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Promoting and maintaining diversity in contemporary hardwood forests: Confronting contemporary drivers of change and the loss of ecological memory☆

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ABSTRACT

Declines in the diversity of herbaceous and woody plant species in the understory of eastern North American hardwood forests are increasingly common. Forest managers are tasked with maintaining and/or promoting species diversity and resilience; however, the success of these efforts depends on a robust understanding of past and future system dynamics and identification and application of appropriate silvicultural interventions. We review how historical timber harvesting and land use, increases in deer population sizes, invasive species, and contemporary forest management practices interact to erode ecological memory and increase resilience debt of hardwood forests of eastern North America. The erosion of ecological memory and growing resilience debt in these forests pose significant challenges for forest managers because they alter the response of forests to management from the understory to overstory. Differences in how much ecological memory these systems retain, as well as the mosaic of interacting factors influencing contemporary dynamics, preclude a one size fits all management approach. That being said, our review has identified a host of common factors and pathways that can be manipulated. The approach we propose requires a more thoughtful understanding of the forest understory as the foundation upon which resilient systems are built. Which silvicultural levers will have the greatest utility clearly depend on the ecological context of the forest, and a willingness to experiment and adapt. We offer a conceptual model and recommendations for managers confronting novel plant communities and uncertain system dynamics.

1. Introduction

Foresters managing hardwood forests in eastern North America have long assumed that if they understood a species' autecology and tailored their treatments accordingly, then silvicultural outcomes should be relatively predictable. However, managers are increasingly confronted by unpredictable and/or undesirable outcomes, creating greater uncertainty as to which technique(s) to use. The decline in the efficacy of some techniques may be attributable, at least in part, to compounding and interacting factors that erode ecological memory (defined in Section 2) in managed forests. These patterns are most evident in forest understories where changes in diversity and composition are well-documented, but their importance not always recognized in the context of forest management. The lack of predictability, and

importance of the understory to biodiversity and forest dynamics, suggests that maintaining ecosystem services requires managing these forests as complex adaptive systems where ecosystem functions and services emerge as a result of feedbacks among external factors and interacting components (Puettmann et al., 2009).

The vast majority of plant diversity in temperate hardwood forest ecosystems resides in the understory, which includes all herbaceous plants and shrubs. This stratum also functions to regulate regeneration processes of forest tree species cultivated by forest managers, underscoring its importance in perpetuating forest community resilience and provisioning of ecosystem services (Gilliam, 2014). Declines in diversity and the development of novel understory communities may therefore be harbingers of larger changes to the entire forest ecosystem representing latent losses in the diversity, resilience and long-term sustainability of overstory vegetation and ecosystem services. Greater novelty and decreasing diversity and heterogeneity of understory communities in eastern North American hardwood forests are increasingly common (Rooney et al., 2004; Rogers et al., 2008). The factors associated with these changes are complex, but have generally been attributed singularly or interactively to changes in land use, forest management, and natural disturbance regimes; increases in ungulate abundance; and introductions of invasive species.

Herein, we review potential drivers of understory dynamics that may be singularly or interactively degrading ecological memory and resilience, thereby reducing the efficacy of using historic plant communities as predictors of system response. Based on this review, we offer a conceptual model and recommendations for managers confronting novel plant communities and uncertain system dynamics. In light of changing climate conditions and current and emerging stressors to native plant communities, we focus on the restoration of ecological memory, resilience and function to this important layer.

2. Ecological memory

Ecological memory is the information and material legacies—in essence the adaptations, individuals, and materials that persist after disturbance—that guide ecosystem reorganization after disturbances, and shape response to future disturbances (Johnstone et al., 2016; Jõgiste et al. (2017)). The less ecological memory that persists through disturbance, the lower the resilience or ability to return to the pre-disturbance state. Resilience debt is the loss of resilience not apparent until the next occurrence of disturbance, possibly leading to unexpected transition to a new state after a routine disturbance occurs (Johnstone et al., 2016). When ecological memory is totally lost and an ecosystem cannot return to its original state, the result is a novel ecosystem (Hobbs et al., 2013).

What factors could overcome the resilience of eastern North American hardwood forests, and what changes could be leading to resilience debt? We pose that degradation of ecological memory is a limitation to restoring and maintaining understory plant diversity. In the following sections, we discuss key drivers, their interactions and context dependence, in order to further knowledge regarding ecological memory and its role in the restoration and sustainable management of eastern North American hardwood forests.

2.1. Forest harvesting and land use

Early forest harvesting at the time of European settlement in eastern North American hardwood forests (c. 1850–1920) tended to be exploitative, harvesting valuable trees with little consideration for the residual forest (Whitney, 1994). Furthermore, following this cutover during European settlement, many areas of forest were retained in non-forest land-uses, particularly areas of fertile soils with suitable climates that were utilized for agriculture. During the Great Depression, many areas of marginal farmland were abandoned and returned to forest, often intermixed with second-growth forest that regenerated following

logging. As the abundance of virgin forests declined and future wood supplies became more uncertain, silvicultural systems were developed to manage these second-growth forests based on systems utilized in Europe, regional scientific research, and the experience of forest managers. Changes in the composition, structure, and function of understory plant communities related to agricultural use and abandonment, exploitative forest harvesting, and subsequent silvicultural systems are well documented (Flinn and Marks, 2007; Burton et al., 2009; Wyatt and Silman, 2010; Sabatini et al., 2014). However, we are only beginning to understand their consequences for forest dynamics and functions in the long-term.

The silvicultural systems which became prevalent vary by region, with silviculture of northern hardwoods forests dominated by uneven-aged systems while silviculture utilized in the central and southern hardwoods tended to be even-aged systems. This dichotomy in silviculture approaches was likely due to variation in the species composition of the forests (and their synecology), environmental constraints, local timber markets, forest management objectives, and the historical context of forest management in the region. While the majority of these silvicultural systems are considered more sustainable than the exploitative harvesting of the past, their effect on the ecological memory of these forests has varied and forest managers in some regions are increasingly confronted by unpredictable, less desirable outcomes of their activities. These less desirable outcomes may be particularly pronounced in regions where forest management has become constrained to one silvicultural paradigm with little variation in the silvicultural systems implemented across the region.

