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# Ecological Impacts of Energy-Wood Harvests: Lessons from Whole-Tree Harvesting and Natural Disturbance

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Recent interest in using forest residues and small-diameter material for biofuels is generating a renewed focus on harvesting impacts and forest sustainability. The rich legacy of research from whole-tree harvesting studies can be examined in light of this interest. Although this research largely focused on consequences for forest productivity, in particular carbon and nutrient pools, it also has relevance for examining potential consequences for biodiversity and aquatic ecosystems. This review is framed within a context of contrasting ecosystem impacts from whole-tree harvesting because it represents a high level of biomass removal. Although whole-tree harvesting does not fully use the nonmerchantable biomass available, it indicates the likely direction and magnitude of impacts that can occur through energy-wood harvesting compared with less-intensive conventional harvesting and to dynamics associated with various natural disturbances. The intent of this comparison is to gauge the degree of departure of energy-wood harvesting from less intensive conventional harvesting. The review of the literature found a gradient of increasing departure in residual structural conditions that remained in the forest when conventional and whole-tree harvesting was compared with stand-replacing natural disturbance. Important stand- and landscape-level processes were related to these structural conditions. The consequence of this departure may be especially potent because future energy-wood harvests may more completely use a greater range of forest biomass at potentially shortened rotations, creating a great need for research that explores the largely unknown scale of disturbance that may apply to our forest ecosystems.

**Keywords:** aquatic ecosystems, biodiversity, biofuels, carbon storage, energy-wood, forest productivity, natural disturbance, whole-tree harvesting, woody debris, saproxylic organisms

The recent emphasis on renewable, alternative energy sources has focused considerable attention on expanding energy production from forest-derived biomass worldwide. As it becomes

economically feasible to use energy-wood (EW; *sensu* Benjamin et al. 2010), it is likely that removal of forest residues such as tree tops, branches, and leaves, as well as other typically nonmerchantable components such

as bark and stumps, will increase (Norton et al. 2003). Therefore, the US Departments of Energy and the Interior have issued a formal memorandum of understanding that supports the utilization of woody biomass as energy-wood (EW), incorporating it in their definition as “the harvest, sale, offer, trade, and/or utilization of woody biomass to produce the full range of wood products, including timber, engineered lumber, paper and pulp, furniture and value-added commodities, and bioenergy and/or biobased products such as plastics, ethanol, and diesel” (Norton et al. 2003, p. 2).

During the energy crisis in the late 1970s, EW was primarily procured in North America through whole-tree harvesting (WTH), which differs from conventional harvesting (CH) in that the entire above-ground portion of the tree is removed (Figure 1). With WTH, tops and limbs may be chipped for pulp or used in small burning facilities, with the remainder marketed for roundwood (Klass 1985, Mitchell 1992). Partly in response to this increased use of

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wood for energy during that time, numerous studies across North America examined the impacts of WTH on ecosystem properties, including soil nutrients and water quality (Davis 1976, Hornbeck and Kropelin 1982, Johnson et al. 1982, Mitchell 1992, Sabourin et al. 1992). Given the recent resurgence of interest and technological advances associated with the use of EW, there is much that can be learned from a reexamining of these WTH studies. For example, although the forest industry in Fennoscandia is developing technology that allows greater efficiencies in using forest residues such as smaller diameter trees and stumps (Hakkila 2006), this more intensive type of harvesting has not yet been applied to a great extent in North America.

A key change in management philosophy occurring since the last push for energy-wood harvesting (EWH) has been the development of forest management strategies that emulate natural disturbance (ND) regimes. These management strategies leave complex patterns of residual vegetation and arrangement of residual structures (Figure 2) and thereby maintain forest composition and structure within the historic range of variation generated by disturbance (Keane et al. 2009). This approach has been proposed as a coarse-filter strategy for maintaining native biodiversity within managed forested landscapes and includes implementing harvest patterns to mimic the historic spatial scale, frequency, and severity of naturally occurring canopy mortality events ranging from single-tree fall gaps created by wind and other disturbance agents to landscape-scale stand-replacing events driven by mixed-severity fire regimes (Hunter 1999, Seymour et al. 2002). The uncertain and complex aspects of NDs can be difficult to use as management targets but provide insights into the temporal and spatial characteristics of ecosystem processes emerging from historic ND regimes (Landres et al. 1999). It is not hard to imagine that there is potential for EWH to diverge from the range of conditions created by NDs (Lorimer and White 2003), given the possibility for shortened rotations and a larger focus on even-aged cutting methods. Greater exploration of the potential changes to forests resulting from EWH, especially with removal of residues and previously nonmerchantable wood (Figure 1), is needed to determine whether it represents a disturbance that is fundamentally different from CH or WTH, which it more closely resembles. By the same token,

identifying and characterizing the stand attributes and/or processes that are influenced by EWH are imperative when the extent that EWH differs from the historic range of variation in disturbance effects is assessed (Cyr et al. 2009).

An important distinction between EWH and WTH is that with the former, the focus is on the end product and not necessarily on the techniques used for harvesting the forest (Rittenhouse et al. 2012). EW can be derived from many types of harvesting methods and cutting systems. Given current market constraints, the most economically available supply of EW comes from non-competitive markets in which forest residues are integrated as part of commercial sales for timber and pulpwood (Becker et al. 2009). In addition, there is considerable interest in using EW derived from thinning treatments and uneven-aged systems. However, the vast majority of EW is currently procured as part of regeneration harvests in even-aged systems to overcome costs associated with transportation to existing processing facilities (Benjamin et al. 2010, Becker et al. 2011). Future development of the EW market through higher chip prices could improve the cost efficiency of smaller thinning operations and uneven-aged harvest methods (Becker et al. 2009).

Although there are a wide range of forest types within the region encompassed by this review, the most common commercial forest types include aspen (*Populus tremuloides* Michx.), birch (*Betula* L.), lowland conifers (e.g., *Picea mariana* Mill. and *Larix laricina* [Du Roi] K. Koch), and pine (*Pinus resinosa* Aiton, *Pinus banksiana* Lamb., and *Pinus strobus* L.) within the Lake States and spruce-fir (*Picea rubens* Sarg. and *Abies balsamea* [L.] Mill.), northern hardwoods (e.g., *Acer saccharum* Marshall and *Betula alleghaniensis* Britton), oak-hickory (*Quercus* L. and *Carya* Nutt.), and pine (*Pinus resinosa*

Aiton, *Pinus banksiana* Lamb., and *Pinus strobus* L.) within the northeastern states. Of these, EWH is most commonly being applied to those forest types in which even-aged regeneration methods are most common (i.e., aspen, birch, pine, spruce-fir, and oak).

Given that the most common methods of harvesting for EW are currently even-aged systems, we chose to focus this review on the expected impacts of even-aged EWH on ecosystem structure and function. Our overall objective was to summarize existing knowledge to anticipate the impacts of EWH on carbon stocks, nutrients, terrestrial biodiversity, and associated aquatic ecosystems. Where possible, our review builds on knowledge to highlight what we can expect from EWH. In addition, we examine the impacts of EWH within the context of how ND regimes influence ecosystem structure and function, and highlight where departures and similarities exist between the latter and EWH. Whereas EWH is receiving substantial attention across the globe, the majority of our review draws on forest research from north temperate and subboreal forests.

