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Review

Are Secondary Forests Ready for Climate Change? It Depends on Magnitude of Climate Change, Landscape Diversity and Ecosystem Legacies

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Abstract: In this review and synthesis paper, we review the resilience of secondary forests to climate change through the lenses of ecosystem legacies and landscape diversity. Ecosystem legacy of secondary forests was categorized as continuous forest, non-continuous forest, reassembled after conversion to other land uses, and novel reassembled forests of non-native species. Landscape diversity, including landforms that create varied local climatic and soil conditions, can buffer changing climate to some extent by allowing species from warmer climates to exist on warm microsites, while also providing refugial locations for species that grow in cool climates. We present five frames that allow forest managers to visualize a trajectory of change in the context of projected regional climate change, which are: Frame 1 (persistence), keep the same dominant tree species with little change; Frame 2 (moderate change), keep the same tree species with large changes in relative abundance; Frame 3 (forest biome change), major turnover in dominant tree species to a different forest biome; Frame 4 (forest loss), change from a forest to a non-forest biome; and Frame 5 (planted novel ecosystem), establish a novel ecosystem to maintain forest. These frames interact with ecosystem legacies and landscape diversity to determine levels of ecosystem resilience in a changing climate. Although forest readiness to adapt to Frame 1 and 2 scenarios, which would occur with reduced greenhouse gas emissions, is high, a business as usual climate change scenario would likely overwhelm the capacity of ecosystem legacies to buffer forest response, so that many forests would change to warmer forest biomes or non-forested biomes. Furthermore, the interactions among frames, legacies, and landscape diversity influence the transient dynamics of forest change; only Frame 1 leads to stable endpoints, while the other frames would have transient dynamics of change for the remainder of the 21st century.

Keywords: boreal forest; climate adaptation; ecosystem legacy; landscape diversity; temperate forest; transient dynamics

1. Introduction

Potentially major impacts of climate change pose significant issues for adaptation of forests and appropriate management responses. While land management can be adapted to any foreseeable change—even transitions to a different forest type or from forest to grassland—adaptation of the forest via management has a complex set of limitations that varies greatly among climate change scenarios, landscape contexts, and ecosystem legacy status for a given forest. Forest adaptation via management may be feasible or not, depending principally on the interactions between ecosystem legacies lending natural adaptability to forests, which may be enhanced or reduced by management actions, and the magnitude of climate change expected on a given landscape.

To understand the interaction between management and forest adaptation to climate change, a brief review is needed of resilience [1], resilience debt [2], and ecosystem legacy and related concepts, including information and material legacies, ecological memory, and legacy syndrome [3,4]. For purposes of this paper, these concepts are broadened to include not only pulse disturbances like wind storms and fires, but also temperature and other continuous changes associated with climate change (press disturbances) that will also impact sustainability in terms of regeneration and growth of trees and competition among tree species.

Three strategies of adaptation to climate change—incremental, anticipatory, and transformational —have been conceptualized for future climate scenarios [5]. These correspond roughly with the resistance (forestall impacts and protect valuable resources), resilience (improve the capacity of ecosystems to return to desired conditions after disturbance), and facilitation (actively facilitate transition of ecosystems from current to new conditions) approaches of Millar et al. [6]. Additionally, the anticipatory/resistance strategy incorporates the non-management or passive response (e.g., [7]). Briefly, the choice of appropriate management response depends on anticipated change: low, medium, and high magnitude [8]. For cases of low magnitudes of climate change, sufficient levels of ecosystem legacies and high ecological resilience, minimal management may be needed to allow forests to resist change (i.e., resistance). For increasing magnitudes of climate change where innate ecological resilience is not high enough to resist change, management may be directed at increasing the ecological resilience of the forest. At some magnitude of change, no adaptation of the existing forest is possible (e.g., a transition to a completely different forest type or forest to non-forest). In such cases, managing for facilitation of the change and a graceful transition may be the best course of action.

