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Challenges facing gap-based silviculture and possible solutions for mesic northern forests in North America

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Gap-based silvicultural systems were developed under the assumption that richness, and diversity of tree species and other biota positively respond to variation in size of harvest-created canopy gaps. However, varying gap size alone often does not meet diversity objectives and broader goals to address contemporary forest conditions. Recent research highlights the need to consider site factors and history, natural disturbance models, within-gap structure and recruitment requirements in addition to light resources for desired tree diversity. This synthesis brings together silvicultural developments and ecological literature on gap-based management, highlighting interactions with other factors such as microsite conditions, non-tree vegetation and more. We pose a revised concept for managers and researchers to use in prescriptions and studies focused on integrated overstory and understory manipulations that increase structural complexity within and around canopy openings.

Introduction

Managing tree diversity is both a goal of sustainable forest management and an approach to enhance ecosystem resilience and adaptability (Millar *et al.*, 2007; Mori *et al.*, 2013). For some forests, a method of managing tree diversity is to emulate patterns of natural disturbances. The creation of openings in the forest canopy, or gaps, has been of particular interest because gaps in unmanaged forests known for gap-phase dynamics can be associated with a diverse collection of regenerating tree species (Runkle, 1982). Gap-based silvicultural systems have experienced widespread application and adoption at different points in history for various ecological and economic reasons; these systems involve harvesting overstory trees singly or in groups for the purpose of tree regeneration (O'Hara, 2002). Gap-based silviculture can sustain the provisioning of desired products and ecosystem services by maintaining a diversity of tree species (Coates and Burton, 1997). In this regard, the incorporation of canopy gaps within silvicultural practices may also enhance forest resilience or adaptability to stressors, perturbations or environmental change (Millar *et al.*, 2007; Puettmann, 2011; Mori *et al.*, 2013). Gap-based systems, therefore, present an opportunity for further development and application in forest management of a broader range of objectives, including resilience and adaptability.

Canopy gaps are caused by natural agents (i.e. insect, disease, wind, ice and fire) in all forests, but, in managed forests, the primary agent is timber harvest, where overstory trees are removed singly or in groups or patches (hereafter, 'harvest gaps'). Managers interested in regenerating a particular species prescribe gap characteristics favouring the species' shade tolerance and other regeneration requirements. For example, in northeastern US northern hardwood forests dominated by shade-tolerant American beech (*Fagus grandifolia* Ehrh.) and sugar maple (*Acer saccharum* Marshall), a large gap size (e.g. >0.3 ha patch) will favour the establishment of *Populus* spp., *Betula* spp. and other shade-intolerant species (Leak *et al.*, 2014). Deliberate manipulation of harvest gap size is a straightforward approach for managers because it can be efficiently incorporated into timber harvest operations. However, regeneration outcomes from gap-based management are often inconsistent with theoretical predictions of regeneration responses (Raymond *et al.*, 2006; Bolton and D'Amato, 2011; Matonis *et al.*, 2011; Kern *et al.*, 2013; Forrester *et al.*, 2014). These inconsistencies could be due to other gap characteristics (e.g. gap shape, aspect, etc.) (Prévost and Raymond, 2012) and forest conditions (e.g. seed bed, seed source, advance regeneration, competing vegetation and damaging agents such as herbivores) (Willis *et al.*, 2015) that vary with, or independently of, gap size.

Our goal is to propose a revised concept of gap-based silviculture that recognizes the complexity of gap attributes and functions. Here, we review pertinent scientific literature, summarize recent findings and critique long-standing views of harvest gap use and application. We focus on the premise that gap-based approaches can help meet sustainable forest management objectives, such as encouraging a diversity of canopy tree species. Our approach is different from previous studies and reviews (Muscolo *et al.*, 2014; Zhu *et al.*, 2014) because we focus on implementation and outcomes of gap-based management. We also focus on gap-based management in mesic forests of northcentral and northeastern North America. In these forests, wind is a primary disturbance agent and unmanaged forests are characterized by uneven-aged structure and diverse mixtures of hardwood and conifer species (Runkle, 1982; Frelich and Lorimer, 1991), because this approach is deemed appropriate for these forests (Coates and Burton, 1997). Moreover, we address factors (seed source, damaging agents, etc.) that limit the efficacy of gap size in promoting diversity and have broad applicability to forest management in other countries.

Background

Silvicultural systems and harvest gaps

Harvest gaps have a long history in silviculture. The integration of harvest gaps into silvicultural systems, which include a specified method of regenerating trees after harvest, fall into two overarching families: selection and irregular shelterwood systems (Table 1). Both seek to maintain, or restore, uneven-aged (multi-aged) stand structures (Smith *et al.*, 1997; O'Hara, 2014).

Selection systems are used to develop balanced, uneven-aged stands composed of multiple cohorts or age classes of trees, distributed across approximately equal areas of growing space. This structure, in theory, sustains a given yield of timber over time (Schutz, 1997; Spathelf, 1997). Single-tree selection is commonly applied by maintaining a specific diameter distribution with a target residual density, volume and maximum diameter. Gaps as wide as the crowns of dominant trees are dispersed throughout the forest and created when these trees are cut singly (and in tandem with tending of the below-canopy trees) throughout a managed stand at each harvest entry.

Area-based group selection is a classic example of the integration of harvest gaps into balanced uneven-aged stand management. Size of harvest gaps are greater than mature crown widths (~100 to 2000 m^2) and close through the infilling of regenerating saplings (Webster and Lorimer, 2005; Poznanovic *et al.*, 2013). Harvest gap size and density are planned over space and time to regenerate new spatially discrete cohorts that independently undergo stand development to maturity. Area-based group selection is simple to use and, like single-tree selection, creates an even flow of merchantable timber that can be harvested sustainably at short intervals within the stand (Leak and Gottsacker, 1985; Matthews, 1989).