## EWH and Ecosystem Structure and Function

### Forest Structure

NDs strongly influence forest structure through their effects on the spatial and temporal distribution and abundance of biomass, including live trees, foliage, and deadwood (Table 1). Harvesting also influences structure. For instance, whereas the amount of fine woody debris often increases immediately after clearcutting due to logging slash inputs (McCarthy and Bailey 1994), the levels of coarse wood typically decline due to the displacement, fragmentation, and crushing of decayed logs by equipment (Hautala et al. 2004). In general, the effects of harvest-

## Management and Policy Implications

Energy-wood harvesting has the potential to impact a wide range of ecosystem characteristics. This review focuses specifically on potential harvest effects on forest structure, carbon storage, nutrient retention, maintenance of biodiversity, and associated aquatic ecosystems. Although the geographic scope of the review is northeastern North America, the principal messages should be broadly applicable to other temperate regions and forest types. This review incorporates some of the wealth of information that has been gained from whole-tree harvesting studies, which are especially applicable for assessing the potential impacts of energy-wood harvesting. The information summarized here will be useful to both scientists and forest practitioners, particularly those interested in managing for forest-derived biofuels, while simultaneously ensuring the long-term ecological sustainability of forested ecosystems.

**A** Conventional Harvest (CH)



**B** Whole-tree Harvest (WTH)



**C** Intensive harvest for energy-wood



**Figure 1.** Aspen-dominated mesic hardwoods, St. Louis County, Minnesota. Contrast of CH (A) with WTH (B) and intensive EWH (C) of red pine forest, Potlatch Corporation, Minnesota. CH typically removes only the bole of merchantable trees, whereas WTH removes all aboveground tree biomass from the site. Piles seen in EWH include nonmerchantable trees, deadwood, and tops bundled for removal and chipping.

ing on forest structure are largely dependent on disturbance severity and frequency but less so on whether the ecosystem is mesic or fire-dependent (Table 1).

A key difference between ND and traditional harvesting (CH and WTH) is the degree to which both live tree and deadwood legacies are retained after the disturbance. Much of the biomass killed by stand-replac-

ing ND (e.g., severe fires) is retained on site in the form of snags or downed logs (Table 1; Franklin et al. 2007). Gap-scale disturbances on mesic sites create localized accumulations of downed logs and snapped trees and a high degree of spatial heterogeneity in the distribution of these features (Table 1). In contrast, forest harvesting typically removes these structural elements. With CH,

logging slash serves as the primary deadwood legacy left on site (McCarthy and Bailey 1994), whereas WTH results in a more thorough removal of living biomass from the stand, with deadwood coming primarily from incidental breakage of crowns during harvesting.

Another contrast between ND and harvesting is the amount, size, and composition of live tree legacies. Most stand-replacing NDs leave some number of live trees (Table 1; Franklin et al. 2007). Moreover, these trees can span a range of sizes from saplings to very large individuals. In fact, larger trees are more likely to survive some disturbances, such as surface fire. In contrast, both CH and WTH, when applied in even-aged management, remove all or most merchantable stems. Even with use of retention guidelines, which are increasingly common among various land management organizations (Franklin and Johnson 2012), residual trees in commercial harvests may often be smaller diameter, nonmerchantable stems (D'Amato et al. 2009). Because of the integral role these legacies play in regulating ecosystem processes (Spies 1998), these alterations can have cascading effects on other ecosystem functions, including carbon and nutrient retention and cycling and sustainability of biodiversity.

Given the high levels of biomass utilization possible with EWH, including previously nonmerchantable living stems, there could be greater carbon impacts on structure than with WTH (Table 1). In addition, EWH may include the removal of sound downed logs and snags and in many regions includes the removal of stumps (Walmsley and Godbold 2010; Table 1).

### Carbon Stocks

Natural and harvesting disturbances often have measurable impacts on ecosystem carbon stocks. Insights about the potential consequences of EWH on carbon stocks can be identified from studies of other disturbances. Much of the aboveground carbon in forest ecosystems is stored in live woody biomass (Fahey et al. 2010), although dead woody material can be a substantial component in some ecosystems (Bradford et al. 2009). Differences in impacts on aboveground carbon pools can be pronounced between NDs and harvesting disturbances. The impact of NDs on aboveground carbon depends on disturbance type (Table 2). On mesic sites, windthrow and insect or disease mortality result in modest short-term car-

**A** Post Natural Disturbance – Fire



**B** Post Natural Disturbance - Wind



**Figure 2.** Jack pine forest, Superior National Forest, Minnesota. Post-ND stand structure resulting from stand-replacing fire (A) and wind (B).

bon release. Although widespread insect outbreaks can have substantial carbon consequences over regional scales (Kurz et al. 2008), stand-replacing wildfires have more dramatic short-term impacts on carbon stocks, by releasing carbon stored in foliage and organic soil layers and modest portions of carbon stored in woody material (Kashian et al. 2006, Bond-Lamberty et al. 2007, de Groot et al. 2009, Bradford et al. 2012). In contrast, harvesting has an obvious and dramatic impact on carbon stored in above-ground biomass, removing all or most livebole biomass in even-aged CH and much of the live branch biomass in WTH (Table 2). EWH would remove as much live, above-ground carbon as WTH and potentially even more if typically nonmerchantable material such as small diameter and poorly formed stems are also removed. Even greater carbon reductions would occur with deadwood and stump removal.

Recovery of carbon stored in above-ground biomass after harvesting or stand-replacing NDs has been well characterized globally in chronosequence studies (Pregitzer and Euskirchen 2004) and specifically in parts of the northern forest (Bradford and Kastendick 2010). However, these recovery patterns may only apply when soil fertility

has not been altered by the disturbance. Repeated harvesting that removes nutrient capital may decrease productivity and change long-term patterns of carbon storage and cycling (Thiffault et al. 2010). This potential decline in soil fertility may be an important point of divergence between EWH and ND. Simulation modeling studies, often parameterized from WTH studies, suggest that intensive harvesting, i.e., short rotations and/or WTH, could cause long-term decreases in productivity and eventually reductions in ecosystem carbon storage (Rolff and Agren 1999, Peng et al. 2002, Nunery and Keeton 2010).

Carbon stored in soil is another large pool, although one that is less affected by harvesting or NDs (Norris et al. 2009). The initial influence of harvesting, either CH or WTH, on soil carbon stocks is highly variable, depending on climate, soil type, and vegetation (Hoover 2011), but generally results in modest short-term decreases in carbon (Johnson and Curtis 2001, Nave et al. 2010). Much of this decrease occurs in the organic soil (Nave et al. 2010), possibly as a consequence of physical disturbance that mixes forest floor biomass into the mineral soil. Under certain conditions, such as those in conifer-dominated forests, WTH appears

to decrease soil carbon stocks more than CH (Johnson and Curtis 2001), and subsequent soil carbon recovery is influenced by the recovery of vegetation (Johnson et al. 2002). Dissolved organic carbon exports are typically higher for a brief period after harvest, and these increases are more pronounced in WTH than CH (Kreutzweiser et al. 2008). The effects of EWH on belowground carbon stocks should be generally similar to those of WTH, (i.e., initial short-term declines in surface soil carbon followed by recovery). However, if EWH involves increased utilization of fine-wood residues and, more intensively, stump removal, then impacts to soil carbon could exceed those associated with WTH.

