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Promoting structural and species diversity in Great Lakes northern hardwoods: a conceptual model and its application

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Forest ecosystems are shaped by their historical disturbance regime. Structural and species diversity are driven by disturbance frequency, patch size and microsite disturbance severity in forests across the globe. Forest management in Lake State northern hardwoods, however, has primarily used high-frequency, low- to moderate-severity canopy disturbance and low-severity microsite disturbance harvesting techniques such as single-tree selection. Catastrophic disturbances during European settlement followed by the widespread and long-term use of uniform approaches to forest management have homogenized managed forests and created a need to emulate a fuller range of historically prevalent natural disturbances. We present a conceptual model based on complex adaptive forest management that proposes five primary factors including mean patch size, proportion disturbed, frequency, degree of exposed mineral soil and coarse woody debris input. This model demonstrates the need for a greater range of silvicultural systems to more closely emulate the range of variability associated with natural disturbance regimes. In Great Lakes northern hardwoods, using a greater variety of silvicultural systems including those with larger patch cuts and greater soil disturbance, may restore and promote structural and tree species diversity in these forests by creating greater microsite heterogeneity. Applying this conceptual model to forests more broadly, while still considering regionally specific factors, may help restore species and structural diversity and ultimately, ecosystem resilience.

Introduction

Long-term use of systematic forest management has tended to simplify the structure of forests worldwide (Hall *et al.*, 2003; Angers *et al.*, 2005; Montes *et al.*, 2005; Neuendorff *et al.*, 2007; Yoshida *et al.*, 2017). A shift in natural disturbance severity such as reduced gap sizes due to fewer large trees, and subsequent declines in species diversity owing to fewer suitable germination sites (Woods, 2000; Schulte *et al.*, 2007; Zhang *et al.*, 2012), could make forests less resilient to future disturbances and consequently less economically reliable (Niese and Strong, 1992; Dymond *et al.*, 2014, 2015). Evidence suggests that the long-term implementation of uniform management reduces structural diversity (Angers *et al.*, 2005; Neuendorff *et al.*, 2007) and species functional trait diversity (Neuendorff *et al.*, 2007; Curzon *et al.*, 2017), which are integral components of ecosystem resilience and resistance (Yachi and Loreau, 1999; Elmqvist *et al.*, 2003; Tilman *et al.*, 2006; Downing *et al.*, 2012). Higher functional trait diversity can contribute to greater complementarity or greater functional redundancy, which consequently strengthen resilience or resistance, respectively (Downing *et al.*, 2012). Ecosystem resilience is an especially critical attribute in the face of global change if novel disturbance regimes become predominant (Holling, 1973; Elmqvist *et al.*, 2003; Drever *et al.*, 2006; Messier *et al.*, 2013; Derose and Long, 2014).

In this paper, we review the importance of natural disturbances to forest composition, structure and function and discuss the impact of European settlement and forest management practices on forests using northern hardwoods in the Great Lakes region as a case study. Furthermore, we propose a conceptual model to demonstrate the mismatch between historical natural disturbance regimes and settlement and forest management disturbances on a stand scale. Finally, we posit that forest managers need to implement a greater range of silvicultural systems to adequately emulate natural disturbance regimes and maintain forest ecosystem resilience. We discuss an example specific to Great Lakes northern hardwoods, though our conceptual model can be applied to forests across the globe using five identifiable components of disturbance.

Historical natural disturbance regimes

Disturbance effects on landscape-level patterns

Natural disturbances are fundamental processes in forest ecosystems across the globe. Pickett and White (1985) define a disturbance as 'any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment'. Niches created by natural disturbances, for example, are largely credited with maintaining ecosystem biodiversity (Ricklefs, 1976; Denslow, 1980). Moreover, stand structure, plant community composition and biogeochemical cycles are often highly correlated with the regional disturbance regime (Pickett and White, 1985; Oliver and Larson, 1996; Halpin and Lorimer, 2016). As such, ecosystems are strongly influenced by their disturbance history.

