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CONCEPT PAPER

Understanding compositional stability in mixedwood forests of eastern North America[1]

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Abstract: Mixedwood forest composition, or co-dominance of hardwood and softwood species, has been interpreted as both stable and unstable. Through review of existing theory, we propose a conceptual model to understand mixedwood compositional stability in boreal and temperate forests of eastern North America. We first review the current theory that the strength of neighborhood effects (i.e., species ability to self-replace under their own canopy) is essential to understanding stability such that when self-replacement is strong for both dominant hardwood and softwood species, composition is stable except at extreme disturbance severities. In contrast, when mixedwood forests are dominated by negligible or weak affinities to self-replace, composition is unstable and sensitive to changes in disturbance. Our new concept further posits that changes in both the disturbance severity and its vertical direction are essential to understanding stability. For example, where moderate-severity surface fires (which impact forests from below) cease and are replaced by moderate-severity blowdowns (which impact forests from above), instability can occur even when disturbance severity is unchanged. We therefore pose and discuss an extension to current theory to provide a new unifying concept of stability for mixedwood forests and, more broadly, for mixed-species forests.

Key words: mixed-species forests, deciduous-coniferous mixtures, regeneration strategy, neighborhood effects, compositional resilience.

Résumé : La composition des forêts mixtes, dans lesquelles il y a codominance d'espèces feuillues et résineuses, a été décrite comme étant stable ou instable. En se fondant sur la théorie existante, nous proposons un modèle conceptuel pour comprendre la stabilité de la composition des peuplements mixtes dans les forêts boréale et tempérée de l'est de l'Amérique du Nord. Nous explorons d'abord la théorie actuelle selon laquelle la force des effets de voisinage (c'est-à-dire la capacité des espèces à s'autoremplacer sous leur propre couvert) est essentielle pour comprendre la stabilité. Ainsi, lorsque l'auto-remplacement est fort pour les espèces dominantes de feuillus et de résineux, la composition est stable sauf si l'intensité des perturbations est extrême. En revanche, lorsque les forêts mixtes sont dominées par des espèces dont la capacité à s'auto-remplacer est négligeable ou faible, la composition est instable et sensible à des changements de perturbation. De plus, notre nouveau concept postule que des changements d'intensité de la perturbation et de sa direction verticale sont nécessaires pour comprendre la stabilité. Par exemple, lorsque des feux de surface d'intensité modérée (qui affectent les forêts par le bas) cessent et sont remplacés par des chablis d'intensité modérée (qui affectent les forêts par le haut), un état instable peut s'établir même si l'intensité de la perturbation demeure inchangée. Par conséquent, nous proposons et discutons d'une extension de la théorie actuelle pour introduire un nouveau concept unificateur de stabilité pour les forêts composées de feuillus et de résineux et, plus généralement, pour les forêts composées de plus d'une espèce. [Traduit par la Rédaction]

Mots-clés : forêts mixtes, mélanges de feuillus et de résineux, stratégie de régénération, effets de voisinage, résilience compositionnelle.

Introduction

Forests cover approximately one-third of the Earth's land area, support biodiversity and ecosystem processes, and provide jobs, commodities, materials, food, and fuel to societies (FAO and UNEP 2020). Tree species composition of forests controls many of these goods and services, given the large variation in individual species' traits guiding characteristics such as productivity, nutrient cycles, economic value, and preferred habitat (Mestre et al. 2017). Thus, the compositional stability of forests is important to the maintenance of a range of traditional and contemporary ecosystem services (Millar et al. 2007; Puettmann 2011; Mori et al. 2013).

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Compositional stability has been defined as the ability of the current assemblage of species to resist or adjust to change such as disturbance (sensu Halpern 1988). Compositionally stable forests may undergo significant changes in other stand structural features but retain a similar mix of dominant tree species (e.g., Barker Plotkin et al. 2017). Stability in forest composition at a given location depends largely on the interaction of individual species' traits with multiple factors, including past disturbance, abiotic site characteristics, and the current stage of forest development and succession. In some cases, disturbance or management may be necessary to maintain composition (e.g., Fisher and Terry 1920). Furthermore, stability at the scale of tree lifespans (hundreds of years) may occur at a landscape scale of multiple stands even if not all stands are stable (Johnson 1992).

Although forest stability results from complex interaction of many factors, conceptual models have been successfully utilized to explain forest stability over time. Two prevalent stand-based models follow high-intensity disturbance that eliminates most pre-disturbance aboveground vegetation and reach biomass or structural stability after four phases (Bormann and Likens 1979; Oliver and Larson 1996). In the Bormann and Likens (1979) model, stability is based on biomass and nutrient accumulation over developmental phases (reorganization, aggradation, transition, and steady state). In the Oliver and Larson (1996) model, stability is based on canopy structure changes with stand development phases (initiation, stem exclusion, understory re-initiation, and old growth – complex). In both models, stands eventually become structurally stable with time (i.e., steady state or old growth – complex), but neither model is focused explicitly on stability of composition, which limits their application to mixed-species stands. The neighborhood-effect theory of forest dynamics, by contrast, focuses on stability of composition rather than structure and is based on a cusp-catastrophe model that is dependent on interactions among species traits, successional status, and disturbance regimes rather than the passage of time alone (Frelich 2002, 2016). In this model, forest composition can be stable in any phase of stand development and for any period of time when the prevailing disturbance regime complements the traits of the dominant species to self-replace under their own canopy.

A special case of forest composition is the mixture of hardwood and softwood species wherein neither composes more than 75%–80% of aboveground live biomass, also known as "mixedwood" forests. Mixedwood forests can be found throughout North America and around the world (Hoshino et al. 2002; Seavy and Alexander 2011; Vickers et al. 2021). In eastern North America alone, these forests are estimated to cover 19 million hectares (Vickers et al. 2021). Greater understanding of mixedwood forests is important for retention of biodiversity (Macdonald and Fenniak 2007), resilience to changing climate (Kabrick et al. 2017), and response to disturbance regimes (Hély et al. 2001) as well as a range of forest products (MacDonald 1995) compared with hardwood or softwood forests. In eastern North America, softwood species in most mixedwood stand types are both needle-leaved and evergreen, whereas the companion hardwood species are broadleaved and mostly deciduous (Woodward et al. 2004). A general disturbance regime for mixedwood forests does not exist; disturbance regimes in mixedwood forests vary in type, severity, and frequency (Kabrick et al. 2017; Kenefic et al. 2021). Similarly, both hardwood and softwood species can be associated with early or late succession, because dominant hardwood and softwood components in eastern North American mixedwood forests range widely in shade tolerance, lifespan, mature size, and other traits (Table 1; Appendix A). Thus, generalizing mixedwood forests beyond their hardwood–softwood composition can be difficult but is crucial for understanding their ecological relationships and developing appropriate silvicultural systems for their management.

Variability across mixedwood forest types makes explaining stability of mixedwood composition difficult. Some mixedwood stands are compositionally stable, retaining a similar mix of hardwood and softwood species for thousands of years even as disturbance severity varies, e.g., eastern hemlock (*Tsuga canadensis* (L.) Carrière) – northern hardwoods (Frelich et al. 1998); whereas others are much more sensitive, changing composition with disturbance, e.g., red spruce (*Picea rubens* Sarg.) – balsam fir (*Abies balsamea* (L.) Mill.) – hardwoods (Amos-Binks and MacLean 2016). Other mixedwood forests exist at the stand scale only under limited disturbance type, severity, and frequency combinations, e.g., pine (*Pinus* spp.) – oak (*Quercus* spp.) forests of the Appalachian Mountains region (Brose and Waldrop 2010). These contrasting scenarios of mixedwood forest stability have not been unified conceptually.