### Nutrient Retention

Nutrient dynamics after forest disturbance are influenced by fine-wood abundance and growth of residual and reestablishing vegetation (Shortle et al. 2012). Understanding how natural and harvesting disturbance influences amounts of fine wood and rates of vegetation regrowth offers insight into the potential effects of EWH on nutrient pools. Periodic losses of nutrients occur when gaps are created through ND. Loss of the overstory increases the rate of mineralization within gaps (Dittman et al. 2007). Nitrogen (N) and phosphorus (P) are the primary nutrients exported as leachate after ND, but they are less mobile in forest ecosystems where ground vegetation and organic forest layers remain intact (Johnson 1995, Martin and Hornbeck 2000).

In the case of stand-replacing fire, considerable amounts of N may become available in the form of  $\text{NH}_4^+$  and  $\text{NO}_3^-$ , as well as P in enriched ash, which could be exported unless used by recolonizing vegetation (Certini 2005). The magnitude of losses can be characterized by the amount and quality of residues as well as by the abundance and composition of remaining vegetation (Table 3). Harvesting in fire-prone forests reduces cation retention relative to ND (Table 3). For example, Duchesne and Houle (2008) found that with WTH of balsam fir (*Abies balsamea* [L.] Mill.) in boreal forests, the reduction of litter and slash led to depleted calcium (Ca), potassium (K), and magnesium (Mg) in the soil. Losses of K were of particular significance with WTH because as much as 5 times the amount of K was stored in tree biomass versus soil pools, leading to losses of roughly 44% of available short-term K. Whereas

**Table 1. Structural attributes of stands after ND and various types of stand replacement harvesting disturbance.**

Attribute	After ND		CH		WTH		EWH	
	Mesic <sup>a</sup>	Fire-dependent <sup>b</sup>	Mesic	Fire-dependent	Mesic	Fire-dependent	Mesic	Fire-dependent
Live tree abundance <sup>1</sup> (stems ha <sup>-1</sup> )	260–825	133–520	Substantial impact with abundance increasing with time since harvest	Substantial impact with abundance increasing with time since harvest	Similar to CH	Similar to CH	Similar to CH and WTH/potential for greater impacts if submerchantable trees are harvested for feedstocks	Similar to CH and WTH/potential for greater impacts if submerchantable trees are harvested for feedstocks
Coarse deadwood biomass <sup>2</sup> (Mg ha <sup>-1</sup> )	12–32	18–31	Modest increase in coarse deadwood from logging slash	Modest increase with an increase in coarse deadwood from logging slash	Minimal increase in coarse deadwood from breakage	Minimal increase in coarse deadwood from breakage	Similar to WTH/potential for great impacts if existing coarse wood is collected as a feedstock	Similar to WTH/potential for great impacts if existing coarse wood is collected as a feedstock
Fine deadwood biomass <sup>3</sup> (Mg ha <sup>-1</sup> )	2–7	1–5	Substantial increase in fine deadwood from logging slash	Substantial increase in fine deadwood from logging slash	Minimal increase in fine deadwood from breakage	Minimal increase in fine deadwood from breakage	Similar to WTH	Similar to WTH
Stumps/roots (Mg ha <sup>-1</sup> )	2–5 <sup>4</sup>	3–6	Substantial increase in stumps after harvest	Substantial increase in stumps after harvest	Similar to CH	Similar to CH	Potential for substantial decrease in stumps and roots after stumps are extracted for feedstocks	Potential for substantial decrease in stumps and roots after stumps are extracted for feedstocks

“Minimal,” “modest,” and “substantial” refer to broad categories of disturbance severity, corresponding to approximately <20, 20–50, and >50% change immediately after disturbance, with differences representing the range of values, respectively. <sup>1</sup>Trees ≥10 cm dbh; <sup>2</sup>downed wood and snags ≥10 cm in diameter; <sup>3</sup>downed wood <10 cm in diameter; <sup>4</sup>fine root biomass. Sources: Foster and Boose (1992), Boose et al. (2001), Fisk et al. (2002), Frelich (2002), Rothstein et al. (2004), D’Amato et al. (2008, 2011), Ravenscroft et al. (2010), Bradford et al. (2012), Hoover et al. (2012), Kashian et al. (2012), Klockow (2012), Rittenhouse et al. (2012).

<sup>a</sup> Forest systems generally occupying sandy loam or finer soils for which the predominant disturbance regime is characterized by an absence of stand-replacing fires and a predominance of gap-scale disturbances, including wind, ice, insects, and disease. Return intervals for stand-replacing wind events are quite variable (450–10,500 yr) with coastal areas experiencing hurricanes (85–380 yr). The extent of wind-driven canopy mortality is event-specific and variable (e.g., hurricane damage can range from 0.04 to 37 ha). Stand-replacing fires occur on much longer rotation intervals (>500 yr). Therefore, the values for these systems correspond to those documented for mature mesic forest ecosystems with a history of gap-scale disturbance.

<sup>b</sup> Forest systems generally occupying coarse textured soils for which the predominant disturbance regime is characterized by either mixed-severity or high-severity fire regimes. Return intervals for stand-replacing fire vary by soils and dominant species; for example, on droughty soils dominated by pine barrens, stand-replacing fires typically occurred roughly every 25–100 yr, whereas mixed-pine forest experienced return intervals of around 100–250 yr. Typical patch sizes for intensely burned areas with canopy mortality range from 50 to 200 ha.

**Table 2. Carbon attributes of stands after ND and various types of stand replacement harvesting disturbance.**

Attribute	After ND		CH		WTH		EWH	
	Mesic <sup>a</sup>	Fire-dependent <sup>b</sup>	Mesic	Fire-dependent	Mesic	Fire-dependent	Mesic	Fire-dependent
Aboveground carbon (Mg C ha <sup>-1</sup> )	25–300	25–200	Large losses typically recovered over ~100 yr	Large losses; recovered over ~100 yr; potential decline and loss in productivity	Large losses; recovered over ~100 yr; potential decline and loss in productivity			
Soil carbon (Mg C ha <sup>-1</sup> ) <sup>1</sup>	50–100	25–100	Minimal impacts	Minimal impacts	Minimal impacts	Minimal impacts	Potential decline and productivity loss	Potential decline and productivity loss

“Minimal,” “modest,” and “substantial” refer to broad categories of disturbance severity, corresponding to approximately <20, 20–50, and >50% change immediately after disturbance, with differences representing the range of values, respectively. <sup>1</sup>Soil carbon stocks refer to forest floor and near-surface (typically 10–20 cm) mineral soil. Sources: Foster and Boose (1992), Boose et al. (2001), Fisk et al. (2002), Frelich (2002), Wang et al. (2003), Pregitzer and Euskirchen (2004), Rothstein et al. (2004), Gough et al. (2007), D’Amato et al. (2008, 2011), Bradford and Kastendick (2010), Nave et al. (2010), Ravenscroft et al. (2010), Bradford et al. (2012), Hoover et al. (2012), Kashian et al. (2012), Klockow (2012), Stephens et al. (2012), Rittenhouse et al. (2012).