In the northern hardwood forests of the Great Lakes region, early exploitation led to the selective removal of several economically important species including white pine (*Pinus strobus* L.) and eastern hemlock (*Tsuga canadensis* (L.) Carrière), which directly impacted overstory diversity and seed availability for regeneration in the understory, and complete overstory removals or cutover areas to develop farms or provide wood for new markets. This was followed (for the last 50 + years) by single-tree selection, or partial cuttings, which resulted in further reduction of diversity by reducing many of the moderately shade-tolerant species (e.g. yellow birch, *Betula alleghaniensis* Britton; and northern red oak, *Quercus rubra* L.), and increased dominance of very shade-tolerant maple species, particularly sugar maple (*Acer saccharum* Marsh.) (Crow et al., 2002; Angers et al., 2005; Webster and Lorimer, 2005; Webster and Jensen, 2007). Single-tree selection harvests individual trees scattered uniformly across the stand, retaining a relatively dense canopy and only creating small, ephemeral gaps resulting in relatively low understory light levels (Nyland, 2002). The harvest of trees is repeated regularly, with a harvest cycle of typically 10–20 years, hypothetically yielding a consistent volume of wood for any particular stand or forest. While the utilization of this silvicultural system was developed based on the best available knowledge of species autoecology and natural disturbance regimes to manage for the economically important sugar maple (Eyre and Zillgitt, 1953; Arbogast, 1957), forest managers are now finding that the low light levels in the forest understory have impeded the regeneration of more light-demanding species, leading to declines in species diversity (Crow et al., 2002; Angers et al., 2005; Webster and Lorimer, 2005; Webster and Jensen, 2007; Burton et al., 2009). Furthermore, forest management has reduced coarse woody debris (Goodburn and Lorimer, 1998), which is an important germination microsite for some species (McGee and Birmingham, 1997; Marx and Walters, 2008). In response to this diversity decline, forest scientists and managers experimented with the use of gap-based systems that create larger canopy gaps to increase understory light levels with the aim of promoting mid-successional species and increasing tree species diversity (Webster and Lorimer, 2005; Shields and Webster, 2007; Shields et al., 2007; Prevost et al., 2010; Klingsporn et al., 2012; Prevost and Raymond, 2012; Poznanovic et al., 2013). However, the success of these gap-based systems in terms of increasing species diversity has been variable (Kern et al., 2017).

In contrast to the northern hardwood forests, the oak-mixed hardwood forests in the central region of North America have been managed using a wider range of silvicultural systems, including clearcutting, shelterwood, seed tree, and group selection systems (Parker and Merritt, 1994). However, these silvicultural systems have predominantly been accompanied by fire suppression (Nowacki and Abrams, 2008). The endemic disturbance regime of these forests typically included anthropogenic frequent, low-severity fires that favored oak species (*Quercus* spp. L.), whose investment in belowground growth allows them to resprout after frequent top-kill by fire (Dey, 2014). The lack of fire in these hardwood forests has led to the proliferation of shade-tolerant, fire-sensitive species in the understory of mature stands, while the use of clearcutting and group selection has resulted in dominance by early seral species such as tulip poplar (*Liriodendron tulipifera* L.) and black cherry (*Prunus serotina* Ehrh.) (Jenkins and Parker, 1998). As a result, oak species have encountered a regeneration bottleneck across the region (Dey, 2014).

Finally, across hardwood forests of eastern North America, the harvest of valuable tree species while leaving residual poor quality trees ("high-grading") is still common despite strong scientific evidence that this practice is unsustainable (Eyre and Zillgitt, 1953; Pond et al., 2014). Understory impacts associated with high-grading are not well understood, especially for herbaceous species, but likely correspond to harvest timing and intensity, equipment choice, and whether provisions were implemented to reduce the introduction of invasive species. Impacts to tree regeneration are more obvious because high-grading targets the removal of financially valuable trees and/or tree species, which alone can reduce overstory diversity and therefore seed availability for woody regeneration in the understory. Further, if high-grading also emphasizes removing well-formed, fast-growing individuals, degradation of population genetics can result through leaving poorly-formed, non-vigorous individuals (Kenefic and Nyland, 2005; Nyland, 2005). Residual stand structure of these high-graded stands are often dominated by low-value and shade-tolerant tree species in the understory.

2.2. White-tailed deer herbivory and associated impacts

White-tailed deer (*Odocoileus virginianus*) abundance has historically varied across the hardwood forest of eastern North America. Within this region, deer populations declined in response to habitat loss and unregulated hunting following European settlement, reaching a low point in the early 20th century when the species was scarce or absent across much of its historic range (Leopold et al., 1947). Residual populations remained in the Upper Peninsula of Michigan and parts of Pennsylvania and New York (Leopold et al., 1947), and such areas served as population sources for reintroductions into areas where deer were extirpated (Anderson, 1997; Whitaker, 2010). With the decline in predators, regulation of hunting, and the regrowth of forest after land abandonment during the Great Depression, deer populations rebounded, reaching historic highs in the 1960s–1980s across much of eastern North America and have remained at elevated levels since (Rooney, 2001). The resulting history of chronic herbivory has created deleterious effects in many forest stands throughout the region (Rooney and Waller, 2003). In some cases, past peaks in deer abundance have had lingering and persistent effects even after densities declined, with cascading impacts on other trophic levels (Nuttle et al., 2011, 2014).

The effects of overabundant deer on understory plant communities have been well-documented. Studies have identified decreased plant species diversity (Webster et al., 2005; Habeck and Schultz, 2015), decreased density of palatable herbaceous and woody species (Webster and Parker, 2000; Nuttle et al., 2014) and increased density of other, less palatable and/or browse tolerant species (Stoeckler et al., 1957; Rooney et al., 2000; Horsley et al., 2003; Griggs et al., 2006; Matonis et al., 2011; Nuttle et al., 2011), in response to chronic herbivory. Many of the herbaceous species lost from communities following long-term chronic herbivory are palatable long-lived perennials that are often

dispersal limited (Webster et al., 2005; Royo et al., 2010). Once locally extirpated, these species are slow to re-establish from distant populations, contributing to a negative legacy of reduced species richness of the herbaceous layer (Rooney et al., 2004; Thiemann et al., 2009).

Prior to extirpation, herbaceous species subjected to chronic herbivory may undergo demographic changes including reduced flowering and reproduction (Augustine and Frelich, 1998; Knight et al., 2009a), truncated age distributions (Jenkins et al., 2007), and reduced stature of adult plants (Augustine and Frelich, 1998; Jenkins et al., 2007; Knight et al., 2009a). Effects on herbaceous species result not only from direct herbivory, but from indirect effects as well. For example, jack-in-the-pulpit (*Arisaema triphyllum* (L.) Schott) is largely avoided by deer as a food source, but in areas with high deer populations, the species displays reduced height (Webster et al., 2001; Heckel et al., 2010), reduced seed rain, and male-biased sex ratios as a result of reduced water penetration associated with soil compaction and reduced litter thickness (Heckel et al., 2010).