To our knowledge, a general model of compositional stability in relation to cumulative disturbance for mixedwood forests has not been developed. The underlying species traits and prevailing disturbance regimes are highly variable within and across mixedwood forest types. We propose that a general model is possible if the interaction of species traits by mixedwood component (hardwood–softwood) and disturbance regime are considered. To do this, we re-examine the neighborhood-effect theory of forest dynamics, first proposed by Frelich and Reich (1999) and later updated by Frelich (2002, 2016), which uses both species traits and disturbance regimes to explain compositional stability. The theory has previously been applied to two eastern mixedwood stand types, eastern hemlock – hardwoods landscapes and spruce (*P. glauca* (Moench) Voss) – fir – hardwoods (*Populus*–*Betula* spp.) stands, to demonstrate compositional stability over long time frames with varying disturbance as well as compositional instability over long time frames without disturbance (i.e., succession), respectively. However, the theory has not been conceptualized broadly for mixedwood forest stability in relation to cumulative disturbance. Thus, we first discuss the neighborhood-effect theory in its current form at the stand scale, relating it generally to mixedwood stands, highlighting caveats, and specifying possible predictions using the model. Then, we propose some new adaptations to the current neighborhood-effect theory to establish a conceptual model of compositional stability focused at the stand scale for one or more tree generations (10s to 100s of hectares and years) — the scale of conservation and management — broadly for mixedwood forests of eastern North America. Here, we delve into the underlying hardwood–softwood traits and overriding effects of cumulative disturbance severity for mixedwood forests. Throughout, we use the term "disturbance" as inclusive of both natural (e.g., wildfire, wind events, insect infestations, etc.) and silvicultural (e.g., timber harvest, prescribed fire, etc.) disturbances. We focused our examples on pine–oak mixtures (e.g., shortleaf pine (*Pinus echinata* Mill.) – *Quercus*, pitch pine (*P. rigida* Mill.) – *Quercus*, white pine (*P. strobus* L.) – *Q. rubrum*), highly unstable over any time period, because stability concepts for these mixedwood forests have received less attention in the literature than mixtures such as hemlock–hardwood and spruce/fir–hardwood that express high stability over a range of cumulative disturbance severities or transient successional properties, respectively. In addition, pine–oak forests are important commercial forests, and understanding composition stability to provide a range of ecosystem services has important applications.

Neighborhood-effect theory

The neighborhood-effect theory of forest dynamics proposed by Frelich (2016) uses a cusp-catastrophe model (Frelich and Reich 1999; Frelich 2002) to predict how forest composition at the stand and landscape scales will respond to two control variables: (1) a gradient of "cumulative disturbance severity" over a given time

Table 1. Neighborhood effects (disturbance-activated and overstory–understory), shade tolerance, and successional status of species identified in mixedwood forests (hemlock–hardwood, spruce/fir–hardwood, white pine – red oak, shortleaf pine – oak, and pitch pine – oak) of eastern North America (forest types listed in Kabrick et al. 2017; Kenefic et al. 2021).

Common name[a]	Scientific name	Mixedwood component	Disturbance-activated[b,c,e,f]	Overstory–understory[b,d,e,f]	Shade tolerance[e,f]	Successional status[e,f]	Hemlock–hardwood	Spruce–fir–hardwood	White pine–red oak	Shortleaf pine–oak	Pitch pine–oak
Red maple	*Acer rubrum* L.	Hardwood	+	+	Tolerant	Mid	×	×	×	×	
Sugar maple	*Acer saccharum* Marshall	Hardwood	–	+	Tolerant	Late	×	×		×	
Yellow birch	*Betula alleghaniensis* Britton	Hardwood	0	0	Intermediate	Mid	×	×	×		
Black birch	*Betula lenta* L.	Hardwood	0	0	Intermediate	Mid			×		
Gray birch	*Betula populifolia* Marshall	Hardwood	0	–	Intolerant	Early		×			
American beech	*Fagus grandifolia* Ehrh.	Hardwood	+	+	Tolerant	Late	×	×			
American hophornbeam	*Ostrya virginiana* (Mill.) K. Koch	Hardwood	0	+	Tolerant	Late	×				
Bigtooth aspen	*Populus grandidentata* Michx.	Hardwood	+	–	Intolerant	Early		×			
Quaking aspen	*Populus tremuloides* Michx.	Hardwood	+	–	Intolerant	Early		×			
White oak	*Quercus alba* L.	Hardwood	0	0	Intermediate	Mid			×	×	×
Scarlet oak	*Quercus coccinea* Münchh.	Hardwood	0	–	Intolerant	Mid				×	×
Southern red oak	*Quercus falcata* Michx.	Hardwood	0	0	Intermediate	Mid				×	×
Northern red oak	*Quercus rubrum* L.	Hardwood	0	0	Intermediate	Mid				×	×
Post oak	*Quercus stellata* Wangenh.	Hardwood	0	–	Intolerant	Early				×	×
Black oak	*Quercus velutina* Lam.	Hardwood	0	0	Intermediate	Mid			×	×	×
Basswood	*Tilia americana* L.	Hardwood	0	+	Tolerant	Late	×				
Balsam fir	*Abies balsamea* (L.) Mill.	Softwood	–	+	Tolerant	Late	×	×			
White spruce	*Picea glauca* (Moench) Voss	Softwood	0	+	Intermediate	Late	×	×			
Red spruce	*Picea rubens* Sarg.	Softwood	0	+	Tolerant	Late		×			
Shortleaf pine	*Pinus echinata* Mill.	Softwood	0	–	Intolerant	Early				×	
Pitch pine	*Pinus rigida* Mill.	Softwood	+	–	Intolerant	Early					×
Eastern white pine	*Pinus strobus* L.	Softwood	0	0	Intermediate	Mid	×		×		
Northern white-cedar	*Thuja occidentalis* L.	Softwood	–	+	Tolerant	Late		×			
Eastern hemlock	*Tsuga canadensis* (L.) Carrière	Softwood	–	+	Tolerant	Late	×		×		

Note: The "+", "–", and "0" indicate that neighborhood effects are positive, negative, or neutral, respectively. An "×" indicates presence in the mixedwood type.

[a] Kabrick et al. (2017).

[b] Frelich (2002).

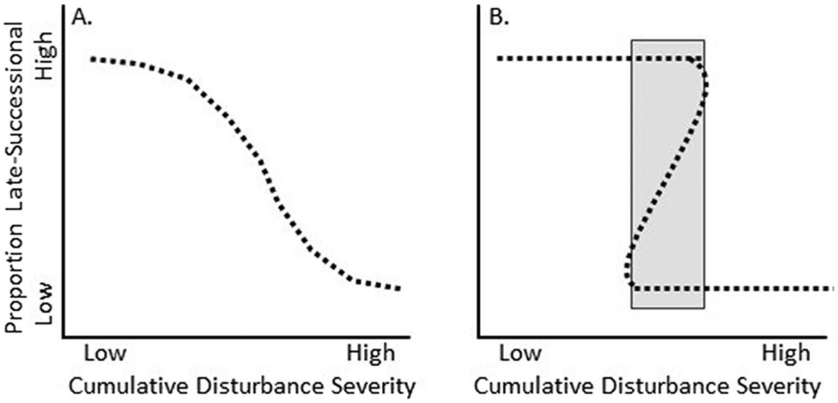
[c] Neighborhood effect is in response to stand-killing fire, as described by Frelich (2002) and Frelich and Reich (1999).