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similar losses can be seen due to stand-replacing wildfire (Brais et al. 2000), CH typically leaves fine branches, leaves, and whole crowns on site to decompose over a long period of time, slowly releasing nutrients (Thiffault et al. 2007). EWH has the potential to leave very small amounts of residual woody material after harvest, which would

eliminate much of the slowly released nutrient pool typically available after CH.

In mesic forests (e.g., northern hardwoods mixed with aspen and birch), ND such as windthrow, disease, and insects operate on a fine scale, creating gaps of varying sizes (0.0004–0.1 ha; Seymour et al. 2002). Changes in microclimate and its in-

teractions with vegetation affect patterns of nutrient availability and retention (Finzi et al. 1998, Prescott 2002, Cobb 2010). Small single-tree gap sizes (88–230 m<sup>2</sup>) release small pulses of nutrients that are assimilated by colonizing vegetation and belowground soil biota (McGee et al. 2007). As gap sizes increase, the potential for nutrient export to

**Table 3. Nutrient attributes of stands after ND and various types of stand replacement harvesting disturbance.**

Attribute	After ND		CH		WTH		EWH	
	Mesic <sup>a</sup>	Fire-dependent <sup>b</sup>	Mesic	Fire-dependent	Mesic	Fire-dependent	Mesic	Fire-dependent
Standing whole tree (kg/ha)			Minimal impacts with slash retention; lag in nutrient accrual until vegetation regrowth	Minimal impacts with slash retention; lag in nutrient accrual until vegetation regrowth	Potential for modest loss and low accrual until vegetation regrowth	Potential for modest loss and little accrual until vegetation regrowth; impacts less than those for nutrient-rich sites	With short rotations, potential for substantial decline in nutrients and deficits in Ca, K, and Mg	With shorter rotations, potential for modest decline, deficits in Ca, K, and Mg
N	170–615	23–33 <sup>c</sup>						
P	22–80	2.0–2.38 <sup>c</sup>						
K	117–375	11.4 <sup>c</sup>						
Mg	32–60	2.5–2.6 <sup>c</sup>						
Ca	200–340	16 <sup>c</sup>						
Forest floor organic litter layer (kg/ha)								
N	197–1,738	764–2,850						
P	21–86	17–32						
K	31–80	36						
Mg	37–130	45						
Ca <sup>d</sup>	48–486	288						
Mineral soil pools (kg/ha)								
N	3,625–5,900	1,411						
P	914–2,520	550						
K	986–13,820	36						
Mg	4,091–11,900	11						
Ca	569–16,701	89						

<sup>a</sup>“Minimal,” “modest,” and “substantial” refer to broad categories of disturbance severity, corresponding to approximately <20, 20–50, and >50% change immediately after disturbance, with differences representing the range of values, respectively. Sources: Hornbeck and Kropelin (1982), Freedman et al. (1986), Macadam (1987), Mann et al. (1988), Huntington and Ryan (1990), Foster and Boose (1992), Brais et al. (2000), Boose et al. (2001), Frelich (2002), McLaughlin and Phillips (2006), Duchesne and Houle (2008), LeDuc and Rothstein (2010), Ravenscroft et al. (2010).

<sup>b</sup> Forest systems generally occupying sandy loam or finer soils for which the predominant disturbance regime is characterized by an absence of stand-replacing fires and a predominance of gap-scale disturbances, including wind, ice, insects, and disease. Return intervals for stand-replacing wind events are quite variable (450–10,500 yr) with coastal areas experiencing hurricanes (85–380 yr). The extent of wind-driven canopy mortality is event-specific and variable (e.g., hurricane damage can range from 0.04 to 37 ha). Stand-replacing fires occur on much longer rotation intervals (>500 yr). Therefore, the values for these systems correspond to those documented for mature mesic forest ecosystems with a history of gap-scale disturbance.

<sup>c</sup> Forest systems generally occupying coarse textured soils for which the predominant disturbance regime is characterized by either mixed-severity or high-severity fire regimes. Return intervals for stand-replacing fire vary by soils and dominant species; for example, on droughty soils dominated by pine barrens, stand-replacing fires typically occurred roughly every 25–100 yr, whereas mixed-pine forest experienced return intervals of around 100–250 yr. Typical patch sizes for intensely burned areas with canopy mortality range from 50 to 200 ha.

<sup>d</sup> Nutrient values from standing jack pine (Foster and Morrison 1976) were adjusted by proportion of standing biomass after stand-replacing wildfire (Bradford et al. 2012).

<sup>e</sup> Soil profile depths sampled varied but were generally to a depth of 10–70 cm.

adjacent forest increases. For example, work in northern hardwood and eastern hemlock (*Tsuga canadensis* [L.] Carrière) forests compared nutrient pools within large windthrow gaps (diameters of 300–2,000 m<sup>2</sup>) with adjacent forest and attributed the reduced levels of exchangeable base cations, such as Ca, K, and Mg, within gaps, as well as less available nitrate, to leaching losses (Scharenbroch and Bockheim 2007). Whereas CH provides residual slash inputs at a much larger scale (5–25-ha patches; McDonald et al. 2006, D’Amato et al. 2009), the frequency of disturbances (Runkle 1982) is lower than that of ND in mesic forests. The extent of inputs of slash on the landscape through CH differ compared with those of ND, particularly in mixed-wood aspen forests, where ND from insect and disease can create periodic inputs of nutrients every 10 years through canopy mortality affecting from 5.5 to 17.8% of the landscape (Reinikainen et al. 2012). In comparison, EWH, with complete removal of canopy trees and probable decreases in residual woody debris, would probably have much

lower short-term retention of nutrients than CH.

In general, removal of large amounts of forest residues can decrease availability of Ca, K, and Mg in the soil, all of which are important to tree health (Federer et al. 1989). The recovery of nutrient pools is highly dependent on stand development and past stand conditions, presenting a challenge for determining the range of possible responses (Yanai et al. 1999). For example, the availability of nutrients may be in part due to the variability in wood residues and associated wood decay fungi in place after harvest (Shortle et al. 2012). In landscapes where Ca is already limited, increased removal of slash and reduced litter inputs may have important long-term consequences for site fertility (Hornbeck et al. 1990, Grigal 2004, Shortle et al. 2012). There are, however, situations in which WTH may be somewhat similar to conditions created during historical NDs, such as on chronically nutrient-poor sites that have experienced frequent stand-replacing wildfire (Rothstein and Spaulding 2010). However, even in this

case, WTH does not completely emulate the biogeochemical conditions created by fire that make nutrients more stable in the soil (Thiffault et al. 2007).

## EWH and Biodiversity

EWH has the potential to have a substantial impact on species richness and community composition for a variety of organisms. The mechanisms may be direct, in the case of woody plants that are harvested. More likely, the mechanisms will be indirect, resulting from removal of the overstory, disturbance to the understory, soil, and forest floor, and loss of coarse and fine woody debris.