At high population densities, deer have had a profound effect on forest regeneration in many parts of the eastern North American hardwood forests where woody species are browsed in the winter until herbaceous species emerge in the spring (Webster et al., 2005). Differences in browse preference and tolerance across species may result in shifts in relative dominance under different levels of herbivory. For example, in many parts of eastern North America deer herbivory has contributed to the scarcity of oak species reproduction (McEwan et al., 2011; Kern et al., 2012; Dey, 2014) and helped promote dominance by less palatable species such as American beech (*Fagus grandifolia* Ehrh.) and black cherry (Horsley and Marquis, 1983; Waller and Alverson, 1997; Jenkins et al., 2015). Similarly, heavy deer browsing has combined with shrub competition in forest openings to greatly reduce regeneration success of yellow birch (Horsley et al., 2003; Kern et al., 2012) and allowed the recruitment of less palatable and/or more browse tolerant species (Walters et al., 2016). Conversely, two conifers, eastern hemlock and northern white cedar (*Thuja occidentalis* L.) are heavily browsed during winter when deer congregate under mature conifer canopies (Rooney and Waller, 2003). While sugar maple and other hardwood species are also browsed, their ability to resprout allows them to persist, driving composition towards hardwood dominance in many conifer forests (Anderson and Loucks, 1979; Witt and Webster, 2010; Salk et al., 2011). In other areas browse intensity can be so severe that sugar maple is also eliminated and replaced by less browse preferred/more browse tolerant species such as ironwood (*Ostrya virginiana* Mill.) or by nothing at all (Matonis et al., 2011).

In addition to its direct effects on seedlings, deer herbivory can also increase the dominance of competing herbaceous vegetation. For example, high deer browse pressure has been shown to increase the cover of ferns and sedges (Horsley and Marquis, 1983; Randall and Walters, 2011; Nuttle et al., 2014) and invasive herbaceous species, such as garlic mustard (*Alliaria petiolata* (M. Bieb.) Cavara & Grande) (Knight et al., 2009b) and Japanese stiltgrass (*Microstegium vimineum* (Trin.) A. Camus) (Webster et al., 2008). In some cases, these effects may be reversible if deer browse pressure were simply relaxed. Based upon paired exclosures and demographic modelling, Kalisz et al. (2014) predicted that a garlic mustard population in Pennsylvania would go extinct in the absence of deer. Similarly, after deer were excluded for 10 years, Webster et al. (2008) observed that woody vegetation overtopped Japanese stiltgrass and the resulting shade greatly reduced cover of the non-native grass. In other cases, reversal may require active management and/or a much longer timeframe, for example shifts in the density and composition of tree regeneration requires long periods of time (Matonis et al., 2011). In addition to reinforcing the dominance of invasive plants, deer also serve as seed dispersers for a range of non-native species (Williams and Ward, 2006).

Deer herbivory may also have indirect effects on other components of forest ecosystems. Exclosure studies have revealed increased soil compaction (Heckel et al., 2010; Shelton et al., 2014; Sabo et al., 2017),

reduced litter layer thickness (Heckel et al., 2010; Bressette et al., 2012), and reduced abundance and species richness of litter and soil arthropods (Bressette et al., 2012; Lessard et al., 2012) in the presence of deer. Furthermore, in areas where deer congregate in the winter, deer may create an early spring nitrogen pulse that may lead to persistent shifts in plant community composition (Tahtinen et al., 2014). Results from areas where deer do not migrate to winter habitat are more mixed. For example, Bressette et al. (2012) documented decreased nutrient availability and higher arbuscular mycorrhizal fungal inoculum potential in exclosures, two trends that were not observed in an exclosure study by Shelton et al. (2014).

When considered *en masse*, the effect of chronic herbivory may reduce ecosystem resilience through species loss, alterations to biogeochemical processes, and changes in forest structure resulting from regeneration failure. Chronic herbivory may further interact with other factors, such as invasive species and historic land use, to reduce ecological memory and further contribute to resilience debt. The interplay of these and other ecological factors highlight the difficulty of quantifying resilience, and identifying management actions to reduce its degradation in forest ecosystems.

2.3. Invasive species

Invasive species have had significant effects on the diversity of the herbaceous and tree regeneration layer in eastern North American hardwood forests. Pathogen, plant, and insect invasions change essential resources, stand structure, and trophic interactions that affect the diversity of ground-layer plants. Moreover, chronic species invasions are long-lasting and the long-term effects on species diversity are unclear.

There are a large number of pathogen, plant and insect invasions that have occurred in the hardwood forests of eastern North America that may have directly or indirectly impacted the forest understory. Catastrophic epidemics such as chestnut blight (*Cryphonectria parasitica* Murr. Barr), Dutch elm disease (*Ophiostoma ulmi* (Buism.) Nannf. and *Ophiostoma novo-ulmi* Brasier.), hemlock woolly adelgid (*Adelges tsugae*), emerald ash borer (EAB, *Agrilus planipennis* Faimaire), and butternut canker (*Sirococcus clavigigneti-juglandacearum* Nair, Kostichka & Kuntz) have resulted in widespread, near complete mortality of host species and likely have decreased or currently are decreasing tree diversity in the understory. Another example, beech bark disease (BBD) — an introduced insect-fungus (*Cryptoccoccus fagisuga* Lindinger – *Neonectria* spp. Woollenweber) disease complex — is an example of a persistent, chronic invasion disturbance that is altering the structure of many northern hardwood forests in eastern U.S. and Canada (Houston, 1994). BBD kills canopy dominants of the host tree American beech and the mortality event triggers root sprouting of beech seedlings in the forest understory (Houston, 1994). As a result, a deeply-shaded understory beneath beech sapling thickets develops, other canopy species such as sugar maple regenerate poorly, and floral diversity of the ground-layer is reduced (Hane, 2003; Cale et al., 2013). BBD is expected to affect the full range of beech within the next 30 years (Morin et al., 2007) and create second killing fronts in areas where the disease has existed for decades (Giencke et al., 2014). The long-lasting effects of BBD on biodiversity and tree regeneration are largely unknown (Cale et al., 2017).