Forest ecosystems across North America are no exception. A defining feature of eastern hemlock (*Tsuga canadensis* (L.) Carrière) – white pine (*Pinus strobus* L.) – northern hardwood forests in the Great Lakes region, for example, is the range of severity of windthrow disturbances under which these species evolved (Frelich and Lorimer, 1991; Whitney, 1987, 1994; Hanson and Lorimer, 2013). Though some species such as eastern hemlock and American beech (*Fagus grandifolia* Ehrh.) have more limited distribution, Great Lakes northern hardwoods generally had similar natural disturbance regimes across their range. Large windthrow events typically had high severity but long-return intervals, while small windthrow events had relatively low severity but short-return intervals. For example, Zhang *et al.* (1999) estimated a presettlement rotation period of 722 year for catastrophic windthrow (>1.0 ha) in northern hardwoods in the Luce District of Upper Michigan, and Canham and Loucks (1984) estimated a return time of 1210 year for windthrow >1.0 ha when pooling all forest types across northern Wisconsin. Though catastrophic blowdowns were rare, an extensive gradient of blowdown severity existed ranging from treefall to stand-leveling. A rotation period of 94 and 236 years was estimated for moderate (≥140 km h^{-1}) and severe (≥180 km h^{-1}) windthrow, respectively, in northern hardwoods across the Great Lakes region from Minnesota to New York (Frelich and Lorimer, 1991). Moreover, frequent low-severity windthrow (51–69 years for >10 per cent canopy removal) maintained hemlock – hardwood dominance in western Upper Michigan (Frelich and Lorimer, 1991; Frelich, 2002). The small gaps created by treefall allowed shade-tolerant species to persist, while larger gaps promoted the recruitment of less tolerant species such as yellow birch (*Betula alleghaniensis* Britt.). To contrast, severe fire typically had much longer return intervals. Catastrophic fire reached a rotation period upwards of 2600 year in Upper Michigan (Frelich and Lorimer, 1991; Zhang *et al.*, 1999). Despite their infrequency, catastrophic disturbances were critical for maintaining diversity in these forests (Woods, 1984, 2000; Frelich, 2002). Species such as white pine, red oak (*Quercus rubra* L.) and paper birch (*Betula papyrifera* Marshall) were recruited following fires that exposed mineral soil and decreased competition from sugar maple (*Acer saccharum* Marshall; Frelich, 2002). Finally, evidence suggests that indigenous people used fire as a management tool, though the extent of intentional fire use varied among regions and forest types (Whitney, 1994; Zhang *et al.*, 1999).

Disturbance effects on microsites

While disturbances of stand-level or greater patch size affect whole forest ecosystems, species-specific responses are driven by changes under microsite conditions such as light availability, surface soil moisture, temperature and available nutrients. Such factors are important for plant germination and survival and are frequently driven by patch size and abundance of both exposed mineral soil and coarse woody debris (Roberts and Gilliam, 1995; Roberts, 2004; Bailey *et al.*, 2012). Light availability, for example, often structures understory plant communities and, consequently, tree seedling communities (Scheller and Mladenoff, 2002; Burton *et al.*, 2014; Sabatini *et al.*, 2014). Moreover, gaps created by windthrow or treefall have been shown to promote both plant species diversity and functional diversity in ecosystems across the globe due to differences in light requirements and shade tolerance among species (Ricklefs, 1976; Denslow, 1980; Kern *et al.*, 2014a). Small canopy disturbances such as treefall favour shade-tolerant species, while large canopy disturbances such as severe windthrow typically favour shade-intolerant species. Shade-tolerant understory herbs often respond negatively to the wide fluctuations in temperature and moisture typically resulting from disturbances that simultaneously increase light availability (Small and McCarthy, 2002). Moreover, the highest densities of shade midtolerant yellow birch and tolerant hemlock have been found in the southern edges of large gaps after 2 (Raymond *et al.*, 2006) and 10 (Poznanovic *et al.*, 2014a, 2014b) growing seasons, owing to the creation of adequate germination substrate but relatively little tolerance for wide fluctuations in temperature or rooting zone moisture.

Surface soil moisture is highly heterogeneous among microsites throughout forest stands due to differences in aspect, vegetation cover, underlying soil substrate, organic matter content and topographic location. Natural disturbances such as windthrow and wildfire can further increase heterogeneity of soil moisture among microsites (Peterson *et al.*, 1990; Ritter *et al.*, 2005; Poznanovic *et al.*, 2014b). Small-scale disturbances generally maintain greater consistency in soil moisture, while large-scale disturbances generally create greater variability in soil moisture (Guo *et al.*, 2002). For example, previous work has demonstrated that soil moisture increases with gap size immediately following harvest, likely a result of less canopy interception and fewer trees transpiring (Burton *et al.*, 2014). On the other hand, rapidly invading shrubs may instead decrease soil moisture (Royo and Carson, 2006). Furthermore, soil moisture and light availability are often correlated and consequently affect the composition of tree recruits in gaps (Poznanovic *et al.*, 2014b).