When the impacts of EWH on biodiversity are evaluated, it is important to determine whether the disturbance causes changes that are outside the natural range of variation in disturbance for the system and/or impedes recovery of species to acceptable levels or at acceptable rates (Royo and Carson 2006). Ground-layer plants, deadwood-dependent organisms, and ground-dwelling animals and some birds

**Table 4. Biodiversity attributes of stands after ND and various types of stand replacement harvesting disturbance.**

Attribute	After ND		CH		WTH		EWH	
	Mesic <sup>a</sup>	Fire-dependent <sup>b</sup>	Mesic	Fire-dependent	Mesic	Fire-dependent	Mesic	Fire-dependent
Ground layer plant species richness	2–8 (vas. m <sup>-2</sup> ) 3–7 (vas. 0.5 m <sup>-2</sup> ) 7–8 (vas. + nonvas. m <sup>-2</sup> )	10–25 (vas. 400 m <sup>-2</sup> ) 2–15 (nonvas. 400 m <sup>-2</sup> ) 9–16 (vas. 0.5 m <sup>-2</sup> )	Minimal to modest increase for vas.; minimal change of nonvas.	Modest increase of vas.; minimal change for nonvas.	Similar to CH for vas.; potential decrease for nonvas.	Modest increase of vas.; potential decrease of nonvas.	Similar to WTH	Similar to WTH
Ground-layer plant community composition	Composition relatively stable	Modest change; more early successional species	Minimal to modest change; loss of residual species	Similar to ND; vary by degree of mineral soil exposure	Modest change; more early successional species, reduced residual species	Similar to ND	Similar to WTH; substantial change possible	Similar to WTH; substantial change possible
Saproxylics	Composition and richness stable, assuming gap disturbance	Postfire shifts in composition, favoring fire-adapted species	Reductions with less woody debris and smaller log diameters	Less known, probably reduced from ND	Further reductions over CH due to loss of FWD; slow recovery	Less known, probably reduced from CH	Greater impact (less CWD; short rotations)	Less known, probably reduced from WTH
Herpetofauna <sup>c</sup>	Similar to reference; abundance stable over time assuming gap-scale disturbance	Low natural richness; abundance affected by intensity of disturbance	Changes proportional to intensity and scale of harvest; recovery rapid with regrowth	Changes proportional to intensity and scale of harvest; recovery rapid with regrowth	Impact greater than CH	Impact greater than CH	Impact greater than WTH; short rotations	Impact greater than WTH; short rotations
Small mammals <sup>c</sup>	Similar to reference condition; abundance stable with time assuming small-scale disturbance	Lower natural richness, favoring generalists; abundance affected by intensity of disturbance	Changes proportional to intensity and scale of harvest; most species recover with regrowth	Changes proportional to intensity and scale of harvest; most species recover with regrowth	Significant impacts; less slash and hard mast; most species recover with regrowth	Significant impacts; less slash and hard mast; most species recover with regrowth	Similar to WTH; greater potential impacts with shorter rotations	Similar to WTH; greater potential impacts with shorter rotations
Birds	Similar to reference condition; abundance stable with time assuming small-scale disturbance	Periodic disturbance by fire creates a mosaic of early and late successional communities	Minimal to substantial change proportional to intensity and scale of harvest; most species should recover with regrowth	Minimal to substantial change proportional to intensity and scale of harvest; most species should recover with regrowth	Greater impacts than CH; modest effects, most species should recover with regrowth	Greater impacts than CH; modest effects, similar to fire; recover with regrowth	Greater impacts than CH and WTH, potential substantial effects due to nutrient depletion	Greater impacts than CH and WTH (removal of FWD and CWD), potential for modest effects due to nutrient depletion

<sup>a</sup> “Minimal,” “modest,” and “substantial” refer to broad categories of disturbance severity, corresponding to approximately <20, 20–50, and >50% change immediately after disturbance, with differences representing the range of values, respectively. Plant species may include either vascular (vas.) or nonvascular (nonvas.) species. CWD, coarse woody debris; FWD, fine woody debris.

<sup>b</sup> Forest systems generally occupying sandy loam or finer soils for which the predominant disturbance regime is characterized by an absence of stand-replacing fires and a predominance of gap-scale disturbances, including wind, ice, insects, and disease. Return intervals for stand-replacing wind events are quite variable (450–10,500 yr) with coastal areas experiencing hurricanes on intervals from 85 to 380 yr. The extent of wind-driven canopy mortality is event-specific and variable (e.g., hurricane damage can range from 0.04 to 37 ha). Stand-replacing fires occur on much longer rotation intervals (>500 yr). Therefore, the values for these systems correspond to those documented for mature mesic forest ecosystems with a history of gap-scale disturbance.

<sup>c</sup> Forest systems generally occupying coarse textured soils for which the predominant disturbance regime is characterized by either mixed-severity or high-severity fire regimes. Return intervals for stand-replacing fire vary by soils and dominant species; for example, on droughty soils dominated by pine barrens, stand-replacing fires typically occurred roughly every 25–100 yr, whereas mixed-pine forest experienced return intervals of around 100–250 yr. Typical patch sizes for intensely burned areas with canopy mortality range from 50 to 200 ha.

<sup>d</sup> It is difficult to generalize faunal species responses because different species respond differently to disturbance.

represent taxa that are most likely to be affected by EWH in ways that exceed responses to ND.

### Ground-Layer Plant Communities

There are numerous studies that examined changes in the ground-layer plant community after ND. The general finding is that substantial changes do occur naturally in both richness and community composition, with the magnitude of change dependent on degree of reduction in tree cover, understory vegetation disruption, and forest floor and soil disturbance (primary disturbance axes *sensu* Roberts 2004). The magnitude of changes along these axes depends on the type of disturbance and the type of ecosystem (i.e., fire-prone or mesic; Table 4). Proliferation of early successional species is com-

mon after stand-replacement disturbances such as fire (Dyrness 1973, Haeussler et al. 2002, Moola and Vasseur 2008). However, when vegetative parts or dormant seeds of predisturbance late-successional species survive, especially on mesic sites after wind, these species may persist as advanced regeneration or reestablish large populations early in stand development (Dyrness 1973). Disturbances that are technically stand-replacing, but leave some overstory intact and have minimal disturbance of understory vegetation and forest floor, will have postdisturbance, ground-layer plant communities with greater similarity to the predisturbance condition than stands with little or no residual overstory (Halpern et al. 2005).

Many studies have compared plant spe-

cies dynamics in logged stands with those in stands initiating after ND, typically fire (Haeussler et al. 2002, Haeussler and Bergeron 2004, Hart and Chen 2008). Most of these studies involved something other than WTH (Halpern 1989, Halpern and Spies 1995, Roberts and Zhu 2002) or were ambiguous about the harvest system (Hughes and Fahey 1991, Gilliam et al. 1995, Peltzer et al. 2000). Despite these limitations, there are similarities of response that emerge, which may be important to consider in the context of EWH. Many studies demonstrate that ground-layer composition of harvested stands is more similar to mature conditions than in stands after natural fires, often due to greater survival of individuals and species from the predistur-

bance stand after harvest and the addition of early successional species after fire (Abrams and Dickmann 1982, Rees and Juday 2002, Haeussler and Bergeron 2004). Greater changes can be expected when clearcutting is combined with forest floor and mineral soil disturbance (Roberts and Zhu 2002), which is more likely with EWH. Finally, there is evidence that ground-layer plant communities converge to compositions similar to the reference condition within several to many decades, regardless of the disturbance (Gilliam et al. 1995, Rees and Juday 2002, Roberts and Zhu 2002). However, the potential for loss of rare species is a large concern, and given that few studies have examined ground-layer response specifically after intensive EWH, the changes in plant community composition are not known.

