973; Dahlgren & Driscoll, 1994; Likens et al., 1970, 1998; D. R. Warren et al., 2007). Research at HBEF led to the discovery of acid rain and contributed greatly to today´s understanding of its impact on biogeochemical flux and cycling and on forest growth (Likens et al., 1972, 1996, 1998).

The diverse research at HBEF produces a large number of scientific findings, especially in relation to northern hardwood forest ecosystems. These findings are relevant to long term management of natural resources such as water supply and quality, timber yield, forest health and growth, and wildlife.

## Forest-stream interactions and dynamics

### Disturbances and structural development of natural forest ecosystems

Forest communities are subject to change over time, and so are forest development concepts. Traditionally, broadly applied models of forest development describe four distinct stages of forest succession: stand initiation, stem exclusion, gap formation/understory re-initiation, and old growth (F. H. Bormann & Likens, 1979; Oliver & Larson, 1996). Franklin *et al.* (2002) developed a new concept of dynamic forest succession with multiple pathways. They state that composition, function, and structure are important attributes of a forest ecosystem. Composition describes the variety and proportion of species present in a forest ecosystem. Functions or services carried out by forest ecosystems include productivity, conservation of nutrients, regulation of hydraulic cycles, habitat for biodiversity, and many others (Ried et al., 2005).

The character of a forest is often described by its structural complexity. Franklin *et al.*, (2002) define the attribute structure as structural elements such as trees, snags, and logs and the variability of these elements. Structural elements can be dispersed or aggregated. Hence, the spatial arrangement of structural elements is also a component of the attribute structure.

The importance of stand structural attributes is increasingly recognized for multiple reasons. First and foremost, structure is the attribute most often manipulated in forest management practices. Ecosystem functions highly depend on structure (Thom & Keeton, 2019). Structure is often used as proxy for functions (e.g. productivity) or for organisms that are difficult to measure directly, such as cavity dwelling animals (Franklin et al., 2002). Tree species diversity, tree size, and condition, influence structural diversity, and hence ecosystem structure and function. Old trees often exhibit features like decay cavities, large-diameter branches, and distinct bark features, which contribute to the structural diversity of a stand. Large live trees generate larger snag and log structures that have distinct ecological roles simply because of their size. Uprooted trees create structural features like tip-up mounds and pits, and contribute to soil mixing (B. T. Bormann et al., 1995; Šamonil et al., 2010). LWD on the forest floor and standing dead trees are structures of significant importance. Continuous foliage distribution throughout the canopy contributes significantly to structural diversity in old-growth forests and enhances biodiversity (Carey & Johnson, 1995; Lindenmayer et al., 2000; Parker, 1997; Parker & Brown, 2000; Ruggiero et al., 1991). Canopy gaps lead to the establishment of dense cohorts of trees, which produce densely shaded areas within stands.

Several processes, such as reproduction, growth, breakdown, and death of trees, are associated with structural development of forest stands. Most of these processes operate throughout much of the sere and not only in a single stage. Particular processes may be associated with certain stages in stand development because they may dominate in these stages. For instance, disturbances like wind, insect outbreaks, disease, low-intensity fires etc,. kill trees, generate biological legacies, and establish new cohorts of trees. Therefore, these processes are often associated with stand initiating disturbances.

However, these disturbances operate throughout succession and enhance spatial heterogeneity within the stand (F. H. Bormann & Likens, 1979). Disturbances at gap-level subsequently generate more and more within-stand spatial heterogeneity. Therefore, forests with chronic and catastrophic disturbance regimes develop a mosaic of patches with cohorts at multiple developmental stages and incorporate all stand developmental processes simultaneously.

Phases of stand structural development have been described in several publications (F. H. Bormann & Likens, 1979; Carey & Curtis, 1996; Oliver & Larson, 1996; Spies & Franklin, 1996). However, recognizing the fact that natural forest development happens continuously, rather than in a series of distinct stages, the classification in developmental stages may seem arbitrary. Franklin et al (2002) distinguish eight developmental stages in stand development: Disturbance and legacy creation, cohort establishment, canopy closure, biomass accumulation / competitive exclusion, maturation, vertical diversification, horizontal diversification, and pioneer cohort loss. In structurally diverse forests these developmental stages can co-occur in spatial and temporal proximity (Franklin et al., 2002).

*1. Disturbance / legacy creation stage*

A high intensity natural disturbance, like windthrow or fire, initiates stand development. The disturbance provides conditions that favour the development of a new cohort of trees. Natural disturbances hardly ever eliminate all structural elements from the previous stand. These persisting living and dead structures e.g., large remnant trees, are described as biological legacies (Franklin et al 2002, Franklin and MacMahon 2000). Remnant shade-tolerant trees can support re-establishment of these species in mature stands with limited seed sources by increasing seed availability (Keeton 2000). At a landscape level, a natural disturbance pattern creates habitat islands with diverse structural legacies and unique environmental conditions (Foster et al, 1998. Keeton 2000). Post-disturbance conditions after a traditional clear-cut differ greatly in comparison to the conditions following a natural disturbance. Traditional clear-cutting results in low levels of large woody debris and no legacy of overstory trees persists (Franklin et al., 2002).

*2. Cohort establishment stage*

During cohort establishment, a new generation of trees is established. This phase is typically completed most rapidly when the new cohort forms from surviving regeneration. This suggests that cohort establishment actually preceded disturbance and legacy creation (Franklin et al., 2002).

*3. Canopy closure stage*

During canopy closure, trees re-stablish site dominance. This brief phase can be viewed as a transition between cohort establishment and biomass accumulation. However, it is a phase of rapid development and dramatic change. Light levels in the understory are being reduced to a great extent. Some species like shrubs, herbs and lichens are being suppressed or eliminated while saprophytes and invertebrate detrivores thrive. Canopy closure happens more rapidly on highly productive sites (Franklin et al., 2002).

*4. Biomass accumulation/competitive exclusion stage*

In this period of young stand development, the tree cohort thoroughly dominates the site. Rapid growth and biomass accumulation, competitive exclusion, and density-dependent mortality within the tree cohort, characterize this phase (F. H. Bormann & Likens, 1979). Species diversity declines as a result of shading and suppression of many understory plants (Franklin et al., 2002).

*5. Maturation stage*

During maturation stage the pioneer tree cohort reaches maximum height and crown spread. The mass of large woody debris is at a minimum level. Overstory tree mortality shifts from density dependent to density-independent causes like insects, disease, and wind. Overstory trees begin to exhibit signs of decline. Individual trees grow in height, width, and crown spread while biomass levels approach an asymptote. Sub-lethal damage like broken and multiple tops, top and hole decay, and brooming increases niche diversification. The understory community, including shade-tolerant trees, is being re-established as the thinning canopy of overstory dominants allows more light to reach the forest floor (Franklin et al., 2002).

### *6. Vertical diversification stage*

This phase is characterized by significant development of late-successional or old-growth forest attributes like the re-establishment of canopy continuity between the ground and upper tree crowns. Overstory trees are increasingly decaying, which results in large woody debris approaching levels typical for old-growth stands. Density independent tree mortality dominates, which leads to initiation and expansion of gaps. Damage and mortality of canopy trees continues to generate structural complexity and enhances niche diversification. Communities of bryophytes and foliose lichens are developing (Franklin et al., 2002).

### *7. Horizontal diversification stage*

As a result of gap creation and expansion, the stand evolves into multiple structural units. Heavily shaded areas develop where dense patches of shade-tolerant species have reached the mid or upper canopy. At this point, the light environment is controlled primarily by shade-tolerant species and not by remaining trees from the pioneer cohort, which are continuously decaying. Gaps result from disturbances that create contagious tree mortality, such as wind, many diseases, and insects (Franklin et al., 2002).

### *8. Pioneer cohort loss stage*

Shade-intolerant species are present in the sere but canopy gaps are too small for their successful reproduction. However, the structural influence of a large pioneer species may continue for several centuries after the death of the last individuals, because of the large snags and logs that persist (Franklin et al., 2002).

*Structural endpoint of stand development*

As outlined by Franklin et al., (2002), these eight stages are characteristic of a sere initiated by a catastrophic disturbance. The sere is composed of a mixture of pioneer shade intolerant species and shade-tolerant species. Franklin & Fites-Kaufmann, (1996) describe the functional late-successional stand as a mosaic of structural units, which is shaped by natural disturbances.

## Multiple pathways in forest development

Structural complexity has largely been associated with late-successional forests in temperate systems (F. H. Bormann & Likens, 1979; Franklin et al., 2002; Oliver & Larson, 1996). Franklin and Fites-Kaufmann, (1996) suggest to view the functional late-successional stand as a mosaic of structural units. Recent research describes multiple pathways of forest development and the potential emergence of structural complexity in the immediate post-disturbance (Donato et al., 2012; Lorimer & Halpin, 2014; Meigs et al., 2017). Donato et al., (2012) suggest that even early-successional forests can exhibit structural complexity similar to that in old-growth forests. They point out that conventional models of forest succession as described by F. H. Bormann & Likens, (1979) and Oliver & Larson, (1996) are often based on managed stands post timber harvest (e.g. a clear cut), that were structurally simplified after the removal of biological legacies. After stand initiation, these evenly aged and structurally simple stands would go through a stem exclusion phase before gaining structural complexity towards later successional stages of gap formation / understorey re-initiation. Structural complexity would be highest in old-growth stands (F. H. Bormann & Likens, 1979; Oliver & Larson, 1996). However, in naturally regenerating forests, some aspects of structural complexity may arise much sooner than expected under conventional forest succession models (Donato et al., 2012). Natural disturbances rarely eliminate all structural elements from the preceding stand (Franklin et al., 2002). The persisting living and dead structures, described as biological legacies, differ greatly among disturbances (Franklin et al., 2000, 2002). As a result, natural succession following these disturbances is highly variable and often deviates from succession described in conventional models (Donato et al., 2012; Franklin et al., 2002; Turner et al., 2009). Some stages may be prolonged while other stages, like canopy closure, may be skipped entirely. Qualities describing structural complexity in both young stands and old growth forests include horizontal and vertical heterogeneity, large standing snags, abundant large diameter woody debris, the co-existence of shade-tolerant and shade-intolerant species, a well-developed understory and diverse growth rates (Donato et al., 2012). Hence, a significant proportion of eventual old-growth complexity may already be determined in this early stage.

## The importance of legacy trees

Biological legacies have a large influence on ecosystem recovery following a disturbance. Franklin et al., (2000) define biological legacies as the organisms, organic materials, and organically generated environmental patterns that persist through a disturbance and are incorporated into the recovering ecosystem. Biological legacies include organisms persisting as seeds, spores, or surviving individuals, dead structures like snags, logs, and other woody debris or animal carcasses, and also spatial patterns generated by biotic processes (Franklin et al., 2000). The persistence of a dense layer of understory tree saplings and sprouts after a wind-throw event is a common example of biological legacies in northern hardwood forests (Foster et al., 1997). Structural legacies (both living and dead), lifeboat species that would otherwise disappear from a site after disturbance by providing habitat, substrate, and food source (Franklin et al., 2000; Gibbons & Lindenmayer, 1996; Lindenmayer & Franklin, 1997; Mazurek & Zielinski, 2004). For example, some birds or epiphytes strongly depend upon the existence of large remnant trees or cavity trees (Edman et al., 2016; Franklin et al., 2000; Lundquist & Mariani, 1986; North et al., 1999). Legacy trees can ameliorate microclimatic conditions that promote survival and reestablishment of organisms after a disturbance (Franklin et al., 2000). Persisting structures enhance the structural complexity in post-disturbance ecosystems and promote landscape connectivity (Donato et al., 2012; Foster, Knight, et al., 1998; Franklin et al., 2000, 2007). Legacy trees promote species which depend on dead wood or live trees in early succession while sustaining ecosystem functions (Gustafsson et al., 2010). The persistence of mature trees as biological legacies after wildfire has been reported in Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) stands of the northwestern United States (Franklin et al., 2002; Goslin, 1997; Zenner et al., 1998). Keeton & Franklin, (2005) report positive effects of remnant old-growth western hemlock (*Tsuga heterophylla*) and western red cedar (*Thuja plicata*) on reestablishment of shade-tolerant conifers in mature Douglas-fir

(*Pseudotsuga menziesii*) stands. Increased bat activity and elevated numbers of birds, especially at legacy trees with basal hollows, show that legacy trees add significant habitat value to managed coastal redwood forests in California (Mazurek & Zielinski, 2004). North et al., (1999) highlight the importance of remnant old-growth trees and snags in regenerating stands as foraging habitat for Northern Spotted Owls in forests of the Olympic Peninsula and in the North Cascade Range of Washington State.

Northern hardwoods of the Great Lakes and New England regions are characterized by a wind-gap disturbance regime, promoting the development of structurally complex, multi-cohort mixed-species stands (Franklin et al., 2007; Frelich & Lorimer, 2015). Typical legacies of a wind-gap disturbance include numerous boles on the forest floor, some large live trees, and snags (Franklin et al., 2007). Infrequent, intense storms can substantially impact northern hardwood forests (Cooper-Ellis et al., 1999). Foster et al., (1997) and Cooper-Ellis et al., (1999) report high survival of trees following a hurricane simulation experiment. Survival varied considerably with damage type (bent trees > snapped trees > uproots) and tree species.

Few studies address the function of legacy trees in northern hardwood forests. Halpin & Lorimer, (2016) report shorter post-disturbance recovery times of stands with large residual trees compared to even-aged stands. DeGraaf et al., (1992) and Paragi et al., (1996) suggest that larger trees with cavities provide important habitat for many birds and mammals of northern hardwood forests, such as piliated woodpecker, porcupine, raccoon, fisher, gray fox, little brown myotis and big brown bat. Keeton et al., (2007) studied the effects of forest age on LWD loading in streams draining old-growth, and mature northern hardwood forests with and without remnant old-growth trees in the Adirondacks. The average in-stream LWD volume at mature sites with old-growth remnants was higher than at mature sites without remnants, but no significant difference could be detected because of the small sample size. Many knowledge gaps regarding the abundance of legacy trees in the Northeast and their functions in northern hardwood forests remain, and further research is needed.

## Legacy tree retention

The largest and oldest trees at HBEF are remnants from the pre-settlement period (Whittaker et al., 1974). Many of these trees were of undesirable timber quality or of poor form, which saved them from being cut when the Hubbard Brook Valley was logged in the 1800s and early 1900s (Holmes & Likens, 2016; Whittaker et al., 1974). Today legacy tree retention (synonyms include green tree retention, variable retention and retention felling) is a common component of ecologically based silvicultural systems (Gustafsson et al., 2012). Silvicultural guidelines and forest practice laws vary strongly between countries, states and regions (Gustafsson et al., 2010). The concept of retention forestry originated in the Pacific Northwest in the 1980s. By the late 1990s, retention forestry was an established practice in the northwestern United States and southwest Canada, and was specified in policy and regulations in California, Oregon, Washington and British Columbia. At this time, the first studies and applications in the eastern United States emerged. In Europe, the retention approach was first introduced in Sweden, Finland and Norway, where legislations and guidelines for harvest operations were adapted to incorporate environmental concerns in the 1990s and 1980s (Gustafsson et al., 2012). In tropical regions of Asia, Africa and America, reduced impact logging is practiced as a sustainable harvest method (Dykstra, 2012; Putz et al., 2008). This concept was derived from selective logging and includes the retention of biological legacies as a part of harvesting operations (Meijaard et al., 1994). Especially in managed forests, the retention of key elements of stand structural complexity, such as large living and dead trees, is an important conservation measure. (Lindenmayer et al., 2006) A review paper by Gustafsson et al. (2010) reveals, that within several studies in northern Europe, retention trees have noticeable effects on forest characteristics, including biodiversity patterns. While retention trees do not maintain the characteristics of intact mature forests, they ameliorate the consequences of clear-cutting on biota and provide substrate for early-successional species (Gustafsson et al., 2010). Depending on regulations and conservation objectives, trees can be retained in patches or as dispersed single trees (Gustafsson et al., 2012). Retention levels are often expressed as number of retained trees and aboveground timber value per hectare in case of dispersed retention or as percentage of harvest area in case of aggregates. Specific requirements for retention trees often include a minimum diameter and tree species (Gustafsson et al., 2012). Generally, larger volumes and more trees seem to maintain diversity better (Gustafsson et al., 2010). Lie et al., (2009) recommend retaining old and large trees in patches to maintain biodiversity of epiphytic lichens in Norway. In northern hardwood forests, structural complexity enhancement, which includes retention of large diameter trees and snags, leads to increased large woody debris volumes and enhanced carbon storage (Ford & Keeton, 2017; Keeton, 2006; Nunery & Keeton, 2010).