Natural disturbances also greatly affect available nutrient dynamics. As with soil moisture, small disturbances generally maintain greater consistency in available nutrient levels while large disturbances typically create a pulse of available nutrients. Though often dependent on remaining vegetation, rates of nitrogen mineralization and nitrification generally increase after disturbances due to the large input of organic matter, subsequent increase in microbial activity and less uptake by trees (Likens *et al.*, 1970; Attiwill and Adams, 1993). Moreover, the composition of canopy trees has a large effect on soil nutrient dynamics. Sugar maple-dominated stands have high rates of nitrogen mineralization and nitrification, while hemlock-dominated stands have lower rates of nitrogen mineralization and nitrification, largely due to differences in leaf chemistry between species (Lovett and Mitchell, 2004; Lovett *et al.*,. 2004). On the other hand, Mladenoff (1987) observed the opposite trend under recently created treefall gaps.

Surface soil moisture and available nutrients are also often correlated with the abundance of coarse woody debris, which has a higher and more stable moisture content when compared with mineral soil and leaf litter (Jurgensen *et al.*, 1997; Laiho and Prescott, 2004; Bailey *et al.*, 2012). For example, coarse woody debris adsorbs up to 220 per cent of its dry mass in water, compared with 20–40 per cent for mineral soil (Fraver *et al.*, 2002). The ability of decaying woody debris to retain soil moisture and unique fungal communities appears to favour yellow birch and hemlock regeneration, which often have greater germination and survival on decaying woody debris (Marx and Walters, 2008; Poznanovic *et al.*, 2014a). Decaying logs further provide substrate for fungi important in nutrient cycling and symbiotic relationships (Heilmann-Clausen and Christensen, 2003; Poznanovic *et al.*, 2014a; Dove and Keeton, 2015).

The interacting effects of natural disturbances and competing vegetation can further influence regeneration dynamics. For example, the longevity of raspberry (*Rubus* spp.) seeds and prolific growth of raspberry following a disturbance make it an important competitor in some northern hardwood forests following disturbance (Donoso and Nyland, 2006; Kern *et al.*, 2017). Moreover, Kern *et al.* (2013a) found that the abundance of competing shrubs increased with gap size. Another strong competitor, sedge (*Carex* spp.) reproduces vegetatively, a trait that allows it to spread rapidly without relying on seed germination (Hale *et al.*, 2006; Powers and Nagel, 2009). The abundance of raspberry and sedge in recently disturbed (natural and anthropogenic) northern hardwoods is a prime example of the systematic rise of recalcitrant understory layers worldwide due to interacting effects of management and elevated levels of herbivory (Royo and Carson, 2006).

Recent disturbance regimes

European settlement-related disturbances

The Great Lakes forests fuelled rapid industrial growth and settlement during the late nineteenth century. Extensive areas of pine forest were logged within several decades during this period, referred to as the 'cutover' (Wales, 1939; Whitney; 1994; Gough, 1997). Following the cutover, largely unintentional slash fires of residual debris nearly eliminated remaining biological legacies such as seed banks, coarse woody debris, symbiotic organisms, organic nutrients and advance regeneration that would otherwise promote ecosystem resilience (Whitney, 1987; Johnstone *et al.*, 2016). As a result, these two major successive disturbances dramatically altered forest cover by favoring sprouting species such as maple, oak, paper birch and aspen (*Populus tremuloides* Michx. and *P. grandidentata* Michx.). Rapidly growing white-tailed deer (*Odocoileus virginianus*) densities from 1920 to 1940s (Leopold *et al.*, 1947) further favoured a transition from conifers to hardwoods (Ross *et al.*, 1970; Rooney and Waller, 2003; Zenner and Peck, 2009). Following the peak of logging in the Great Lakes around 1892, almost all merchantable pine and hemlock were logged by 1920 (Whitney, 1987; Williams, 1989). When pine was almost depleted in Michigan by the 1890s, a new focus on hardwoods emerged. Consequently, the primary lumber species shifted by 1912 from pine to sugar maple (Whitney, 1987).