In contrast, irregular uneven-aged approaches, such as those often created through irregular shelterwood systems, are unbalanced among age classes in space and time when applied at the stand level. Irregular uneven-aged stands do not contain the age-class distribution necessary to produce a constant yield of mature trees at short harvest intervals indefinitely (Smith *et al.*, 1997). Irregular approaches can be useful when balanced approaches, such as single-tree selection, are not suitable or where species composition is not necessarily suited to selection systems; for instance, irregular shelterwood system is an approach to manage forests with highly heterogeneous stocking, quality and merchantability due to past, exploitive partial cutting (Lussier and Meek, 2014).

The group selection and irregular shelterwood systems currently applied in North America (Hawley, 1921) were originally developed in Central Europe in the eighteenth century to maintain mixed-species stands in order to avoid timber resource shortages and exploitation (Puettmann *et al.*, 2009). This meant regenerating species intermediate in shade tolerance in gaps embedded within a matrix of shade-tolerant tree species, such as European beech (*Fagus sylvatica* L.) (Matthews, 1989; Brumme and Khanna, 2009; Puettmann *et al.*, 2009). As such, a common measure for evaluating the degree of success of these systems has been their ability to regenerate and maintain mixed-species stands containing a range of species with varying degrees of shade tolerance in

Table 1 Classification of silvicultural systems and variants using gaps, according to the arrangement of gap makers and the target stand (Smith, 1986; Nyland, 2002; Raymond *et al.*, 2009)

Gap makers		Target stand structure	
Scale	Spatial arrangement	Balanced uneven-aged	Irregular uneven-aged
Single-tree	Random, depends on the location of trees to harvest	Single-tree selection cutting	Extended irregular shelterwood (uniform)
Multiple-tree	Random, depends on the location of trees to harvest	Hybrid single and group selection cutting	Continuous cover irregular shelterwood
Multiple-tree	Systematic, area-based, spatially clustered area to regenerate	Group-selection cutting Patch-selection cutting	Expanding gap irregular shelterwood

the canopy layer (O'Hara *et al.,* 2007). Successful application of gaps to meet regeneration goals has been most common when applied in forest conditions similar to the region from which these systems originated (i.e. similar range of tree species shade tolerance and regeneration strategies; Sendak *et al.,* 2003) or where systems were modified to account for local ecological and site conditions (Kelty *et al.,* 2003). The greatest documented success in maintaining tree diversity outside of Europe has been in the northern hardwood forests of northern New England (Leak and Filip, 1977) where large gaps or patches (>0.1 to 0.2 ha) are harvested and cleaned of less desirable advance regeneration (Leak, 2003). Smaller gaps have been successful in hemlock–hardwood forests on poorer sites in the upper Great Lakes region (Webster and Lorimer, 2005) and northern Maine, US (McClure and Lee, 1993; Sendak *et al.,* 2003). As a result, the hypothesis that gap-based approaches can meet sustainable forest management objectives, such as promoting canopy tree diversity, have persisted in management guides in eastern North America for decades (Eyre and Zillgitt, 1953; Leak and Filip, 1977; Larouche *et al.,* 2013).

Ecological theory and natural gaps

Ecological theories predict that canopy gaps can function to maintain diversity. Following natural gap creation, nutrients and moisture generally become more available and light can follow strong gradients in the understory from closed forest canopy to open and no forest canopy (Palik *et al.,* 1997; Raymond *et al.,* 2006; Prévost and Raymond, 2012; Burton *et al.,* 2014; Walters *et al.,* 2014). Species with different life history traits may specialize on different segments of the gap size gradient (i.e. niche partitioning) allowing them to coexist (Grubb, 1977). For instance, species with small seeds, rapid height extension and low-shade tolerance are predicted to regenerate successfully in large gaps with high light availability, while species with large seeds, deep root systems and high-shade tolerance are predicted to regenerate successfully in low light conditions of small gaps or along the edges of larger gaps (Figure 1). This concept assumes that additional regeneration requirements (e.g. seed supply, substrate) of a regenerating species are also met.

Several studies have shown that natural tree-fall gaps play a determining role in the regeneration of tree species in tropical (Denslow, 1987; Uhl *et al.,* 1988), temperate (Runkle, 1981, 1982; Kneeshaw and Prévost, 2007) and boreal ecosystems (Greene *et al.,* 1999; McCarthy, 2001). At the gap scale, regeneration studies generally show that tree seedling density and recruitment of less shade-tolerant species all increase as gap size increases and the effect is greater in harvest than natural gaps (Dale *et al.,* 1995). Thus, the notion that gap-based approaches can meet sustainable forest management objectives, such as maintaining or restoring tree diversity, appears substantiated by empirical studies of natural tree-fall gaps.

Scrutinizing outcomes of gap-based silviculture

Unmet regeneration goals

Despite the aforementioned successes of gap-based approaches, empirical data supporting the role of natural gaps in maintaining tree species diversity at the gap and stand scale is limited. In fact, failures in the application of gap-based silvicultural systems are evident in eastern North America (Stephens *et al.,* 1999; O'Hara, 2002; Schuler, 2004; Bolton and D'Amato, 2011). In some cases, gaps were largely void of tree regeneration (Matonis *et al.,* 2011). In other cases, gaps were dominated by a single, non-target species (Forrester *et al.,* 2014); indeed, numerous studies have documented that species composition remains largely dominated by shade-tolerant species, even in large gaps (Arseneault *et al.,* 2011; Poznanovic *et al.,* 2013; Forrester *et al.,* 2014). Similarly, studies explicitly examining gap partitioning have generally shown that although tree species do sort along gradients of light availability, the magnitude of effects are variable and often small, because factors other than light (in the following section) contribute to tree regeneration patterns (Falk *et al.,* 2010; Gasser *et al.,* 2010; Bolton and D'Amato, 2011; Kern *et al.,* 2013).