The overall objective of this paper is to illuminate the responses and resilience of forests to different magnitudes of climate change and their interactions with ecosystem legacies, and landscape diversity. We present a framework for managers to evaluate the potential response of a given forest to changing but uncertain future conditions, focusing on secondary forests and the development of novel conditions under climate change. We use the southern boreal forest ecotone with temperate forests, savannas and grasslands as an illustrative example, although the concepts developed can be applied to other forest types. First, however, we clarify our usage of several concepts and terms in widespread use.

2. Definition of Secondary Forests

The simplest definition of "forest" is a large area dominated by trees. Many other definitions are used globally for different purposes that add precision by incorporating tree density, tree height, land use, legal standing, ecological function, and disturbances that may render an area temporarily treeless [9,10], as well as including woodlands and trees outside forests [11,12]. Tropical deforestation, and more generally the past and continued destruction of primary forests worldwide, have given rise to the concept of secondary forests that describe much of the world's forest cover. Despite widespread usage, the term "secondary forest" in practice is ambiguous [13]. The main points of contention have been about naturalness (resulting from human or natural disturbance of primary forest), the intensity and extent of disturbance, and nature of the vegetation that develops. Here we consider second growth to be any forest which was clearcut, or converted to other land uses (most commonly agriculture), and reforested or afforested with natural or planted regeneration. This definition excludes some common types of forests including primary forests subject to low-intensity selective logging, low-intensity, small-scale extractive activities (e.g., for non-timber forest products), or affected by small-scale natural disturbance. Regardless of these nuances, all types of forests may have the condition of intactness—continuous overstory or cover over time. Over a large enough area, continuous forests create their own interior conditions of generally somewhat cooler temperatures and higher humidity than in open areas outside of the forest.

3. Forest Resilience and Legacy Concepts as Related to Secondary Forests

Resilience is another widely used term with different underlying concepts and assumptions [1]. As borrowed from engineering, resilience refers to the ability of a system to return to the same state after a perturbation. Engineering resilience assumes the existence of a single equilibrium state. Holling's definition of ecological resilience [14] provides for the possibility of multiple equilibria. Socio-ecological resilience considers that natural and social systems are strongly coupled [15] and remains within the same regime, essentially maintaining its structure and functions following disturbance. Socio-ecological resilience assumes a system is capable of self-organization, learning, and adaptation [16].

Differences among the definitions were summarized by [1]: engineering resilience focuses on recovery of the system to a pre-disturbance state [17]; ecological resilience includes both resistance and recovery of the system, such that several quasi-equilibria are possible within the historical range of variability in composition and structure [4,18]; and social-ecological resilience adds adaptive capacity and transformational ability [19]. Nikinmaa et al. [1] posit that the three resilience conceptualizations are hierarchical: socio-ecological resilience subsumes ecological, which in turn subsumes engineering resilience. Recovery after disturbances such as fires, logging, and windstorms have often been studied, as have resilience after conversion to agriculture and reforestation. Most studies focused on relatively short-term conditions, employing the engineering resilience concept. Engineering resilience, however, is ill-suited to changing conditions under climate change, which better applies the ecological resilience framework [1]. Thus, we use the ecological resilience concept, which also has widely varied implications for disturbance under future climate [2].

The meaning of resilience changes depending on the spatial scale being examined. At stand and landscape scales, resilience is understood as the likelihood of return to the same stand composition, or for landscapes composed of many stands, after disturbance. In contrast, at the regional scale, the issues of concern are whether changing climate will cause change to a different forested biome or from a forested to non-forested biome (i.e., less concern over dominant tree species). Here we posit that ecological resilience depends on the interactions between climate change and ecosystem legacies of secondary forests and landscape diversity.

3.1. Ecosystem Legacies and Memory

Forest resilience to climate change is shaped by ecological memory of past ecological states, as transmitted by ecosystem legacies [4]. Ecosystem memory is the totality of post-disturbance ecosystem legacies [4,20]. Ecosystem legacies persist through change (disturbance) and shape the future responses to climate change and disturbances. Various disciplines have used the concept of legacies to describe conditions that persist after disturbance; these include disturbance, biological, soil, land-use, and silvicultural legacies that overlap in complex ways [4]. Ecosystem legacies are further classified as information legacies (species adaptations) and material legacies (individuals, seeds, woody material, and nutrient pools). Ecosystem legacies are stated in positive terms, rather than the mixture of positive (e.g., biological) and negative (e.g., land-use) legacies [2]. Ecosystem legacies describe what passes through the disturbance filter, rather than what was lost [4]. Thus we avoid terms such as "bad ecological memories' [21].