[d] Neighborhood effect is in response to windstorm-caused canopy damage, as described by Frelich (2002) and Frelich and Reich (1999).

[e] Burns and Honkala (1990).

[f] USDA Forest Service (2003).

Fig. 1. An interpretation of the cusp-catastrophe model (Frelich 2002) of forest composition: (A) traits of canopy trees are impartial or detrimental to self-replacement (i.e., neutral or negative neighborhood effects); (B) traits of canopy trees favor self-replacement (i.e., positive neighborhood effects). Line slope indicates compositional stability, where slope of 0 is stable and a slope greater than 0 or less than 0 is relatively unstable. The grey box highlights a range of disturbances in which either composition could exist.



period and (2) "neighborhood effects" of dominant species in the stand (Fig. 1). We review these control variables and note areas for development.

Cumulative disturbance severity

In the neighborhood-effect theory, cumulative disturbance severity is net disturbance-caused tree mortality (or cumulative proportion of trees killed, excluding density-dependent, self-thinning mortality) over a given time period (Frelich 2002). Higher values of cumulative disturbance severity occur when mortality resulting from disturbance events exceeds recovery between events. A given level of cumulative disturbance severity may result from multiple, mild events at high frequency or a single, severe event. Therefore, the current theory treats disturbance as an integrated variable of "cumulative disturbance severity" (Frelich and Reich 1999; Frelich 2002).

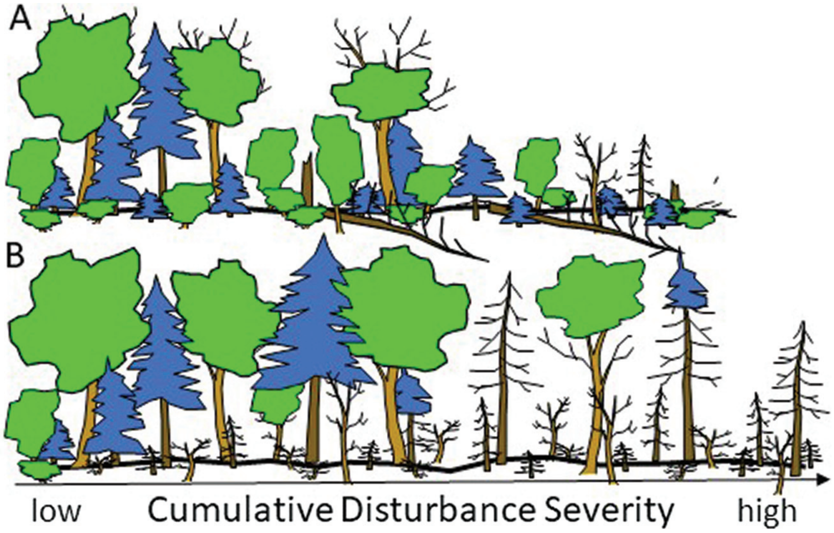
We found this variable difficult to interpret for different disturbance regimes (e.g., type, size, frequency, intensity, etc.). For example, "low" cumulative severity could represent wind disturbances affecting a few trees in the overstory only (e.g., individual treefall gaps or crown defoliation) or effects of low-severity fire disturbances affecting seedlings in the forest understory only (e.g., spot surface fires). This distinction is not well developed in the model. In mixtures of eastern hemlock – hardwoods, the dominant hardwood (sugar maple, *Acer saccharum* Marshall) uses treefall gaps to self-replace, but equally low-severity understory disturbances such as a spot fire would be detrimental to self-replacement of this fire-sensitive species (Canham 1989; Hengst and Dawson 1994). Likewise, cumulative low-severity disturbances in the understory such as frequent surface fires essential for the regeneration of both pines and oaks in pine–oak mixtures can be important, but the same level of cumulative disturbance severity in the overstory would have the opposite effect, allowing the release and recruitment of other species in the understory and the eventual change in overstory composition (Dey and Hartman 2005; Nowacki and Abrams 2008). Furthermore, "moderate" cumulative disturbance severity could represent a range of disturbances that occur in either the understory or overstory (e.g., surface fire or moderate to large wind events, respectively) and with high heterogeneity (e.g., Hanson and Lorimer 2007). "High" cumulative severity could represent disturbances that create mortality in the over- and under-story canopy layers (e.g., severe insect infestations followed by fire), affecting both canopy layers. Overall, a number of complexities related to cumulative disturbance type and effects on canopy layers, in addition to cumulative severity of disturbance, influences composition, but they are not detailed in the current theory.

Neighborhood effects

In the neighborhood-effect theory, the other primary control variable is neighborhood effects (Frelich and Reich 1999; Frelich 2002). Neighborhood effects are processes mediated by canopy trees that operate in favor of (positive), to the detriment of (negative), or impartial to (neutral) their self-replacement (i.e., regeneration) at the time of canopy mortality (Frelich 2002). Frelich and Reich (1995) identified two major categories of neighborhood effects: those related to overstory–understory relationships (e.g., shading, litter, seed rain, or presence of an understory seedling bank via advance regeneration) and those activated by disturbance (e.g., via canopy, e.g., serotinous cones, or soil seedbanks, or root and stump sprouts). Neighborhood effects occur at scales smaller than stands, because they represent individual trees to groups of trees and form important links between tree species traits, site (e.g., soil condition, slope, water table depth), and disturbance (Frelich 2016).

As with "cumulative disturbance severity", neighborhood-effect theory treats tree traits as a single, complex variable of "neighborhood effects". We found this variable to be potentially too general to explain the strengths of species' affinities to replace themselves and too strict in scale of self-replacement. While positive, neutral, and negative neighborhood effects do explain the probability of self-replacement, they do not indicate strength or variation within neighborhood effects type, especially for positive neighborhood effects. For instance, the strongest version of a positive neighborhood effect is when a mature tree survives the disturbance, i.e., the same individual continues to control the microsite, whereas seed banks represent a relatively weaker neighborhood effect, as propagules of the species originally occupying the microsite are not the same genetic individual and must still compete for the site. The strength of vegetative replacement is between these, depending on ability to sprout, which varies greatly among species (Del Tredici 2001), by tree age and diameter (Johnson et al. 2019), and on the disturbance severity. In addition, neighborhood effects are focused on self-replacement at the individual-tree scale; however, self-replacement may occur beyond the canopy of an individual tree such that the overall stand composition remains stable at stand or patch scales. Overall, we found neighborhood effect strength and scale, in addition to feedback effect (positive, neutral, negative), to be informative to understanding the stability of forest composition.

Fig. 2. The tree mortality effects of disturbance direction across a range of cumulative disturbance severity; severity represents minimal leaf area loss at low levels and maximum leaf area loss at high levels. (A) When disturbance direction initiates from above starting in the canopy and then to the understory, smaller trees are killed progressively as cumulative disturbance severity increases. (B) In contrast, when disturbance direction initiates from below starting in the understory and then to the overstory, larger trees are progressively killed as cumulative disturbance severity increases. Even at the same total severity level and starting from the same stand conditions, very different post-disturbance structure may result. While cumulative severity and leaf area loss is similar between the two disturbance directions, the resulting stand structure varies. Note that this illustration depicts an array of post-disturbance structures possible within a neighborhood scale. At the scale of a stand, it is likely that a given severity level will actually result in a range of post-disturbance structures from one neighborhood to the next. [Colour online.]