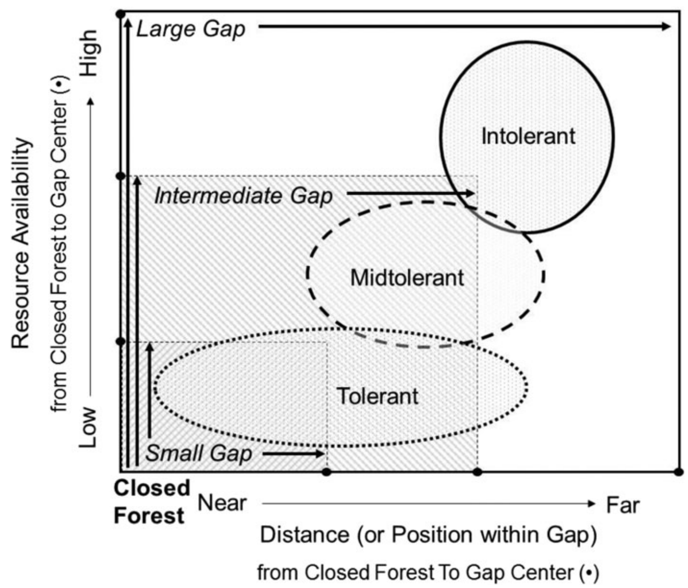

Figure 1 An illustration of the gap partitioning (Grubb, 1977) as the conceptual relationship for shade tolerance strategies with plant essential resources (*y*-axis) and within-gap position (*x*-axis). Stress and competition constrain tolerance groups within the gap. Species with tolerant strategies dominate in gap edge positions. Intolerant species dominate in gap positions far from gap edge. Mid-tolerant species are intermediate in distance from edge to tolerant and intolerant species, and, as a result, composition is differentiated by gap position. Gap size is also partitioned with intolerant species unique to large gaps (white, entire response surface), mid-tolerant species dominating in intermediate gaps (down, right hatching) and shade-tolerant species dominating small gaps (down, left hatching).

Regeneration factors beyond gap size

Basic regeneration requirements are often not met with harvest gaps alone. For example, seed availability may strongly restrict the number of species that can establish in harvest gaps (Caspersen and Saprunoff, 2005). This limitation can arise from a lack of proximate seed bearing trees, low fecundity, a depauperate seed bank or seed predation (Clark *et al.,* 1998; Raymond *et al.,* 2003). Additionally, many species, especially those with small seeds, can be limited by the availability of favourable substrates for germination, including bare mineral soil and highly decayed coarse woody debris (Gray and Spies, 1997; Caspersen and Saprunoff, 2005; Marx and Walters, 2008; Weaver *et al.,* 2009; Willis *et al.,* 2015). In northern hardwood forests of North America, these substrates are less common due to a history of management activities aimed at removing trees before they die and/or decay and an emphasis on low impact harvest practices that create little surface disturbance (Goodburn and Lorimer, 1998; Wolf *et al.,* 2008; Burton *et al.,* 2009; Olson *et al.,* 2011).

Furthermore, advance tree regeneration (i.e. tree seedlings and saplings that established prior to the creation of harvest gaps) and non-tree vegetation can offset gap size effects on seedling establishment. Advance regeneration often outcompetes seedlings establishing post-gap creation and can 'capture' gaps as a result of an initial size advantage (Webster and Lorimer, 2005; Dietze and Clark, 2008). In some cases, species present as advance regeneration are often the few species that are the most shade tolerant and most tolerant of other factors negatively impacting growth and survival (e.g. ungulate browsing (Royo and Carson, 2006)). As a result, advance regeneration may dominate canopy recruits regardless of gap size or light availability (Madsen and Hahn, 2008; Forrester *et al.,* 2014). In hardwood forests, sprouts from damaged trees or stumps from cut trees have root energy stores that allow rapid response and canopy ascension following gap creation. Regeneration from sprouting can comprise a large proportion of tree regeneration (Dietze and Clark, 2008; Forrester *et al.,* 2014). Not surprisingly, recruitment of less-tolerant tree species following gap creation is particularly successful in areas where existing advance regeneration is felled along with overstory trees (Leak, 2003) or where low-quality sites limit the abundance of advance regeneration (Webster and Lorimer, 2005).

Many other factors limit the response of tree regeneration to gap size. These include, but are not limited to, root competition with shrubs (Engelman and Nyland, 2006; Montgomery *et al.,* 2010), below-ground resource limitations (Walters *et al.,* 2014) and extreme microenvironments (Strong *et al.,* 1997). Moreover, variation in edaphic factors within and among harvest gaps and across soil, and bedrock gradients can lead to variation in species performance unrelated to the effects of gap size on light availability (Gray and Spies, 1997; Bigelow and Canham, 2002; Van Couwenberghe *et al.,* 2010; Walters *et al.,* 2014). These complex interactions can make the regeneration of species mixtures including light-demanding tree species particularly difficult to manage.