The stronger the ecological memory, the greater the resilience to changing climate. Wilderness areas, primary forests (i.e., never logged), and some secondary forests (intact, continuously forested areas that have been relatively undisturbed for at least the last two centuries), are better positioned to maintain resilience and ecosystem services in a changing climate than other, younger secondary forests [22]. Even for these latter forests, resilience in a changing climate has major dependencies on the factors discussed below that are fixed for a given landscape, such as landscape diversity. However, at least when all other factors are equal, continuous forests are more resilient [23].

An edited pattern of ecosystem legacies, a legacy syndrome, contains complex relationships that allow many aspects of disturbance regime and traits of dominant tree species to interact in mutualistic fashion to facilitate ecological function on a given landscape [4]. A mismatch is likely to occur when either environmental tolerance of the foundational tree species or safe space for disturbance regime is exceeded, leading to a loss of ecological memory and transition to different vegetation types [2]. Two possible trajectories are to a novel ecosystem or to a degraded state, with a permanent decline in productivity and capacity to regulate environmental processes [18]. In either direction, there is less ecological memory, and new relationships among species that confer resilience are not necessarily well established. Ecological functions (productivity, retention of nutrients) and ecosystem services (maintaining biodiversity, timber production and CO_2 sequestration) are likely to be at lower levels than in forests with strong ecological memory.

3.2. Resilience Debt

Resilience debt [2] or memory debt [18] represents a loss of resilience due to misalignment of information legacies and climate change-related disturbances which is only apparent after disturbance and climate change have occurred. Thus, if the same disturbance (type and severity) as historically occurred should occur again, the forest could drastically change when the resilience debt comes due. In other words, disturbances that formerly perpetuated the forest now lead to change, in which case the forest is outside of the safe operating space for the disturbance or climate regime. Ecosystem memories can facilitate change in a direction away from the historical natural condition, away from desired management outcomes, for example that favor invasive species [21]. To tie concepts of ecosystem legacies, resilience, and resilience debt together, we can say that high resilience scenarios (with high ecosystem legacies and low resilience debt) maintain existing conditions, while moderate resilience scenarios allow some stands to remain the same, and most or all stands change in low resilience scenarios (with low ecosystem legacies and high resilience debt, Figure 1). Furthermore, the level of resilience for a given forest in a changing climate comes about due to the relative magnitudes of ecological resilience and climate change opposing one another.

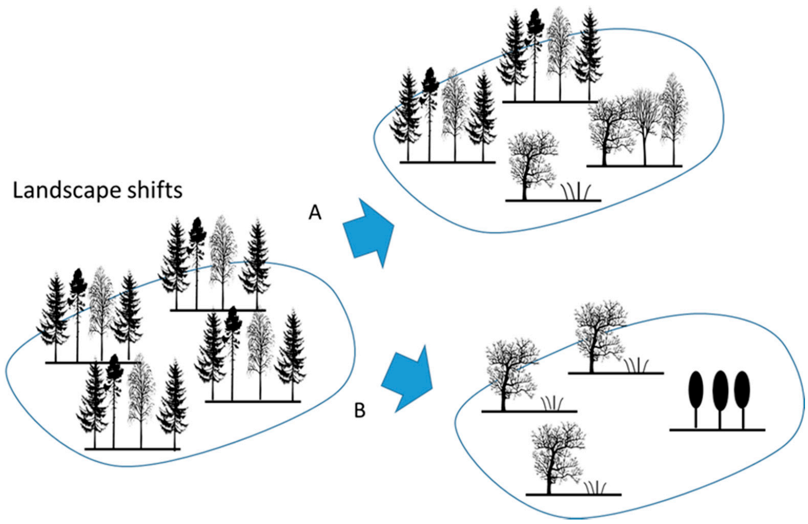

Figure 1. Landscape shifts for southern boreal forest for future scenarios with low and high magnitudes of climate warming. **A**. Low magnitude of warming allows some boreal stands to persist while other stands convert to temperate forest or savanna; this is a moderate resilience scenario. **B**. High magnitude of warming causes loss of all boreal stands and their replacement by either savanna or artificial planted forest; this is a low resilience scenario.