## Forest structure and age influence wood loading in streams

In the absence of human interference, successional processes and natural disturbances shape forest structure (F. H. Bormann & Likens, 1979; Franklin et al., 2002; Frelich & Graumlich, 1994; Lorimer, 1977; Runkle, 1982). Previous studies suggest that forest age and structure have a large influence on in-stream ecosystem processes (Keeton et al., 2007; D. R. Warren et al., 2009). Density-dependent tree mortality is high during stand development and maturation stage, which results in a high potential for LWD accumulation in streams (Franklin et al., 2002). However, these logs are often smaller in size and their functions in stream geomorphology are limited. Keeton et al., (2007) suggest that wood functions in streams increase with late seral development, when logs reach a diameter of 30 cm or more, and within channel accumulations increase. At later stand developmental stages, density independent factors, like disturbances such as fire, disease, pathogens, and wind or ice storms, have a large impact on forest structure and lead to LWD accumulation in streams (Franklin et al., 2002; Frelich & Graumlich, 1994; Hanson & Lorimer, 2007). Structural complexity is generally high in old-growth forests (Franklin et al., 2002; Mcgee et al., 1999). Frequent small scale disturbances like disease, and wind or ice storms dominate forest dynamics in old–growth forests of the northeastern United States (Frelich & Graumlich, 1994; Lorimer & White, 2003; Mcgee, 2000; Ziegler, 2002). Warren *et al.* (2009) suggest that volume and frequency of LWD is most closely associated with age of the dominant canopy trees. It has also been observed that streams surrounded by old-growth forests exhibit higher LWD loading compared to streams of mature forests and that LWD loading is higher in stands with high basal area (Keeton et al., 2007; Valett et al., 2002). Pools and debris dams occur more frequently in streams surrounded by old-growth forests (Bilby & Ward, 1988; Valett et al., 2002).

## Forest structure determines light availability in forested headwater streams

Light is an important factor limiting productivity in temperate-forest streams (Gregory, 1980; Hill et al., 1995; Kiffney et al., 2004). The structure of riparian forests impacts stream processes by determining the amount and spatial distribution of light fluxes to headwater streams (Keeton et al., 2007; D. R. Warren et al., 2013). Thus, changes in structure and composition of riparian forests can alter light flux and stream primary production, which subsequently impacts in stream nutrient dynamics and higher trophic level production (Boston & Hill, 1991; McTammany et al., 2007; Noel et al., 1986; Sobota et al., 2012). Warren *et al.*, (2013) suggest that light influx on small headwater streams is highest following high intensity disturbances like clear-cuts, fires, or large windstorms. Re-establishment of particularly woody vegetation decreases light availability, as the canopy develops and ultimately closes over the stream. Franklin *et al.*, (2002) highlight that there are multiple pathways in forest development. Shading was reported to increase sharply during the "canopy closure" phase and to reach a maximum during the "biomass accumulation / competitive exclusion" phase of stand development. In this phase, an even-aged cohort of trees competes for resources and density dependent tree mortality is high. During stand development, density independent tree mortality and non-stand replacing disturbances create a more complex canopy and lead to gap formation which results in increased light availability below the canopy. These canopy gaps also increase light flux to associated streams (Curzon & Keeton, 2010; Stovall et al., 2009).

Light influx promotes primary production and algal growth, increases in-stream nutrient uptake, and can cause shifts in stream food webs (Murphy, Hawkins and Anderson, 1981; Boston and Hill, 1991; Power and Dietrich, 2002; Stovall, Keeton and Kraft, 2009; Hill, Smith and Stewart, 2010; Warren *et al.*, 2016; Bechtold *et al.*, 2017). Terrestrial carbon is a major energy source in small headwater streams (Fisher & Likens, 1972; Vannote et al., 1980). However, recent research using stable isotopes stresses the relative importance of algal carbon in stream food webs, even when algal standing stocks are low (Brito et al., 2006; Lau et al., 2009; A. O. Y. Li & Dudgeon, 2008; McCutchan & Lewis, 2002; McNeely et al., 2007; Schmid-Araya et al., 2012)

Warren, *et al.*, (2016) suggest that light availability reaches a minimum during the stem-exclusion phase, 20 to 60 years after a stand replacing event. Consequently, stream Gross Primary Production (GPP), light variability, nutrient processing, and the amount of autochthonous carbon transferred to higher trophic levels in the stream food web all reach their minimum at this time. They suggest that with increasing canopy complexity during stand development, canopy gaps form and create patches of light that increase light availability and variability in streams. This results in an increase in GPP (assuming no nutrient limitation), which increases autochthonous carbon in the stream food web. There is evidence that in forested headwater streams a moderate increase in light has positive effects on growth and production of fish via bottom-up processes (Kiffney et al., 2014; Kiffney & Roni, 2007; Murphy et al., 1981).

## Large woody debris and its functions in forested streams

Large wood is an important component of woodland river ecosystems. Gurnell *et al.*, (2002) indicate that tree species composition and forest structure, climate and the hydrological regime, fluvial geomorphology, as well as river and woodland management influence the relationship between large wood and the physical characteristics of stream ecosystems. Aside from affecting flow hydraulics, mineral- and sediment transfer, and the geomorphology of streams, wood plays an increasingly important role in creating a diversity of habitat patches for a wide range of organisms at different stages of their life cycles.

### Woody debris in small, medium and large streams

Functions of wood in streams are variable and depend on a large number of factors. Gurnell et al. (2002) explain the role of LWD in fluvial processes. They suggest that the size of a wood piece in relation to the size of the river influences its storage, dynamics, and functions in the stream. Wood pieces appear large in comparison to channel width in "small" streams. In these scenarios the majority of wood pieces are longer than the width of the stream channel. "Medium" streams are wider than the size of most wood pieces and "Large" streams have widths greater than the length of all the wood pieces delivered to them. Gurnell *et al.*, (2002) compare the functions of woody debris in small, medium, and large streams:

In "small" streams wood pieces tend to remain close to where they were delivered to the stream. Pieces are often oriented perpendicular to direction of flow. They provide important structures in the stream and control rather than respond to the hydrological and sediment transfer characteristics of the stream. Contact to soil and frequent wetting and drying result in increased decay rates (Bilby et al., 1999).

In "medium" sized streams, the combination of wood length and form becomes important for the stability of wood within the channel. Large pieces of wood function as traps for smaller pieces and form wood accumulations (debris dams). Flow regime and buoyancy of the wood affect wood transport.

Channel geometry controls delivery, mobility, and breakage of wood in "large" streams. Wood retention depends on the distribution of flow velocity and on the channel pattern. A large amount of wood accumulates at the channel margins. The quantity of in-stream woody debris depends largely on the degree of contact between the active channel and the forested floodplain and islands. Keller & Swanson, (1979) report similar findings. They suggest that woody debris concentrations are highest in small headwater streams and decrease downstream.

## Large woody debris affects the hydrology and geomorphology of streams

Wood influences the hydraulics of flows within stream channels by acting as roughness elements (Gurnell et al., 2002). Quantity, position, and orientation of wood pieces have different impacts on flow patterns, flow resistance, and the water surface profile (Gippel et al., 1996; W. J. Young, 1991). Particularly in smaller streams, wood increases flow complexity and water retention (Ehrman & Lamberti, 1992).

LWD can have a great impact on channel morphology. For example, Keller & Swanson, (1979) report that debris dams can partially or completely block the stream channel. Blockages can lead to erosion of the stream bottom or bank, deposition of sediments and debris which facilitates the creation of mid channel bars and braided channels, and backwater situations upstream of the debris dam which may lead to meander cutoffs (Keller & Swanson, 1979). In steep streams, debris dams facilitate the development of plunge pools and create falls and cascades, which leads to a stepped stream profile (Heede, 1972; Keller and Swanson, 1979). Keller and Swanson (1979) suggest that this phenomenon may result in dissipation of much of the stream's energy. Woody debris and a stepped stream profile influence the exchange between stream water and ground water (Harvey & Bencala, 1993; Wondzell & Swanson, 1999). Montgomery *et al.*, (1995) and Gurnell and Sweet, (1998) reported a positive correlation between frequency of large woody debris accumulations and pools.

## Woody debris influences biogeochemical processes

Woody debris creates obstructions, which lead to enhanced mineral and organic sediment storage and nutrient retention in stream ecosystems (Bilby & Ward, 1988; Hedin et al., 1988; D. M. Thompson, 1995). Debris dams, for example, are hot spots for anaerobic microbial transformation of inorganic nitrogen into gaseous form. This denitrification process leads to loss of nitrogen gas from the system (Bilby & Likens, 1980; Steinhart et al., 2000). In contrast, wood removal leads to sediment scour, loss of organic matter, and changes in channel morphology (Beschta, 1979; Bilby & Likens, 1980; Gurnell & Sweet, 1998; Klein et al., 1987; Smith et al., 1993). A study at Bear Brook at HBEF revealed that the removal of debris dams led to a dramatic increase in export of organic carbon from the system (Bilby & Likens, 1980).

## Woody debris as energy source in headwater streams

Terrestrial organic matter is an important energy source for aquatic food webs in headwater streams, particularly where dense canopy covers cause shading and reduce in-stream primary production (Anderson & Sedell, 1979; Vannote et al., 1980). A study at HBEF revealed that Bear Brook is highly heterotrophic, receiving 99 % of its energy from the surrounding forest (Fisher & Likens, 1972). This paradigm in stream ecology has been challenged by recent studies, highlighting the relative importance of autochthonous carbon in stream food webs, even though algal standing stocks may be low (Brito et al., 2006; McCutchan & Lewis, 2002; McNeely et al., 2007). However, LWD provides structural habitat for algae and serves as a stable substrate for heterotrophic fungi and bacteria (Gurnell et al., 1995; Sabater et al., 1998; Sinsabaugh et al., 1991). Leaf litter and the associated microbial biomass are a major food source for many aquatic invertebrates (Gurnell et al., 1995; Vannote et al., 1980). Although leaves are of higher nutritional value and can be degraded faster, LWD can function as a reliable long-term food source for several years (Gurnell et al., 1995). Certain invertebrates have specialized on processing raw wood (Anderson et al., 1978). A detritus-based invertebrate community can be an important food source for organisms of higher trophic levels, like predatory invertebrates and fish (Hall et al., 2000, 2001; Mundie, 1974; Wallace et al., 1999).

## Woody debris provides habitat for biodiversity

The complex physical structure of woodland streams and their wood pieces and accumulations provide a diversity of food source and habitat for a wide range of organisms at different stages of their life cycles (Gurnell et al., 2002; Harmon et al., 2004). Before 1970, wood was often considered as a hindrance for fish migration and a cause of oxygen depletion in streams (Harmon et al., 2004). Woody debris may contain organic compounds that are potentially lethal to aquatic organisms (Harmon et al., 2004). Leachates of Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*) bark were toxic to humpback salmon (*Oncorynchus gorbuscha*) fry (Buchanan et al., 1976). The adverse effects of western redcedar (*Thuja plicata*) on coho salmon (*Oncorhynchus kisutc*) seem to be restricted to freshly logged areas with high amounts of *Thuja* slash or streams with naturally high accumulations of debris (Peters et al., 1976). Excessive amounts of logging waste can also lead to Oxygen depletion which often affects fish populations (Harmon et al., 2004). Fishery managers often face difficult decisions when it comes to removal of woody debris dams. The removal of a large debris dam may benefit fish passage, however it has to be considered how this intervention will affect the stream channel and the load of suspended elements (Beschta, 1979).

Recent research shows the beneficial roles of LWD in the formation and stabilization of fish habitat. Wood loading has been positively correlated with the diversity of both macroinvertebrates and fish (Angermeier & Karr, 1984; Benke et al., 1985; Elliott, 1986; Smock et al., 1985, 1987, 1992). Woody debris is often associated with high densities and biomass of macroinvertebrates (Smock et al., 1987). Especially in streams with sandy bottoms, which are unsuitable for colonisation, woody debris provides a stable habitat for macroinvertebrates (O'Connor, 1992; Wallace & Benke, 1984).

Woody debris, pools, and backwaters created by woody debris, are especially important as rearing habitat for juvenile fish (Gurnell et al., 1995). Deep pools provide important refuge during low-flow events and pool volume and biomass of some fish species is positively correlated (Gurnell et al., 1995). Backwaters accumulate detritus and are important foraging sites for fish feeding on drift organisms (Gurnell et al., 1995). A meta-analysis by Mellina & Hinch, (2009) revealed that the removal of woody debris after clear cutting is accompanied by a decrease in pool number and size and has negative effects on the salmonid biomass of forested streams of the United States, Canada and Sweden. Increased bedload transport after woody debris removal may have negative impacts on aquatic biota and may lead to scour or excessive burial of salmonid eggs (Smith et al., 1993)

## Forest management impacts wood loading in streams

Forest management can have major impacts on stream flow quantity and quality (I. C. Campbell & Doeg, 1989). Research at HBEF has vastly contributed to understanding the effects of forest management practices on stream ecosystems. All vegetation on Watershed 2 (W2) was cut and vegetation regrowth was inhibited for two years by application of herbicides. Likens *et al.*, (1970) report dramatic changes in stream water quantity and composition following this event. Stream flow increased by 39% in the first year and 28% in the second year. Stream water concentrations of most ions increased, especially nitrate, which almost continuously exceeded the health levels recommended for drinking water. Stream water temperatures were higher and fluctuated more after deforestation compared to the undisturbed condition. Higher temperature and the increased availability of light and nutrients led to dense algal blooms during summers following the operation. A study by Hedin et al., (1988) revealed that deforestation had a major effect on the persistence and abundance of debris dams and on sedimentation. After clearcutting followed by herbiciding of the experimental watershed W2, the number of debris dams decreased dramatically while sediment export increased. Similar findings have been reported in other studies (Bosch & Hewlett, 1982; Fredriksen, 1971; Golladay et al., 1987; Tebo, 1955). Several authors have mentioned large amounts of logging waste and excessive sedimentation following forest operations, which can have negative effects on stream ecology and biota (Burns, 1972; Graynoth, 1979; Harmon et al., 2004). Years after logging, the change in stand structure continues to affect stream ecosystems, but the long-term effects of forest management practices on large woody debris loading in streams remain poorly understood. The amount of large woody debris may decline because of the absence of mature trees in the regrowing forest, or remain high for some time after deposition of logging waste, or may even increase when the presence of clear cuts makes the surrounding forest prone to disturbances (Bilby & Ward, 1991; Bragg, 2000; Gomi et al., 2001; Kreutzweiser et al., 2005; Montgomery et al., 1995).

## The line-intercept method for large woody debris estimation

In most surveys in-stream LWD is assessed by counting and measuring every piece of large wood within a reach. This technique is accurate and effective, but often time consuming. The line-intercept method (LIM) for wood volume estimation as developed by Warren and Olsen, (1964) and modified by Van Wagner, (1968) has been widely applied in forest surveys (Marshall et al., 2000, 2003; Waddell, 2002; D. R. Warren et al., 2013; Woldendorp et al., 2004; Woodall & Monleon, 2008). The LIM assumes that all pieces of wood are cylindrical, horizontal and randomly oriented (Van Wagner C. E., 1968). Non-random orientation of woody debris can affect the accuracy of the estimate (Howard & Ward, 1972; Van Wagner C. E., 1968).

Few studies have used a line-intercept approach for assessing woody debris in stream ecosystems (Gippel et al., 1996; D. R. Warren et al., 2008; M. K. Young et al., 2006). Wallace and Benke, (1984) were the first to apply the LIM in streams. They quantified wood volume in two subtropical coastal plain streams by establishing a series of transects perpendicular to stream flow. A similar modification of the LIM has been applied by O'Connor, (1992), Gippel et al., (1996) and Baillie et al., (1999). An alternative application of the LIM is to estimate wood volume along a transect running through the stream thalweg. Valett et al., (2002) estimated LWD volume in small headwater streams by running a single longitudinal transect through the stream thalweg, rather than multiple perpendicular transects. Few studies have evaluated the accuracy of the LIM for estimating LWD volume in streams. Gippel et al., (1996) found that a series of multiple perpendicular transects across a lowland Australian river overestimated wood volume in comparison to a total wood census and aerial photographs. D. R. Warren et al., (2008) compared line-intercept estimates and census techniques in small, constrained stream reaches of the western Adirondacks. The stream reaches ranged from approximately 2 m to 11 m in width and 120 m to 250 m in length. For each reach, they estimated wood volume and frequency by counting and measuring all pieces of LWD that intercepted a longitudinal transect running through the center of bankfull width. The estimates of wood volume were highly correlated with the results of a complete wood census, while the LIM slightly overestimated wood volume, particularly in streams with high wood loading. Regarding wood volume and frequency, they did not find a significant difference between the LIM estimates and the census. However, the predictive power of frequency estimates was weaker than for volume estimates. According to the results of this study stream size does not affect the accuracy of the LIM for streams up to 8 m bankfull width. Hence, D. R. Warren et al., (2008) suggest that line-intercept surveys are an effective method for estimating in-stream large wood volume in small constrained streams.

## Climate change and forested ecosystems of the future

### Forests of the future

Climate change is one of the greatest threats to forest ecosystem services and biodiversity (Sala et al., 2000; Schröter et al., 2005; Thomas et al., 2004). Shifts in temperature and precipitation are expected to vary throughout biogeographic regions, resulting in more or less favourable conditions for tree growth and forest development (Lindner et al., 2010). As the risk of extreme weather events increases and disturbance regimes change, the adaptive capacity of forests becomes extremely important (Lindner et al., 2010; Seidl et al., 2017; Thom et al., 2017).

Climate sensitivity of forest ecosystems may vary with changes in structure and composition, induced by forest aging and disturbance regime (Boulanger et al., 2018; Pan et al., 2011; Thom et al., 2017). Older forests, which are characterized by higher structural and functional complexity, may be better at buffering climate change effects than younger forests with low complexity (Frey et al., 2016; Martin et al., 2018; I. Thompson et al., 2009; Urbano & Keeton, 2017). Forests with old remnant trees / legacy trees, may have greater capacity to sustain favourable microclimates for habitat specific biota than younger forests (Franklin et al., 2002; Fritz et al., 2009).