Challenges

Contemporary environmental and operational conditions are also different from those under which silvicultural systems and underlying ecological theory were originally developed. Over the past century, human modifications of disturbance and trophic regimes have contributed to changes in forest plant biodiversity worldwide (Dale *et al.,* 2001, Frelich, 2002; Chazdon, 2003; Roberts, 2004). These conditions can alter, limit or even nullify expected patterns of tree regeneration following gap creation (Royo and Carson, 2006; Kern *et al.,* 2012; Nuttle *et al.,* 2013). Resulting declines in tree species diversity may diminish the capacity of forests ecosystems to provide the range of goods and services people value (Chapin *et al.,* 2000).

First, the pool of species capable of regenerating within gaps is decreasing. Populations of specific tree species (e.g. white pine [*Pinus strobus* L.], yellow birch [*Betula alleghaniensis* Britton], eastern hemlock [*Tsuga canadensis* (L.) Carrière], red spruce [*Picea rubens* Sarg.]) have been reduced as a result of historical logging activities, including 'high-grade' logging, resulting in seed source limitations and reducing the potential for recruitment in gaps (Keeton and Franklin, 2005; Schulte *et al.,* 2007; Burton *et al.,* 2009). Moreover, Dutch elm disease (*Ophiostoma ulmi* [Buisman] Nannf.), emerald ash borer (*Agrilus planipennis* Fairmaire) and hemlock woolly adelgid (*Adelges tsugae* [Annand]) have functionally eliminated their host species across millions of forested hectares of North America (Anagnostakis, 1978; Loo, 2009). These changes not only reduce the likelihood that these species will successfully regenerate in gaps (Papaik *et al.,* 2005; Vose *et al.,* 2013) but also dramatically alter environmental conditions (Boettcher and Kalisz, 1990; Canham *et al.,* 1994; Burton *et al.,* 2011). Therefore, sustaining many of these species with reduced populations proves increasingly complicated in contemporary forests.

Second, canopy gaps created via harvesting, or the sudden widespread mortality of trees due to pests, pathogens or drought, can also trigger the monopolization of the forest understory by a limited number of native and exotic plant species (Huenneke, 1983; Eschtruth *et al.,* 2006; Gandhi and Herms, 2010). This response may occur as a result of the historical legacy of exploitive harvesting. For instance, historical logging was typically more severe than natural disturbances and may have resulted in more homogenous distribution of a persistent soil seed bank of *Rubus* species (Mladenoff, 1987; Tappeiner *et al.,* 1991; Hyatt and Casper, 2000). As a result, after harvest, a thick shrub layer can develop and dampen the effect of the gap on tree regeneration (Kern *et al.,* 2012). The development of 'recalcitrant' vegetation layers can slow, alter or even arrest tree regeneration trajectories following harvest gap creation making sustainable forest management challenging without the explicit consideration and control (e.g. chemical or mechanical treatments) of this vegetation (e.g. reviewed by Sullivan and Sullivan, 2003; Royo and Carson, 2006). Additionally, a major challenge being faced by forest managers in the northeastern US is beech sprouting, particularly on poorer sites where beech is more abundant. Prolific sprouting is triggered physiologically as a response to both beech bark disease (primarily *Nectria coccinea* var. *faginata)* (Houston, 2001). Beech sprouts can form dense understories both within closed canopy forests and in gaps, outcompeting other regeneration, including species that might be more desirable commercially such as sugar maple and yellow birch (Nyland *et al.,* 2006). Increasingly beech control is viewed as a necessary component of gap-harvesting operations where sprouting is a problem (Bédard *et al.,* 2014). For instance, cleaning at the time of harvest has been effective in diminishing recalcitrant layers of beech and increase the abundance of regeneration for other tree species (Leak *et al.,* 2014).

Moreover, contemporary forests are also affected by dynamic, intensified trophic interactions that can exert considerable control over post-disturbance plant dynamics (Frelich *et al.,* 2012). Forests worldwide have experienced large increases in populations of both native and introduced ungulates (Persson *et al.,* 2000; Côte et al., 2004; Perea et al., 2014). Browsing by overabundant ungulates, such as white-tailed deer (*Odocoileus virginianus* Zimmerman), can shift species composition, reduce abundance of browse-sensitive plant species and cause localized extirpations of browse-preferred species (McInnes et al., 1992; Russell et al., 2001; Rooney and Waller, 2003; Côte et al., 2004; Carson et al., 2014). Within gaps, ungulate browsing can shift competitive hierarchies leading to situations where browse tolerance, rather than shade tolerance, determines competitive success and persistence in the community (Tripler et al., 2005; Eschtruth and Battles, 2008; Krueger et al., 2009). For example, ungulate browsing has been shown to severely limit tree establishment in large gaps created by windthrow, thereby altering successional rates and pathways (Proll et al., 2014). Indeed, recent experiments have shown that ungulates can nullify the expected increase in shade-intolerant or mid-tolerant trees species following gap creation (Kern et al., 2012; Nuttle et al., 2013; Thomas-Van Gundy et al., 2014), yet indirectly increase herbaceous diversity through their consumption of woody shrubs and seedlings (Royo et al., 2010). Effects of harvest gaps on forest regeneration trajectories are often strongly linked to herbivory where ungulate populations exceed historical levels, which can result in regeneration failures following canopy gap creation (Kuijper et al., 2009; Matonis et al., 2011; Kern et al., 2012; Forrester et al., 2014).

Finally, the invasion of European and Asian earthworms (*Lumbricus terrestris* L. and *Amynthas hawayanus* Rosa) into previously earthworm-free soils of North America (e.g. New England, Lake States and Canada) further disrupts soil structure, nutrient availability and mycorrhizal associations (reviewed by Frelich et al., 2006; Forey et al., 2011). Both soil acidity and climate affect *L. terrestris* invasion in North America (Moore et al., 2013). Experimental evidence suggests *A. hawayanus* may be only limited by climate, suggesting potentially more widespread effects than *L. terrestris* (Moore et al., 2013). Earthworm colonization has been linked to alterations in plant communities, including declines in recruitment of mycorrhizal species (e.g. *A. saccharum*; Hale et al., 2006) and a concomitant shift towards dominance by small-seeded non-mycorrhizal species (e.g. *Carex* spp. Holdsworth et al., 2007; Powers and Nagel, 2008).