3.3. Landscape Diversity and Forest Resilience

As climate changes, ecosystem legacies will interact with another important factor that can confer more orderly ecosystem responses, namely landscape diversity—variation in landforms, soil texture, and substrate chemistry (pH and nutrient levels) at scales from 10 s of m to 10 s of km. In particular, diversity of land forms and soil textures allows coexistence in close proximity of vegetation types adapted to varied temperature and moisture regimes. In essence, a diverse landscape with many different legacy syndromes in operation can allow some of them to expand while others contract, with relatively short distances for foundational species to move while the climate changes [24]. Thus, we have a landscape-scale, spatial version of the biodiversity insurance hypothesis [25].

Landscape diversity plays a major role in allowing for natural adaptation to climate change to take place [24]. Temperature lies upon the landscape like a quilt, with patches of different temperatures due to solar radiation differences according to aspect and slope steepness. Furthermore, temperature variation combined with variation in albedo, wind patterns, evaporation, and soil texture, also leads to similar variation in soil moisture [26]. For a given landscape, there can be landforms harboring species in unique places that could become a dominant cover type over large spatial extents in a warmer climate. Steep equatorward slopes, for example, or sandy soils could represent future warmer temperatures and drought stress. Similarly, there may currently be places of potential refuge for species that may be displaced on most of the landscape in the future. For example, areas with deep silty soils with high water holding capacity, low areas that receive cold air pooling at night, or poleward-facing slopes may be wetter, cooler refugia for species otherwise ill-adapted to drier, warmer climate, allowing, for example, boreal stands to persist on the landscape as temperate forests develop in warmer parts of the landscape [26], (Figure 2A).

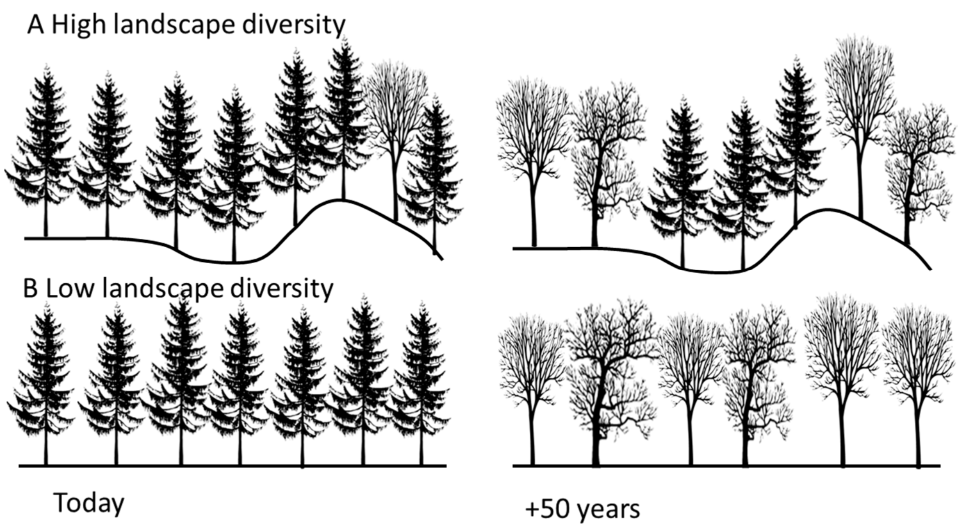

Figure 2. Impacts of landscape diversity on forest change in a warming climate at the trailing (southern) edge of the boreal forest and leading (northern) edge of temperate deciduous forest. (**A**) High landscape diversity scenario has preexisting maple on a south facing aspect (facing right in this figure) which expands by year 50 and maintains boreal forests in lowlands receiving cold-air pooling and on north facing aspects (facing left in this figure). (**B**) Low landscape diversity scenario experiences larger changes in composition and loses diversity as the climate warms.