Mean annual temperatures across the northeastern United States have been warming steadily since the 1970s (Hayhoe et al., 2007). Most forests in this region are still recovering from 19th century clearing and are structurally more simple and younger compared to pre-European settlement (Foster, Motzkin, et al., 1998). The vegetation of the Northeast may profit from the predicted lengthening of the growing season and decline of frost days (Hayhoe et al., 2007). Aging temporal and boreal forests develop greater structural complexity which may increase niche availability and promote ecosystem functions like carbon storage (Crow et al., 2002; Mcgee et al., 1999; Urbano & Keeton, 2017). However, many challenges remain. A warming climate will likely exacerbate problems associated with invasive species, and will alter important interactions and synchrony between plants and pollinators, pests, diseases, and weeds (Walther et al., 2002; Weltzin et al., 2003). It remains poorly understood how species composition and structure will change as these forests develop, and how these changes will affect ecosystem services and biodiversity. Thom *et al.*, (2019) suggest that ecosystem service and biodiversity indicators, like total ecosystem carbon, timber growth and species richness, are sensitive to climatic changes and vary with forest age. Their findings suggest that younger forests of the boreal–temperate ecotone of eastern North America may be more sensitive to climate change compared to older forests, and that the mix of ecosystem services and biodiversity provided by younger forest may shift as a consequence of climate change, while remaining stable in old forests.

However, forests themselves are important climate regulators. Forests do not only ameliorate climate extremes, they also function as important carbon sinks (K. T. Davis et al., 2019; Nunery & Keeton, 2010). It will therefore be crucial to maintain and protect old-growth forest ecosystems, their processes, functions and biodiversity (Franklin, 1993; Luyssaert et al., 2008; Noss, 1999). In commercially used forests it will become increasingly important to manage forests for late-successional or old-growth characteristics by enhancing structural complexity, which will promote carbon sequestration and mitigate climate change (Ford & Keeton, 2017; Gunn et al., 2014; Keeton, 2006; Thom & Keeton, 2019).

## Streams of the future

Freshwaters of different regions vary in their responses to climate change (Schindler, 1997). Climate change will affect rainfall distribution, and therefore soil moisture, runoff, and water supplies to catch basins will change (Hengeveld, 1990). Stream flow of low-order and headwater streams is closely related to weather patterns and climate (Brooks, 2009; Lull & Sopper, 1966; Vogel et al., 1997, 1999). It can be expected that stream water temperature will increase with air temperature (Eaton & Scheller, 1996; Stefan & Preud'homme, 1993). Maximum precipitation intensities are projected to increase in the northeastern United States, which would lead to positive trends in high-flow events (Demaria et al., 2016; Poff et al., 1996). Evapotranspiration, runoff and drought frequency are expected to increase over time (Hayhoe et al., 2007). In general, simulations indicate that climate change is likely to drive a re-distribution of stream flow in the Northeast, with a general tendency towards more streamflow in winter and spring and less in summer and fall (Hayhoe et al., 2007).

Changes in flow regimes and flow characteristics of low-order streams would strongly affect stream ecology (Rolls & Bond, 2017). Reduction of base flow may lead to declines in population sizes or local extinction of species and reduced species richness (Benejam et al., 2010; Boulton, 2003; Kupferberg et al., 2012). Increases in discharge variability may lead to population declines due to increased mortality of eggs, larvae and adults, reduced species richness, and altered species composition (Casas-Mulet et al., 2014; Freeman et al., 2001; Paetzold et al., 2008; Perkin & Bonner, 2014; Schmutz et al., 2014). An increase in stream temperature may lead to reduction of habitat for cold water species (Eaton & Scheller, 1996). Extremes of water flow and temperatures can reduce recruitment and survival of anadromous salmonids (Jonsson & Jonsson, 2009) In-stream productivity and water temperature are highly dependent on light availability, which is regulated by shading effects of the forest canopy (Johnson, 2004; D. R. Warren et al., 2013). Streams running through riparian forests of greater structural complexity are more likely to exhibit channels in better geomorphic condition and may therefore be more resilient to flood events (Keeton et al., (2017). Forests may have an increasingly important role in buffering climate effects on small headwater streams (K. T. Davis et al., 2019; Zwieniecki & Newton, 1999).

# CHAPTER 2: REMNANT OLD-GROWTH TREES ENHANCE LARGE WOODY DEBRIS LOADING IN LOW-ORDER STREAMS OF NORTHERN HARDWOOD FORESTS


## Abstract

New England's landscapes are characterized by secondary forests that are still recovering from 19$^{th}$ century clearing and land use. It remains poorly understood how forest-stream dynamics and associated ecosystem services will change as these forests develop towards a late-successional condition. This study addresses this knowledge gap by investigating the effects of riparian forest structure on wood loading of 13 low-order streams draining mature northern hardwood forests at the Hubbard Brook Experimental Forest (HBEF) in New Hampshire. We assessed in-stream large woody debris (LWD) along 300 m longitudinal transects within 13 stream reaches using the line-intercept method (LIM) and a total wood census (TWC). We also sampled in-stream habitat features, such as pools and debris dams, and measured attributes of riparian forest structure. We applied multi-hierarchical Bayesian models to investigate the effects of forest structure on in-stream LWD loading and the effects of LWD loading on pool frequency and debris-dam frequency. We used a paired-t-test to compare the results of the LIM and the TWC. Forest structure affected LWD loading, indicating strong effects of big tree density and dead tree density among other structural attributes. Debris dam frequency strongly depended on LWD frequency, while pool frequency depended on stream geomorphology. The LIM and the TWC delivered significantly different results when 50 m long stream sections were compared, which suggests that the accuracy of the LIM depends on transect length. The results show that biological legacies like remnant old-growth trees are important structural attributes promoting LWD in low-order streams. Retaining large diameter trees in managed forests is an essential measure to maintain ecosystem processes, functions and biodiversity of forests and streams. Our findings also demonstrate that determination of adequate transect length is necessary before using the LIM for in-stream LWD assessments.

# 1. Introduction

Riparian and streamside forested ecosystems provide a wide range of ecosystem functions and services, such as hydrologic regulation, pollutant uptake and filtration, flood resilience and habitat for biodiversity (Gilvear et al., 2016; Keeton et al., 2017; Meyer et al., 2005; Nunery & Keeton, 2010; Ried et al., 2005; D. R. Warren et al., 2016). Large woody debris (LWD) and LWD accumulations (debris dams or wood jams) are important features in forested stream ecosystems (Gurnell et al., 2002; D. R. Warren et al., 2009). A number of studies have documented the influence of wood loading on channel geomorphology and a variety of stream processes in different parts of the world (Gomi et al., 2001; Gurnell & Sweet, 1998; Powell et al., 2009; Richmond & Fausch, 1995). Some of these have evaluated the dynamics of wood loading, such as spatial distribution and accumulation rates in relation to disturbances and forest age, along streams in northern hardwood forests of northeastern North America (Keeton et al., 2007; Kraft et al., 2011; D. R. Warren et al., 2007, 2009; D. R. Warren & Kraft, 2008). However, it remains poorly understood which key attributes associated with stand structural complexity have the largest impact on in-stream LWD loading. This study aims to advance our understanding of the influence of forest structure on LWD in streams running through temperate forests, helping watershed managers to improve related ecosystem functions.

## 1.1 Forest and stream dynamics

Forest structure, age, and dynamics affect wood loading in streams. Changes in forest structure over time and space are shaped by the interaction of successional processes and both human and natural disturbances (F. H. Bormann & Likens, 1979; Franklin et al., 2002; Frelich & Graumlich, 1994; Lorimer, 1977; Runkle, 1982). Previous studies suggest that forest age and structural development at the stand scale have a large influence on in-stream ecosystem processes (Keeton et al., 2007; D. R. Warren et al., 2009). Density-dependent tree mortality is high during self-thinning and maturation stages, which results in a high potential for LWD to recruit into streams (Franklin et al., 2002). However, these logs are often smaller in size, their functions in stream geomorphology are limited, and loss rates (e.g. decay, physical transport) are high. Keeton et al., (2007) suggest that wood functions in streams increase with late seral development, when logs reach a diameter of 30 cm or more, and within-channel accumulations increase. At later stand developmental stages, density independent mortality, such as natural disturbances like fire, disease, pathogens, wind and ice storms, accelerate rates of LWD recruitment and accumulation in streams (Franklin et al., 2002; Frelich & Graumlich, 1994; Hanson & Lorimer, 2007).

A range of low to moderate intensity disturbances, like insect outbreaks, or wind- and ice storms, dominate forest dynamics in late-successional and old-growth forests of the northeastern United States (Fahey et al., 2020; Kosiba et al., 2018; Meigs & Keeton, 2018). These intermediate-severity disturbances transfer significant amounts of carbon from live to dead pools by creating high volumes of downed coarse woody detritus (Meigs & Keeton, 2018). Warren et al., (2009) suggest that age of the dominant canopy trees is a robust predictor of volume and frequency of LWD in forested streams of the Northeast. It has also been observed that streams draining old-growth forests exhibit higher LWD loadings compared to streams draining mature forests, and that LWD loadings are higher in stands with high basal area (Bilby & Ward, 1991; Keeton et al., 2007). The proportion of LWD-formed pools to boulder-formed pools is higher in old-growth stands compared to mature stands of hardwood forests in the Adirondacks (Keeton et al., 2007).

Old-growth and late successional stands are often characterized by high structural complexity and elevated volumes of LWD (Franklin et al., 2002; Mcgee et al., 1999). Structural complexity can include elements such as a continuous vertical foliage distribution, variable horizontal densities including gaps and anti-gaps, high amounts of large woody debris, elevated densities of snags and large live legacy trees. Intermediate-severity disturbances alter light availability patterns, while creating legacies with high structural complexity (Meigs et al., 2017; Meigs & Keeton, 2018).

## 1.2 Forests at HBEF – the legacy

Partial harvesting of the forests in the Hubbard Brook Valley began in the early 1800s and intensified in the early 1900s. Between 1907 and 1915 harvest was directed towards merchantable red spruce (*Picea rubens*), along with some balsam fir (*Abies balsamea*) and hemlock (*Tsuga canadensis*). Later hardwoods were cut for bobbins and pulp. In 1921 the Hubbard Brook Valley was incorporated in the

White Mountain National Forest. After that, the vegetation remained largely undisturbed, apart from some salvage logging following a hurricane in 1938 and the experimental harvesting between the mid-1960s and the 1980s (Holmes & Likens, 2016).

Today, HBEF is one of the most comprehensively studied landscapes on Earth (Holmes & Likens, 2016). Forest and stream interactions have been studied using the paired, small-watershed approach. This approach is based on a simple concept: Watersheds are defined as water catchment basins or discrete drainage areas. Stream networks are fed by precipitation. Some of the water entering the watershed ecosystem by precipitation is returned to the atmosphere by evapotranspiration. The runoff collects in a stream. At HBEF, nine small headwater catchment basins have been designated as experimental watershed-ecosystems. These watersheds have gauging weirs where stream water flow and chemistry are measured to calculate nutrient fluxes. Because any two watersheds are not necessarily similar and cannot be considered as scientific "control", adjacent or nearby watersheds are referred to as "reference" watersheds (Holmes & Likens, 2016). Whole watershed manipulation experiments were conducted to test the effects of clearcutting, whole tree harvest, strip cuts, and other disturbances on nutrient budgets, stream water yield and chemistry, forest development, and many other ecosystem processes (F. H. Bormann et al., 2010; Burton & Likens, 1973; Dahlgren & Driscoll, 1994; Likens et al., 1970, 1998; D. R. Warren et al., 2007).

The unusual land use history of the forests in the Hubbard Brook Valley results in a forest structure that differs from many or most secondary forests in the Northeast. Intermediate intensity cutting and removal of large amounts of red spruce in the early 1900s left behind yellow birch (*Betula alleghaniensis*), hemlock and other species that comprise the legacy trees today. Removing most of the mature red spruce increased light levels, thereby releasing the advanced regeneration already present in the understory. This history resulted in multi-aged, second-growth northern hardwood forests with remnant old growth elements, such as standing dead wood and large downed woody debris and large legacy trees (Holmes & Likens, 2016). We would expect that in-stream LWD loadings at HBEF are higher than in other secondary forests of the region but lower compared to old growth forests (Keeton et al., 2007).

### 1.3 The role of large woody debris in streams

Large woody debris (LWD) supports a wide range of processes and functions in stream ecosystems. Wood recruitment into streams occurs either as a result of individual tree mortality or after disturbances of different scales, affecting multiple trees in the riparian forest (D. R. Warren et al., 2009). LWD deposited and subsequently transported by high flows in streams leads to formation of debris dams, which, in turn, sometimes create both scour (above) and plunge (below) pools (Andrus et al., 1988; Bisson et al., 1987; Gurnell & Sweet, 1998; Keller & Swanson, 1979; Montgomery et al., 1995). LWD, debris dams and pools play key roles in many physical, chemical, and biological processes. They alter channel geomorphology, influence nutrient cycling and sediment retention, affect flood resilience and provide habitat for various biota, including fish and macroinvertebrates (Bilby & Likens, 1980; Dahlström & Nilsson, 2004; Groffman et al., 2005; Keeton et al., 2017; Ogren & King, 2008; Roni & Quinn, 2001). Debris dams, for example, are hot spots for anaerobic microbial transformation of inorganic nitrogen into gaseous form. This denitrification process leads to loss of nitrogen gas from the system (Bilby & Likens, 1980; Steinhart et al., 2000). For example, a study at Bear Brook, a low-order stream at HBEF with similar characteristics to the streams included in this study, revealed that the removal of debris dams led to an 18 % increase in export of dissolved organic carbon, an increase of 632 % in export of fine particulate organic carbon and an increase of 138 % in export of coarse particulate organic matter from the system (Bilby & Likens, 1980).

### 1.4 In-stream LWD dynamics

Multiple factors influence longevity, orientation and mobility of LWD in streams. Wood enters the stream as a result of individual tree mortality or as a consequence of disturbances that affect multiple trees (D. R. Warren et al., 2009). Physical abrasion / breakdown and fluvial transport lead to wood export from streams (D. R. Warren et al., 2009). Decay rates are variable and depend largely on tree species and the position of the LWD piece in the stream bed. Frequent drying and wetting results in higher decay rates compared to fully submerged pieces (Bilby et al., 1999). Studies suggest that hardwoods generally decay faster than conifers and that decay rates decrease with increasing stream size (Bilby et al., 1999; Melillo et al., 1983). Stream size also plays an important role regarding mobility and orientation of in-stream LWD. In small streams, where channel width is less than the length of the majority of wood pieces, LWD tends to remain close to where it entered the stream (Gurnell et al., 2002). Bilby & Ward, (1991) state that 40 % of LWD pieces are oriented perpendicularly to the axis of flow in streams of southwestern Washington with less than 7 m channel width. In larger streams, wood tends to be oriented downstream (Bilby & Ward, 1991; Chen et al., 2006).

Based on previous research, we predicted that forest structure, as well as stream characteristics like bankfull width and gradient, influence LWD loading in streams of HBEF. Mobility of in-stream LWD depends on streamflow, bank stability and particularly on length of LWD relative to bankfull width (Gurnell et al., 2002; Lienkaemper & Swanson, 1987; M. K. Young, 1994). Large logs are more likely to remain in the stream for a longer period of time and act as a trap for smaller pieces of wood. Wood mobility is especially low in small streams with low bankfull width (Likens & Bilby, 1982).

Streams included in this study were of first and second order and had an average bankfull width ranging from 2.7 m to 7.6 m. The line-intercept method (LIM) for LWD assessment relies on the assumption that wood is randomly oriented. Bilby & Ward, (1991b) and Chen et al., (2006) report that wood tends to be oriented perpendicular to direction of stream flow in small streams, which would lead to an overestimation of LWD volume using the LIM. However, D. R. Warren et al., (2008) applied the LIM at streams of similar size in the Adirondacks and suggest that the LIM is an effective method for in-stream LWD volume estimation. We assume that most LWD pieces remain relatively close to where they enter the low-order streams of HBEF. Ergo, we propose that LWD loading at a particular site is directly influenced by the structure of the surrounding forest.

### 1.5. Hypotheses and study objectives

The primary objective of the study was to investigate the relationship between forest structure and in-stream LWD loading, with particular focus on the role of large legacy trees. We hypothesize that in-stream LWD loading can be linked to structural attributes of the surrounding forest and that the unique character of these stands with large legacy trees leads to enhanced LWD loading in streams of HBEF.

Previous studies have reported LWD to be a strong predictor for pool frequency and debris dam frequency (Dahlström & Nilsson, 2004; Montgomery et al., 1995; Richmond & Fausch, 1995). We hypothesize that LWD loading is positively associated with debris dam and pool formation in low-order forested streams at HBEF. Understanding this relationship would inform a range of studies exploring processes related to stream geomorphology and in-stream habitat structure.