Contemporary forest conditions thus pose many challenges to silviculture, making business-as-usual models no longer reliable. While these challenges were often unknown or non-existent when silvicultural and ecological basics were developed, the objectives for which forests are managed have also broadened to include many non-commodity values. Important steps forward in gap-based silviculture include adapting management practices to account for contemporary forest conditions, a broader array of ecosystem goods and services including sustainability, and increasing resilience and adaptability in general.

Moving forward in concept

Developing silvicultural systems that enhance ecosystem resilience and adaptability by maintaining or restoring tree diversity continues to be of high relevance. In particular, tree diversity may enhance ecosystem resilience and resistance to challenges facing forest management, such as host-specific pests and pathogens and extreme events induced by climate change (Millar et al., 2007; Mori et al., 2013). Diversity of overstory trees can stabilize the provisioning of desired ecosystem services, including species-specific products, in the context of such changes (Tilman and Downing, 1994) and has a cascading effect on diversity of other biota, which, collectively, can influence the range of traits and capability of forests to respond to stressors, perturbations or environmental change (Chapin et al., 2000; Barbier et al., 2008). Thus, promoting tree diversity is not only one of the many goals in sustainable forest management in and of itself but also an approach to maintaining a broader range of species and ecosystem functions.

Applying the ever-growing knowledge of natural disturbance ecology to silviculture is integral to experimentation, innovation and adaptation in sustainable forestry practices. Variation in structural and functional conditions within stands and on the landscape facilitates diversity and resilience. Thus, understanding natural disturbances and stand dynamics is one part of a larger conceptual approach that advances gap-based forest management.

Comparing how current silvicultural systems do or do not approximate natural disturbance effects provides context to current or potential management options (Figure 2) (Seymour et al., 2002). For example, the frequent small canopy gaps resulting from individual-tree mortality due to a light-intensity disturbance (e.g. natural senescence) overlap gap characteristics resulting from single-tree selection (Figure 2) (Seymour et al., 2002). Moreover, if a large gap is used in an irregular shelterwood harvest, it might emulate an opening size resulting from a moderate-intensity disturbance, such as a localized windstorm (e.g. a microburst or tornado) (Figure 2) (North and Keeton, 2008).

Although gap-based silviculture does not emulate all aspects of natural gaps, in general, it has been proposed as a flexible system that can be adjusted to emulate the frequency, size and distribution of gaps resulting from natural disturbance specific to a forest type (Coates and Burton, 1997). The latter authors outline a step-by-step process to do this in practice. For

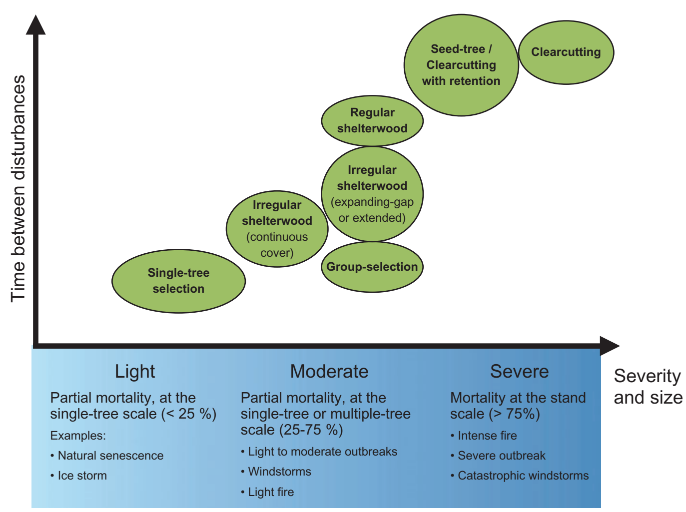

Figure 2 Conceptual framework situating silvicultural systems according to a gradient of severity, size and frequency of disturbances at the stand scale (adapted from Raymond et al., 2013).

example, unmanaged mesic northern hardwood forests in the Great Lakes region are characterized by random, single-tree mortality that result in an average of ~10% canopy disturbance per decade but with more intense disturbances from other factors such as storms at much longer intervals (e.g. >40% canopy disturbance – every 500 years) (Frelich and Lorimer, 1991). Within the constraints of economically defensible harvest practices, this disturbance regime could be approximated by prescribing single-tree harvests interspersed with small group (<500 m^2) harvests and patches of unharvested forest, removing 10–20 per cent of the overstory on cutting cycles ranging from 18–25 years). Varying gap size and cutting cycle length in addition to maintaining unharvested patches would help to more closely mimic the random component of individual-tree mortality than the typical dispersed single-tree selection techniques, and it would allow for the provisioning of dead trees and snags (Angers *et al.,* 2005; Newbery *et al.,* 2007). Superimposed upon this management regime would be infrequent (e.g. every 200+ years) higher intensity (e.g. >500–2500 m^2 openings) that would mimic elements of a moderate–severity storm in this forest type (Hanson and Lorimer, 2007). Although this approach is posed to increase tree diversity, the idea has not been validated in practice, and current information questions its potential for increasing diversity in the face of high deer populations (Kern *et al.,* 2013; Walters *et al.,* In Press).