With high landscape diversity, species already present may expand without having to move very far, or contract their spatial extent but still persist, as the climate changes—thus a diverse forested landscape as a whole could be more resilient to climate change than a low-diversity, flat landscape that has low species diversity (Figure 2B). In essence, diverse landscapes lead to strong ecosystem legacies and ecological memory at the landscape scale, despite the fact that patches of some forest types present may have weak ecosystem memory.

In highly diverse landscapes, a forest type or tree species that currently has a small spatial extent may become the dominant cover type in a changing climate. The whole suite of species needed for future ecosystem function may be present and do not need to disperse far. Importantly, the more small inclusions there are of a currently minor, but future dominant type, the faster it can expand as the climate warms [27].

Magnitudes of climate change and landscape position within a given region (leading edge versus trailing edge with respect to warming climate) will interact with ecosystem legacies and landscape diversity to influence the ultimate outcome for change in a given forest landscape, and determine the potential for management actions to enhance forest ecosystem services. Leading edges of the range for tree species, forest types, or biomes are defined as edges towards a cooler climate, generally poleward or higher elevation edges (there are local or regional exceptions due to cold air pooling in basins with certain shapes and lake or ocean effects), while trailing edges are defined as usually equatorward or lower elevation edges.

Although low-magnitude climate change may not challenge the abilities of ecosystem legacies, landscape diversity, and management to work together to mitigate effects of climate change, the higher climate change scenarios are likely to overwhelm all ecosystem legacies of the currently dominant forest type everywhere on the landscape (Figure 1B), perhaps even the strongest legacy syndromes in primary forests. Information legacies can become useless for adaptation to large magnitudes of warming, leading to large resilience debt when formerly routine disturbances occur, mismatch of disturbance regime and species traits in the legacy syndrome, and status outside of safe operating space [2]. Furthermore, large magnitudes of warming climate may overwhelm landscape and structural diversity, exceeding the ability of even the vegetation type on the warmest parts of a diverse landscape to thrive, leading to a period of chaotic reorganization.

4. Secondary and Planted Forest Legacies

Depending on the origin of secondary forests, the level (or strength) of ecosystem memory and maintained legacies can be quite variable. Over sufficient time, some planted forests can develop characteristics similar to secondary forests, including legacies. Continuity of forest cover is an over-arching characteristic.

4.1. Continuous Forest, Second Growth Legacy

These forests originated following harvesting without an intervening period of conversion to other land uses [4,23]. Often these were harvested during winter in high latitudes, perhaps by clearcutting, but without soil tillage. They have a strong memory in terms of legacies—species composition of the tree layer and soil. However, early successional species could dominate due to high light availability at the time of tree establishment, or in some cases dominants could be late successional species because shade-tolerant species in the understory were released post-harvest or retained from the previous stand. These could be even-aged or uneven-aged at this time.

4.2. Non-Continuous Forest with Reassembled Native Legacies

Forests can develop on land abandoned after human conversion for other uses, often from abandoned agriculture or pasture [23]. A forest legacy is reassembled via natural processes, in which species composition (information legacy) is similar to that of continuous secondary forest. Structural legacies, however, such as large trees, gaps, and coarse woody debris likely will be absent. This occurs in situations where many native species are present in scattered locations (for example along minor water courses or windbreaks), but can still spontaneously assemble former communities when human activity ceases. These are for the most part post-agricultural lands that had scattered continuous forests on the landscape nearby (e.g., farm woodlots) and few or no invasive species were present.

4.3. Non-Continuous Forest with Novel Reassembled Legacies

A novel community of species can assemble on abandoned land, including mostly non-native species that can move easily across long distances, or that were purposely planted. These tend to be on land more recently abandoned by other uses than reassembled legacy sites, so that propagules of invasive species were present in many nearby locations. These could be completely novel in species composition with all species put there by people. Legacies reassemble, but develop an ecosystem memory that tends to drive succession in an undesired direction.