A secondary objective of the study was to compare different techniques for sampling LWD loading in streams. We applied and compared two methods for LWD assessment in this study. These are the line intercept method (LIM) and the total wood census (TWC) method. The LIM for wood volume estimation as developed by Warren and Olsen, (1964) and modified by Van Wagner, (1968) has been widely applied in forest surveys (Marshall et al., 2000, 2003; Vacik et al., 2000; Waddell, 2002; D. R. Warren et al., 2013; Woldendorp et al., 2004; Woodall & Monleon, 2008). Few studies have used a line-intercept approach for assessing woody debris in streams (Gippel et al., 1996; M. K. Young et al., 2006). D. R. Warren et al., (2008) compared LIM estimates to a TWC in stream reaches of the western Adirondack region, ranging from 120 m to 250 m in length. They suggest that the LIM is an effective method for estimating in-stream large wood volume in small constrained streams (D. R. Warren et al., 2008). To inform future choice of transect length for the LIM and to test the accuracy of the LIM at streams of HBEF we tested the hypothesis that the LIM delivers similar results to a TWC along stream sections of 50 m length, and along stream reaches of 300 m length.

## 2. Material and Methods

### 2.1 Study area and sites

Our study was conducted at the  Hubbard Brook Experimental Forest (HBEF), which is a 3,162 ha bowl-shaped basin located in the White Mountains of New Hampshire, U.S.A. ( 43°56´N, 71°45´W) (Schwarz et al., 2001). Elevations range from 252 m to 1,015 m (Schenck Bailey et al., 2003). Slopes range from 0 % to 70 % with an average of 16 %. The climate is predominately continental with annual precipitation averaging about 1,360 mm, much of it in the form of snow (Schenck Bailey et al., 2003; Schwarz et al., 2001). The northern hardwood forests are dominated by *Betula alleghaniensis, Fagus grandifolia* and

*Acer saccarum,* with minor components of *Tsuga canadensis, Acer pensylvanicum, Acer rubrum, Betula papyrifera*, *Fraxinus americana* and *Populus tremuloides*. *Abies balsamea* and *Picea rubens* predominate in higher elevations, especially on north-facing slopes (Schenck Bailey et al., 2003). The bedrock is composed of sulphidic schist and calc-silicate granulite from the Rangeley Formation and Kinsman Granodiorite (Bailey et al., 2004). The predominant soil type is spodosol, a well-drained, acidic, and relatively infertile soil type with distinctive layers. Spodsols occur under forests in cool, moist climates (Holmes & Likens, 2016). After extensive logging in the early 1900s the forests of the Hubbard Brook Valley were incorporated into the White Mountain National Forest in 1921. Since then the vegetation remained largely undisturbed except some salvage logging after a hurricane in 1938, and experimental harvesting in the mid-1960s and 1980s (Holmes & Likens, 2016).

The Hubbard Brook Valley is oriented in an east-west direction with predominantly north and south facing slopes. The valley is drained by the Hubbard Brook, which is about 14 km long and has 16 major tributaries. Overall, the valley contains approximately 100 km of perennial streams and 25 km of ephemeral streams. Stream flow is lowest during the summer months and peaks in April with the snow melt. Water temperatures range from just above 0 °C to average of 18 °C in summer. From June to October, headwater streams are heavily shaded by the forest canopy, which results in low variability in temperature. Stream waters contain low concentrations of dissolved elements and nutrients, and are moderately acidic, with an average pH of 5.5 (Holmes & Likens, 2016).

Field data were collected among 13 tributary streams of the main stream of Hubbard Brook Watershed (). Data were collected along one 300 m reach (or transect) per stream. Selected reaches were low order (1 or 2) perennial headwater streams. Mean bankfull width ranged between 2.7 m and 7.6 m. Mean stream gradient reached from 5.8 % to 19.9 %. The forests surrounding these streams have remained largely undisturbed since 1920, and can be described as mature with scattered remnant old-growth trees left after partial harvesting in the 19th and early 20th centuries (Holmes & Likens, 2016). An exception was a study reach in Watershed 4 (W4), one of the experimental watersheds. Watershed 4 was strip cut between 1971 and 1975; dominant trees regenerated following cutting were 48 to 52 years of age in 2019 (Burton & Likens, 1973; D. R. Warren et al., 2007).

## 2.2 Stream data collection

Stream and forest surveys were conducted in June and July 2019. In each of the 13 streams, a field tape was laid out along a 300 m longitudinal transect in the center of the bankfull channel. The transect was sub-divided into six sections, each with a length of 50 m.

We applied two methods for the assessment of in-stream LWD. The first was the line-intercept method (LIM), following Warren et al., (2007). Using this method, we only recorded LWD pieces that were intercepting the transect. LWD has been defined as dead wood > 1 m length and > 10 cm diameter at intercept (Andrus et al., 1988; Raikow et al., 1995; Richmond & Fausch, 1995). We recorded the position of the LWD piece along the transect, and measured the diameter at intercept with an accuracy of 0.05 m. We recorded species and decay class (1 to 5) following Sollins et al., (1987).

In addition, we conducted a total wood census (TWC) and assessed all LWD along the 300 m stream reach. LWD was defined as dead wood > 1 m length and > 10 cm diameter at any point. We recorded the position along the transect for every piece meeting the criteria, and measured the length to the nearest 0.5 m. We measured the diameter at a central point to the nearest 0.05 m.

We recorded all debris dams along the 300 m stream reach. Debris dams were defined as accumulations of woody debris with at least two or more pieces of wood with a diameter >1 cm accumulating around one core piece of large woody debris (≥ 1 m in length and ≥ 10 cm in diameter).

We recorded pools along the 300 m stream reach. Pools were defined as sections of the stream channel where water is impounded within a closed topographical depression (Abbe & Montgomery, 1996). Pools must meet certain characteristics to be defined as pools, following Pleus et al., (1999). Pool characteristics vary according to stream size. For streams with a mean bankfull width between 2.5 m and 4.9 m, a pool must have a residual depth of 0.2 m. The residual depth is the difference between the depth at the deepest point and the depth at the outflow point. The area at residual depth (or deeper) must be at least 1 $m^2$. For streams with a mean bankfull width between 5.0 m and 9.9 m the residual depth must be at least 0.25 m, and the area at residual depth or deeper must be at least 2 $m^2$.

### 2.3 Forest data collection

We conducted forest surveys on four variable radius plots within the adjacent forested corridor along each of the 13 stream reaches. At W8 there were six plots to capture structural variability. Forest inventory plots were distributed among four sections of each reach (two on each side, one upstream, the other downstream). Plot centers were located along a corridor running parallel to the stream, at a distance of one maximum tree height from the bank. We determined maximum tree height by measuring the height of the highest canopy trees at every site with an Impulse 200 laser range finder (Laser Technology Inc., Centennial, Colorado, USA). We measured canopy tree height for three to five canopy trees and recorded an average. Plots were located on this corridor to ensure that LWD originating from the plot had the potential to contribute to in-stream LWD. Plots were located at a random point along this corridor. We used a Garmin GPSMAP 64s handheld to record the coordinates at plot center (Garmin Ltd., Olathe, Kansas, USA). We measured gradient and aspect using an inclinometer and a compass, respectively. We used a wedge prism (2.3 metric basal area factor) for the forest inventory. For live trees as well as standing dead trees, we recorded diameter at breast height (dbh, 1.37 m), species, and decay stage (1 to 9) following Sollins et al., (1987). We used the laser range finder to measure the height of dead trees.

### 2.4. Calculation of biometrics

We used the computer software NED3 to calculate 31 forest structure parameters for each site (n = 13) (see Table 2 and Table 4 ) (Twery & Thomasma, 2014).

The following parameters were calculated for each stream (n = 13) and for each stream section (n = 78) (see Table 1 and Table 3): bankfull area in $m^2$, mean bankfull width in m, mean gradient in percent, LWD volume estimate of the LIM, LWD volume of the TWC, LWD frequency estimate of LIM in stems per 100m, LWD frequency of the TWC in stems per 100m, debris dam frequency in debris dams per 100m, pool frequency in pools per 100m.

## 2.5 Statistical analysis

Data analysis was performed using the R language and statistical computing environment (R Core Team, 2020). The packages dplyr (Wickham et al., 2020) and reshape2 (Wickham, 2007) were used for data organization. The packages rstanarm (Goodrich et al., 2020), nlme (Pinheiro et al., 2020) and lme4 (Bates et al., 2015) were used for model building. We used the packages MuMIn (Barton, 2020), bayesplot (Gabry & Mahr, 2020) and loo (Vehtari et al., 2020) for model selection. We used ggeffects (Lüdecke, 2018) for computing marginal effects and ggplot2 (Wickham, 2016) and ggpubr (Alboukadel, 2020) for data visualisation.

### *2.5.1 Investigating the relationship between in-stream LWD and forest structure*

Our first hypothesis is that multiple aspects of forest structural complexity, and particularly large legacy trees, affect in-stream LWD loading.

We used Bayesian generalized linear models (GLMs) to analyse the relationship between forest structure and in-stream LWD and the effects of LWD loading on pool and debris dam frequency. The Bayesian approach best fit the structure of our dataset, considering the large number of parameters, the nested study design, and the relatively small sample size in each group. We used a nested study design where we analysed 78 stream sections of 13 streams. 6 sections (50 m in length) belonged to one stream, or site. We had stream parameter data for all individual stream sections. We used LWD volume and LWD frequency as evaluated in the TWC. Forest structure parameters were assessed per site, so we used the forest structure data recorded at a site for all 6 stream sections of the site. Models were built using data for the 78 stream sections (50 m in length). We used forest and stream parameters as fixed effects and site as the only random effect.

Bayesian modelling was also deemed robust, as it is increasingly used in ecological studies, ranging from predicting single-species population dynamics to understanding ecosystem processes (Dixon & Ellison, 1996; Ellison, 2004; Shen et al., 2003; Toivonen et al., 2001). In the field of forest ecology, Bayesian approaches have been used for modelling diameter distribution, aboveground tree biomass, tree growth, stand level height and volume growth, individual tree mortality, stand basal area distribution, carbon storage, forest ecosystem services and biodiversity (Bullock & Boone, 2007; Clark et al., 2007; Green & Strawderman, 1996; R. Li et al., 2012; Metcalf et al., 2009; Nyström & Ståhl, 2001; D. Thom et al., 2019; Thom & Keeton, 2020; Zapata- et al., 2012).

#### 2.5.1.1. The relationship between LWD volume and forest structure

To avoid collinearity between predictor variables in our models, we checked for correlations among forest-and stream parameters using the Pearson´s correlation coefficient r. A threshold of $|r| = 0.7$ has been suggested as an appropriate indicator for when collinearity starts to distort model estimates and prediction (Dormann et al., 2013). If two or more parameters were correlated with $|r| > 0.7$, we tested the correlation between these parameters and the response (LWD volume). Of the correlated parameters, only the parameter with the highest correlation with the response remained for model building, the others were omitted. This parameter selection process resulted in a set of 16 independent parameters. We scaled and zero-centered the selected parameters and used them as predictor variables for building GLMs.

Bayesian GLMs with group-specific terms were built using the `rstanarm` package in R (Goodrich et al., 2020). We used a log transformation for the response variable LWD volume. The first model included the response log(LWD volume in $m^3*ha^{-1}$) and all 16 parameters as predictors and the random effect of the site.

In a stepwise elimination process, we omitted one parameter in every step, resulting in a new model. Parameters were omitted following standardized criteria. First, we compared the mean effect of all parameters in the model. Then, we omitted the parameter with the lowest mean effect in the next model. If two parameters had the same lowest effect, we compared the standard deviation of the effect. In this case we omitted the parameter with the highest standard deviation of the effect. In case mean effect and standard deviation of the effect were the same, we compared the 10 % and 90 % intervals and omitted the parameter with the higher difference between the 10 % and the 90 % value. This approach resulted in a set of 19 candidate models. We used the expected log predictive density (elpd) as an information criterion to identify the most parsimonious model and performed predictive checks. We visually checked the residuals of the models for normal distribution. We compared the mean Bayesian $R^2$ and mean leave-one-out (LOO) $R^2$ and created marginal effects plots for all parameters included in the best fitting model.

#### 2.5.1.2 Relationship between LWD frequency and forest structure

We used a similar approach to investigate the relationship between in-stream LWD frequency and forest structure. We used a threshold of $|r| > 0.6$ for the parameter selection because a selection with a threshold of $|r| > 0.7$ resulted in a rank deficient model matrix. The parameter selection process with a threshold of $|r| > 0.6$ resulted in a set of 12 parameters, that we scaled and zero-centered and used for model building. The first model included the response sqrt(LWD frequency in stems*100 $m^{-1}$) and all 12 parameters as predictors and the random effect of the site. The stepwise elimination process as described above resulted in 12 models. Then we compared these models using the elpd as information criterion. We performed predictive checks and checked residuals for normal distribution. We compared the mean Bayesian-$R^2$ and mean LOO $R^2$ and created marginal effects plots for all parameters included in the best fitting model.

### *2.5.2 Relationship between LWD, debris dams and pools*

Our second hypothesis assumes that LWD promotes the formation of debris dams and pools. We used a similar Bayesian approach to test this hypothesis.

#### 2.5.2.1. LWD and debris dams

We built Bayesian GLMs to investigate whether debris dam frequency is related to LWD loading and stream profile. We analysed the 78 stream sections (50 m in length) and accounted for the random effect of the site. The first model included LWD volume, LWD frequency, mean bankfull width and mean gradient as predictors of debris dam frequency and the random effect of the site. We applied the stepwise elimination process as described above for models with different transformations of the response, which resulted in a set of 13 models. We then compared the elpd of these models and performed predictive checks. Residuals were visually tested for normal distribution. We calculated mean Bayesian $R^2$ and mean LOO $R^2$ values, and created marginal effects plots for the parameters in the final model.

#### 2.5.2.2. LWD and pools

We used a similar approach to investigate whether pool frequency depends on LWD loading or stream profile. The first model included LWD Volume, LWD frequency, mean bankfull width and mean gradient as predictors for pool frequency and the random effect of the site. We applied the stepwise elimination process for models with different transformations of the response. This resulted in a set of 15 models. We compared the elpd of these models, and performed predictive checks. Residuals were visually tested for normal distribution. We calculated mean Bayesian $R^2$ and mean LOO $R^2$ values and plotted marginal effects for the parameters in the final model.

### *2.5.3 LWD inventory method comparison*

The third hypothesis assumes that the LIM delivers similar results compared to the TWC. To test this hypothesis, in-stream LWD volume per hectare was assessed and estimated in two different ways. The LIM as developed by Warren and Olsen, (1964) and Van Wagner C.E., (1968), as modified by Shiver and Borders, (1996) uses the following equation to calculate LWD volume per ha:

$$V_{LIM} = (\frac{\pi^2}{8L}) \sum d_i^2$$

where $V_{LIM}$ = the estimated wood volume in cubic meters per hectare, L = transect length in meters, and d = log diameter in centimetres. We assumed a cylindrical log shape for volume estimates using the total wood census and calculated LWD volume per ha using the equation

$$V_{TWC} = \frac{\pi * \left(\frac{d}{2}\right)^2 * l}{A}$$

Where $V_{TWC}$ = the estimated wood volume in cubic meters per hectare, d= log diameter in meters, l = log length in meters and A= area of the bankfull in ha. The two volume estimates were compared.

The Pearson´s correlation between the two volume estimates was calculated for the 50 m stream sections (n = 78) and for the 300 m stream reaches (n = 13). Pairwise Wilcoxon signed-rank tests were performed to compare the volume estimates for each 50 m section (n = 78) as well as the mean volume estimates for each stream (n = 13).

# 3. Results

## 3.1 Forest structure influences LWD loading

The results supported our primary hypothesis that forest structure, and particularly large legacy trees, affect LWD loading in streams, although there was a wide range of variability in wood loading across the streams we sampled (Figure 2, Figure 3). Big tree density and density of dead trees were important predictors for both LWD volume and frequency.

### *3.1.1 Forest structure and LWD volume*

LWD volume was also highly variable at the resolution of 50 m long stream sections, ranging from 3.94 $m^3$*$ha^{-1}$ to 344.50 $m^3$*$ha^{-1}$. LWD volume of stream reaches varied between 16.32 $m^3$*$ha^{-1}$ and 127.10 $m^3$*$ha^{-1}$. The streams had an average LWD volume of 55.55 $m^3$*$ha^{-1}$ (Figure 2). This variability could be attributed to a number of forest structural parameters based on the Bayesian statistical models. For example, the best fitting and most parsimonious model explained the relationship between in-stream LWD volume and forest structure as a function of eight forest structure parameters and bankfull width.

In-stream LWD volume showed positive relationships with big tree density and the standard deviation (sd) of basal area. In-stream LWD volume was negatively related to live tree density, percentage of conifers, mean bankfull width, sd of big tree density, relative density, dead tree density, and quadratic mean diameter (QMD) (**Figure** 4).

### *3.1.2 Forest structure and LWD frequency*

Density of big trees, dead tree density, and QMD all influence LWD frequency in streams based on our results. LWD frequency was highly variable within reaches (i.e. as measured at the scale of stream sub-sections), ranging from 4 to 62 logs per 100 m. This range was slightly narrower at whole stream reach scales, with mean LWD frequency varying from 15 to 40 pieces per 100 m (Figure 3. The average LWD frequency among the sampled streams was 24 pieces per 100m. The most parsimonious model describing the relationship between LWD frequency and forest structure contained five parameters. However, the elpd differences between models were marginal and ranged from 0.2 to 6.3. QMD and big tree density exhibited a positive relationship with LWD frequency. This compared with dead tree density, sd of QMD, and sd of big tree density, which were all negatively related to LWD frequency (Figure 5).