Forest management practices

Major advances in silviculture for the northern hardwoods were developed between 1930 and 1950s. Though many approaches were developed, single-tree selection became widespread in the western Great Lakes, with approximately 85 per cent of non-industrial managed land using uneven-aged management comprised primarily of single-tree selection (Jacobs, 1987; Kern *et al.*, 2014b). Under single-tree selection, trees are extracted singly and dispersed across a range of diameter sizes until a residual basal area goal is reached, then repeated every 10–20 years (e.g. Wisconsin DNR *Silviculture Handbook*, 2002). This silvicultural system primarily favours shade-tolerant species such as sugar maple by creating openings of approximately 0.004–0.03 ha on a decadal basis (Crow *et al.*, 2002; Wisconsin Forest Management Guidelines, 2011; Kern, *et al.*, 2014b). In addition to its low-severity canopy removal, winter harvesting with low-impact machinery further minimizes soil microsite disturbance, limiting opportunities for trees that require bare mineral soil to regenerate. Frequent harvest entries, upper diameter limits proposed by the widely used Arbogast Guide (Arbogast, 1957) and mill preferences also limited development of old-senescent trees and large coarse woody debris, further homogenizing stand structure by decreasing microsite variability created when large trees are toppled by windstorms and ultimately reducing the abundance of several economically valuable species such as yellow birch (Webster and Lorimer, 2005; Neuendorff *et al.*, 2007; Shields *et al.*, 2007; Salk *et al.*, 2011).

Several recent studies have demonstrated the declining structural and species diversity of northern hardwoods due to management practices. Neuendorff *et al.* (2007) reported an increase in the relative density of sugar maple and concurrent decrease in relative density of yellow birch after 40 years of single-tree selection in an Upper Michigan northern hardwood forest. Seedling and sapling layers were dominated by sugar maple in both managed stands and stands unmanaged since European settlement, but unmanaged stands had greater species richness. Moreover, in sugar maple-dominated forests of southwest Quebec, the continuous application of selection cutting created dense foliage layers throughout the stand understory due to the large post-harvest recruitment of advance regeneration (Angers *et al.*, 2005). The authors suggest that the long-term application of selection systems in sugar maple-dominated forests may yield homogenized stand structure and composition, along with limited biodiversity at the stand and landscape scale. Also in southwest Quebec, Doyon *et al.* (2005) observed that low horizontal heterogeneity within single-tree selection stands was significantly correlated to avian assemblages and ultimately recommended the application of more diverse silvicultural systems. On a landscape scale, Schulte *et al.* (2007) summarized anthropogenic disturbances and found an increase in dominance of both sugar and red maple from pre- to post-settlement in the Great Lakes states of Minnesota, Wisconsin and Michigan due to the initial widespread harvesting of pine followed by repeated slash fires and finally, the widespread and long-term application of single-tree selection.

Emerging disturbances

Though historically prevalent natural disturbances continue to shape forest ecosystems, several additional influences have arisen since settlement due to regional and global change. The effect of increasing white-tailed deer populations on regeneration in Great Lakes northern hardwood forests has been well-documented in the last two decades (Alverson *et al.*, 1988; Rooney and Waller, 2003; Powers and Nagel, 2009; Kern *et al.*, 2012), particularly because deer populations in northeastern Wisconsin and southern Upper Michigan are relatively high (WDNR, 1998; Rooney and Waller, 2003; Powers and Nagel, 2009; Sabo *et al.*, 2017). The survival of preferentially browsed seedlings, including sugar maple, is compromised in regions with high deer populations due to intense herbivory, leaving behind unpalatable and economically undesirable species such as ironwood (*Ostrya virginia*; Matonis *et al.*, 2011). High deer herbivory further promotes the rapid spread of Pennsylvania sedge (*Carex pensylvanica*) by decreasing the cover of preferentially browsed herbs, seedlings and saplings, therefore reducing competition for resources (Powers and Nagel, 2009).

European earthworms represent another major influence on regeneration dynamics in northern hardwood forests. European earthworm invasion likely exacerbates the negative impacts of deer herbivory by dramatically altering soil conditions and consuming the forest floor, which sugar maple seeds rely on as a germination substrate (Hale *et al.*, 2006, Corio *et al.*, 2009). For example, Corio *et al.* (2009) found lower seedling stem counts of sugar maple in heavily earthworm-invaded stands when compared with less invaded stands. Moreover, earthworm invasion is often highly correlated with the spread of Pennsylvania sedge, further complicating tree regeneration dynamics in impacted forests (Bohlen *et al.*, 2004; Hale *et al.*, 2006).