However, natural disturbances are inherently 'messy'. They seldom produce the simplified environments replicated in field experiments and targeted by traditional silvicultural systems (Franklin *et al.,* 2007). Rather, natural disturbances leave behind numerous biological legacies, including live and dead organisms and biologically derived structures and patterns (Franklin *et al.,* 2000). A growing body of research has highlighted the importance of these legacies in maintaining or restoring structural and taxonomic diversity following both natural and anthropogenic disturbances (McGee *et al.,* 1999; Mazurek and Zielinski, 2004; Hyvärinen *et al.,* 2005; Keeton, 2006; Sullivan *et al.,* 2008; Roth *et al.,* 2014). For instance, a silvicultural study in Vermont, US (Keeton, 2006) tested a variety of harvest gap sizes, with structural retention in the larger openings (0.05 ha mean). The study showed that a variety of small gap and group selection with retention techniques can help maintain a range of non-tree biota in managed forests (McKenny *et al.,* 2006; Smith *et al.,* 2008; Dove and Keeton, 2015). Similarly, other studies examining within-gap retention of seed trees and legacy trees have demonstrated the ability of these systems to increase richness of tree species, while also providing enriched structural conditions via high survival rates of retained overstory trees within gap environments (Poznanovic *et al.,* 2013; D'Amato *et al.,* 2015). Nonetheless, trade-offs may exist regarding level of within-gap live tree retention and the ability to recruit species of lesser shade tolerance (D'Amato *et al.,* 2015).

In addition, early attempts to compare silvicultural systems with natural disturbance have focused on the extreme disturbance regimes, such as high-frequency, small-scale (gap forming) or low-frequency, large-scale (big fires, hurricanes, etc.) with less emphasis on moderate-intensity disturbances (Seymour *et al.,* 2002). Moderate-intensity disturbances, in particular, create more spatial complexity than conveyed by the concept of discrete canopy gaps and early ideas about gap-based management (Nagel *et al.,* 2006; Hanson and Lorimer, 2007). After a moderate-intensity wind-throw event, remnant trees both living and dead are abundant and well-distributed within these blowdowns, both dispersed as individuals and aggregated in clumps (Curzon and Keeton, 2010). Conversely, the amount and pattern of intact undisturbed forest (i.e. the matrix, or 'anti-gap' sensu Franklin *et al.,* 2002), lightly disturbed portion and residual trees within larger gaps are irregular in distribution as well. As a result, gap fraction, canopy closure and light availability show a high degree of spatial variation (Figure 3). Moreover, harvest scenarios based on moderate-intensity wind disturbance with a range of gap sizes increased species and trait diversity of

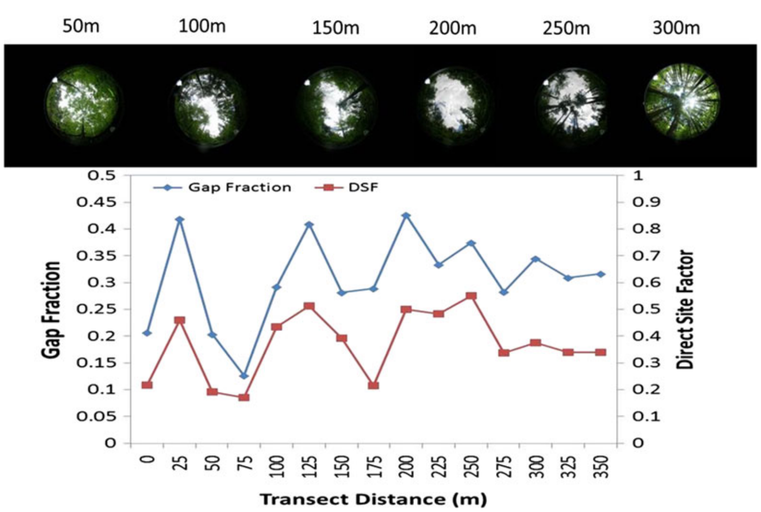

Figure 3 Spatial variability in canopy openness 4 years after a moderate-intensity windstorm in a uneven-aged, mixedwood forest in the Adirondack Mountains of New York, US. Canopy openness was measured with hemispheric photographs (top panel) and canopy metrics (bottom panel) following a transect through the middle of the blowdown event. Gap fraction (primary vertical axis) represents the ratio of canopy in open sky. Direct Site Factor (DSF, secondary vertical axis) is a measure of light availability or ratio of direct light below the canopy to direct light above (Keeton unpublished).

ground-layer vegetation from uncut forest conditions (Kern *et al.*, 2014).

The resulting regeneration patterns after multiple partial mortality disturbance events are far more complex than a simple gap model (Figure 1) would assume as well. In comparison with a model in which regeneration occurs only in gaps, regeneration can respond to spatially offset light, such as transient sunflecks originating from a break in the canopy that is not directly overhead (Figure 3) (Canham *et al.*, 1990; Van Pelt and Franklin, 2000). This spatial dynamic also creates a diversity of tree ages and sizes both within and among patches. The outcome is quite different from the conception of an uneven-aged forest as simply the aggregate of multiple even-aged patches (Goff and West, 1975).

Lastly, regeneration delays may be viewed as failures or opportunities if trade-offs with wood productivity are acceptable. Fully stocked, dense tree regeneration in all gaps within a short time period following gap creation is desired in commodity-driven forestry but is inconsistent in unmanaged forests. Lags in regeneration following gap creation can, in some contexts, provide opportunities to achieve management goals other than tree regeneration. For example, regeneration lags may be important for maintaining a broad range of early successional specialists and associated wildlife species (Swanson *et al.*, 2010). Early successional specialists in gaps may include non-tree vegetation such as shrubs (e.g. *Rubus* sp.) and non-vascular plants such as bryophytes that play important roles in nutrient cycling (Bormann and Likens, 1979; Turetsky, 2003), forage and mast production (Stransky and Roese, 1984) and provisioning of habitat (Smith *et al.*, 2001). Variability in stocking of regeneration in gaps develops spatial and temporal complexity within a managed stand and likely contributes more broadly to ecosystem resilience (Churchill *et al.*, 2013).