### 3.2 Function of LWD in streams

Our results supported the hypothesis that LWD loading influences debris-dam frequency, but pool frequency depended on stream geomorphology rather than LWD loading.

#### *3.2.1 LWD enhances debris dam frequency*

The potential for debris dams to form is highly dependent on LWD frequency based on our results. We reached this conclusion because the best fitting and most parsimonious model for the relationship between debris dams and LWD loading described debris dam frequency as a function of LWD frequency rather than LWD volume or stream profile (**Figure** 6). Debris dam frequency and LWD frequency exhibit a strong positive correlation (Pearson´s r = 0.80). Yet the strength of these relationships was influenced by the high degree of variability within our dataset. For example, debris dam frequency (averaging 9 dams per 100 m of stream channel) ranged from 0 to 12 debris dams per 50 m stream section. Debris dam frequency among streams varied between 3 and 18 debris dams per 100 m (Table 3).

#### *3.2.2 Pool frequency depends on stream geomorphology*

In our data, pool frequency appeared to be more strongly related to stream profile than to LWD loading, possibly due to the very high abundance of boulders, which also form pools. The best fitting and most parsimonious model for pool frequency included only mean bankfull width and mean gradient as predictors (Figure 7). Pool frequency varied between 0 and 8 pools per stream section. Among stream reaches, pool frequency ranged between 0 and 10 pools per 10 m. The average among the surveyed streams is 5 pools per 100 m (Table 3).

### 3.3. Accuracy of the LIM is scale dependent

Our results did not support the hypothesis that the LIM and the TWC deliver similar estimates on a scale of stream sections (50 m in length). However, no significant difference between the two methods was detected on the scale of stream reaches (300 m in length). The results showed a clear scale dependency in the relative accuracy of the two methods we tested for estimating wood loading in stream channels (Figure 8). The volume estimates resulting from the LIM correlate with the volume estimates resulting from the TWC. LWD volume estimates using the LIM ranged from 2.46 $m^3*ha^{-1}$ to 144.95 $m^3*ha^{-1}$ for 50 m sections and from 15.05 $m^3*ha^{-1}$ to 74.63 $m^3*ha^{-1}$ for 300 m stream reaches. LWD volumes assessed in the TWC ranged from 3.94 $m^3*ha^{-1}$ to 344.50 $m^3*ha^{-1}$ for 50 m sections and from 16.32 $m^3*ha^{-1}$ to 127.10 $m^3*ha^{-1}$ for 300 m stream reaches. The volume estimates of the 50 m stream sections correlated positively with Pearson´s r = 0.6627091. The volume estimates for the 300 m stream reaches were positively correlated with Pearson´s r = 0.7763514.

The results of the pairwise Wilcoxon signed-rank test where volume estimates of the 78 50 m sections were compared, suggest that there is a significant difference (p-value = 0.001338) between the volume estimates of the LIM and the volume estimates of the TWC.

The equation for the best fitting linear regression line (p-value = 3.865e-11, adjusted $R^2 = 0.4318$) relating the LIM LWD volume estimate and the LWD volume resulting from the TWC is as follows for comparison of 50 m sections:

$$(LIM - LWD\ volume) = 0.49 * (TWC - LWD\ volume) + 13.14$$

The equation for the best fitting linear regression line (p-value = 0.001804, adjusted $R^2 = 0.5666$) relating the LIM LWD volume estimate and the LWD volume resulting from the TWC is as follows for comparison of 300 m stream reaches:

$$(LIM - LWD\ volume) = 0.43 * (TWC - LWD\ volume) + 19.90$$

In contrast, the results of the pairwise Wilcoxon signed-rank test where volume estimates of the 13 300 m stream reaches were compared suggest that there is no significant difference (p-value = 0.1677) between the volume estimates of the LIM and the volume estimates of the TWC.

# 4. Discussion

## 4.1. Remnant old-growth trees enhance LWD loading in streams

Our results support the hypothesis that forest structure, and particularly large legacy trees, influence LWD loading in streams. The relationship between in-stream LWD and forest structure is complex. In-stream LWD loading is closely linked to a set of forest and stream characteristics, including the presence and abundance of large diameter remnant old-growth (or "legacy") trees. Our study reveals that big tree density and dead tree density are important predictors for both LWD volume and LWD frequency.

### *4.1.1. Drivers of in-stream LWD volume*

In-stream LWD volume can be described as a function of big tree density, live tree density, percent conifers, mean bankfull width, sd of big tree density, sd of relative density, dead tree density, quadratic mean dbh and sd of total basal area. The relative effect of each individual parameter is interpreted in the following sub-sections.

#### 4.1.1.1. Big tree density enhances LWD volume

As suggested by Keeton, Kraft and Warren, (2007) we expected large remnant trees to increase structural complexity of the second growth stands at HBEF and to enhance in-stream LWD loadings. Our results clearly supported this hypothesis. The strong positive effect of big tree density on in-stream LWD volume and the low standard error suggest that remnant old-growth trees enhance LWD loading in streams of HBEF. Big trees are important structural elements of old growth forests, which generally exhibit higher terrestrial and in-stream LWD loadings (Bauhus et al., 2009; Bilby & Ward, 1991; Burrascano et al., 2013; Franklin et al., 2002; Keeton, 2006; Keeton et al., 2007; Keren & Diaci, 2018).

#### 4.1.1.2. Live tree density reduces LWD volume

In-stream LWD volume decreases with increasing density of live trees. A possible explanation for this negative relationship is that young stands with high densities of living trees are characterized by low amounts of dead wood. Density dependent tree mortality in these stands may be high, but the resulting woody debris stems are often relatively thin compared to later seral stages and may result in high woody debris frequencies rather than volumes (Franklin et al., 2002).

#### 4.1.1.3. Conifer percentage reduces LWD volume

In-stream LWD volume decreases when percentage of conifers increases. This relationship stands in contrast to findings of Harmon *et al.*, (2004), who mention that in general deciduous forests produce less coarse woody debris than coniferous forests and that conifers decay slower than deciduous trees. A possible explanation why there appears to be more LWD in streams surrounded by deciduous trees is that mortality of particularly large beech trees may be elevated because of beech bark disease (Forrester et al., 2003; Van Doorn et al., 2011). Dieback of these large trees may significantly contribute to in-stream LWD volume.

#### 4.1.1.4. Bankfull width reduces LWD volume

The results suggest a negative relationship between LWD volume and mean bankfull width. This stands in contrast to findings of Chen *et al.*, (2006), who found that LWD volume increases with bankfull width in streams of the southern interior of British Columbia. Cordova *et al.*, (2007) report that LWD volume and bankfull width:depth ratio is negatively correlated in streams of the midwestern United States, but that bankfull width does not have a significant influence on LWD volume. However, Keeton et al., (2007) discovered that in-stream LWD volume decreases with increasing bankfull width in low-order streams of the western Adirondacks, streams that seem very similar to the ones surveyed at HBEF. They mentioned the possibility of increased discharge and heavy ice flows at some of their sites as a reason for this negative relationship. We observed piles of large woody debris accumulating around trees growing in close proximity to the stream bank at some of the larger streams surveyed at HBEF. These large pieces of wood may have been blown out of the streambed during high flow events. Long term data recording stream flow at HBEF suggest that elevated discharge and high flow events occur in spring following snow melt (J. L. Campbell et al., 2011; Schenck Bailey et al., 2003).

#### 4.1.1.5. Variability in big tree density reduces LWD volume

Standard deviation of big tree density and LWD volume exhibit a negative correlation. Standard deviation of big tree density was included in the model as a parameter describing the variability of big tree density per site. According to Franklin *et al.*, (2002) the attribute structure does not only include individual structures such as trees, snags and logs, but also the variability of these structures. As an example, we would not expect an old-growth forest to be composed of predominantly big trees. We would rather expect a mosaic of different age classes in a structurally complex forest. Assuming that in-stream LWD volume increases in a structurally more complex forest we would expect in-stream LWD volume to increase with the variability of big tree density. This makes our results difficult to interpret. In general, sites with high densities of big trees showed intermediate variability in big tree density. Sites with lower densities of big trees showed very little variability or higher variability than stands with high big tree density. It is possible that in-stream LWD and standard deviation of big tree density show a negative relationship because sites with low variability in big tree density often had lower big tree densities. Also, it is possible that four variable radius plots are not enough, or at an inadequate scale, to describe the variability within a stand.

#### 4.1.1.6. Variability in relative density reduces LWD volume

Similarly, in-stream LWD volume seems to decrease as the standard deviation of relative density increases. Following a concept of forest development in multiple pathways as suggested by Franklin et al., (2002), we would expect a structurally complex forest to be composed of patches with different age classes and therefore a high variability of relative density. As Keeton et al., (2007) suggest, we would expect more LWD in streams surrounded by structurally complex forests. However, our results show that high variability of relative density results in less in-stream LWD volume. The effects of this parameter, however, are accompanied by high standard errors when sd of relative density decreases. This means that for sites with low variability in relative density, the effects on in-stream LWD volume are generally positive but very uncertain in magnitude. It is possible that the standard deviation between four plots is not an adequate measure for describing variability in relative density, and more plots or differently scaled plots would be needed to increase the accuracy of this parameter.

#### 4.1.1.7. Dead tree density reduces LWD volume

In-stream LWD volume decreases with increasing density of dead trees. A general assumption would be that streams surrounded by forests bearing high amounts of dead wood would also exhibit high LWD loadings. It must be noted that in this study only standing dead wood has been assessed, but not downed woody debris on the forest floor. This is likely the reason why streams surrounded by high densities of standing dead wood exhibit lower LWD volumes than streams with low densities of standing dead trees (where dead trees may be scattered across the forest floor as downed woody debris e.g., as a result of a windstorm). Especially the mountainside vegetation is subject to frequent disturbances by windstorms (Bormann et al., 1970). Windstorm created legacies are characterized by few remaining large living trees, snags and high amounts of downed logs (Cooper-Ellis et al., 1999; Franklin et al., 2002). We observed patches with windthrow legacies. These patches had low densities of living and dead trees, but high abundances of downed logs, which in some cases directly contributed to in-stream LWD loading.

#### 4.1.1.8. QMD reduces LWD volume

In-stream LWD volume decreases as QMD increases. The QMD is a measure for average tree diameter commonly used in forestry as a surrogate for arithmetic mean basal area (Curtis & Marshall, 2000). Old-growth forests are characterized by higher QMD (Burrascano et al., 2013). We would expect in-stream

LWD volume to increase with basal area as suggested by Keeton et al., (2007), and therefore also with increasing QMD. It is difficult to explain why our data suggest a negative relationship between in-stream LWD volume and QMD. It is likely that sites with younger, thinner trees at HBEF have high rates of inter-stem competition and self-thinning and, therefore, dead wood recruitment into stream channels (Bormann et al., 1970). This could potentially lead to increased LWD volumes in streams of these stands. However, more research is needed to confirm this hypothesis.

#### 4.1.1.9. Variability in basal area enhances LWD volume

In-stream LWD increases with increasing standard deviation of total basal area. The standard deviation of total basal area describes the variability of basal area within the stand. The positive relationship between in-stream LWD volume and sd of total basal area supports the assumption that a complex forest structure, which is characterized by cohorts of trees at different age classes resulting in patches with different basal area, promotes in-stream LWD (Franklin et al., 2002). However, to investigate this relationship in further studies, we suggest more than four plots to capture variability in basal area.

### *4.1.2 Drivers of in-stream LWD frequency*

In-stream LWD frequency can be described as a function of QMD, big tree density, dead tree density, sd of QMD and sd of big tree density. The relative effects of the individual parameters are interpreted in the following sub-sections.

#### 4.1.2.1. QMD enhances LWD frequency

LWD frequency increases with QMD. This relationship is supported by findings of other researchers. Bilby and Ward, (1991) suggest that in-stream LWD frequency is elevated in old-growth forests compared to second-growth forests in Southwestern Washington. Burrascano *et al.*, (2013) report that old-growth forests generally exhibit higher QMD and higher LWD volumes than second growth forests.

Since the surveyed sites at HBEF are second growth forests with old growth elements, we would expect increasing LWD frequencies with elevated QMD. Our results support this assumption.

#### 4.1.2.2. Big tree density enhances LWD frequency

LWD frequency increases with big tree density. Since big trees are important structural elements of old growth forests and streams draining old-growth forests are characterized by higher LWD frequencies, we expected an increase of LWD frequency with increasing density of big trees (Bauhus et al., 2009; Bilby & Ward, 1991; Burrascano et al., 2013; Franklin et al., 2002; Keeton, 2006). Our results clearly support this assumption.

#### 4.1.2.3. Dead tree density reduces LWD frequency

LWD frequency decreases with increasing density of dead trees. This relationship is similar to the negative relationship between LWD volume and density of dead trees. One possible explanation for this relation is that only standing dead trees were assessed to describe dead tree density. Standing dead trees may not be a good predictor for downed woody debris on the forest floor or in-stream LWD, which is obviously no longer standing.

#### 4.1.2.4. Variability in QMD reduces LWD frequency

LWD frequency is negatively related to the standard deviation of QMD. Sd of QMD is a measure describing the variability of QMD in the stand. Following the concept of Franklin *et al.*, (2002), we would expect a forest with high structural complexity to be composed as a mosaic of cohorts at different age classes and therefore also at different diameters. We would expect high variability in QMD to create a more complex structure, which would enhance in-stream LWD frequency. However, our results do not support this assumption. It is possible that relatively young stands with low variability in diameter, experience high competitive exclusion and density dependent mortality, which contributes high frequencies of LWD to streams draining these stands (Franklin et al., 2002). It is also possible that the variability among four plots does not adequately describe the spatial heterogeneity of QMD within a stand. A more intensive sub-sampling regime might be required to capture this variability.

#### 4.1.2.5. Variability in big tree density reduces LWD frequency

LWD frequency decreases with increasing standard deviation of big tree density. This relationship does not support our assumptions and is difficult to explain. Assuming that a structurally complex forest with high LWD frequencies is composed of cohorts at different age classes, we would assume that the variability of big tree density leads to an elevated LWD frequency in streams draining these forests (Bilby & Ward, 1991; Franklin et al., 2002; Keeton et al., 2007). However, old, remnant trees may no longer be surrounded by cohorts of their age class but may rather be dispersed throughout the forest. It is possible that stands with evenly high densities of big trees contribute more in-stream LWD than stands with variable densities of big trees. However, evidence supporting this assumption is needed. Potentially four variable radius plots per site do not adequately describe the variability of big tree density within a stand.

### *4.1.3 In-stream LWD loading compared to other forests of the region*

Low-order streams at HBEF exhibited elevated LWD volumes but lower LWD frequencies compared to streams draining other mature forests of the region. Keeton et al., (2007) assessed LWD loading in low-order streams surrounded by mature, mature with remnant old-growth trees, and old-growth forests of the Adirondacks. They found average in-stream LWD volumes of 34 $m^3*ha^{-1}$ in mature forests, 126 $m^3*ha^{-1}$ in mature forests with remnant old-growth trees and 200 $m^3*ha^{-1}$ in old growth forests. With 55.55 $m^3*ha^{-1}$ the average LWD volume of streams at HBEF is therefore higher than LWD volumes in streams draining mature forests of the region. These findings underline the unique character of mature stands with old-growth elements at HBEF. In both studies the presence of big legacy trees stands out as an important structural attribute that enhances LWD volume in streams.

Warren and Kraft, (2008) assessed LWD frequency over four years in a forested mountain stream of the eastern Adirondacks. They found between 122 and 158 pieces in the 400 m long reach (30.5 to 39.5

pieces*100 $m^{-1}$). With 24.18 pieces*100 $m^{-1}$ the average of low-order streams at HBEF was lower than reported for the forested stream in the Adirondacks. However, with an estimated stand age between 60 and 80 years, the forest surrounding this reach seems younger than most stands at HBEF, which have been largely undisturbed after 1920 with the exception of experimental logging in some watersheds (Holmes & Likens, 2016). Franklin et al., (2002) mention a high potential for elevated downed woody debris frequencies in younger stands resulting from density-dependent tree mortality.

## 4.2. LWD as an important structural element of low-order streams

Our study reveals that LWD promotes the formation of debris dams, whereas pool formation depends largely on stream geomorphology. LWD frequency is a strong predictor for debris dam frequency, while pool frequency can be associated with bankfull width and gradient. We discuss explanations for these relationships in the following sub-sections.

### *4.2.1. LWD frequency promotes debris dam formation*

LWD frequency is a strong predictor for debris dam frequency. The most parsimonious model for debris dam frequency included LWD frequency as single predictor, with a narrow uncertainty interval. Mean bankfull width, mean gradient and LWD volume did not turn out as important predictors for debris dam frequency. Keeton et al., (2007) report that debris dam frequency was strongly linked to LWD volume. Our results suggest that the number of LWD pieces is more important than LWD volume. The more pieces of LWD present, the more they function as chore pieces and trap other debris. Debris dams alter stream geomorphology, influence sedimentation and nutrient cycling and provide habitat for biodiversity (Bilby & Likens, 1980; Gurnell & Sweet, 1998; Keller & Swanson, 1979; Montgomery et al., 1995; Smock et al., 1987; Steinhart et al., 2000). Debris dam frequency is strongly linked to LWD frequency, which in turn depends on riparian forest structure. Warren *et al.*, (2007) report that debris dam frequencies at HBEF are high in streams draining young forests, low in streams draining forests around 20 to 30 years and increase again as forests mature. We expect debris dam frequency to increase as northern hardwood forests of the Northeast develop towards a later-successional condition. Managing for late-successional or old-growth elements and enhancing structural complexity of riparian forests may also promote debris dams and their ecosystem functions in forested streams (Keeton, 2006).