A few studies have specifically compared WTH with CH or ND. For instance, McInnis and Roberts (1994) demonstrated that WTH resulted in greater disturbance and distinctly different communities of natural tree regeneration than CH in Acadian mixed forests. Framstad et al. (2009) reviewed Swedish boreal forest studies that compared vascular plant communities between CH and WTH. Although they found no significant differences in richness, there were differences in community composition. For example, nitrophilous taxa such as *Epilobium angustifolium* L. appeared to be negatively affected when the tops and branches were removed in WTH, presumably due to reductions in nitrogen availability (Olsson and Staaf 1995, Bråkenhielm and Liu 1998). However, these results have been contradicted by others (Åström et al. 2005). A number of studies have shown that early successional species may be favored with WTH (Bergquist et al. 1999, Åström et al. 2005).

In one of the more comprehensive studies to date, Hart and Chen (2008) examined ground-layer responses to WTH and compared dynamics with those of stands after natural fires in the eastern forest (harvest type specified in Brassard and Chen 2008). They found that ground-layer vegetation, 7 years after WTH in boreal conifer, mixed-wood, and deciduous forests, had higher species richness and significantly different composition relative to those of stands of the same age but of fire origin, a result consistent with the CH (or unknown harvest system) versus fire comparisons cited previously. Long-term results of this study to assess the

potential for convergence are not yet available.

To summarize, after many disturbance events, ground-layer plant communities may converge in species composition and richness over time toward reference conditions. We would expect this to be the case for EWH, considering the results from WTH studies. However, the potential exists for intensive EWH to disrupt plant communities to a greater degree than even WTH if such harvests remove understory vegetation, soil/forest floor, and residual slash to a greater degree than occurs with WTH, especially if stumps are removed. There are few studies that evaluate ground-layer plant community responses to the extreme range of removals associated with EWH and over sufficient time to make predictions with confidence.

### Saproxylic Communities

A large number of species depend on deadwood for all or portions of their life cycle. The persistence of these saproxylic species, primarily wood-decay fungi and beetles, thus depends on an adequate and fairly continuous supply of deadwood. Therefore, saproxylic species, perhaps more than any other species group, are most vulnerable to deadwood reductions resulting from CH, WTH, or EWH operations (Table 4), as these harvests may result in deadwood volumes below the natural range of variation for ND regimes.

These negative consequences are well documented in Finland and Scandinavia, where CH in the past century and WTH in recent decades have greatly reduced both the quality and quantity of coarse woody debris (Söderström 1988, Fridman and Walheim 2000, Rouvinen et al. 2002). Consequently, the richness and abundance of wood-decay fungi has diminished considerably (Bader et al. 1995, Rydin et al. 1997). Similarly, species richness of saproxylic beetles is markedly higher in seminatural forests subject to ND than in forests managed by CH (Martikainen et al. 2000, Similä et al. 2003).

Under ND regimes, the relationship between deadwood attributes and saproxylic species under fire-dependent systems is much less studied than in mesic systems (Table 4). However, results indicate that fire causes a shift in the composition of beetles (Toivanen and Kotiaho 2007, Boulanger et al. 2010) and wood-decay fungi (Junninen et al. 2008, Olsson and Jonsson 2010) and that several rare and/or threatened fungal species may be favored by fire (Olsson and

Jonsson 2010). The effects of CH, WTH, and EWH operations on saproxylic species in these fire-dependent systems remain poorly understood (Table 4).

By removing fine woody debris, WTH and EWH could pose a threat to saproxylic species that use this substrate (Table 4). Recent research has clearly shown the importance of fine woody debris in supporting a rich and diverse saproxylic fungal community, at times more diverse than that found on coarse woody debris (Nordén et al. 2004, Juutilainen et al. 2011, Brazee et al. 2012). Further, both Jonsell et al. (2007) and Brin et al. (2011) found that although fine woody debris (generally >4 cm diameter) did not necessarily have higher richness or diversity of saproxylic beetles than did larger diameter debris, a number of beetle species were significantly associated with or specialized on fine debris. Increased reductions in substrate, whether fine or coarse woody debris, to levels below that found under the natural range of variation would probably translate to reductions in abundance and richness of saproxylic species, owing simply to species-area relationships (Preston 1962; Table 4).

Given that EWH removes existing, nondecayed woody debris, as well as a wide range of living material (e.g., shrubs, boles, tops, and branches) that would otherwise add to the deadwood pool, it probably represents a greater reduction in residual deadwood relative to ND than either CH or WTH (Tables 1 and 4). The low volumes and homogenization of deadwood resulting from EWH would be further exacerbated by short rotations, because they would preclude the accrual of the large and well-decayed logs required by certain fungal species (Bader et al. 1995, Renvall 1995, Kruijs et al. 1999). Thus, EWH, particularly on short rotations, probably represents a greater risk to stand-level, saproxylic diversity, relative to ND regimes, than either CH or WTH (Table 4).

### Amphibians, Reptiles, and Small Mammals

A great number of small vertebrate fauna of north temperate and subboreal forests are favored by shaded, moist, and cooler forest floor conditions provided by large, mature trees (Fredericksen et al. 2000), snags, or downed coarse woody debris (DeGraaf et al. 2006). Tree squirrels (*Sciurus* spp. Linnaeus) and bats (*Myotis* spp. Kaup) use cavities in large diameter standing dead and live trees, and bats roost under loose, exfoliating bark on snags and large,

live trees (Kunz and Lumsden 2003, Taylor 2006, Mumby et al. 2011). Tree squirrels and many other wildlife species are dependent on mature trees for hard mast (i.e., seed) forage (Martin et al. 1951, Nixon et al. 1975, Robertson et al. 2008). Amphibians depend on moist forest floor conditions provided by overstory shading and fine and coarse, downed deadwood (Mitchell et al. 2006).

Forest floor fauna, such as small mammals and herpetofauna (i.e., amphibians and reptiles), are sensitive to canopy disturbance and to decreases in downed woody material (DeGraaf and Yamasaki 2001, Evans et al. 2010). However, a hallmark of most types of ND, particularly on mesic sites, is that there is rarely complete removal of microhabitat structures (Table 1) important for these species (Hansen et al. 1991, Drever et al. 2006). Smaller, gap-scale disturbances, on mesic sites in particular, are most likely to retain favorable forest floor habitat conditions.

The responses of forest floor fauna to stand-replacing disturbances such as wildfire are species-specific and not well documented for much of the northern US forest (Pilliod et al. 2003). What we can surmise is that there are direct and indirect effects of wildfire on forest structure and ecosystem processes that are important to maintaining faunal species. Direct impacts of wildfire, such as mortality, vary due to geographic and landscape features that shape the behavior of a fire, such as fire speed, and landscape features, such as streams and wetlands that provide refuge for fleeing fauna. Indirect impacts that change the structure of the habitat through combustion of fine fuels, loss of canopy, and warming of soils, can have long-term consequences (Pilliod et al. 2003) because most small mammal and herpetofaunal species have small home ranges (DeGraaf and Yamasaki 2001, DeGraaf et al. 2006).