Moving forward in practice

Gap-based silvicultural systems present a range of challenges and opportunities for forest managers (York *et al.*, 2004; Arseneault *et al.*, 2011; Bolton and D'Amato, 2011). They can regulate production and extraction of goods and service and, more generally, enhance forest heterogeneity and biodiversity. However, given contemporary forest conditions, these benefits may not be realized. Although there is a lack of sufficient empirical research and practical experience in many forest types and regions, there are a number of beneficial ways in which gap-partitioning theory and attributes of natural disturbances can be used to help adapt current silvicultural systems to current forest conditions. Consequently, we propose the following principles where operability and economics allow.

Target gap placement

Canopy gaps should be located where their likelihood of successfully promoting desired future conditions is greatest. This may include locating gaps to release patches of desirable advance regeneration (a practice long-advised yet little applied in traditional regeneration systems (Weigel and Parker, 1997)), on aspects conducive to establishment and growth of featured species (Dodson *et al.*, 2014), on landforms particularly susceptible to gap formation (Almquist *et al.*, 2002), in areas of undesirable growing stock or areas of mature or overmature timber (Nyland, 2002), or where seed trees of featured species can be retained within or adjacent to openings (Raymond *et al.*, 2006; Shields *et al.*, 2007; Poznanovic *et al.*, 2013). The landscape context of the opening and its proximity to habitat features is also important to consider, especially if seasonal movements or aggregation of ungulates pose a risk to regeneration (Millington *et al.*, 2010; Witt and Webster, 2010). In addition, planning tools, like ecological classification systems (Kotar *et al.*, 2002; Zenner *et al.*, 2010), which incorporate variation in soil, hydrology and bedrock effects on species performance, could inform gap placement for improved prediction of regeneration outcomes.

Do more than cut trees

Gap-based systems have largely focused on a truncated view of the impacts of canopy disturbance, by primarily emphasizing the levels of canopy mortality in a given harvest or disturbance events. This ignores many of the other associated microsite and structural conditions created by canopy disturbance events that have historically allowed for the maintenance of a diversity of tree species in gap environments. These include exposing bare mineral soil by scarification in wind-disturbed systems to increase seedling densities of light-seeded species within harvest gaps (Raymond *et al.*, 2003; Lorenzetti *et al.*, 2008; Prévost *et al.*, 2010; Willis *et al.*, 2015) where seed trees are present or where direct seeding is considered. In addition, if a recalcitrant non-tree layer of vegetation develops, herbicides (Fournier *et al.*, 2007; Povak *et al.*, 2008; Man *et al.*, 2009; Nelson and Wagner, 2011; Olson *et al.*, 2011), retention of logging debris and trees (Harrington *et al.*, 2013; Dodson *et al.*, 2014) or release cutting (e.g. with brushsaws) may be useful for removing over-represented or undesirable advance regeneration and vegetation. However, choice of competition control may affect diversity of ground-layer plant communities and wildlife habitat in some cases (Swanson *et al.*, 2010; Betts *et al.*, 2013) or insignificantly affect others (Ristau *et al.*, 2011; Stoleson *et al.*, 2011; Trager *et al.*, 2013). Lastly, manipulating woody debris (e.g. leaving logs) and microtopography (e.g creating tip-up mounds) may provide additional heterogeneity similar to natural disturbance effects and may enhance opportunities for diverse regeneration over time and space (Beatty and Stone, 1986; Carlton and Bazzaz, 1998; Keeton, 2006; Smith *et al.*, 2008).

Consider artificial regeneration

In many forests managed using uneven-aged systems (Table 1), natural regeneration has been the default method of regeneration. When and where feasible, artificial regeneration from appropriate seed sources may be a necessary investment for species with establishment limitations (e.g. seed, substrate, etc.). Gap-planted trees, however, can be strongly limited by the same factors impacting natural regeneration (i.e. above- and below-ground competition and deer herbivory) (Kern *et al.*, 2012; Peck *et al.*, 2012; Hebert *et al.*, 2013; Montgomery *et al.*, 2013; Walters *et al.*, 2014), limiting their use for overcoming seed limitation in some areas. In some cases, investing in repellent or fencing temporarily may be worthwhile to protect at least a few tree species of concern during the period when they are within the reach of browsers.

Understand the local landscape context for browsers

Obtain estimates of local ungulate densities and their herbivory effects, and then plan silvicultural systems accordingly to account for browsing. Management decisions may increase or decrease ungulate carrying capacity and, in turn, change the impact that browsers have on the landscape (Rooney *et al.,* 2015). Analysing landscape context for wildlife patterns can steer forest management toward areas with greater possibilities of success. For example, targeting managed stands farther from winter yarding areas (Millington *et al.,* 2010). Additionally, managers may target particular tree regeneration compositions that offer resistance/resilience to browsers although it may be a compromise to promoting tree species diversity. Unfortunately, decreasing ungulate densities via management is rarely socially tenable, and exclosures or repellent to protect regenerating trees are rarely economically feasible for all but the most valuable tree species. A possible alternative is manipulating logging slash and downed crowns to create temporary physical barriers to browsers and provide opportunities for saplings to outgrow the reach of browsers (van Ginkel *et al.,* 2013).