### *4.2.2. Stream geomorphology drives pool formation*

The results show that pool frequency of low-order streams at HBEF depends on mean gradient and mean bankfull width, rather than on LWD volume and LWD frequency. This stands in contrast to Montgomery *et al.*, (1995) and Andrus et al., (1988) who stress the importance of LWD in pool formation. Bilby & Ward, (1991) report that frequency of LWD associated pools decreases with increasing stream size and that LWD associated pools occur more frequently in streams draining old-growth forests compared to streams draining second-growth or clear cut forests of southeastern Washington. Rosenfeld & Huato, (2003) found a weak relationship between pool spacing and LWD abundance in small coastal streams of British Columbia. They also report significantly lower pool spacing in steeper streams and streams with lower bankfull width compared to low-gradient streams and streams with greater bankfull width. Rosenfeld & Huato, (2003) stress the importance of big trees (> 60 cm dbh) in pool formation, warning that the impact of riparian management that reduces the number of large-diameter trees on stream geomorphology may often be underestimated. Kreutzweiser et al., (2005) found that LWD only had little influence on pool formation in boreal streams of Canada and that pool frequency was not related to stream size. Keeton et al., (2007) state that geomorphic variables like boulders and bankfull width also influence pool frequency in Adirondack streams and suggest to consider LWD as subsidy that increases pool-forming potential. It seems that drivers of pool frequency and spacing vary among streams of different regions and ecosystems.

## 4.3. Orientation bias and transect length affect LIM estimates

The accuracy of the LIM is scale dependent and can be greatly reduced if random orientation of LWD is not given. The results of the method comparison suggest that the LIM delivers more accurate volume estimates along the 300 m transects (Pearson´s $r = 0.7763$) than along 50 m sections (Pearson´s $r = 0.6627$). The LIM and the TWC deliver significantly different results according to the comparison of 50 m sections (n = 78) but no significant differences according to the comparison of the 300 m transects (n = 13). This might be due to the small sample size in the stream comparison. The results show that the LIM underestimates LWD volume, particularly as LWD volume increases. D. R. Warren et al., (2008) applied the LIM at 11 stream reaches in mixed hardwood–conifer forests of the western Adirondacks ranging from 120 m to 250 m in length. Their LIM volume estimates were highly correlated with TWC. They suggest that the LIM is an effective technique for estimating LWD loading in small constraint streams. This stands in contrast to the results of this survey. The reason for this discrepancy could be that LWD pieces may not be randomly oriented in the surveyed streams at HBEF. Chen *et al.*, (2006) assessed LWD orientation in streams of British Columbia and found that LWD is primarily oriented perpendicular to the bank in streams with a mean bankfull width < 3 m and predominantly oriented parallel to the bank in streams with a mean bankfull width > 3 m. (Bilby & Ward, 1991) reported 7 m as the bankfull width where wood orientation changes from predominantly parallel to predominantly perpendicular in streams of southwestern Washington. Streams of our survey ranged from 2.71 m to 7.61 m mean bankfull width, with only three streams being < 3 m. Our personal observation was that LWD often accumulated along the stream bank parallel to stream flow. These LWD pieces were not captured with the LIM, which could be the reason why the LIM underestimated LWD volume of these streams. The LIM is often less time consuming than a TWC, but must be used with caution when random orientation of LWD is not given. In streams where LWD is primarily oriented parallel to the stream bank, a set of transects oriented perpendicular to the stream would overestimate LWD volume as in Gippel et al., (1996). In terrestrial settings, effects of orientation bias can be greatly reduced by running two perpendicular transects or three transects at an angle of 120° (Van Wagner C. E., 1968). In streams where random orientation of LWD cannot be assumed, a combination of transects at different angles, similar as applied by Latterell et al., (2006) may be useful.

### 4.4. The importance of big legacy trees for stream ecosystems

Our study reveals the importance of legacy trees for in-stream LWD recruitment. The unique character of the forests at HBEF with mature stands and old-growth elements resulted from historical forest management practices. The selective logging of merchantable trees in the early 1900s left behind smaller trees and trees of undesirable quality, which comprise the legacy trees of today. Previous studies highlight the importance of legacy trees in forest ecosystems (Keeton & Franklin, 2005; Mazurek & Zielinski, 2004; North et al., 1999). Our study brings to light that legacy trees have a major effect on stream ecosystems. Our results show that streams draining stands with elevated densities of big legacy trees exhibit higher LWD volumes and frequencies. Our results also show that LWD frequency enhances debris dam formation in streams of HBEF. Numerous studies list the important role of LWD and debris dams in stream ecosystems, such as flood resilience, sediment retention, nutrient cycling, and habitat diversification (Bilby & Likens, 1980; Dahlström & Nilsson, 2004; Groffman et al., 2005; Keeton et al., 2017; Roni & Quinn, 2001). It will be crucial to maintain these ecosystem services in the future by promoting LWD in streams.

#### 4.4.1. Changing forests and streams

Climate change is one of the greatest threats to forest ecosystems and biodiversity (Sala et al., 2000; Schröter et al., 2005; Thomas et al., 2004). It remains poorly understood how forests will develop in a changing climate and how these changes will affect ecosystem services and biodiversity. Younger forests may be more sensitive towards changes compared to older forests, and the mix of ecosystem services provided by younger forests may change more dramatically while remaining stable in old forests (Thom et al., 2019). Forests with old legacy trees may have greater capacities to sustain favourable microclimates for habitat specific biota than even-aged young forests (Franklin et al., 2002; Fritz et al., 2009).

Climate change will also affect rainfall distributions, soil moisture, runoff, and water supplies to catchment basins. Changes in flow regimes and flow characteristics can strongly affect stream ecology (Rolls & Bond, 2017). Increases in discharge variability, reduction of base flow and an increasing water temperature may lead to habitat loss, declines in populations and species richness, and altered species-compositions (Casas-Mulet et al., 2014; Eaton & Scheller, 1996; Kupferberg et al., 2012; Perkin & Bonner, 2014). By regulating stream flow, nutrient cycling, and providing habitat for various biota, large woody debris could become a key attribute in ameliorating the effects of climate change on low-order streams (Gurnell et al., 2002; Harmon et al., 2004; Keller & Swanson, 1979).

### 4.4.2. Forests ameliorate climate effects on streams

Forests may have an increasingly important role in buffering climate effects on streams. In-stream productivity and water temperature strongly depend on light availability, which is regulated by shading effects of the forest canopy (Johnson, 2004; D. R. Warren et al., 2013). Keeton et al., (2017) suggest that streams running through forests of greater structural complexity may be more resilient to flood events. Forests themselves are important climate regulators and function as carbon sinks (K. T. Davis et al., 2019; Nunery & Keeton, 2010).

## 4.5. Managing the forests of our future

The significant role of forests in the fight against climate change is becoming more and more apparent. It will not only be essential to maintain and protect old-growth forest ecosystems, their functions, processes, and biodiversity, but also to incorporate management practices that promote structural complexity and biological legacies in commercially used forests. An example for ecologically based silviculture, with focus on biological legacies and natural regeneration, is legacy tree retention. The concept of legacy tree retention was established in the Pacific Northwest in the late 1980s and is now applied around the globe (Gustafsson et al., 2012). However, silvicultural guidelines, best management practices, and forest regulations vary strongly between states, regions, and countries (Gustafsson et al., 2010, 2012). The practice of legacy tree retention (sometimes called green tree retention, variable retention, or retention felling) spares selected patches or single trees from being logged during harvest operations. These retained structures have significant effects on forest characteristics, regeneration and biodiversity patterns (Gustafsson et al., 2010; Keeton & Franklin, 2005; Lie et al., 2009). The practice of structural complexity enhancement (SCE) accelerates the development of secondary forests towards old-growth and focuses on the creation of structural complexity by emulating natural disturbance and stand development processes (Fassnacht et al., 2015). Recent research reveals the effectiveness of SCE in enhancing carbon storage and LWD volumes in northern hardwood forests (Ford & Keeton, 2017; Keeton, 2006).

## 5. Conclusion

The unique character of second-growth forests with old-growth elements at HBEF leads to elevated LWD loadings in streams. Our study highlights the importance of large legacy trees as a forest structural attribute, enhancing LWD loading in low-order streams of HBEF. Although the relationship between LWD loading and forest structure was complex and depended on many variables, big tree density was an important predictor for both, LWD volume and LWD frequency. LWD plays an important role in enhancing in-stream habitat diversity by creating debris dams. Our results confirm that debris dam frequency strongly depended on LWD frequency. Pool frequency was closely related to stream geomorphology. The comparison of the LIM and the TWC revealed that the accuracy of the LIM is scale dependent and increases with the length of the transect. We conclude that the LIM is only accurate at larger scales, where there is sufficient distance to intercept enough logs to compensate for missed logs associated with finer scale variability in log distribution. Finally, we want to stress that it will be crucial to adapt management practices that promote legacy trees and in-stream LWD to maintain functionality of forest and stream ecosystems in the future, and to ameliorate detrimental effects of climate change.

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# Figures

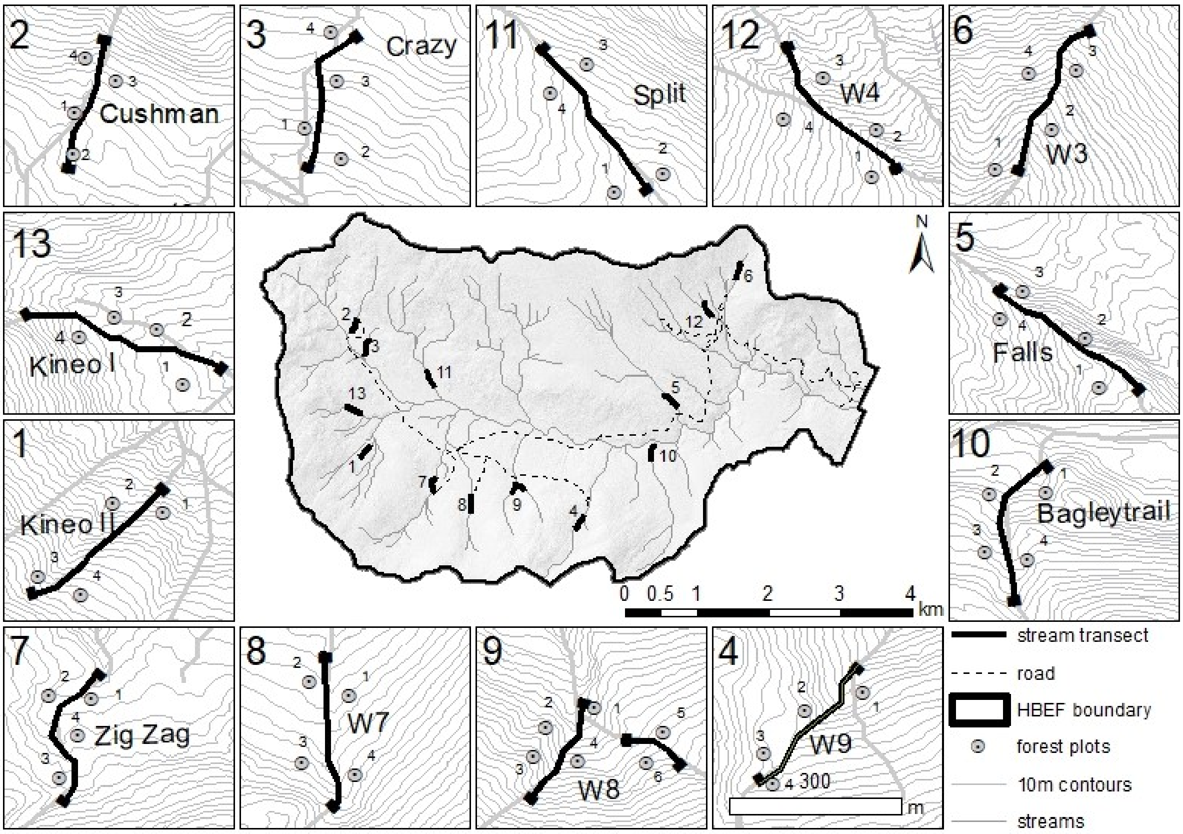


**Figure 1: Locations of study sites at Hubbard Brook Experimental Forest: 1: Kineo2, 2: Cushman, 3: Crazy, 4: W9, 5: Falls, 6: W3, 7: Zigzag, 8:W7, 9:W8, 10:Bagleytrail, 11: Split, 12: W4, 13: Kineo1. This figure includes shapefiles as obtained from Scott Bailey and hubbardbrook.org.**

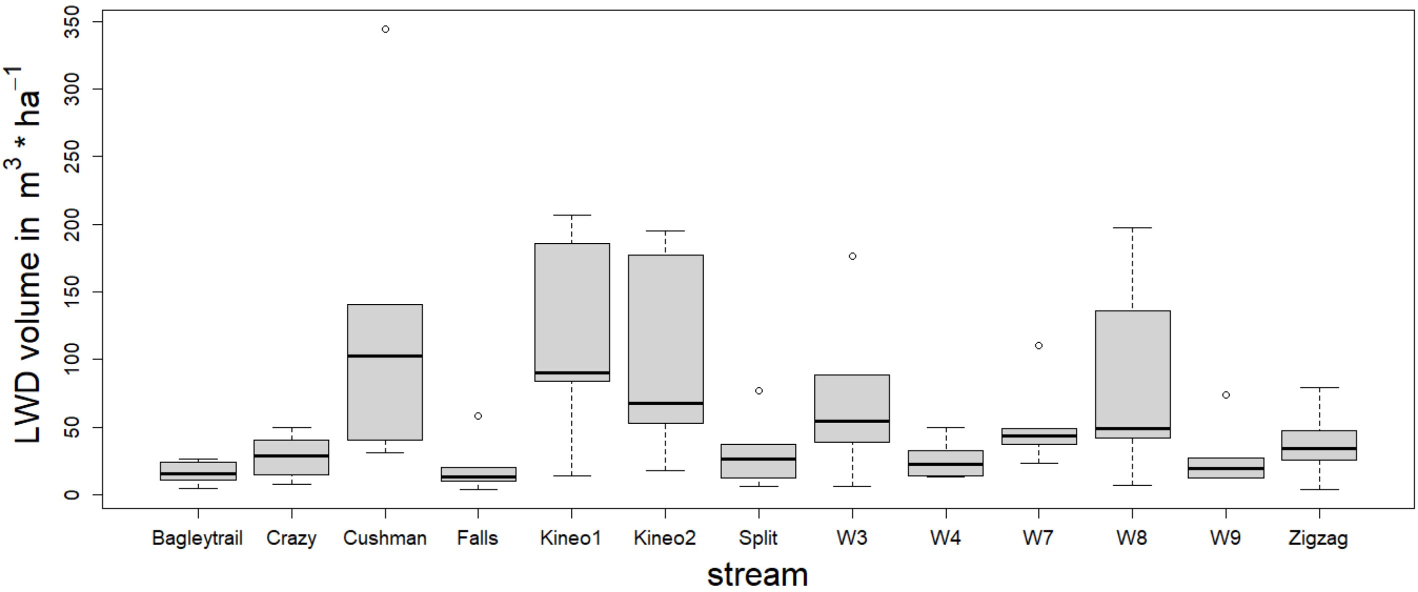


**Figure 2: Boxplots of in-stream LWD volume by stream reach. The box represents the interquartile range (IQR) of the data. The black line represents the median. Whiskers represent reasonable extremes of the data, that do not exceed the distance of 1.5*IQR. Points exceeding this distance (outliers) are plotted as single points.**

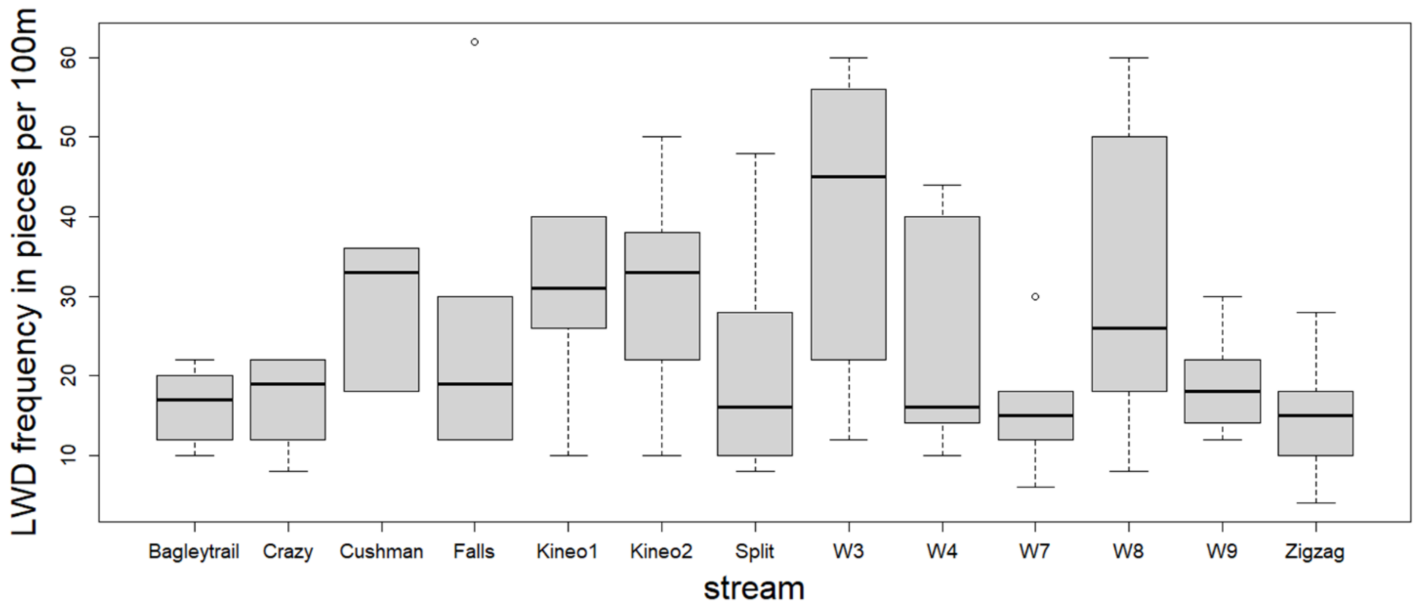


**Figure 3: Boxplots of in-stream LWD frequency by stream reach. The box represents the interquartile range (IQR) of the data. The black line represents the median. Whiskers represent reasonable extremes of the data, that do not exceed the distance of 1.5*IQR. Points exceeding this distance (outliers) are plotted as single points.**