Another example of a persistent, chronic invasion disturbance is the multi-species European and Asian earthworm invasion that is widespread throughout the hardwood forests of eastern North America (Hendrix et al., 2008; Chang et al., 2016). The stage of invasion varies regionally with landscape-wide, late-stage invasions on the Atlantic Plain and southern Great Lakes regions, and variable, multi-front stages of invasion in the northern Great Lakes, Central Hardwoods and New England regions (Frelich et al., 2006; Hendrix et al., 2006; Moore et al., 2017). The extent and effects of invasions are limited in soils that are dry, very coarse textured, or low pH, and by palatability of litter

(Tiunov et al., 2006). Palatability depends on C:N ratio and Ca content of litter (Holdsworth et al., 2012) and is thus low in stands of beech and oak, moderate in sugar maple, and high in red maple (*Acer rubrum* L.), ash (*Fraxinus* spp.), elm (*Ulnus* spp.), aspen (*Populus* spp.), birch (*Betula* spp.) and American basswood (*Tilia americana* L.). Basic impacts of the invasion are increased rates of leaf litter fragmentation, and thinning or elimination of the organic horizon (duff layer) (Hale et al., 2005b; Holdsworth et al., 2012). These forest floor changes lead to drier surface soils and disturbance to the mycorrhizae and fine root symbioses of forest floor plants and tree seedlings (Hale et al., 2006). Nutrients such as N, P, Ca and Mg are also leached from the ecosystem (Hale et al., 2005a; Resner et al., 2015). These changes to the soil can reduce tree growth, reduce native plant diversity, favor graminoids and species that germinate on mineral soil, and facilitate invasive plant species that coevolved with the worms on their home continent (Nuttle et al., 2014; Craven et al., 2017).

Moreover, invasive plants constitute a serious threat to understory diversity in hardwood forests of eastern North America, with non-native shrub species among the most problematic. Many of the most aggressive shrub species originated in East Asia and share an extended autumn leaf phenology that allows them to fix more annual carbon than native competitors (Fridley, 2012). Seeds of most species are animal dispersed, with birds serving as the primary vector (Richardson et al., 2011). Bird dispersal allows invasive shrub populations to expand across fragmented landscapes, where successful establishment is correlated with total edge and the density of roads (Bartuszevige et al., 2006; Flory and Clay, 2006). Once established within a forest, invasive shrub populations typically expand slowly at first, during which time they may not be recognized as a management problem. However, many populations grow exponentially after this lag period, after which they become very difficult to control (Webster et al., 2006). For example, Shields et al. (2014) identified a 10–15 year post-establishment lag period for populations of Amur honeysuckle (*Lonicera maackii* (Rupr.) Herder), after which they rapidly expanded with mature populations consisting of up to 3135 stems (> 1.37 m height) per ha. Shrub populations may have both direct and indirect effects on understory plant communities.

Invasive shrubs reduce the abundance, growth, and survival of many native tree seedlings, often allowing only the most shade-tolerant tree species to persist under mature invasions (Hutchinson and Vankat, 1998; Gorchov and Trisel, 2003; Fagan and Peart, 2004; Shields et al., 2015). In addition, invasive shrubs have been shown to reduce the diversity and cover of herbaceous species (Collier et al., 2002; Gorchov and Trisel, 2003; Hartman and McCarthy, 2008), as well as pollination rates and seed set (Miller and Gorchov, 2004; McKinney and Goodell, 2010). A growing body of research has documented how invasive shrubs alter nutrient cycling in forest ecosystems. Litter layers under invasive shrubs undergo more rapid decomposition (Ashton et al., 2005; Trammell et al., 2012), resulting in a more rapid release of nitrogen that may, in turn, be sequestered by the invasive shrubs (Ehrenfeld et al., 2001; Heneghan et al., 2006; Trammell et al., 2012). In an interesting belowground interaction between invasive species, Heneghan et al. (2007) found a positive correlation between common buckthorn (*Rhamnus cathartica* L.) and invasive earthworm populations, and Madritch and Lindroth (2009) found that removing buckthorn resulted in a 50% reduction in earthworm abundance.

The effects of invasive plants, pathogens, earthworms and insects are a significant threat to ecosystem resilience. In ecosystems with low resilience, rates of invasion can be high, decreasing the native ecological memory and building new and potentially undesirable information and material legacies within the local ecosystem. Thus, the degree of resilience debt after invasion is dependent on the current resilience of the native ecosystem (Schaefer, 2009; Johnstone et al., 2016).

2.4. Context dependencies, interacting and synergistic effects

While changes to land use, herbivory, and invasive species have each impacted the understory of the eastern North American hardwood forests, they also interact with each other resulting in complex and often unexpected outcomes. These interactions may intensify or ameliorate their individual impact on understory plant diversity. Thus, the sign and magnitude of any single effect will be influenced by interactions with other effects, resulting in high levels of context dependency (Chamberlain et al., 2014).

For example, introduced earthworms can interact with high populations of white-tailed deer, land use change and invasive plant species to alter the composition and structure of understory plant communities. Earthworms reduce plant abundance for many species, increasing the deer to plant ratio, which then exacerbates the impact of deer on the remaining plants. Earthworms can favor invasive species by changing the seedbed to mineral soil and in some cases reducing nutrient and water content of the A horizon (Frelich et al., 2006; Eisenhauer et al., 2012; Roth et al., 2015). In deeply shaded understories, plant growth rates of preferred forage species are unlikely to exceed the rate of consumption by deer, which can reduce plant survival and reproduction (Augustine et al., 1998). Low cover and diversity of native plants resulting from deer herbivory and/or earthworms may provide vacant niches that are readily filled by invasive plants, especially following harvesting or overstory disturbances that increase light levels at the forest floor; an effect which may be exacerbated by a warming climate (Eisenhauer et al., 2012; Whitfeld et al., 2014). Introduced plant species (e.g., buckthorn and garlic mustard) benefit under this scenario of combined disturbance, earthworm and deer impacts because many are avoided by deer or are tolerant of herbivory. However, aggressive native species including some ferns, Pennsylvania sedge (*Carex pensylvanica* Lam.) and other graminoids (Fisichelli et al., 2013) may also expand their populations under this scenario. Once dominant, these species may function to exclude native tree seedlings and other native plants (Royo and Carson, 2006; Powers and Nagel, 2009).