4.4. Planted Forest Legacies

Currently existing planted forests, including plantations, can be any of the three forest legacy types described above: continuous forest planted with native tree species; reassembled forest planted with native tree species combined with species that arrived on their own [28]; or novel reassembled forests planted with non-native tree species [29]. Soils could have been plowed or not, and planting could have been performed on open soil or into an intact understory. However, the first two types are most common and, over sufficiently long time, may develop legacies similar to secondary forests. Plantations, especially if intensively managed on relatively short rotation, can develop ecosystem memories with a legacy syndrome miss-matched to the disturbance regime resulting in high resilience debt.

Many secondary forests already have species (or provenances) adapted to warmer climate or drier conditions, but do not have the resilience or ecosystem legacies of primary (old growth, primeval) forests. This is especially important at leading/trailing edges. Although the level of adaptation of tree species to local conditions varies, planted forests, on the contrary, are usually established with locally adapted material and optimized for growth under current conditions. While diverse forests are thought to be more resilient overall, mixed species plantations are rare. Nevertheless, sometimes other species have spontaneously regenerated within gaps in plantations and are helping with resilience to climate change.

5. Resilience Frames and Management Options

We recognize five resilience frames (Figure 3) through which to view forest change at the landscape scale, from a management perspective. In each case these should be interpreted as related to climate change scenarios by the late 21st century and frame the management options available under the specified conditions.

Frame 1, persistence. Keep the current tree species as climate changes, with minor change in forest type due to small shifts in relative abundance among them. This may happen in areas with high landscape and tree species diversity, characterized by high ecosystem memory, continuous forest legacy, and low magnitudes of climate change expected relative to ranges of foundational tree species. Forests are dominated by leading edge or mid-range tree species. Resilience debt is small for the forest as a whole. This is the incremental [5] or resistance [6] adaptation strategy that relies on the ability of native species to adapt to modest changes in climate, via techniques such as stand thinning for drought resistance, maintaining a diversity of tree species, managing to mitigate effects of invasive species that add to stress on the ecosystem, and creating multi-aged stands resistant to wind storms [5,6,21].