Species composition

In the neighborhood-effect theory, the forest tree composition response is defined as the proportion of late-successional tree species in the cusp-catastrophe model (Frelich and Reich 1999; Frelich 2002). The compositional response to disturbance severity can be simply portrayed in two scenarios of neighborhood effects. When neighborhood effects are negative or neutral, composition is unstable, because as cumulative disturbance severity decreases, composition shifts from early- to late-successional species dominance (Fig. 1A). Low-severity disturbances (and (or) longer time periods between higher severity disturbances) result in higher proportions of late-successional species, and vice versa for higher severity disturbances and (or) shorter time periods. For mixedwood forests with negative or neutral neighborhood effects, this means that these forests tend to transition out of mixedwood and into hardwood- or softwood-dominated composition and transition back to mixedwood composition depending on changes in cumulative disturbance severity, assuming seed sources are available. For example, fire suppression limits pitch pine regeneration in pine–oak forests, so composition shifts from mixedwood to increasingly hardwood-dominated composition over undisturbed time (La Puma et al. 2013). An increase in disturbance severity, e.g., wildfire or insect infestations, enables pine regeneration to establish, drawing composition back toward a pine–oak mixture (Brose and Waldrop 2010).

When neighborhood effects are positive, either early- or late-successional compositions persist through a wide range of disturbance severities, even at disturbance severities that would also maintain the opposite composition (Fig. 1B). Graphically, this pattern is represented with two overlapping and parallel lines. The horizontal portions of each line in Fig. 1B indicate the range of disturbance severities capable of maintaining a given mixture, depending on the prior composition of a stand (Frelich 2002). When the lines are connected, two "cusps" appear (Fig. 1B), at which increasing or decreasing cumulative disturbance severity is no longer compatible with dominance by the pre-existing early- or late-successional species (Frelich 2002). For instance, very high severity disturbances may be needed to shift late-successional composition dramatically, beyond the upper cusp (Fig. 1B), and alter forest composition to early-successional dominance for decades (D'Amato et al. 2018), e.g., a major wind disturbance must be followed by a major wildfire event to shift eastern hemlock – hardwoods to jack pine (*P. banksiana* Lamb.) – aspen (Frelich 2002). For mixedwood forests in which both the dominant hardwood and softwood species possess positive neighborhood effects, this means that these forests stay in mixedwood composition over a wide range of cumulative disturbance severities. An important consideration for this theory is that site-specific conditions may further influence any neighborhood effects and (or) cumulative disturbance effects, which will further adjust the degree of composition stability (i.e., the slopes of the line or positions of the cusps; Fig. 1) within the model (Frelich et al. 1998; Frelich 2016).

Predictions

The predictions of the neighborhood-effect theory can be summarized as follows (Fig. 1): (1) forests dominated by species with positive neighborhood effects (e.g., serotinous seed rain after fire or release of a seedling bank from suppression after wind or insect damage) have a better ecological memory of pre-disturbance composition (Johnstone et al. 2016), at stand scales over a wider range of cumulative disturbance severities (wide range of little to no slope in Fig. 1B), than forests dominated by species with neutral or negative neighborhood effects (shown as a narrow range of little to no slope in Fig. 1A); (2) disturbances of similar cumulative disturbance severity can result in either early- or late-successional stable compositions when positive neighborhood effects are present (overlapping and parallel lines in Fig. 1B), whereas a range of cumulative disturbance severity results in unstable early- to mid-successional composition when neutral or negative neighborhood effects are present (continuous single line in Fig. 1A); and (3) there are four broad categories that emerge from a scaled-up impact of neighborhood effects and are applicable to stand-scale applications:

Table 2. Distribution of mature plant propagation strategies to self-replace after disturbance (adapted from Rowe 1983) by neighborhood effect strength and vertical direction of disturbance (disturbance from above or from below, explained in Fig. 2) for major species found in some mixedwood forests of eastern North America.

Strategy (Rowe 1983)	Neighborhood effect strength	Disturbance from above	Disturbance from below
Resist, mature individuals survive the disturbance	Strong positive	HW: sugar maple, yellow birch	HW: white oak, black oak, scarlet oak, chestnut oak SW: shortleaf, pitch, white pines
Endure, belowground structures survive and regenerate vegetatively	Moderate positive	HW: beech, basswood	HW: red maple, aspen, northern red oak SW (seedling stage): pitch pine, shortleaf pine
Evade, re-establishes though stockpiled seed in soil or canopy or through seedling banks in the understory	Weak positive	HW: sugar, red maple, beech SW: hemlock, red spruce, fir	HW: pin cherry SW: pitch pine
Invade, re-establishes from offsite seed	Neutral	HW: sugar, red maple, beech, oaks SW: fir	HW: yellow, paper birches SW: most conifers
Avoid, re-establishes once site returns to a condition suitable for seedling establishment	Negative	HW: paper birch, aspen, pin cherry SW: white, shortleaf, pitch pines	HW: sugar maple, beech, basswood SW: red spruce, hemlock, fir

Note: HW, hardwood tree species; SW, softwood tree species. (Note that all species may invade at some point.)

(*a*) stable late-successional, (*b*) unstable late-successional, (*c*) stable early-successional, and (*d*) unstable early- to mid-successional forests (Frelich 2016). Depending on the successional status of the dominant hardwood and softwood, any of these combinations are possible for mixedwood forests.

A new view of stability for mixedwood forests

For mixedwood forests of eastern North America, the existing theory is easiest to apply to relatively stable early- or late-successional forests. In these forests, the co-dominant hardwood and softwood species both have traits, or neighborhood effects, that match a wide range of cumulative disturbance severities, allowing them to replace themselves, stabilizing composition. For generally unstable early- to mid-successional forests such as oak-dominated hardwood forests or pine-dominated softwood forests "…a sequence of disturbances of equal severity and uniform temporal spacing would be needed to keep composition the same — an unlikely scenario except perhaps for frequently burned savannas…" (Frelich and Reich 1999). Previous research indicates that pine–oak mixtures are maintained by periods of frequent surface fires, a disturbance from below, for pine and oak establishment under nearby adult trees, followed by periods of infrequent but more severe crown fires, wind events, insect infestations, or harvesting activities, i.e., disturbance events that kill canopy trees and release advance pine regeneration (Little 1979; Guyette et al. 2007; Stambaugh et al. 2007). This compositional stability scenario for pine–oak forests is difficult to conceptualize with the current model (Fig. 1A) for two reasons. First, complex disturbance regimes must be simplified to cumulative disturbance severity and specific effects of disturbance type are not apparent, especially at moderate-severity levels or those affecting different canopy layers. For example, pine–oak mixtures require both changes in severity (low to high) and type (fire to wind) of disturbance that create a complex moderate-severity regime; however, as presented, stability under moderate-severity regimes is not apparent. Second, the composition axis is focused on proportion of late-successional species only. Neither mid-successional species, which differ in traits from late-successional species (Table 1; Appendix A), nor forest types containing a low frequency of late-successional species such as pine–oak are directly interpreted from the model.