While the effects of earthworm invasion on tree regeneration are largely indirect, other non-native pests have caused devastating declines in native tree species through direct impacts. Beech bark disease complex (*Cryptococcus fagisuga Lindinger* and *Nectria coccinea var. faginata* (Pers.) Fr.), emerald ash borer (*Agrilus planipennis* Fairmaire), European gypsy moth (*Lymantria dispar dispar* L.) and oak wilt (*Bretiziella fagacearum* (T. W. Bretz) J. Hunt) are several examples of non-native invasive pests which have greatly impacted Great Lakes forests (Gandhi and Herms, 2010; Pugh *et al.*, 2011; Lovett *et al.*, 2016). The death of important tree species such as American beech, ash (*Fraxinus* spp.) and oak (*Quercus* spp.) can have large indirect effects on plant community ecology and biogeochemical cycles, not to mention the large economic impacts (Aukema *et al.*, 2011; Lovett *et al.*, 2016).

Yet another threat, climate change will likely impact Great Lakes forests as deviations from historical temperature and precipitation trends are likely to cause shifts in plant species composition. Higher winter temperatures may favour species currently at their northern range, while negatively influencing species currently at their southern range. Combined with less frequent but more intense precipitation events, drought-tolerant species (e.g. oaks and aspen) may fare better than less drought-tolerant species such as sugar maple, yellow birch and eastern hemlock (Handler *et al.*, 2014). Though restoration efforts are typically guided by historic species composition, this reliance may prove irrelevant in the face of climate change (Harris *et al.*, 2006).

Disturbance-based forest management

The emergence of ecological forestry and complexity science has offered insights into how forests can be managed as disturbance-based, complex adaptive systems (Drever *et al.*, 2006; Messier *et al.*, 2013). Disturbance-based silviculture uses regionally specific natural disturbance regimes as blueprints for management practices to maintain adaptive and resilient forest ecosystems (Drever *et al.*, 2006; Messier *et al.*, 2013).

Rather than focusing management on a single objective such as timber production or wildlife habitat, managing forests for ecosystem resilience requires the holistic consideration of ecosystem components, temporal and spatial scales and their interactions, which also helps maintain ecosystem services (Messier *et al.*, 2013). Ecosystem services are benefits provided by the provisional, regulating, cultural and supporting components of an ecosystem (*Millenium Ecosystem Assessment*, 2005). Without the ability of a forest ecosystem to quickly recover from a perturbation, people cannot reliably depend on the forest for the services it provides. Managing forests as complex adaptive systems therefore fits well within the framework of ecosystem services. For example, a resilient forest ecosystem can provide clean water, timber and fibre. It mitigates unexpected flooding disasters because it has evolved under its current (albeit, pre-climate change) disturbance regime (Seymour and Hunter, 1999). A resilient forest ecosystem can naturally purify water by filtering contaminants, absorbing nutrients and preventing soil erosion, though this depends on the successional state of the forest. It provides aesthetics and recreational opportunities and further provides spiritual benefits by maintaining species diversity, and consequently species that may be historically important to indigenous and local communities (Gadgil *et al.*, 1993, Emery *et al.*, 2014). Functional trait diversity, which often links above and belowground processes (Bardgett and van der Putten, 2014; Alberti *et al.*, 2017), is another key component of ecosystem resilience (Elmqvist *et al.*, 2003; Downing *et al.*, 2012; Whitfield *et al.*, 2014). The functional trait diversity of a resilient ecosystem may help maintain a balanced nutrient budget and regulate species populations, consequently limiting the opportunity for invasion (Davis *et al.*, 2000; Downing *et al.*, 2012).

The increasing threats of climate change and species invasion require adaptability in management techniques. Though the severity of future natural disturbances is unpredictable, applying a variety of silvicultural systems using historically prevalent natural disturbances as a management blueprint, within the natural range of variability, gives the ecosystem greater potential to maintain productivity, stability and resilience (Drever *et al.*, 2006; Messier *et al.*, 2013, Nolet *et al.*, 2018).