Silvicultural treatments may amplify the effects of ungulates and invasive species. Canopy gaps have been shown to concentrate herbivory in gaps (Alverson et al., 1988; Stewart et al., 2000; Kuijper et al., 2009); gap-based silviculture may therefore be unsuccessful at regenerating tree species or maintaining biodiversity in the ground-layer where deer population densities are high, even with additional enrichment plantings (Kern et al., 2012). These interactions may further depend on canopy gap size, however (Tahtinen et al., 2014). For example, the probability of tree regeneration being browsed declines with increasing opening size and *Rubus* abundance (Murray et al., 2016; Walters et al., 2016). Pennsylvania sedge has been observed to increase in abundance immediately following canopy gap creation where deer populations are high (Burton et al., 2014) and form a thick carpet in forests with a long history of deer abundance and selection silviculture (Powers and Nagel, 2009; Randall and Walters, 2011). Timber harvesting operations may facilitate the dispersal of introduced and invasive plant and earthworm species within and among forest stands on logging equipment. The removal of wood boles and associated reductions in downed wood during logging further reduce ecological memory, potentially providing opportunities for these species to spread (e.g., Harrington et al., 2013). Effects of harvesting intensity on invasive plant species are species-specific, varying from transient increases in local abundance (e.g., Burton et al., 2014) to persistent and widespread compositional shifts (e.g. glossy buckthorn, Fagan and Peart, 2004; Burnham and Lee, 2010; Hausman et al., 2010). However, where deer occur in lower densities, they can promote diversity in harvest gaps (Royo et al., 2010; Murray et al., 2016). Although harvesting intensity and habitat loss and fragmentation are not causally related, negative effects of harvesting intensity on understory plant communities are expected to be amplified in smaller, more isolated stands because source strength for regenerating plant communities is
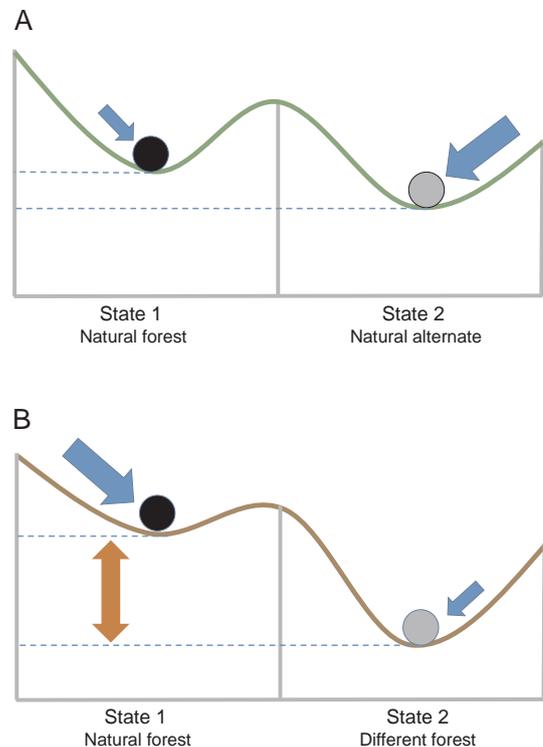
Fig. 1. Conceptual ball and cup diagram of alternate forest states. (A) Alternate states on a natural landscape with high ecological memory where tree species in the dominant successional state are in synch with disturbance regime (State 1, black ball) and alternate caused by an unusually severe disturbance (State 2, gray ball). Differences between the states are relatively small compared to B, and forces tending to push State 1 over the cup to State 2 are relatively minor and met with large resistance, while major forces are required to return to State 1 (blue arrows). (B) Forest states in ecosystems with impaired ecological memory. Due to resilience debt, forces pushing towards State 2 are large while forces pushing back towards State 1 are small (blue arrows). Resistance to state transition from 1 to 2 is small, while resistance in the opposite direction is large, and the more factors impairing ecological memory in play (deer browsing, fragmentation, invasive species, etc.), the larger the difference in the two states (orange arrow). Understory communities can transition to novel states (State 2 in B) before overstory tree communities, which can sit near the tipping point for decades. Novelty in understory communities, therefore, can provide an indication of resilience debt in forest overstory tree assemblages. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

generally weaker (i.e., they have low ecological memory).

2.5. Degradation of ecological memory

In summary, many eastern North American hardwood forests are besieged by contemporary changes in disturbance regimes; historically high ungulate populations; invasive plants, diseases and pest introductions; and climatic changes. Compounded with contemporary land use changes and the persistent deleterious legacy effects from European settlement, forest resilience mechanisms (Frelich and Reich, 2010) may be overwhelmed, leading to a loss of ecological memory. The higher and more severe the number of such changes in a given forest, the more likely a resilience debt exists (Johnstone et al., 2016), and the greater the number of species that could have population bottlenecks that lead to local or regional extirpation. The resulting lower native species richness in a typical forest stand has been termed biotic impoverishment, while the higher likelihood that a few robust species will dominate is called biotic homogenization (Rooney et al., 2004). Species that are ultimately destined for extinction due to inability to reproduce, but which persist due to long lifespans of the existing individuals, comprise the extinction debt (Rogers et al., 2009).