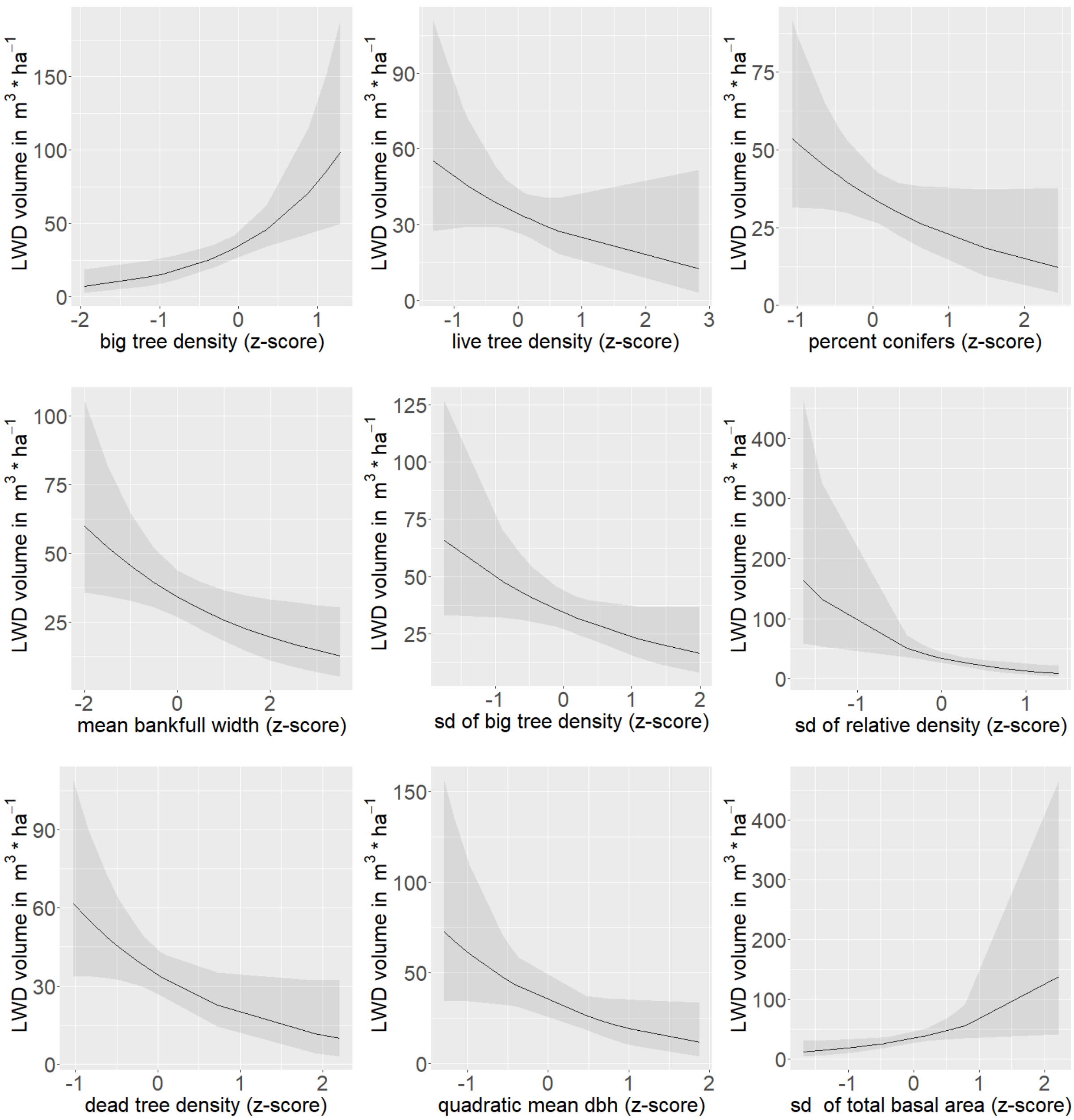


**Figure 4: Marginal effect plots for parameters included in the most parsimonious model describing the relationship between in-stream LWD volume and forest structure. Parameters have been standardized (z-score).**

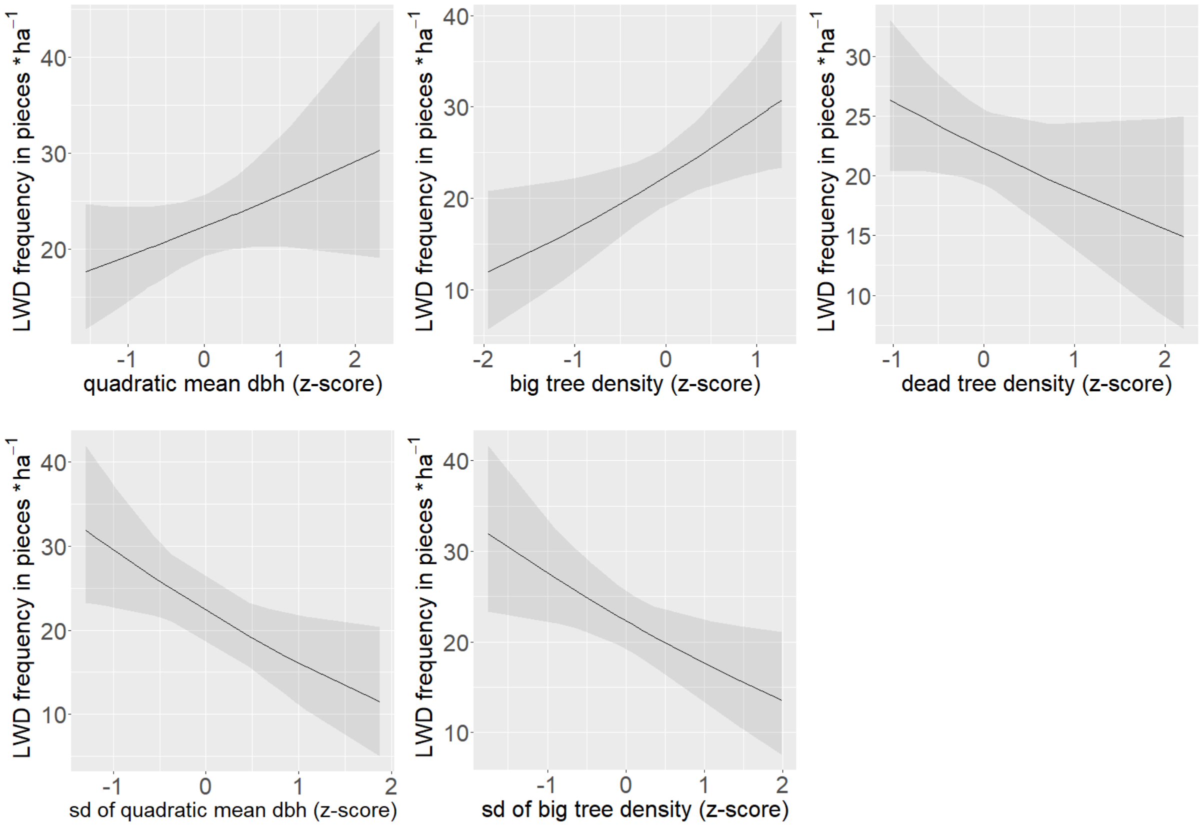


**Figure 5: Marginal effect plots for parameters included in the most parsimonious model describing the relationship between in-stream LWD frequency and forest structure. Parameters have been standardized (z-score).**

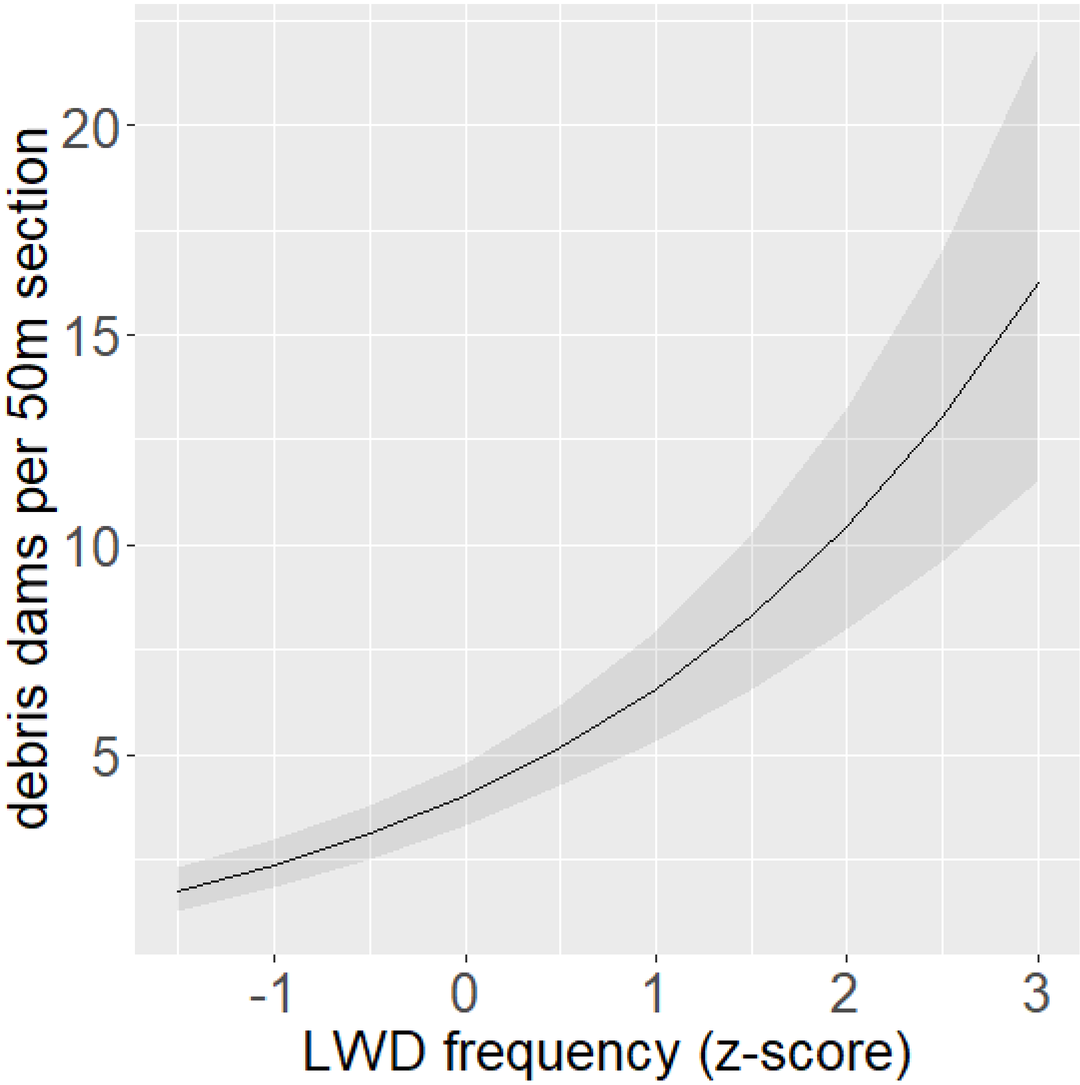


**Figure 6: Marginal effects for LWD frequency as single parameter included in the most parsimonious model describing debris dam frequency. Parameters have been standardized (z-score).**

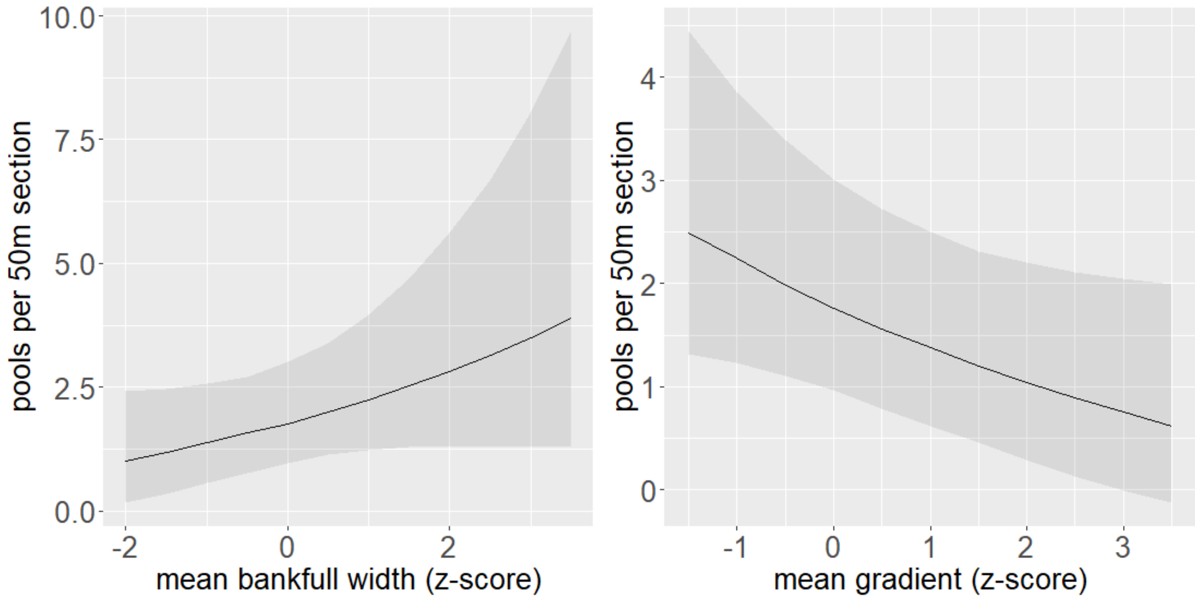


**Figure 7: Marginal effect plots for parameters included in the most parsimonious model describing pool frequency. Parameters have been standardized (z-score).**

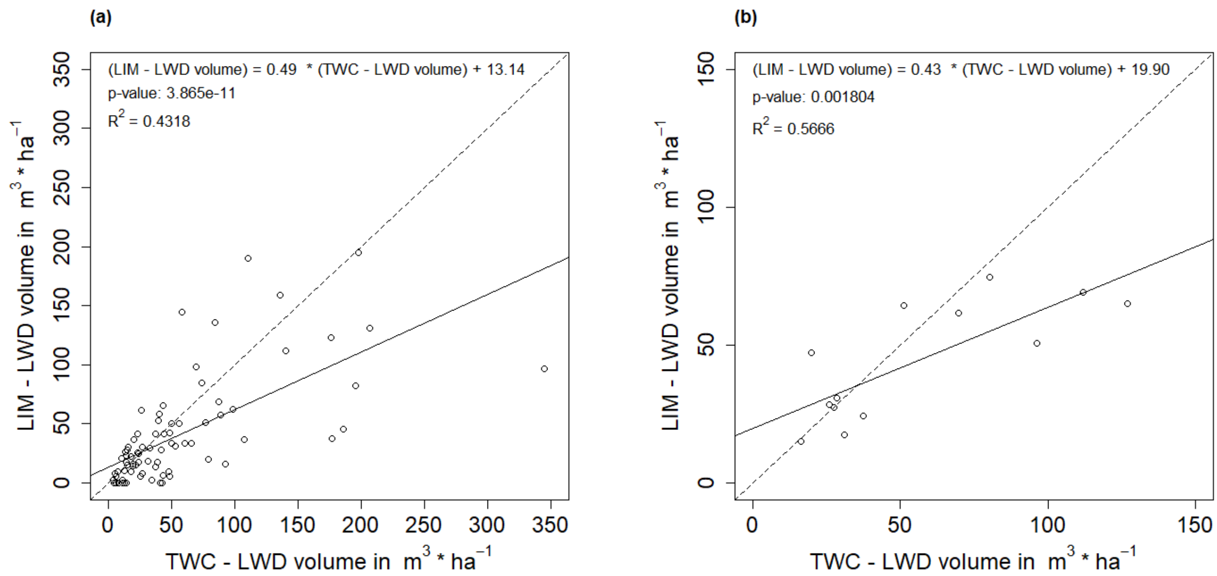


**Figure 8: LWD volume estimates for (a) stream sections of 50 m length and for (b) stream reaches of 300 m length.**

# Tables

**Table 1: Descriptions and units of stream parameters.**

| stream parameter | unit | description |
|---|---|---|
| channel area inventoried | $m^2$ | area of stream channel |
| mean bankfull width | m | mean width of stream channel |
| mean gradient | % | mean gradient of stream |
| LIM - LWD Volume | $m^3*ha^{-1}$ | large woody debris volume estimate using the Line Intercept Method |
| TWC - LWD Volum | $m^3*ha^{-1}$ | large woody debris volume calculated after a Total Wood Census |
| LIM - LWD Frequency | $stems*100m^{-1}$ | large woody debris frequency estimate using the Line Intercept Method |
| TWC - LWD Frequency | $stems*100m^{-1}$ | large woody debris pieces counted in the Total Wood Census |
| debris dam frequency | $debris\ dams*100m^{-1}$ | numper of debris dams per 100m (or per stream section of 50m if specified) |
| pool frequency | $pools*100m^{-1}$ | numper of pools per 100m (or per stream section of 50m if specified) |