Conceptual models to identify gaps in management and find solutions

Identifying management gaps

Historically, there has been a mismatch between silvicultural practices and regionally specific disturbance regimes on a stand scale. As Figure 1 illustrates, treefall is characterized by a relatively small mean patch size, small proportion of stand disturbed, low degree of exposed mineral soil, low coarse woody debris input, but relatively high frequency. Consequently, microsites with a thick leaf litter layer overlaying pit-mound topography, and little understory light availability, are common across stands which historically experienced treefall as the dominant disturbance regime and are particularly favourable for sugar maple and American beech regeneration (Tubbs, 1977; Frelich, 2002; Kern *et al.* 2013b; Gauthier *et al.*, 2016). On the other hand, windthrow events that have lower disturbance frequencies combined with greater mean patch size, more exposed mineral soil and more coarse woody debris input tended to favour additional species such as hemlock, yellow birch, aspen and white pine (Frelich, 2002; Webster and Lorimer, 2002; Prévost and Raymond, 2012). Furthermore, high-severity fires were at the opposite end of the spectrum from treefall by having relatively low frequency combined with high mean patch size, high degree of exposed mineral soil and high input of coarse woody debris (albeit charred) consequently favoring a greater abundance of pioneer species such as paper birch and aspen (Frelich, 2002). Overall, the large range of these disturbances tended to maintain greater structural and species diversity than seen today.

Historical management practices, on the other hand, have focused on the extremes of these disturbances. The cutover, including subsequent slash fires, most closely emulated high-severity fires (high on all axes of Figure 2). Single-tree selection has since been the dominant silvicultural system in forests with planned management, yet represents only a narrow range of each axis (Figure 2). Single-tree selection is typically characterized by a moderately small mean patch size, intermediate proportion of stand disturbed, moderately high-frequency and moderately low coarse woody debris input (Després *et al.*, 2016). Additionally, the degree of exposed mineral soil is largely dependent on soil conditions during harvest and the type of machinery (Napper *et al.*, 2009). For example, deep snow cover during winter harvesting often minimizes soil disturbance while in contrast, little or no snow cover during harvesting will increase the degree of soil disturbance, particularly if the soil is not frozen (Berger *et al.* 2004; Kern *et al.*, 2006). Though several studies have recommended a variety of harvesting systems to maintain structural and species diversity (Doyon *et al.*, 2005; Nolet *et al.*, 2018), silvicultural systems which emulate the full range of disturbances between these two extremes have, until recently, received little attention. In 1957, Arbogast explicitly stated that yellow birch requires the occasional patch cut of ~0.04 ha near a seed tree, in addition to exposed mineral soil, to emulate the favourable conditions for germination and survival provided by higher severity disturbances (Arbogast, 1957). More recent guidelines have recommended larger gaps (Wisconsin Department of Natural Resources, 2011) or greater use of regular and irregular shelterwoods (Raymond *et al.*, 2009; Lussier and Meek, 2014; Raymond and Bédard, 2017); however, these have yet to be intentionally implemented on a large scale and monitored long term.

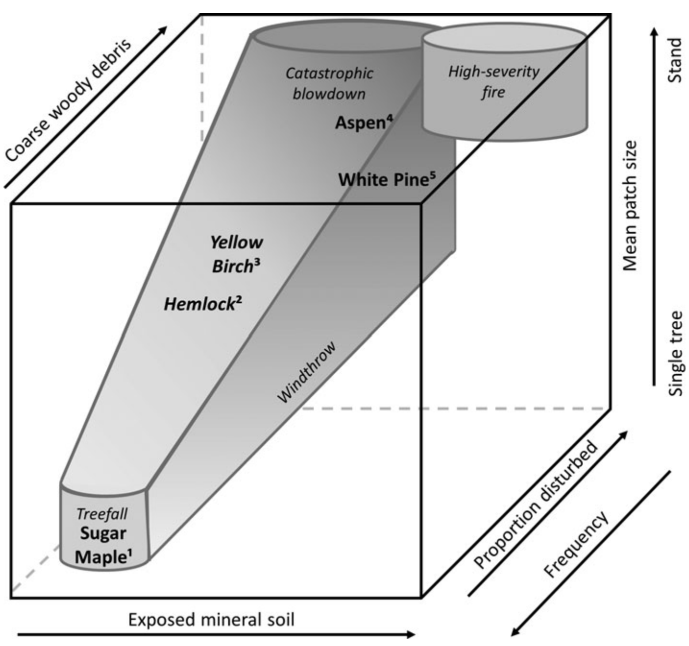

Figure 1 Conceptual model showing historically prevalent disturbance regimes in Great Lakes northern hardwoods, and the tree species best promoted by the resulting microsite conditions. Historical disturbances were variable, promoting a large diversity of tree species across the landscape. Italicized species have shown evidence of decline in Great Lakes northern hardwoods. [1](Tubbs, 1977; Kern *et al.*, 2013a; Beaudet *et al.*, 2014); [2](Frelich and Lorimer, 1991; Scharenbroch and Bockheim, 2007; Marx and Walters, 2008); [3](Gastaldello *et al.*, 2007; Lorenzetti *et al.* 2008; Gauthier *et al.*, 2016; Lambert *et al.*, 2016); [4](Peltzer *et al.*, 2000; Rich *et al.*, 2007; Schulte *et al.*, 2007; Vodde *et al.*, 2015); [5](Frelich and Lorimer, 1991; Reich *et al.*, 2001; Rich *et al.*, 2007; Vodde *et al.*, 2015).