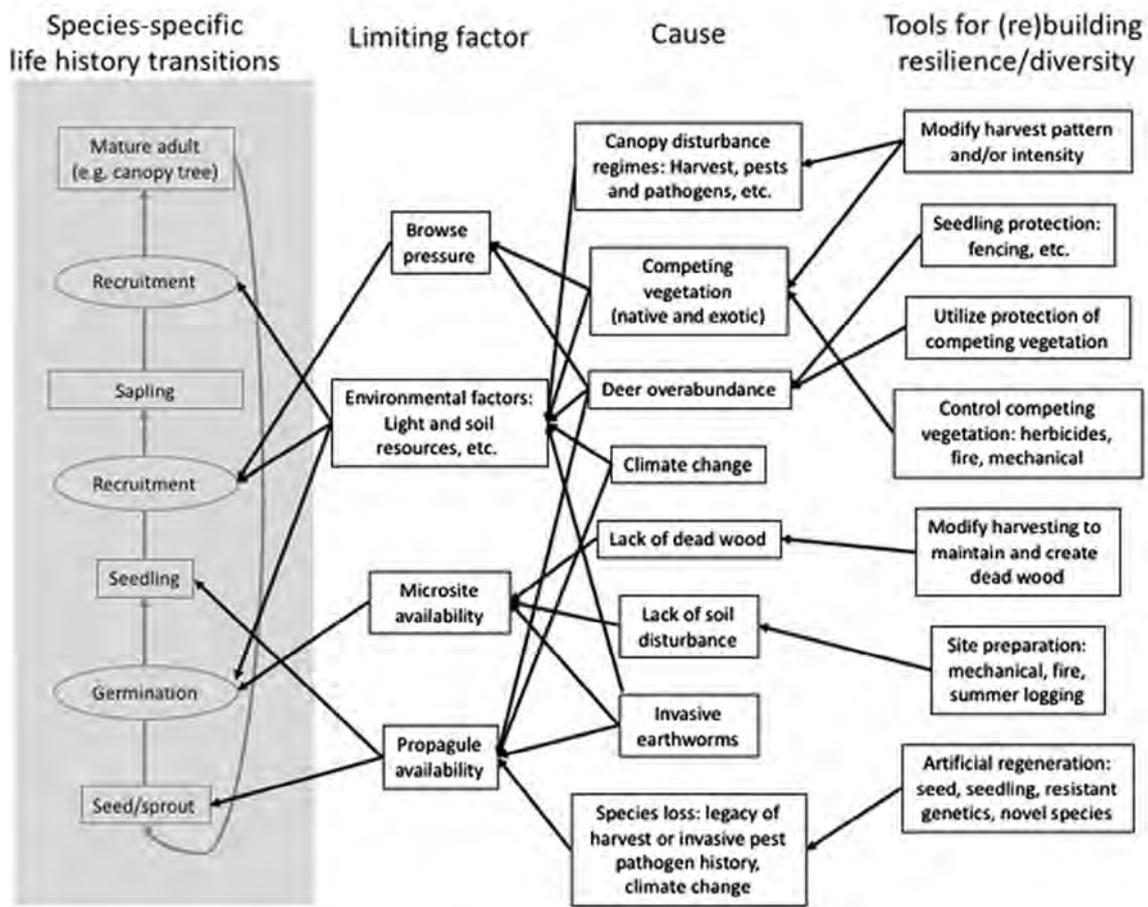Ecological memory enabled by biological and material legacies can

Fig. 2. Conceptual diagram of challenges to hardwood forests, their impact on stand dynamics, and potential silvicultural options.

be disrupted to varying degrees (Fig. 1). Pre-European settlement forests developed under different combinations of natural disturbance regimes and long-term Native American burning regimes. Syndromes with species traits in synch with disturbance type and severity fostered high post-disturbance memory across many forest types (Frelich, 2016). The cutover carried out by European settlers mimicked natural disturbance types to some extent; for example, winter clearcutting that left the seedling/herbaceous plant layer intact under the snow and clearcutting followed by slash burning had similarities to large-scale natural windthrow and high-intensity fires, respectively. Thus, most species were able to recover and the cutover itself caused only a moderate loss of ecological memory. However, what happened after the cutover varied tremendously across the hardwood forest region, and created a mosaic of subregions with varying degrees of "bad ecological memories", biotic impoverishment and extinction debts.

Those areas that were quickly reforested after the cutover—mostly in the northern Lake States—did well during the first several decades, with large tracts of forest in mid to late-successional stages by the late 20th Century. However, as reviewed above, increasing white-tailed deer populations, earthworm invasion, catastrophic pest and pathogen epidemics and forest management practices subsequent to the cutover have begun to strain ecosystem resilience in some places. For example, an average 19% loss of plant species richness occurred in stands revisited after 50 years in northern Wisconsin, even on these largely intact landscapes (Rooney et al., 2004), and clear sets of 'winner' and 'loser' species with certain traits have emerged (Wiegmann and Waller, 2006).

In other parts of the hardwood forest region, oak forests formerly had frequent, low intensity fires. Fire exclusion by fragmenting the landscape and fire suppression started the process of mesophication of these forests (Nowacki and Abrams, 2008). The resulting high resilience

debt meant that most disturbances (natural or anthropogenic) would release understory shade-tolerant, fire-intolerant species and prevent return to the oak-dominated state. At the landscape and regional scales, diversity was lost as the portion of late-successional stands grew, a process that has been accelerated by increased precipitation in the early phases of climate change, but which may reverse in later phases as evaporation from increased temperatures outpaces increased precipitation and dries some forests enough to potentially limit late-successional species like maple (Frelich et al., 2017).

Deforestation and conversion to agriculture occurred in some areas, and resulted in nearly total loss of ecological memory at stand to landscape scales. Recovery from this loss is a very slow process and often depends on the rare long-distance dispersal of such vital biological legacies as seeds of many plant species and mycorrhizae. If contiguous conversion to agriculture occurred over 100–1000 s of km^2, then the loss of temporal-spatial continuity for many native species, and ongoing susceptibility of afforested stands to entry and dominance by non-native species brought by settlers, could lead to novel ecosystems (Jõgiste et al. (2017)). Differences between afforested agricultural lands and lands reforested immediately after logging can persist for centuries to millennia (Foster et al., 2003). Forest remnants in the agricultural landscapes of the southern Lake States and Corn Belt have fared the worst of all hardwood forests in the eastern U.S. For example, Rogers et al. (2008) observed a 25% loss in plant species richness over 50 years in southern Wisconsin forests. Throughout the lower Midwest, forests are highly fragmented with high edge to interior ratios, isolation from other forests, late-stage earthworm invasions and corresponding infestations of invasive shrub and herbaceous species, high deer populations, and probably continuing high extinction debts that will take some time to be 'paid'.

Given the changes in disturbance regime, climate, landscape configuration and intractable presence of invasive species, managers will need a more detailed understanding of forest resilience, ecological memory, and their relationships with biodiversity, to facilitate restoration or ensure a graceful transition to future novel ecosystem conditions.

Given the steep hill that many forests must overcome to return to State 1 in forests with impaired memory (Fig. 1B) as compared to natural conditions (Fig. 1A), there may be two conceptual endpoints for rebuilding resilience via silvicultural treatments. The first is restoring State 1 conditions using historic or less degraded current ecosystems as references and templates for restoration, and the other is building resilience in novel ecosystems. The former could be preferable in situations where there is greater ecological memory such that less intervention is required (i.e. the hill is not as steep and high); whereas, the latter could be applied in situations where restoring State 1 conditions is prohibitively expensive or unattainable given contemporary stressors that are very difficult (e.g. very high deer populations) or impossible to directly overcome (e.g. climate change, invasive earthworms). To encompass the complete spectrum of conceptual goals, we propose to use the term 'restoration' to apply to the goal of maintaining or increasing resilience in forests including, but not limited to, restoring State 1 and/or reference conditions. Furthermore, given our goal of increasing resilience via increased diversity, we use the two terms interchangeably.