Clearcutting, whether in CH or WTH, is clearly different in scale than gap-based ND on mesic sites. However, under CH, clearcutting may be reasonably similar to natural fire disturbance on fire-prone sites (Table 4). Specifically, CH can be similar to less severe wildfire when adequate amounts of legacy structures are retained and when ground-layer vegetation is conserved. The abundance and quality of these structural habitat features can be greatly diminished with WTH and with EWH in particular. As such, impacts on forest floor fauna may be outside the range of variation that occurs with smaller scale, less intense, natural gap

disturbance. For instance, even with residues retained in CH, amphibians were more abundant in the uncut stands than in clearcut stands (deMaynadier and Hunter 1995). Semlitsch et al. (2008) found that amphibians, especially salamanders, emigrate from clearcut sites to adjacent uncut habitat. The effects of CH were greater for salamanders, especially lungless plethodontids, than for anurans (i.e., frogs and toads), which seem more tolerant of the warmer and drier forest floor microclimate characteristic of clearcut stands.

### Avian Communities

The effects of conventional forestry on birds in the northcentral and northeastern United States is reasonably well understood. For example, the removal of tree cover in CH results in the replacement of birds typical of mature forests with early-successional species (DeGraaf 1991, Costello et al. 2000, King and DeGraaf 2000).

The general pattern of bird species turnover is expected to be similar among CH, WTH, and EWH, despite the latter two approaches resulting in notably less large deadwood than in CH stands (Table 1). These habitat features provide important foraging, nesting, and roosting opportunities for birds (Healy and DeGraaf 1989, Welsh et al. 1992, Zheng et al. 2008). Whereas WTH and EWH are expected to result in lower quality habitat than CH, EWH can reduce these important structural features more than WTH and ultimately result in the lowest quality habitat for birds.

The impacts of WTH and EWH on soil nutrients relative to CH is another means by which these harvesting methods could affect birds. Birds on more productive sites experience higher reproductive success, presumably as the result of higher soil nutrient levels (Seagle and Sturtevant 2005). Experimental manipulations have shown that Ca supplementation increased ovenbird (*Seiurus aurocapilla* Linnaeus) territory density by 80% and clutch size by 7%, suggesting that nutrient levels have a substantial influence on abundance and a modest, yet potentially biologically significant, effect on reproduction (Pabian and Brittingham 2011). If WTH operations deplete soil nutrients more than CH, then lower quality habitat would be expected, and to the extent that higher wood removal in EWH results in greater depletion than WTH, EWH would again create the poorest bird habitat.

Despite the likelihood that EWH cre-

ates lower quality habitat than CH, it could still be valuable for regional bird conservation by increasing the representation of early-successional habitats within forested landscapes. Early-successional “shrubland” birds are the subject of considerable conservation concern, given recent declines in bird populations (Askins 1993, Brawn et al. 2001, Hunter et al. 2001). Although early-successional habitat created by EWH is poorer quality than that for CH, given the lack of important structural features and lower soil nutrient levels, it supports more shrubland birds than unmanaged or uneven-aged forests. Thus, EWH could still constitute an important component of landscape-level conservation strategies for these declining species by providing additional commercial incentive for creating early-successional habitat. This could be particularly important on lands that are designated as areas for managing wildlife, yet are marginal for timber production. Managers on these sites would otherwise have to apply costly noncommercial treatments such as mowing or prescribed fire to create and maintain early-successional habitat for declining wildlife species.

### EWH and Aquatic Ecosystems

Aquatic ecosystems, particularly lower order streams, are influenced by ND in the adjacent forest (Table 5). A large body of research has defined a suite of hydrologic, physical, and chemical adjustments to aquatic ecosystems and reinforced the importance of ND regimes (i.e., timing, magnitude, and frequency) for sustaining the structure and function of aquatic ecosystems (Resh et al. 1988, Allan 2004). At the same time, the role of harvesting disturbance (Chamberlain et al. 1991) has been a major topic for research, with much emphasis placed on methods that reduce potential negative impacts.

Natural and harvesting disturbances influence the interception, retention, and cycling of water, energy, and materials by the terrestrial ecosystem, changing delivery rates to surface waters. Reduction in evapotranspiration caused by basal area removal increases water yield during the growing season (Hornbeck et al. 1993, 1997). Removal of overstory vegetation can increase light penetration to streams, with resulting increases in water temperature (Moore et al. 2005). Soil and forest floor disturbance increases the flux of fine sediment to streams and lakes (Waters 1995), increasing the in-

**Table 5. Aquatic ecosystem attributes after ND and various types of stand replacement harvesting disturbance.**

Attribute	After ND		CH		WTH		EWH	
	Mesic	Fire-dependent	Mesic	Fire-dependent	Mesic	Fire-dependent	Mesic	Fire-dependent
Nutrients, sediment, water	Mature and old-growth forests retentive of water, nutrients, and sediment, assuming gap disturbance in watershed and riparian area	Fire results in pulsed release of nutrients and sediment; increased water yield	Increase in nutrient and sediment relative to ND; increased water yields; recovers with regrowth of vegetation	Patterns similar to mesic	Greater impact than CH (CWD and FWD removal); potential for acidification with greater removal of biomass and base cations	Similar to mesic	Similar to WTH but potentially greater impact (large biomass removal and shorter rotations)	Similar to WTH but potentially greater impact (large biomass removal and shorter rotations)
Light	Light regimes relatively stable	Increases in light if disturbance extends into riparian area	Increases in light relative to ND; recovers with regrowth of vegetation	Similar to ND but more extreme if few residual trees remain in riparian area	Similar to CH	Similar to CH	Similar to CH	Greater impact than CH and WTH (if tree biomass removal is complete in riparian area)
Deadwood	Relatively stable contribution of large wood to aquatic system	Deadwood recruitment U-shaped over time	Deadwood recruitment U-shaped over time	Similar to ND	Deadwood recruitment U-shaped over time	Reduction in deadwood recruitment over ND and CH with removal of tops	Potential for reduced input relative to CH and WTH (greater removal of woody biomass in riparian area)	Potential for reduced input relative to CH and WTH (greater removal of woody biomass in riparian area)
Biotic	Increased light from gaps increases productivity; favors autochthonous over allochthonous production; large wood recruited to channels provides habitat for a wide range of taxa	Postfire productivity dependent on magnitude of sediment and nutrient inputs	Context-dependent; increased productivity in light- or nutrient-limited systems if temperature/sediment increases not great; declines in wood-dependent habitats and species	Similar to mesic except more vulnerable to negative effects of excessive sediment, temperature and nutrients	Potential for long-term reduction stream productivity in nutrient-limited systems; greater risk to acid-sensitive species due to greater biomass removal	Same as mesic	Impacts exacerbated compared with WTH	Same as mesic

CWD, coarse woody debris; FWD, fine woody debris.

put of nutrients. The increased light and higher nutrients frequently increase autochthonous primary production (Plante and Downing 1993, Quamme and Slaney 2003), whereas canopy removal can reduce or alter the type of leaf litter inputs affecting trophic structure (Ulrich et al. 1993, Nislow and Lowe 2006). ND, such as wind and insect outbreaks, can increase coarse wood inputs over the short term but may cause longer-term decreases due to the reduction of coarse wood sources (Bragg 2000).