**Table 2: Descriptions and units of forests structure parameters. Parameters were calculated with the software NED-3 (Twery & Thomasma, 2014)**

| forest structure parameter | unit | description |
|---|---|---|
| forest type | category | forest type that most closely matches species composition of overstory after NED2 Reference Guide |
| canopy closure | % | mean percentage of canopy closure |
| basal area total | $m^3*ha^{-1}$ | mean basal area of live and dead trees |
| basal area live | $m^3*ha^{-1}$ | mean basal area of live trees |
| basal area dead | $m^3*ha^{-1}$ | mean basal area of dead trees |
| relative density | % | mean trees per area ratio after Sollins, (1987) |
| QMD | cm | mean quadratic mean diameter of trees in stand |
| big tree density | $stems*ha^{-1}$ | mean density of trees with dbh ≥ 50cm |
| total tree density | $stems*ha^{-1}$ | mean density of living and standing dead trees |
| live tree density | $stems*ha^{-1}$ | mean density of living trees |
| dead tree density | $stems*ha^{-1}$ | mean density of standing dead trees |
| basal area conifers | $m^3*ha^{-1}$ | mean basal area of conifer trees |
| percent conifers | % | mean percentage of total basal area made up by conifer trees |
| AGB total | $t*ha^{-1}$ | mean above ground biomass including living and standing dead trees |
| AGB live | $t*ha^{-1}$ | mean above ground biomass of living trees |
| AGB dead | $t*ha^{-1}$ | mean above ground biomass of standing dead trees |
| sd of canopy closure | % | standard deviation of canopy closure |
| sd of basal area total | $m^3*ha^{-1}$ | standard deviation of basal area of live and dead trees |
| sd of basal area live | $m^3*ha^{-1}$ | standard deviation of basal area of live trees |
| sd of basal area dead | $m^3*ha^{-1}$ | standard deviation of basal area of dead trees |
| sd of relative density | % | standard deviation of trees per area ratio after Sollins 1987 |
| sd of quadratic mean dbh | cm | standard deviation of quadratic mean dbh of trees in stand |
| sd of big tree density | $stems*ha^{-1}$ | standard deviation of density of trees with dbh ≥ 50cm |
| sd of total tree density | $stems*ha^{-1}$ | standard deviation of density of living and standing dead trees |
| sd of live tree density | $stems*ha^{-1}$ | standard deviation of density of living trees |
| sd of dead tree density | $stems*ha^{-1}$ | standard deviation of density of standing dead trees |
| sd of basal area conifers | $m^3*ha^{-1}$ | standard deviation of basal area of conifer trees |
| sd of percent conifers | % | standard deviation of percentage of total basal area made up by conifer trees |
| sd of AGB total | $t*ha^{-1}$ | standard deviation of above ground biomass including living and standing dead trees |
| sd of AGB live | $t*ha^{-1}$ | standard deviation of above ground biomass of living trees |
| sd of AGB dead | $t*ha^{-1}$ | standard deviation of above ground biomass of standing dead trees |

**Table 3: Stream characteristics. Except for area, these values are mean values over 300 m stream reaches**

| site | channel area inventoried $m^2$ | mean bankfull width m | mean gradient % | LIM - LWD Volume $m^3*ha^{-1}$ | TWC - LWD Volume $m^3*ha^{-1}$ | LIM - LWD frequency $stems*100m^{-1}$ | TWC - LWD Frequency $stems*100m^{-1}$ | Debris dam frequency $dams*100m^{-1}$ | Pool frequency $pools*100m^{-1}$ |
|---|---|---|---|---|---|---|---|---|---|
| Bagleytrail | 1488.50 | 4.96 | 13.92 | 15.05 | 16.32 | 4.33 | 16.33 | 8.00 | 9.00 |
| Crazy | 814.25 | 2.71 | 9.33 | 30.84 | 28.48 | 7.33 | 17.00 | 10.33 | 6.00 |
| Cushman | 864.00 | 2.88 | 12.33 | 65.14 | 127.10 | 9.00 | 29.00 | 12.67 | 4.33 |
| Falls | 2283.75 | 7.61 | 12.92 | 47.13 | 19.85 | 7.33 | 25.67 | 8.67 | 7.33 |
| Kineo1 | 876.75 | 2.92 | 10.50 | 69.04 | 111.78 | 12.00 | 29.67 | 12.67 | 2.33 |
| Kineo2 | 919.25 | 3.06 | 20.67 | 50.79 | 96.22 | 10.33 | 31.00 | 12.00 | 9.33 |
| Split | 1531.50 | 5.11 | 5.83 | 17.52 | 31.01 | 4.67 | 21.00 | 4.67 | 1.00 |
| W3 | 1234.50 | 4.12 | 19.92 | 61.69 | 69.75 | 13.00 | 40.00 | 18.00 | 2.67 |
| W4 | 926.75 | 3.09 | 17.33 | 28.38 | 25.76 | 10.33 | 23.33 | 12.33 | 1.67 |
| W7 | 1135.00 | 3.78 | 6.92 | 64.36 | 51.00 | 8.00 | 16.00 | 3.33 | 8.00 |
| W8 | 923.90 | 3.20 | 12.08 | 74.64 | 80.19 | 9.50 | 31.33 | 12.67 | 0.00 |
| W9 | 990.75 | 3.30 | 13.50 | 27.26 | 27.38 | 5.67 | 19.00 | 7.67 | 8.33 |
| Zigzag | 1448.25 | 4.83 | 7.17 | 24.21 | 37.32 | 1.67 | 15.00 | 4.67 | 2.67 |

**Table 4: Forest structure per stream reach. Forest type: SNH = spruce-northern hardwoods, NH = northern hardwoods, HH = hemlock-hardwoods**

| | Bagleytrail | Crazy | Cushman | Falls | Kineo1 | Kineo2 | Split | W3 | W4 | W7 | W8 | W9 | Zigzag |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| forest type | SNH | SNH | SNH | HH | NH | SNH | SNH | NH | NH | NH | SNH | SNH | SNH |
| canopy closure % | 86.89 | 93.44 | 99.43 | 93.94 | 72.43 | 88.39 | 91.20 | 82.10 | 92.61 | 84.34 | 98.22 | 82.54 | 100.00 |
| basal area total m2*ha-1 | 32.71 | 39.60 | 36.16 | 43.62 | 28.12 | 39.03 | 38.45 | 35.01 | 31.57 | 28.70 | 37.88 | 44.19 | 44.19 |
| basal area live m2*ha-1 | 29.27 | 33.29 | 30.42 | 36.16 | 20.66 | 35.58 | 30.42 | 28.12 | 29.27 | 24.10 | 32.14 | 33.29 | 40.17 |
| basal area dead m2*ha-1 | 3.44 | 6.31 | 5.74 | 7.46 | 7.46 | 3.44 | 8.03 | 6.89 | 2.30 | 4.59 | 5.74 | 10.90 | 4.02 |
| relative density % | 86.89 | 111.92 | 105.31 | 105.26 | 74.33 | 92.22 | 96.80 | 87.96 | 108.60 | 86.24 | 106.17 | 82.54 | 134.12 |
| QMD cm | 17.39 | 21.31 | 19.16 | 21.87 | 20.38 | 21.73 | 24.51 | 29.08 | 15.87 | 22.67 | 17.48 | 17.82 | 14.39 |
| big tree density stems*ha-1 | 9.68 | 27.21 | 7.60 | 27.33 | 22.22 | 31.21 | 18.25 | 29.71 | 0.00 | 15.59 | 29.77 | 10.97 | 15.30 |
| total tree density stems*ha-1 | 1376.99 | 1110.78 | 1253.62 | 1160.69 | 862.04 | 1052.81 | 814.88 | 527.21 | 1594.90 | 710.92 | 1581.45 | 1771.95 | 2716.45 |
| live tree density stems*ha-1 | 1330.99 | 1029.01 | 1189.19 | 947.27 | 717.11 | 1032.17 | 677.77 | 419.19 | 1479.03 | 672.67 | 1238.11 | 1396.38 | 2671.06 |
| dead tree density stems*ha-1 | 46.01 | 81.77 | 64.43 | 213.42 | 144.92 | 20.64 | 137.11 | 108.02 | 115.87 | 38.25 | 343.34 | 375.57 | 45.39 |
| basal area conifers m2*ha-1 | 10.33 | 4.59 | 4.02 | 9.18 | 0.00 | 18.37 | 5.17 | 0.57 | 0.00 | 2.30 | 7.65 | 28.70 | 11.48 |
| percent conifers % | 31.58 | 11.59 | 11.11 | 21.05 | 0.00 | 47.06 | 13.43 | 1.64 | 0.00 | 8.00 | 20.04 | 64.94 | 25.97 |
| AGB total t*ha-1 | 200.48 | 282.46 | 245.65 | 283.08 | 201.13 | 244.45 | 272.31 | 275.23 | 173.38 | 201.77 | 254.65 | 237.11 | 273.66 |
| AGB live t*ha-1 | 173.96 | 236.14 | 202.08 | 233.28 | 147.34 | 218.53 | 219.21 | 223.91 | 161.24 | 169.58 | 217.24 | 169.85 | 246.53 |
| AGB dead t*ha-1 | 26.52 | 46.31 | 43.57 | 49.80 | 53.79 | 25.92 | 53.10 | 51.32 | 12.15 | 32.18 | 37.41 | 67.26 | 27.13 |
| sd of canopy closure % | 7.36 | 13.11 | 1.13 | 9.94 | 20.70 | 8.68 | 6.65 | 25.25 | 9.71 | 19.36 | 3.23 | 7.16 | 0.00 |
| sd of basal area total m2*ha-1 | 1.15 | 7.59 | 2.20 | 6.76 | 4.73 | 4.59 | 3.44 | 7.59 | 8.03 | 8.49 | 4.98 | 7.81 | 12.76 |
| sd of basal area live m2*ha-1 | 2.20 | 7.84 | 2.20 | 5.09 | 7.26 | 5.46 | 6.04 | 8.25 | 6.04 | 6.63 | 5.43 | 5.46 | 11.32 |
| sd of basal area dead m2*ha-1 | 2.30 | 2.20 | 2.30 | 4.73 | 3.44 | 1.33 | 4.78 | 2.65 | 3.25 | 4.59 | 3.77 | 3.92 | 2.20 |
| sd of relative density % | 7.36 | 30.35 | 5.43 | 25.97 | 24.14 | 15.89 | 17.36 | 31.37 | 29.14 | 21.65 | 18.03 | 7.16 | 19.24 |
| sd of quadratic mean dbh cm | 6.28 | 6.04 | 4.12 | 5.68 | 3.21 | 6.54 | 3.90 | 6.74 | 2.67 | 8.09 | 3.04 | 2.88 | 4.26 |
| sd of big tree density stems*ha-1 | 7.91 | 17.61 | 5.37 | 5.43 | 13.21 | 11.52 | 19.99 | 10.25 | 0.00 | 7.02 | 12.18 | 8.22 | 23.34 |
| sd of total tree density stems*ha-1 | 622.93 | 521.68 | 538.33 | 791.64 | 334.60 | 643.69 | 223.23 | 257.84 | 1004.65 | 446.02 | 519.80 | 928.03 | 801.78 |
| sd of life tree density stems*ha-1 | 613.56 | 527.98 | 549.34 | 732.01 | 325.45 | 648.72 | 271.64 | 251.88 | 831.14 | 415.42 | 501.23 | 400.65 | 828.78 |
| sd of dead tree density stems*ha-1 | 56.97 | 8.16 | 28.89 | 121.83 | 30.90 | 6.62 | 89.83 | 70.26 | 190.14 | 45.68 | 355.00 | 571.37 | 31.65 |
| sd basal area conifers m2*ha-1 | 4.40 | 2.65 | 4.73 | 14.15 | 0.00 | 8.17 | 5.09 | 1.15 | 0.00 | 1.87 | 5.56 | 10.69 | 10.09 |
| sd of percent conifers % | 4.40 | 2.65 | 4.73 | 14.15 | 0.00 | 8.17 | 5.09 | 1.15 | 0.00 | 1.87 | 5.56 | 10.69 | 10.09 |
| sd of AGB total t*ha-1 | 27.12 | 56.43 | 20.11 | 17.07 | 32.72 | 14.54 | 47.75 | 54.94 | 38.58 | 62.90 | 26.41 | 23.81 | 70.29 |
| sd of AGB live t*ha-1 | 14.13 | 59.24 | 17.59 | 38.81 | 51.93 | 22.73 | 51.56 | 59.42 | 28.29 | 44.23 | 32.29 | 22.84 | 63.68 |
| sd of AGB dead t*ha-1 | 19.77 | 16.95 | 18.50 | 31.88 | 27.78 | 11.07 | 36.67 | 21.87 | 16.73 | 31.69 | 30.76 | 16.89 | 14.61 |

# APPENDIX

## Abstract

New England's landscapes are characterized by secondary hardwood forests that are recovering from 19th century clearing and land use. It remains poorly understood how forest-stream dynamics and associated ecosystem services change as these forests develop towards a late-successional condition. This study addresses this knowledge gap by investigating the effects of riparian forest structure on wood loading of 13 low-order streams draining mature northern hardwood forests at the Hubbard Brook Experimental Forest (HBEF) in New Hampshire. We assessed in-stream large woody debris (LWD) along 300 m longitudinal transects within 13 stream reaches using the line-intercept method (LIM) and a total wood census (TWC). We sampled in-stream habitat features, such as pools and debris dams, and measured attributes of riparian forest structure. We applied multi-hierarchical Bayesian models to investigate the effects of forest structure on LWD loading and the effects of LWD loading on pool- and debris dam frequency. We used a paired-t-test to compare estimates of the LIM to the TWC. Forest structure affected LWD loading, indicating strong effects of big tree density and dead tree density among other structural attributes. Debris dam frequency strongly depended on LWD frequency, while pool frequency depended on stream geomorphology. The LIM and the TWC delivered significantly different results when comparing 50 m stream sections. Our findings highlight the importance of evaluation of adequate transect lengths for further applications of the LIM. We conclude that biological legacies like remnant old-growth trees are important structural attributes which promote LWD in low-order streams.

## Zusammenfassung

Neuenglands Landschaften werden von sekundären Hartlaubwäldern geprägt, die sich von Kahlschlägen und Landnutzung im 19. Jahrhundert erholen. Es ist ungewiss, wie sich Wald-Fluss Dynamiken und assoziierte Ökosystem Dienstleistungen bei fortschreitender Sukzession verändern. In dieser Studie wird der Zusammenhang zwischen Waldstruktur und Vorkommen von grobem Totholz (LWD) in 13 Flüssen erster und zweiter Ordnung im Hubbard Brook Experimental Forest (HBEF) in New Hampshire untersucht. Zur Totholzerfassung wurden die Line-Intercept Methode (LIM) und ein vollständiger Totholz Zensus (TWC) entlang von jeweils einem 300 m langen, in Flussmitte verlaufenden Transekt per Fluss, angewandt. Weiters wurden Habitat Eigenschaften der Flüsse, wie Pools und Debris-Dämme erfasst. In den umliegenden sekundären Hartlaubwäldern wurde die Waldstruktur erhoben. Zur Ermittlung der Beziehung zwischen Waldstruktur und LWD und der Beziehung zwischen LWD und dem Vorkommen von Pools und Debris-Dämmen wurden multi-hierarchische Bayesische Modelle herangezogen. Die Ergebnisse der LIM und des TWC wurden mittels paarweisem t-test verglichen. Das Totholzvorkommen in Flüssen wird von der Waldstruktur, insbesondere von der Dichte dicker und toter Bäume, beeinflusst. Die Frequenz von Debris-Dämmen hängt stark von der Totholzfrequenz ab, während Pool-Frequenz eher von der Geomorphologie des Flusses abhängt. Die Ergebnisse der LIM und des TWC unterschieden sich signifikant, wenn 50 m lange Teilstücke der Transekte verglichen wurden. Unsere Ergebnisse unterstreichen die Wichtigkeit der Evaluation einer angemessenen Transekt Länge vor weiterer Anwendung der LIM. Zusammenfassend stellen wir fest, dass dicke Bäume als biologisches Erbe (biological legacies), wichtige Elemente der Waldstruktur sind, die zu erhöhtem Totholzvorkommen in Flüssen beitragen.