A further mismatch has unfolded between historic disturbances regimes and emerging threats such as deer herbivory, European earthworm invasion, invasive pests and climate change. For example, the disturbance impacts of European earthworm invasions did not exist when historic disturbance regimes predominated. The mean patch size, proportion of stand disturbed, degree of exposed mineral soil, coarse woody debris input and disturbance frequency from these relatively recent disturbances do not overlap historical disturbance regimes and consequently create new disturbance regimes in which current species did not evolve. Promoting forest resilience by increasing stand-scale structural and species diversity could help mitigate the negative impacts of these emerging threats (Nagel *et al.*, 2017).

Though single-tree selection retains canopy cover, aesthetic value and suitable germination sites for shade-tolerant species, its widespread application without the necessary modifications has led to landscape-scale homogenization of Great Lakes forests with planned management (Schulte *et al.*, 2007). This homogenization has resulted in fewer large trees, subsequently reduced gap sizes following windthrow and consequently a decline in suitable germination sites for shade-intolerant and -midtolerant species. The abundance of simplified forests resulting from past land use and management history have now created a need to increase structural and functional trait diversity.

Finding solutions

To capture the range of silvicultural systems which best emulate natural disturbances in northern hardwoods, Figure 2 replaces the historically prevalent disturbance regimes shown in Figure 1 with the silvicultural systems which most closely emulate those disturbances based on mean patch size, proportion of stand disturbed, frequency, degree of exposed mineral soil and coarse woody debris input. For example, sugar maple regeneration is

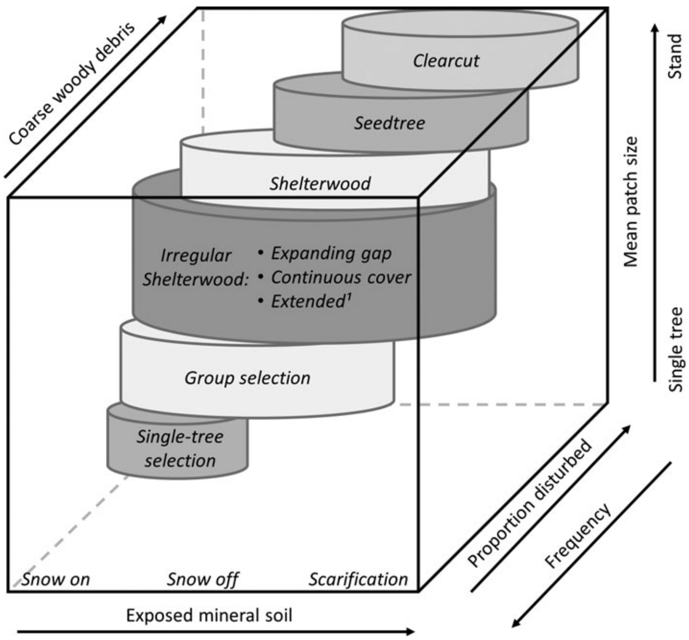

Figure 2 Conceptual model illustrating techniques for restoring tree regeneration diversity based on historic disturbance regime and the species promoted by each disturbance type. Current management of northern hardwoods in the Great Lakes region is typically focused on single-tree selection and small gap cutting. Larger gaps, shelterwood, irregular shelterwood and clearcutting are rarely implemented. [1](Raymond *et al.* 2009).