Thus, we propose a new extension of the interpretation of disturbance and neighborhood effects to conceptualize stability of mixedwood forest composition. To link the neighborhood-effect theory of forest dynamics (Frelich 2016) and its associated cusp-catastrophe model (Frelich 2002) to mixedwood composition, two key concepts must be developed further: (1) the vertical direction of disturbance, i.e., those typically first affecting the overstory (called "disturbances from above" for the purposes of this discussion) or understory (called "disturbances from below" hereafter) and (2) the strength and form of neighborhood effects, which we explain in the following subsections.

Disturbance direction

To facilitate application to the question of mixedwood composition, we propose to interpret cumulative disturbance severity separately by vertical direction of disturbance (i.e., starting in the canopy and then to the understory or vice versa) in addition to degree of tree mortality (Fig. 2). For mortality, the original theory poses mortality of adult trees; we broaden this interpretation to include proportional elimination in leaf area, which would more broadly include mortality of immature trees (i.e., seedling to sapling mortality) and portions of tree crowns (i.e., twig to multiple branch mortality), in addition to mortality of whole, mature trees. This allows for more heterogeneity in resulting stand structure after disturbance. For vertical direction, the original theory combines both. In our extension, disturbances directed from above may have effects ranging in severity from damaging only upper-canopy twigs and branches at low severity (low leaf area mortality) to complete overstory blowdown with secondary crushing of mid- and under-story trees and soil surface disturbance by root pits and mounds (high leaf area mortality; Fig. 2A).

Disturbances from above tend to release existing advance regeneration, whether at once as in a stand-leveling blowdown event or gradually as in chronic individual treefall, but the resulting forests will differ more in structure (even- versus uneven-aged forests) than in composition (dominated by the advance regeneration-forming species). Only at the highest severity, where both overstory and understory (i.e., advance regeneration) trees are killed, will there be significant opportunities for early-successional species to establish and recruit. With this view, disturbances from above would also include snow and ice damage, insect outbreaks, and many forms of timber harvesting. On the other hand, disturbances from below that remain only in the understory may only affect the surface litter at low severity, while intense wildfire at high severity may affect all vegetation layers, killing all understory vegetation (including advance regeneration) and causing high tree mortality (Fig. 2B). When combined, disturbances from above and below create high heterogeneity, especially at moderate cumulative severity.

Disturbances from below tend to damage or kill a high proportion of advance regeneration, whether at once as in a high-severity fire or gradually in frequent surface burns, thus tending to favor

Fig. 3. An interpretation of neighborhood effect strength and direction of cumulative disturbance severity on forest composition (adapted from Fig. 1). (A) Existing model for positive neighborhood effects where alternate compositions can occur (same as grey box in Fig. 1B). A range of disturbance regime severity may maintain composition of either late- or early-successional stands; changes in severity beyond the upper or lower cusps result in abrupt compositional change. (B) We propose that the cusps (black, solid line in panel A, grey line in panel B) results from two curves — one representing the compositional effects of disturbances from above (blue dotted line) and the other representing those of disturbances from below (brown dashed line) when composition includes species with strong neighborhood effects. Disturbances from above maintain late-successional dominance, often by releasing advance regeneration (an overstory–understory neighborhood effect); disturbances from below destroy advance regeneration and facilitate disturbance-activated neighborhood effects of early-successional species. (C) Weak neighborhood effects result in compositions more mixed (inner, light line shades) relative to strong neighborhood effects (outer, saturated line color) at intermediate cumulative disturbance severity levels, converging to a mixed and unstable composition that changes with disturbance severity (grey dot–dash line), similar to that in Fig. 1A. (D) At a given level of cumulative severity, disturbances from above will tend to move a stand's composition toward the upper attractor (dotted line; more late-successional species), and disturbances from below will tend to move the composition toward the lower attractor (dashed line; less late-successional species). (E) Certain disturbances may weaken or strengthen the neighborhood effects of some species. For instance, repeated low-severity fires may reduce late-successional maple regeneration, shifting the upper, blue dotted line downward as their ability to evade disturbance from above is reduced. The same disturbances from below may also enable oak species to accumulate a pool of seedling sprouts (shifting the line further downward as this improves oaks' ability to recapture growing space released from above). (F) After a sequence of low-intensity disturbances has changed the relative effect strengths of component species, as in panel E, the consequences of a given disturbance for a given stand may change. For example, with maple's resilience to disturbance from above reduced while that of oak is increased, the post-disturbance composition following wind (from above) more closely resembles that following fire (from below), unlike the scenario depicted in panel D. Alternative shelterwood cutting scenarios provide examples as well: preparatory cuttings prior to an establishment cut or prescribed burning or herbicide treatments after may change the composition resulting from a final overstory removal. For all panels, line slope indicates compositional stability such that a slope of 0 is stable and a slope greater than 0 or less than 0 is relatively unstable. A stand (star symbol) may occur anywhere in the two-dimensional spaces. [Colour online.]

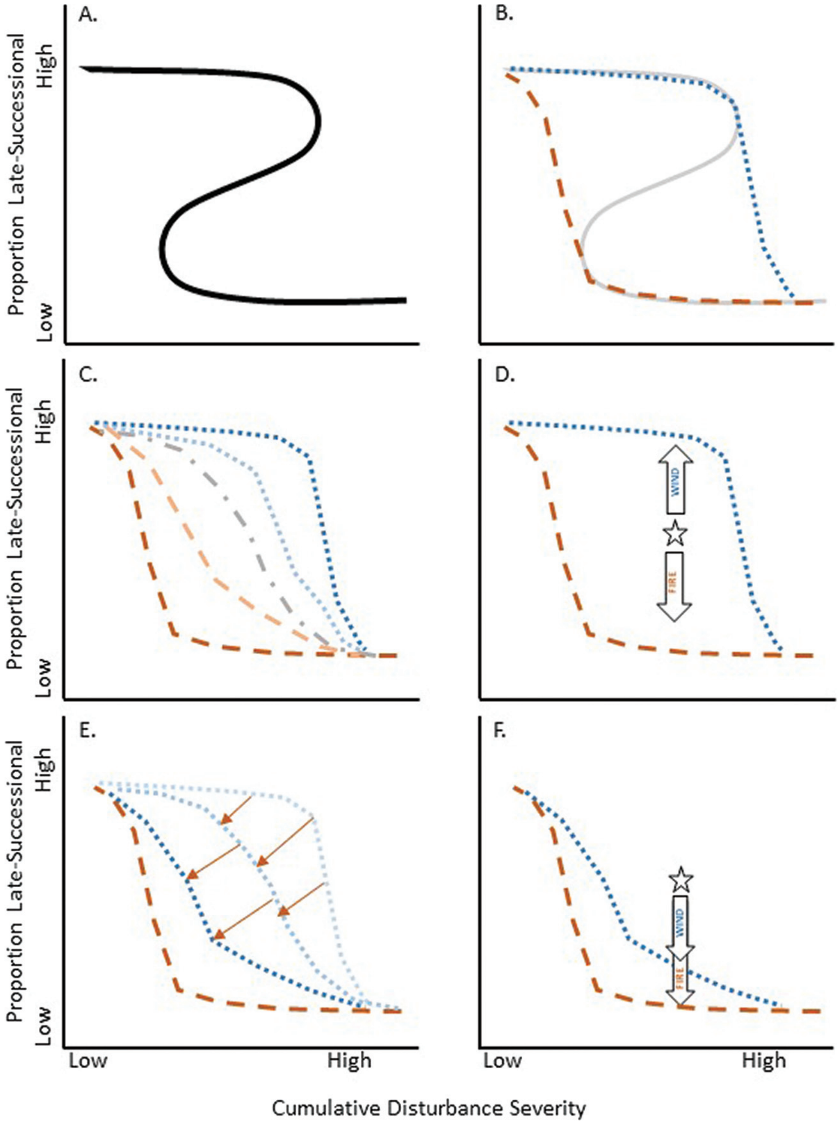


Table 3. Compositional stability category by successional status of dominant species and selected mixedwood forests of eastern North America (forest types listed in Kabrick et al. 2017; Kenefic et al. 2021).