3. A conceptual model for restoring diversity in the eastern North American hardwood forests

Many of the causes of declining ecological memory and resilience in hardwood forests can be characterized by factors affecting transitions in plant life history stages. For trees these include the transitions from seed to seedling, to sapling, and eventually to mature trees (Fig. 2). These factors have species-specific effects, and are integrated over species and individuals, with the aggregate outcome constituting forest stand dynamics. Particular expressions of any one to all of these mechanisms acting additively or interactively, simultaneously or sequentially at different life history stages can pose limiting bottlenecks for life history transitions, with plant species varying in their responses due to trait variation (e.g. palatability to deer, shade tolerance, drought tolerance, and seed size). While the model presented (Fig. 2) focuses on demographic processes associated with the recruitment of overstory tree species, tree seedlings and saplings are a component of the understory and shrubs and herbs in the understory are likely to undergo similar demographic processes even if they do not reach the canopy.

We focus on four important general factors driving forest dynamics: propagule availability, germination/establishment substrate availability, environmental factors impacting growth and survival (e.g. resources), and ungulate browse pressure (Fig. 2). For example, seeds of potential species mixtures need be present to germinate and establish on, for some species, a narrow spectrum of potential substrates. In turn, seedling microsites need to provide sufficient soil resources and light to survive and grow. Then, in order to transition from seedling to sapling stages, trees need to negotiate factors including ungulate browse pressure and understory competition before they can recruit to the canopy.

There are several agents or causes of change in diversity/resilience with most but not all impacting diversity negatively. Each of these acts by affecting the expressions of one or more of the four factors presented (Fig. 2). For example, propagule (seed or sprout) limitation can result from local extirpation through harvest legacies, catastrophic pest and pathogen impacts, forest fragmentation, seed predation, and low seed production resulting from climate change (Caspersen and Saprunoff, 2005; Willis et al., 2016). Further, limited microsites for germination/establishment substrates could result from "gentle" harvest practices that do not expose mineral soil (Raymond et al., 2003; Willis et al., 2015), or selective removal of declining large diameter trees of species that produce high quality decayed wood substrates (e.g. eastern

hemlock; McGee and Birmingham, 1997; Angers et al., 2005; Marx and Walters, 2008).

Although there are a multitude of causes for declining ecological memory and diversity, these losses can be slowed, mitigated, or reversed by management actions that eliminate or circumvent many of the causes and/or their impacts on limiting factors (Fig. 2). For example, overcoming seed limitation by conserving existing seed sources, direct seeding, and/or planting (Shields et al., 2007; Willis et al., 2016); overcoming substrate limitation by scarification (Lorenzetti et al., 2008; Prevost et al., 2010; Willis et al., 2015), or increasing the supply of coarse woody debris (CWD); increasing variability in resource availability by varying harvest patch size (Raymond et al., 2003; Webster and Lorimer, 2005; Prevost et al., 2010; Bédard et al., 2014; D'Amato et al., 2015; Willis et al., 2015; Walters et al., 2016); and suppressing competition from aggressive native and exotic non-tree vegetation and over-represented sub-canopy tree species with herbicides, cutting, or fire (Carlson and Gorchov, 2004; Pergams and Norton, 2006; Gasser et al., 2010; Bolton and D'Amato, 2011; D'Amato et al., 2015; Walters et al., 2016). Invasive insects and pathogens (Morin et al., 2007; Hu et al., 2009; Herms and McCullough, 2014), earthworms (Bohlen et al., 2004; Hale et al., 2005a), and climate change are beyond direct, simple silvicultural manipulation at the stand scale; however, novel manipulations at the stand scale can be used to confront these less controllable factors. Planting tree seedlings with the aim of increasing resilience to change is central to these approaches, including planting species adapted to more xeric or nutrient poor sites in anticipation of climate change and/or earthworm invasion, or genetically improved stock resistant to insects and disease.

For any given silvicultural intervention, however, the model illustrates that ameliorating any single cause and the limiting factor(s) it impacts does not necessarily assure success as another factor operating simultaneously or at a later life history stage may present another bottleneck (Fig. 2). Thus, knowledge of the entire suite of limiting factors and their species-specific impacts is an essential first step to restoring biodiversity.

Assuming the causes of declining diversity and the limiting factors they impact can be identified, realistic goals and prescriptions for restoration of diversity can be developed. Restoration needs, however, to be feasible economically, especially if it is to be accomplished at operational scales on large land bases by public and industrial landowners. The most promising candidates for restoration are forests characterized by single limiting factor bottlenecks, where targeted prescriptions for increasing diversity may be effective at stemming the loss of ecological memory. The level of ecosystem alteration also has a great influence on management goals and silvicultural prescriptions. In forests with high ecological memory, the goal could be to restore a diversity and structure similar to the pre-settlement forest, which could be used as reference for species reintroductions or enhancements.

It is also possible that historical reference conditions are no longer relevant given the level of alteration. Land managers may encounter situations where promoting resilience and diversity via emulating historical reference structures and compositional targets (i.e. returning to State 1, Fig. 1) may not be prudent or even possible. A commonality of the agents causing these situations is that they erode or alter ecological memory to a point where the resilience debt becomes so great that the sites may no longer be capable of supporting historic vegetation assemblages and instead move towards novel states following disturbance. Examples of causes of these situations are climate change, and novel and catastrophic pests and pathogens such as BBD and earthworm invasion (Fig. 2). In these cases, and where ecological memory is low, restoration goals and prescriptions should focus on promoting key processes of forest ecosystems to ensure an efficient functional transition to future novel conditions. As such, singular, "silver bullet" prescriptions for restoration likely do not exist. Instead, we advocate an adaptive approach that considers existing stand conditions, anticipated future changes, and a realistic outlook for what can

reasonably be accomplished with limited resources. One such example is forests beset by the combination of BBD and vulnerability to climate change.

As an addendum to considering causes that are beyond direct management intervention, adapting to the changes brought on by these novel agents might be the best course of action. For example, reductions in organic layer depth created by earthworms could alleviate substrate limitations for smaller-seeded species (Hale et al., 2005b). Under these conditions, natural regeneration or artificial seeding could be used to establish a new cohort of small-seeded species. As another example, widespread mortality caused by emerald ash borer may improve the success of under-planting by increasing light availability and increasing herbaceous vegetation (Burr and McCullough, 2014; Looney et al., 2015, 2017), which can conceal seedlings from browsing (Walters et al., 2016). Mortality from emerald ash borer may also improve the natural regeneration of non-ash species by increasing inputs of coarse woody debris to the forest floor and by increasing resources to residual canopy trees, potentially increasing seed production. Thus, opportunities for restoration may arise from the indirect effects of factors limiting species diversity.