Allow for variability in gap size and shape

Uneven-aged management when applied as single-tree selection tends to result in a high abundance of small gaps relative to the gap size distributions that result from natural disturbances (Lertzman, 1992; Dahir and Lorimer, 1996). Large canopy gaps, while comparatively a rare feature of natural disturbance regimes, may have a disproportionate impact on species diversity and structural heterogeneity (Woods, 2004; Hanson and Lorimer, 2007; Webster and Jensen, 2007). Consequently, consideration should be given to the range and distribution of gap sizes that might be expected under natural disturbance rather than simply the mean or median gap size (Kneeshaw and Prévost, 2007), such that the range of understory conditions facilitates the regeneration of a diversity of tree species (Raymond *et al.,* 2003). Similarly, gap shape tends to become increasingly irregular with increasing opening size (Lertzman and Krebs, 1991). Irregular-shaped openings may enhance resource heterogeneity and soften the visual appearance of larger openings. Thus, moving away from circular and smooth-edged openings will be a step toward promoting variability.

Retain biological legacies

Over the last two decades, the retention of biological legacies has become a key element of ecological forestry, forming the basis, for instance, of the 'variable retention harvesting system' (Franklin *et al.,* 1997). However, legacy or structural retention has largely been viewed within the context of even-aged regeneration systems, such as clearcutting. Retention of wind-firm species within openings can produce desirable microsite conditions, ameliorate aesthetic and ecological impacts and provide a proximate seed source (Shields *et al.,* 2007). Additionally, these trees provide an opportunity to provision for future establishment sites and inputs of coarse woody debris, including standing snags and down dead wood (Fraver *et al.,* 2002). Lastly, depending on the level of retention and its location within the gap, opening size should be adjusted or enhanced during subsequent harvest to facilitate canopy recruitment of target species (Klingsporn *et al.,* 2012; Poznanovic *et al.,* 2014). For example, retained within-gap legacies can dampen sapling height development such that gap closure is more likely by edge trees than by the sapling layer necessitating gap expansion to maintain height growth (D'Amato *et al.,* 2015).

Promote heterogeneity in the non-gap matrix

In unmanaged forests, the 'non-gap' matrix is not uniform. For instance, moderate-intensity natural disturbances, such as windstorms, produce highly heterogeneous residual stand conditions (Woods, 2004; Hanson and Lorimer, 2007). Thus, management activities between gaps can promote similar heterogeneity. Treatments can vary within the stand between doing nothing, marking only access trails, thinning even-aged patches and variable density thinning. Variable density thinning between gaps may be used to enhance heterogeneity (Franklin *et al.,* 2007; Dodson *et al.,* 2012). Irregular shelterwood approaches may also provide a unique opportunity to promote heterogeneity at the stand scale (Raymond *et al.,* 2009).

Experiment and revisit old and untested ideas

Forest ecosystems and operational conditions change over time. Consequently, forest management may best be viewed as an open-ended experiment. As such, consistent terminology, documentation and monitoring of outcomes are needed to advance our understanding of contemporary system dynamics and adapt and codify new techniques. Furthermore, given the rapid pace of change, adaptive management approaches that integrate research and monitoring are needed to respond in real time to changes on the ground.

A recent example of experimenting and revisiting old and untested ideas is the 'expanding gap' or Acadian Femelschlag approach tested in Maine, US (Seymour, 2005), which includes a hybrid of irregular shelterwood harvesting and group selection, retaining legacy trees permanently within group openings that are expanded at each harvest entry. This emulates both gap expansion processes and the biological legacies seen in wind-disturbed forests. Practiced as an area-based prescription on a 100-year rotation, it is only through permanent retention within expanding gaps that trees >100 years of age are maintained within the stand as a whole (Seymour, 2005; North and Keeton, 2008). Continued monitoring will develop and adapt the system with changing forest conditions.

Conclusion

The objective of a harvest gap has been, for decades, to yield forest products while creating the environmental conditions necessary to establish a new cohort of desired tree species or to release an existing cohort. As such, gap-based management appears feasible to enhance ecosystem resilience and adaptation by promotion of tree diversity. Managers are adept at prescribing harvest gap size, shape and density to regulate regenerating tree composition, diversity and area. However, manipulating natural processes with timber harvests often is not simple. Outcomes of harvest gaps may be difficult to predict, particularly in light of contemporary forest conditions.

Adapting silvicultural systems that use harvest gaps and create moderate-intensity disturbances, such as irregular shelterwood, regular shelterwood, group selection or hybrid single-tree and group selection, is a potential first step to develop complexity into managed forests (Table 1; Raymond *et al.,* 2009; Burrascano *et al.,* 2013; Bédard *et al.,* 2014). Applying new ideas such as this may be most appropriate in mature stands reaching the understory reinitiation and old-growth stages (Oliver and Larson, 1996) and in ecosystems driven by light-to-moderate disturbances regimes.

As gap-based approaches continue to develop, emerging technologies will help develop the integration of such ideas into practice. For instance, both remotely sensed and ground-based LIDAR can be used to quantify spatial complexity in canopy structure beyond the more simplistic classifications of gap versus non-gap applied in the past. Approaches like this are being actively tested (Vepakomma *et al.,* 2008; St-Onge *et al.,* 2014; Seidel *et al.,* 2015).

Lastly, and importantly, moving towards a view of spatial and temporal structure in temperate forests as a continuum of possibilities rather than rigid templates or formulas will free silviculturists to experiment with a wider array of practices and outcomes acceptable for diversity goals. However, managing variability in canopy structure, light environments, habitat conditions and scales will be a formidable challenge and trade-off to expectations of commodity-driven forestry. Yet, staying true to the origins of silvicultural approaches in terms of maintaining a diverse mix of tree species will increase the potential for long-term ecosystem resilience and economic sustainability.

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