	Compositional stability[a]		
Successional composition	Stable	Stable after conditioning[f]	Unstable
Mid–late	Eastern hemlock–maple/birch/beech; red spruce/balsam fir–maple/birch/beech[b]		
Early–late			White spruce/balsam fir–aspen/birch[d]
Early–mid	[c]	Pitch pine–oak; shortleaf pine–oak; white pine–oak[g]	Pitch pine–oak; shortleaf pine–oak; white pine–oak[e]

Note: Stable and unstable categories according existing neighborhood-effects theory (Frelich and Reich 1999; Frelich 2002, 2016); Stable after conditioning (see footnote *f*) is a new category proposed in this paper for mixedwood forests composed of early- to mid-successional species undergoing mixed- and moderate-severity cumulative disturbance regimes that include both disturbance direction types (explained in Fig. 2).

[a] Compositional stability in relation to match between the cumulative disturbance severity regime and neighborhood effects of both hardwoods and softwoods.

[b] Wide range of cumulative low- to moderate-severity disturbance from above matched to positive neighborhood effects of both hardwoods and softwoods (Fig. 1B).

[c] Wide range of cumulative moderate- to high-severity disturbance matched from below to positive neighborhood effects, e.g., jack pine – aspen.

[d] Any change in cumulative disturbance severity favoring either positive neighborhood effects of softwoods or hardwoods; temporary mixedwood condition (i.e., midsuccession).

[e] Any change in cumulative disturbance severity neither favoring nor disfavoring neutral neighborhood effects in both softwoods and hardwoods (Fig. 1A).

[f] Compositional stability dependent on cumulative disturbance severity, including a mix of disturbance directions and conditioning to shift neighborhood effect strength in alignment with disturbance regime; new ideas from this paper (Figs. 3E and 3F).

[g] Wide range of cumulative moderate-severity disturbance, including disturbance from below then from above, that condition or strengthen neighborhood effects (from more neutral to more positive) for both softwoods and hardwoods (Fig. 3E).

the perpetuation of early- to mid-successional species otherwise apt to replacement, either in even-aged (result of high-severity, high leaf area mortality) or uneven-aged (result of low-severity, low leaf area mortality) stands. Disturbances from below could include floods and browsing, as well as litter disruption by wildlife (Alexander et al. 1985) and earthworm activity. Seed predation may be considered a disturbance from below, too, if seeds, being tree propagules, are considered the lowest of tree "canopy" layers. In forestry, this would include prescribed fire, brush cutting, and scarification (e.g., salmon blading).

Disturbances from above tend to favor shade-tolerant species that can recruit and establish in the understory (i.e., advance regeneration) and so will advance succession or maintain a late-successional composition. Disturbances from below tend to disfavor understory trees and may produce scarified forest floor conditions that provide substrate and establishment opportunities for early- to mid-successional species. Such disturbances would delay (at low severity) or re-set (at high severity) succession, thus maintaining an early-successional composition. Substrate disturbance is important for species with neutral or negative neighborhood effects to establish in conditions that, if otherwise largely undisturbed, would become dominated by species with positive neighborhood effects. For instance, the cumulative effects of surface fire are important to developing seedling-sprout banks for oaks (Brose et al. 2013). Lastly, the combination of disturbances both from above and from below create complex structural outcomes, especially at moderate-severity levels. A mixed, cumulative disturbance regime is important in the stability of some forests such as pine–oak (Kenefic et al. 2021).

Strength and form of neighborhood effects

To facilitate application to mixedwood composition, we propose to develop another component of neighborhood effects: degree of strength and extent of self-replacement. For self-replacement, the original theory highlights self-replacement through seedlings and saplings that establish and grow beneath the canopy of the same species. For our extension, we broaden this interpretation of self-replacement to include seedling and saplings within a microsite, patch, or stand of adult trees in or near that same microsite, patch, or stand.

For strength, neighborhood effects can be categorized by mechanism and generalized to disturbance direction. We interpret the plant propagation strategies proposed by Rowe (1983) to a gradient of neighborhood effect strength (Table 2). The strongest neighborhood effects are possessed by "resisters", species that possess traits enabling mature individuals to survive the disturbance and thus maintain control of their microsite. For instance, mature white oak survives surface fires, because its thick bark resists the lethal impacts (Stambaugh et al. 2017). "Endurers" are the next strongest: these species persist by surviving belowground and self-replace vegetatively at the same microsite. "Evaders" are species that create a numerical advantage for self-replacement through stockpiled seeds or seedlings. "Invaders" are species with a neutral neighborhood effect, as their prior existence on a site confers no advantage or disadvantage; self-replacement comes from offsite seed sources. Lastly, "avoiders" are species with negative neighborhood effects, as they are unable to self-replace until forest floor conditions return to a state suitable for seedling establishment.

Tree species differ in the set of strategies that they employ, making them more, or less, successful when exposed to disturbances from above versus from below (Table 2). Rowe (1983) developed the formulation with respect to fire, a disturbance from below, to which many late-successional species are avoiders; however, the strategy of a given species should be evaluated with respect to a given disturbance type. Many of these same species form seedling banks of advance regeneration and are evaders of disturbances from above, while others are resisters of different disturbances from below (e.g., herbivory). In mixedwood stands, there are some commonalities among the components of hardwoods and softwoods when considered in the context of neighborhood-effect strengths in the face of disturbances from above and from below (Table 2). Importantly, species can have a suite of strategies that depend on the disturbance direction in addition to severity. For instance, eastern white pine is a resister and an invader with respect to disturbances from below but an avoider or evader of disturbances from above. In a review of silviculture for mixedwoods, lack of seed-bearing trees to invade and maintain mixedwood composition was a common issue in eastern North American mixedwood forests (Kenefic et al. 2021). The intersection of these ideas is foundational to our new extension of the existing theory.

Predictions

With our interpretation of compositional stability, the degree to which strength of neighborhood effects is matched with cumulative disturbance severity determines the stability of mixedwood forest composition. This is based on assumptions that neighborhood effects include self-replacement at the microsite, patch, or stand; that cumulative disturbance severity includes both varying levels of leaf area mortality and disturbance direction; and that seed sources are available to support the species mixture necessary for stability.