4. Restoration in practice: case studies

4.1. Recalcitrant shrub layers

One of the more common structural features in contemporary northern hardwood forests is the presence of a dense, low-diversity shrub and/or tree sapling layer of species that are both shade-tolerant and non-preferred by deer (e.g., native maples and ironwood and/or invasive exotic shrubs; Royo and Carson, 2006; Nowacki and Abrams, 2008; Matonis et al., 2011; Brose, 2016; Roberts et al., 2017). This layer can represent a strong bottleneck to restoration as it outcompetes establishing seedlings and herbaceous vegetation by strongly limiting light availability (Royo and Carson, 2006). Furthermore, this layer may be highly persistent if it is maintained by periodic disturbance and cannot be controlled by mechanical damage from harvesting/or targeted mechanical brushing efforts as most species resprout vigorously (Royo and Carson, 2006; Waldrop et al., 2008; Roberts et al., 2016). Herbicides can provide an effective and cost-efficient near-term tool for remedying this bottleneck (Povak et al., 2008; Miller et al., 2017), but this tool cannot be used in all contexts and jurisdictions. Furthermore, it is critically important to consider the timing and selection of appropriate herbicides, application techniques, and potential impacts to non-target herbaceous species to prevent further erosion of native diversity and ecological memory. Prescribed fire can also be used to treat the sub-canopy tree bottleneck, but it has been shown to be generally ineffective at reducing midstory density once the midstory reaches a critical diameter size (Ryan et al., 2013; Brose, 2016), unless multiple burns can be conducted (Albrecht and McCarthy, 2006; Hutchinson et al., 2012; Arthur et al., 2015; Iverson et al., 2017). Moreover, use of fire can be limited by lack of fuels, inappropriate burning conditions, social/administrative constraints, or because of cost inefficiencies.

Stands characterized by low diversity recalcitrant shrub-sapling bottlenecks typically develop, in part, from some combination of high browse pressure (Matonis et al., 2011), low local species diversity of seeds and sprouts (Schulte et al., 2007; Amatangelo et al., 2011; Willis et al., 2016; Kern et al., 2017), mineral soil and coarse wood substrate limitations (Hura and Crow, 2004; Marx and Walters, 2008; Bolton and D'Amato, 2011; Beaudet et al., 2014), and low light due to single-tree selection harvest regimes (Angers et al., 2005). These factors erode ecological memory and contribute to a growing resilience debt in these forests. Thus, treatment of the recalcitrant shrub-sapling layer alone would likely do little in the long run to restore understory and tree diversity in these systems if the entire suite of limiting factors still persists. Instead, restoration of resilience would require a coordinated regimen that addresses each of the limitations.

4.2. Recovery after beech bark disease

Beech bark disease (BBD) illustrates another case where silviculture must adapt to changing conditions. As reviewed in Section 2.3, decimation of adult American beech populations by this disease complex is often followed by aggressive suckering (Witter et al., 2004; Farrar and Ostrofsky, 2006; Giencke et al., 2014; Jones et al., 2016). Resultant dense subcanopy thickets reduce understory herb cover and outcompete the regeneration of other tree species (Hane, 2003). These thickets then become re-infected before maturity and die back and resprout and die back *ad infinatum* (Jones and Raynal, 1986; Witter et al., 2004). This pattern of persistent subcanopy thickets could compromise long-term productivity and result in further reductions in diversity by limiting canopy recruitment (Cale et al., 2013). A first step in restoration in BBD impacted forests might be reduction of the beech subcanopy with herbicides or other means. However, the likely long-term loss in diversity represented by severe reduction of mature beech justifies the consideration of planting replacement species to circumvent BBD impacts (Fig. 2).

At its most simplistic interpretation, resilience might be maintained by developing and planting resistant genotypes of beech (Sniezko and Koch, 2017). However, there are other considerations, such as the contemporary role of American beech regionally, and options for replacement or enhancement of lost diversity. First, beech is an important producer of hard mast for numerous wildlife species, so maintenance of both ecosystem function and resilience may depend on more than tree species identity when considering options for beech. For example, oaks, hickories (*Carya* spp. Nutt.) and blight-resistant chestnut hybrids (*Castanea* spp. L.) might be considered as alternatives or supplemental to planting resistant beech genotypes.

Another consideration, might be future scenarios of climate change. If in a region where water deficits are expected to increase, then assisted migration of species from drier forest ecosystems could be considered. In northern Michigan, trees now uncommon but abundant prior to European settlement on the most drought prone sites supporting northern hardwoods with a large beech component include white pine and northern red oak (Whitney, 1987; Zhang et al., 2000). These species are found on drier sites than beech, maples, and many other northern hardwoods (Burger and Kotar, 2003) and might be prioritized for local assisted migration via planting on drought prone sites impacted by beech bark disease if greater frequency of drought is predicted. Ideally, the species chosen for migration would be those that best fill the ecological niche created by the loss of the original species, thereby maintaining ecosystem function.

5. Conclusions

The erosion of ecological memory, deleterious legacy effects (novel and undesirable biological and material legacies), and the complex web of stressors facing contemporary hardwood forests of eastern North America pose substantial challenges for the maintenance of biological diversity and productivity. Forests are dynamic and adaptive systems, but it remains uncertain how these systems will respond to the stresses placed on them by demands for forest products, increased dominance by invasive species, new pests and diseases, and changing environmental conditions. In some cases, efforts to restore heterogeneity and diversity from the forest floor up may facilitate successful restoration of desirable developmental trajectories and resiliency. In other cases, managers will be dealing with novel systems with unknown trajectories and dynamics, in which case restoration efforts may help ease the transition and provision important ecological services. In either case, practitioners and researchers need to work together to better understand context-dependent limiting factors and test with clear eyes old, new, and novel approaches to fostering diversity and resilience. Given differences in how much ecological memory these systems retain and the mosaic of factors involved in contemporary dynamics, a simple one

size fits all solution is clearly unattainable. That being said, our review has identified a host of common factors and pathways that can be actively manipulated. The approach we propose requires a thoughtful understanding and view of the forest understory as the foundation upon which resilient systems are built. Which silvicultural levers will have the greatest utility will clearly depend on the ecological context of the forest, but also a willingness to experiment and adapt.

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