The influence of forest disturbance on the distribution, abundance, and diversity of aquatic organisms is complex. Part of this complexity is due to the context-dependent nature of disturbance effects (Nislow 2005). For example, increases in light and nutrients with adjacent harvesting can degrade habitat for stream fish and benthic invertebrates if high temperatures in combination with increased productivity reduce oxygen concentrations. In contrast, for systems in which salmonid production is light- and temperature-limited, these same effects can increase abundance (Nislow and Lowe 2006). In addition, forest disturbance can have strong effects on trophic interactions. In headwater streams, trout populations are highly depen-

dent on terrestrially derived invertebrates as prey (Sweka and Hartman 2008). Removal of vegetation in the riparian zone is likely to have some negative impacts on prey availability, but early-successional vegetation may actually support higher invertebrate production and higher availability of invertebrate prey than does mature forest vegetation (Greene et al. 2008).

Whereas aquatic ecosystems depend on disturbance, there are clearly situations in which harvesting practices result in conditions outside the natural range of variability, with resultant degradation of ecosystem structure and function. These negative effects are strongly influenced by the intensity and type of harvest, suggesting that CH, WTH, and EWH near aquatic systems may have substantially different levels of impact. One important consideration is that whereas streams integrate changes across the whole watershed, those areas directly adjacent to stream channels (i.e., riparian zones) are particularly influential. As a result, some of the effects of forest harvesting, for example, changes in light and temperature regimes, can be largely ameliorated by leaving no- or minimal-harvest buffer zones, a practice that has become a widely adapted and in many

cases mandated by best management practices (Lee et al. 2004).

More intensive and extensive harvesting, as in EWH, is not likely to occur within the riparian zone. Therefore, an important consideration in assessing the physical, chemical, and biological effects of harvesting is distinguishing those processes that are mainly under riparian control (e.g., light and temperature regime, leaf litter, and coarse wood inputs) from those processes that appear to be determined at the whole-watershed scale (e.g., hydrologic regime, base cation, and trace-element dynamics). It is at the latter scale that EWH may impact aquatic systems and the scale at which differences between EWH, WTH, and CH are most likely to be observed (Table 5).

At the stand and small-watershed scale, studies explicitly comparing WTH with CH methods have focused largely on hydrology, nutrients, and geochemistry and have not followed these effects through biological populations and ecosystems in aquatic habitats. For hydrologic regimes, Martin and Hornbeck (2000) observed higher magnitude, short-term effects, and longer-lasting changes in a WTH than in a CH watershed, but differences were relatively minor and

**Table 6. Knowledge gaps and research needs for EWH.**

Attribute	Knowledge gap	Research questions
Structure	Differences between structure after natural disturbance, particularly stand-replacing and heavy partial disturbance, and EWH	What are the impacts of EWH on fine and coarse woody debris, stumps, and structural roots?
Carbon and nutrients	Long-term patterns in carbon and other nutrient dynamics with intensive (stumps, deadwood) and frequent EWH	How susceptible are soils to nutrient depletion with intensive and frequent EWH? How does the potential for nutrient limitation differ with forest and soil type?
Plant communities	Community response to EWH specifically	What is the relationship between amount of biomass removed, particularly of fine and coarse woody debris, and the sustainability of plant communities?
Fine deadwood	Relationship between the abundance and condition of fine deadwood and the composition of saproxylic communities	Do changes in saproxylic communities translate into alterations of ecosystem functioning, particularly patterns and rates of nutrient and carbon cycling and forest productivity?
Vertebrate communities	Impacts of EWH on habitat quality, as measured by structure and nutrient availability, relative to less-intensive harvesting	What are the thresholds of harvest intensity beyond which changes in structure and nutrients fail to support viable populations of birds, ground-dwelling mammals, and amphibians?
Landscapes	Scaling impacts of more frequent and/or more intense energy wood harvests from the stands to landscapes	What are the risks of homogenization of composition and structure of landscapes as frequency and intensity of harvesting increases? What are the dynamics and viability of aquatic species populations over the mosaic of habitats in an "energy-wood" landscape?

were challenging to interpret, given the use of buffer strips in the CH watershed. Overall, differences in hydrologic regimes between CH, WTH, and EWH are likely to depend on the role of retained forest residues such as tree tops in hydrologic routing, but it appears unlikely that these relatively minor differences would strongly influence aquatic habitat conditions. Similarly, differences associated with short-term nutrient dynamics appear to depend strongly on the role of forest residues as sources and sinks. For example, in a study of CH and WTH in North Wales, UK, Stevens et al. (1995) found that the nutrient losses from forest residues caused stream nutrient levels to remain elevated for a longer period in CH watersheds compared with WTH watersheds, where such residues were lacking. Over the longer term, the greater percentage of biomass removal associated with EWH could theoretically result in chronically lower nutrient inputs and lower overall productivity in streams (Table 5), but this has not been tested.

### Gaps in Knowledge

Although there is a tremendous body of work exploring the impacts that WTH and CH have on important ecological processes within forested ecosystems, several key knowledge gaps hamper our ability to anticipate the long-term ecological sustainability of EWH (Table 6). It is a great challenge to adequately characterize the spatial and temporal attributes of ND in comparison with harvesting (Lindenmayer and Laurance 2012). In particular, much is still unknown

about the impacts of multiple interacting disturbances on important ecological thresholds and key legacies (biological, structural, or temporal/spatial patterns) that emerge as an ecosystem reorganizes (Drever et al. 2006) and that are important for regulating ecological function. It is difficult to place EWH within a proper, disturbance-based context without greater understanding of the knowledge gaps highlighted (Table 6). For instance, living biomass forms the primary structure of forests and is the most readily seen aspect of reorganization after disturbance. Longer-term characterization of the stand structures created through ND is needed to better compare stand-replacing and heavy partial disturbance to EWH. There are some key questions that remain to be answered. Some of these include: How much are longer-term carbon and nutrient pools compromised through the more intensive nature of EWH and what time frame is necessary to recover those pools? Given the likelihood that the capacity of soils to maintain nutrients varies, to what extent would the susceptibility of those soils vary with repeated removals of nutrient inputs? Can EWH be conducted in a way that does not compromise the important legacy attributes that support a functioning plant community?

Questions also remain regarding the critical size and spatial arrangement of those legacies, and how they vary by ecosystem. Because there are indications that fine woody debris and coarse woody debris differ not only in nutrient content but also in abil-

ity to provide critical habitat to saproxylic and vertebrate species, further work is needed to quantify these components of the deadwood pool. How much would be needed to maintain the integrity of these communities after EWH? Finally, our review of impacts has focused on stand-scale ecosystem processes. There is a need to consider these impacts in a landscape context to determine threshold proportions and spatial patterns of EWH that result in unacceptable levels of change.

### Conclusions

All forest harvesting, by definition, results in structural and functional conditions that differ from those generated by ND. Studies indicate that compared with ND, there is a general gradient of increasing structural departure ranging from CH to WTH to EWH. In the context of ecosystem sustainability, research to date also appears to indicate that many functional aspects of forests will increasingly depart from conditions generated after ND, along this same harvesting gradient. For these comparisons, WTH studies probably provide the best insight into the potential impacts of EWH on forest structure and function. However, even these studies are limited to consideration of impacts from tree bole and top removal. EWH that includes removal of stumps, large and fine deadwood, and very small-diameter living stems may take us to a largely unexplored region of harvesting impact research (Table 6). We encourage agencies and research institutions to fill these identified knowledge gaps through research

that will provide data to address the long-term ecosystem sustainability of EWH and thus inform decisions concerning the acceptability of forest-derived wood as an important energy source worldwide.

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