First, we pose that intermediate compositions are unlikely in forests composed of species with strong neighborhood effects (between the cusps in the grey box of Fig. 1B), and composition is likely either more early-successional or more late-successional, depending on the direction of the disturbance (two separate lines, Figs. 3A–3B). When composed of either high or low proportions of late-successional species, stands are stable when the neighborhood effects are strongly matched to disturbances from above or from below, respectively. For instance, in late-successional hemlock–hardwood mixtures, eastern hemlock and sugar maple represent the dominant hardwood and softwood, respectively. They both exhibit strong to moderate resistance to disturbances from above (Peterson 2007) (Figs. 3C–3D; Table 2). Furthermore, this hardwood–softwood combination evades the main disturbance from above, wind, as seedling banks in the forest understory, thus employing two positive neighborhood effect traits (Table 1). Mixedwood composition is stable until cumulative disturbance changes direction (e.g., fire following or instead of wind, a disturbance change from above to from below) and negates or diminishes the strength of any pre-disturbance evasion traits (e.g., seedling banks) and resets the forest to early succession and to composition of invaders of disturbances from below such as birches (*Betula* spp.).

A forest composed of weak to neutral neighborhood effects will be unstable when exposed to mixtures of disturbance directions (Fig. 3C). When composition consists of weak to neutral neighborhood effects, disturbances from above provide more or less probability for weak or neutral species to self-replace, while providing conditioning toward late-successional evaders (e.g., hemlock–hardwoods) or vice versa (Fig. 3D). For instance, in a pine–oak mixture of weak to neutral neighborhood effects where disturbances from above prevail at low cumulative severities (e.g., infrequent canopy gaps), pine and oak may fail to regenerate. At the same time, red maple (*A. rubrum* L.), American beech (*Fagus grandifolia* Ehrh), and other shade-tolerant hardwood seedlings may initially invade, then evade the canopy disturbance, and ultimately, dominant the stand through strong neighborhood effects to resist the prevailing disturbance from above regime (e.g., mesophication as described by Nowacki and Abrams 2008).

Furthermore, neighborhood effect strength of a species can change with conditioning of the cumulative disturbance severity and direction (Fig. 3E). At a given level of cumulative disturbance severity, a disturbance regime of one direction may favor a particular neighborhood strength and weaken another. For instance, in early-successional pine–oak mixedwoods, shortleaf or pitch pines and several oaks represent the dominant softwood and hardwood species, respectively. Adult trees of these species exhibit some level of resistance to fire, a disturbance from below (Table 2), which also favors the establishment of pines, the invading softwood component. The hardwood component (oak) of this combination survives fire as seedling-sprouts in the forest understory, a form of advance regeneration that endures repeated disturbances from below (Fig. 3D). At the same time, disturbances from below weaken or negate neighborhood effects of fire avoiders such as maples (Fig. 3E) by killing advance regeneration of those species. The cumulative pine and oak seedling banks created by low-severity fires are eventually released from a change in disturbance direction, a disturbance from above such as insect defoliation (which they evade) (Fig. 3F; Tables 1–2) (MacLean and Clark 2021). Mixedwood composition is stable until cumulative disturbance is low (e.g., fire return interval significantly extended or ceased) and long-term shading diminishes the strength of any pre-disturbance endurance traits (e.g., sprouting) and allows succession to proceed to the gradual invasion of hardwood-dominated evaders (of disturbances from above) such as maples and beech (Table 2).

Given these predictions, we pose our extension to the model (Fig. 3) and example mixedwood forests in Table 3 as follows:

1. Forest composition is stable over a wide range of cumulative disturbance severities when dominant species have strong neighborhood effects that match disturbance direction. For instance, species adapted to "resist" disturbances from below may maintain site dominance for long periods when subjected to modest disturbances from below (Fig. 3B; Table 3, forest types listed in footnotes *b* and *c*).
2. Forest composition is unstable when dominant species are mismatched to the direction of the disturbance, even though disturbance severity has not changed. For instance, an evader of disturbances from above is subjected to disturbances from below (or vice versa); consequently, the forest composition changes (Figs. 3C–3D). In Table 2, sugar maple is listed as an evader of wind disturbance through the survival of seedlings in the understory, but when exposed to fire disturbance, these fire-sensitive seedlings are killed and void the growing space, leading to invasion by other species and shifting stand composition.
3. Species' neighborhood effects can conditionally shift to stronger or weaker neighborhood effect levels through disturbance direction and cumulative severity enabling or circumventing forest compositional stability. For instance, species that are very weak evaders of disturbances from above (e.g., most oaks) may develop an evasive capability if first subjected to disturbances from below that enable the establishment and accumulation of an endurance-adapted seedling-sprout bank. At the same time, the otherwise strong evasion strategy of advance regeneration forming maples is weakened by the same series of disturbances from below (fires). After neighborhood strength is thus conditioned, compositional stability following a disturbance from above may favor the earlier successional species (oaks) that would otherwise be at a disadvantage (Figs. 3E–3F; Table 3, forest types listed in footnote *g*).

Important considerations

There are several important considerations that influence interpretation of compositional stability that are not explored subjects of this article but we mention for context.

- Scale: Mixedwood forests that are generally unstable at scales of neighborhoods to stands can exhibit mixedwood composition at landscape scales, e.g., red spruce/fir–aspen/birch (Colford-Gilks et al. 2012; Amos-Binks and MacLean 2016).
- Site: Mixtures of hardwood and softwood species may also be site-mediated, as with red maple – fir in the boreal–temperate ecotone where local low spots on gently rolling terrain lead to temperature (due to cold air pooling) and water-logging gradients, both of which create a mosaic of habitats for conifer, hardwood, and mixedwood stands (Fisichelli et al. 2013; Looney et al. 2018). Alternatively, site management history can influence stability of mixedwood composition as well (Etheridge et al. 2006; Muñoz Delgado et al. 2019).
- Stand developmental stage: Disturbances occurring at different points in stand development may have different consequences even if the disturbance is of the same magnitude (Frelich 2016). Younger and older trees are susceptible to different damaging agents or respond in different ways to the same agents, e.g., seedlings and saplings of fir and spruce are not susceptible to blowdown events to which their mature

counterparts succumb (Rich et al. 2007). Furthermore, late-development stands may contain substrates, propagules, and regeneration layers absent in earlier development (e.g., Burton et al. 2009) so that a greater variety of stability outcomes may result from a given disturbance.

- Novel change: Lastly, caveats to the ideas presented here include when responses to disturbances are not happening in the historically expected way because the disturbance type or cumulative disturbance severity is novel. For example, elevated browse pressure, invasive species, and anthropogenic disturbances combined can lead to recalcitrant vegetation layers that interfere with the historical match of tree traits of the overstory tree species to the prevailing disturbance regime (Royo and Carson 2006). Similarly, long-term effects of non-native pathogens and pests on native tree species can affect nutrient uptake, forest structure, and productivity through changes in tree species composition (Lovett et al. 2006). These mismatches destabilize composition of the current forest type. Further, climate change can cause resilience debt or the loss or severe degradation of ecological legacies such that adaptive capacity of the forest is lacking or misaligned with novel conditions (Johnstone et al. 2016). Increased atmospheric N deposition has also led to changes in natural and anthropogenic disturbances particularly in the eastern U.S.(Ollinger et al. 1993). For example, Thomas et al. (2010) found both decreased and increased rates of tree growth in response to nitrogen deposition during the 1980s and 1990s within north-central and northeastern U.S. These ecological misalignments potentially destabilize the historical forest composition in both the short and long terms (Williams et al. 2007). Thus, the concept of compositional stability resulting from the alignment of neighborhood effect strength and cumulative disturbance type severity will be weakened or disrupted as forests, including mixedwood forests, undergo novel changes.