best promoted by emulating a regime with small mean patch size, small to moderate proportion of stand disturbed, high frequency, low degree of exposed mineral soil and low coarse woody debris input (Figure 1). The corresponding silvicultural system includes single-tree selection combined with winter harvesting (i.e. snow on) to minimize soil disturbance (Figure 2). However, because single-tree selection traditionally removes up to 40 per cent of the canopy, Nolet *et al.* (2014) proposed a frequent, low-intensity harvesting system which could more closely emulate low-severity disturbances in northern hardwoods. In contrast, yellow birch regeneration requires greater disturbance and is best promoted by a regime with intermediate mean patch size, intermediate proportion of stand disturbed, intermediate frequency, intermediate degree of exposed mineral soil and intermediate coarse woody debris input (Figure 1). Consequently, silvicultural systems for increasing the abundance of yellow birch in northern hardwoods should supplement single-tree selection with larger disturbances such as irregular shelterwoods combined with mechanical scarification and tip-up mounds to increase the degree of exposed mineral soil and coarse woody debris input (Figure 2; Godman and Krefting, 1960; Lorenzetti *et al.*, 2008, Gauthier *et al.*, 2016). An irregular shelterwood begins with an establishment cut similar to a regular shelterwood. Additional cuts are optional, but the two remaining cohorts are always maintained. Regenerating seedlings are protected, can establish and grow for several decades (Raymond *et al.*, 2009). Irregular shelterwood systems and 'structural complexity enhancements' have been recently explored in Québec and New England, respectively, as methods for increasing structural and species diversity in northern hardwoods (Keeton, 2006; Raymond and Bédard, 2017).

In addition to the five main components of disturbances discussed here, regionally specific influences and future interactions must still be considered. Competing vegetation, deer and insect herbivory dynamics and invasive species continually shape forest development and disturbance-based management alone may not sufficiently restore species diversity. The effects of climate change further confound efforts to restore species diversity (Harris *et al.*, 2006; Peters *et al.*, 2013) because a shift in native species abundances and interspecific interactions due to warming temperatures, drought or other effects may make the ecosystem vulnerable to invasive species. The potential for novel interactions consequently makes it difficult to predict regeneration dynamics, but increasing ecosystem resilience with greater structural and species diversity could help prevent ecosystem degradation (Downing *et al.*, 2012; Lindenmayer *et al.*, 2016).

Disturbance spectrum models are not foreign to management literature; indeed, numerous conceptual models have been proposed (Seymour *et al.*, 2002; Kimmins, 2004; Roberts, 2004; Drever *et al.*, 2006; Roberts, 2007; Raymond *et al.*, 2013). Seymour *et al.* (2002) compared management systems with natural disturbances using the 'natural disturbance comparability index', which expresses the deviation of management systems from the upper limit of natural disturbance parameters. This model is useful for quantifying the degree of emulation when limited to patch size and disturbance frequency; however, disturbances are more nuanced than simply patch size and frequency. We expand upon this model by incorporating other important aspects of disturbances that strongly influence regeneration dynamics including coarse woody debris input and degree of exposed soil. Future studies which quantify these additional components along a gradient of natural and management disturbances would further strengthen our conceptual model. Building upon conceptual models, Kimmins (2004) provides a comprehensive qualitative model to demonstrate which seral stages are favoured by various silvicultural systems. Additionally, Raymond *et al.* (2013) compared silvicultural systems to natural disturbances in temperate mixedwood forests based on disturbance severity, size and frequency. The range of comparisons are useful, but these models are limited by the absence of microsite components. A three-axis model proposed by Roberts (2004, 2007) examines characteristics of natural and silvicultural disturbances based on per cent canopy removed, per cent understory removed and per cent forest floor or soil removed or disrupted. Most silvicultural systems were found to only represent a narrow range of these components. These models provide an important foundation for future work, and we have built upon them by incorporating an important temporal gradient. Finally, Drever *et al.* (2006) thoroughly presented a strong theoretical reasoning behind natural disturbance-based management that laid further groundwork for future management objectives. We build upon the above models by explicitly incorporating relevant microsite components and offering specific management systems to emulate the desired natural disturbance.

In conclusion, structural and species diversity are strongly influenced by patch size, proportion of stand disturbed, frequency, degree of exposed mineral soil and course woody debris input. By comparing historically prevalent disturbance regimes to regional silvicultural systems, our conceptual model illustrates the need to emulate a fuller range of natural disturbances to restore and promote species diversity in northern hardwoods in the upper Great Lakes based on these five components. For example, single-tree selection should be supplemented with larger disturbances to promote the regeneration of declining species such as yellow birch. Though our conceptual model is focused on northern hardwood forest ecosystems, it can easily be applied to other forest types using the five identifiable components of disturbance, which are important components of any disturbance type across the globe. Using our conceptual model with other forest types more broadly would further provide a unique qualitative approach for emulating natural disturbances and consequently, promoting forest ecosystem resilience. In all cases, however, regionally specific influences should still be considered.

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Conflict of interest statement

None declared.

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