Management implications and conclusions

Conservation and management of mixedwood forests are important to societal values from commercial forestry to wildlife habitat; however, managing species groups with contrasting autecological traits can be challenging. Where management regimes are mismatched with species composition, mixedwood forests tend to transition out of mixed and into hardwood composition (Kenefic et al. 2021). For instance, disturbances from above such as timber harvesting (from partial cutting to clearcutting) failed to regenerate shortleaf pine, which requires some disturbances from below to regenerate (Jensen and Kabrick 2008). A review of mixedwood forest silviculture noted the difficulty of maintaining the softwood component in mixedwood stands with highly competitive hardwood components (Kenefic et al. 2021). Understanding compositional stability in relation to disturbance is important to the management and conservation of mixedwood stands, and the disturbance focus of the neighborhood-effect theory makes it well suited to understanding how management actions — altering disturbance patterns — affect composition at the stand scale. Thus, the ideas presented here can be applied in management, e.g., prescribed fire to emulate low-severity surface fire.

Mixedwood forests occur in many regions of North America, and several particular softwood–hardwood species combinations occur with such frequency (Vickers et al. 2021) that they are considered ecologically and economically important forest types (Kabrick et al. 2017). Recent studies show potential widespread transitions from mixedwood forest composition to hardwood-dominated forests in eastern North America (Vickers et al. 2021). Conceptual guides such as this article can facilitate conservation and management of mixedwood forest stability to meet societal demand for a range of goods and services.

The neighborhood-effect theory of forest dynamics provided a lens to review compositional stability of mixedwood forests and develop a conceptual guide for mixedwood stability. While the theory did not address mixedwood composition directly, disturbance and neighborhood effects facilitated a generalized understanding of mixedwood composition and stability. In particular, new ideas emphasizing the integration of neighborhood strength and disturbance direction can be adapted as a conceptual tool to managing and conserving mixedwood forests and, more broadly, mixed-species forests. Notably, species with neutral traits such as pine–oak can exhibit compositional stability after the cumulative conditioning of low- to moderate-severity disturbances from below (e.g., surface fires) to facilitate pine substrate invasion and oak seedling-sprouts combined with disturbances from above (e.g., insect infestation) to release advance regeneration and maintain the composition.

In practice, using these ideas might follow these steps. First, the dominant hardwood and softwood species must be identified and evaluated for their traits (e.g., Table 1; Appendix A). Next, the plant strategy for self-replacement and strength of neighborhood effect should be compared with the current disturbance or management regime, including the direction of the disturbance (e.g., Table 2; Fig. 2). The degree of accord or discord will highlight conditions for stable or unstable composition mixtures and opportunities for conservation and management (Fig. 3).

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Appendix A

Brief summary of some softwood and hardwood traits important to mixedwood forest stability

To apply these ideas to mixedwood forests, we highlight the tree traits of hardwood and softwood species. Broadly, each component implies different stand dynamics, phenology, and responses to disturbance with possible synergistic effects that would not be found in either pure softwood or pure hardwood forests (Wagner and Zasada 1991; Ramovs and Roberts 2003;

Augusto et al. 2015). With respect to disturbances, softwood species, in general, tend to be more adapted to disturbances from below than their associated hardwood companions (USDA Forest Service 2003). Importantly, not that all softwoods are more adapted to disturbances from below than are all hardwoods, but that within a given mixedwood, the softwood is more likely to resist or to successfully invade following a disturbance from below. Even among the late-successional softwoods, minor disturbance from below such as disturbance to the forest floor is often beneficial if not required (e.g., Boulfroy et al. 2012).

Softwoods and hardwoods employ characteristically different growth strategies that affect their interactions with each other during stand development in ways that are uniquely different from interactions with others of the same kind (Kittredge 1988; Waskiewicz 2011). Generally, softwoods are less efficient water conduits than hardwood trees, limiting their carbon gain and growth (Bond 1989; Sperry et al. 2006) and resulting in lower seedling and sapling growth rates (Bond 1989; Reich et al. 1998). As a result, recruitment of hardwoods is often greater than that of softwoods, suggesting future dominance of hardwoods and loss of the mixedwood character (Hoshino et al. 2002; Vickers et al. 2021). These traits enhance some hardwood species to be more resistant to disturbances from above.

Moreover, regeneration strategies generally differ among hardwoods and softwoods. In North America, softwood seeds tend to be lighter and more mobile than many of their companion hardwoods, with the important exceptions of birch (*Betula* spp.) and aspen (*Populus* spp.) species. This makes them generally better suited to an invasion strategy after disturbances from below. Undisturbed forest floor litter (low-severity disturbance) can limit softwood invasion strategy. Balsam fir (*Abies balsamea* (L.) Mill.) is one of the few softwoods capable of germinating and establishing on undisturbed forest floor litter (Wang and Kemball 2005). Furthermore, very few softwoods are capable of forming soil seed banks or sprouting from belowground structures; this limits their ability to employ an endure strategy or to evade disturbances from below. Most hardwoods are capable of stump sprouting at some or all developmental stages (Del Tredici 2001); this trait gives hardwoods an endure strategy with respect to disturbances both from below and from above.

The stability of mixedwood forests is also affected by leaf habits. The broad, deciduous leaves of hardwoods are constructed for short lifespans that overlap favorable periods for photosynthesis (Kikuzawa 1991). Evergreen needles of softwoods have long lifespans that reduce nutrient demands for leaf construction and extend opportunities for photosynthesis (Givnish 2002). Softwoods also typically have lower foliar nitrogen and phosphorus contents, lower stomatal conductance under similar environmental conditions, and lower average rates of photosynthetic assimilation per unit leaf area than hardwoods; however, needle retention throughout the year can result in positive net CO_2 assimilation during the spring and fall months when many hardwoods are leafless. Litter inputs tend to be higher in nutrients and decompose more quickly in forests of hardwoods than softwoods (Augusto et al. 2015). As a result, softwoods tend to persist in low-nutrient environments, taking up and returning less nutrients to the forest floor and promoting conditions to self-replace, a positive overstory–understory neighborhood effect (Ericsson 1994). In hemlock–hardwood mixedwood forests, patches of softwood and hardwoods have persisted for 1000–3000 years due to positive neighborhood effects of this kind (Frelich et al. 1993; Catovsky and Bazzaz 2002).

Leaf habit may also influence stability through disturbances from below such as herbivory. In general, softwoods may be less palatable than hardwoods (Reich et al. 1995). In New Brunswick, mixedwood stands were considered important wildlife habitat for ungulates, because of the available hardwood browse and cover provided by softwoods (Morrison et al. 2002); however, selective herbivory on more palatable hardwoods can have long-lasting impacts to recruitment and stability of mixedwood composition (Pastor and Naiman 1992). In some cases, seed predation may be a major factor in the success or failure of co-regeneration of hardwood or softwood species, e.g., seeds of eastern white pine (*Pinus strobus* L.), spruce, and oaks eaten preferentially over fir or red maple (*Acer rubrum* L.) by small mammals (Duchesne et al. 2000; Plucinski and Hunter 2001; Lobo 2014). In general, softwood species are more likely to depend on disturbances from below, at least in mild forms to generate germination microsites in the form of exposed soil patches, as by fallen-tree tip-up mounds or even disruption of the litter layer by small mammals foraging for hardwood seed (Alexander et al. 1985), besides the selective forces of surface fire and browsing.

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