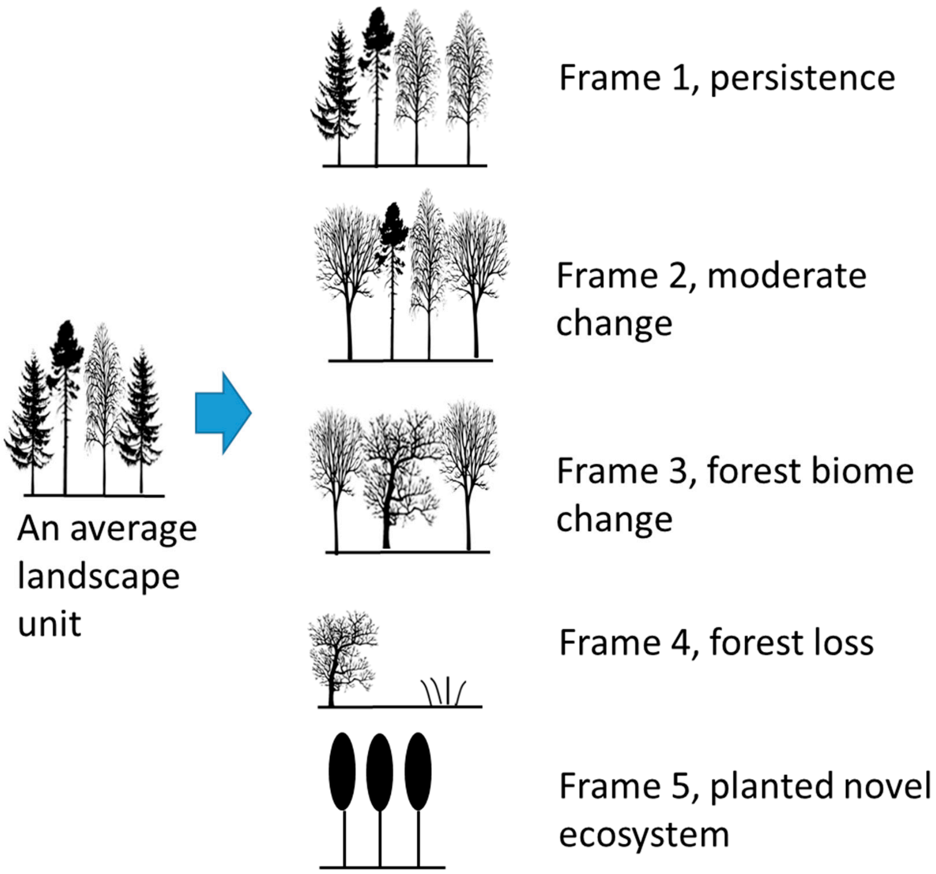

Figure 3. The frames of change in stand types and species composition—a trailing edge southern boreal forest example with leading temperate deciduous forest and oak savanna just to the south. Frame 1, persistence, the same tree species composition is sustained, perhaps with some minor shifts in relative abundance. Frame 2, moderate change, there are substantial changes in relative abundance of dominant tree species. Frame 3, forest biome change, major turnover of species composition, e.g., transition from boreal to temperate species. Frame 4, forest loss, change from forest to non-forest biome (e.g., savanna or grassland). Frame 5, novel ecosystems are established using exotic tree species suited to the new climate.

Frame 2, moderate change. Keep a subset of current tree species, with moderate change in forest type expected. Foundational tree species may include a mixture of leading edge and trailing edge tree species; expected magnitude of climate change, given the level of landscape diversity, would cause loss of the trailing edge species. Frame 2 is generally characterized by moderate levels of ecosystem memory and perhaps some expression of novelty (such as invasive species that are favored by warmer climate or disturbance). Moderate levels of resilience debt exist after disturbance, so that relative dominance among species shifts without creating a novel forest type. Illustrative examples of Frame 2 include transition from dominance by conifers to birch-aspen, already observed in the boreal forest of Alaska and northern Minnesota, as warming climate favors more frequent fires and compound disturbances [2,30] and maple invading boreal conifer forest in northern Wisconsin (Figure 4A–C). Depending on management objectives, the strategy may rely on incremental adaptation by relying on increased dominance of heretofore minor species or anticipatory adaptation by introduction of other species or provenances through assisted migration [31]. Resilience debt is addressed by anticipating changing climate, favoring better adapted species or introducing adapted provenances of foundation species, i.e., a resilience strategy [2,6].

Figure 4. Pre-historic and contemporary transitions of boreal forest in Minnesota and Wisconsin, USA. (**A**) Current boreal forest of black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.) in the Boundary Waters Canoe Area Wilderness, Minnesota. Photo, Elias Anoszko. (**B**) Frame 2 change in a boreal forest. Young paper birch (*Betula papyrifera* Marshall) forest in the Boundary Waters Canoe Area Wilderness. This birch regeneration replaced a coniferous, boreal forest of jack pine (*Pinus banksiana* Lamb.) and black spruce after a windstorm-fire combination in 1999–2006. Photo by Dave Hansen. (**C**) Frame 2–3 change in progress. Sugar maple sapling growing in a boreal balsam fir (*Abies balsamea* (L.) Mill.) and white spruce (*Picea glauca* (Moench) Voss) forest in northern Wisconsin in 2017, where there were no maples 40 years prior; this is a Frame 2 setting now, but could become Frame 3 in the future if maple continues to replace conifers. Photo by Lee Frelich. **(D)** Frame 3 example—temperate sugar maple forest resulting from mid-Holocene transition of boreal forest in a warming climate in western Upper Michigan. Photo by Kalev Jõgiste. **(E)** Frame 4 example—prairie with scattered oak woodland resulting from mid-Holocene transition from boreal forest due to increasing aridity in western Minnesota. Photo by Dave Hansen.

Frame 3, *forest biome change.* This fully anticipatory adaptation strategy maintains a forest of some sort, but with largely different species composition. All foundational tree species are trailing edge, but the landscape of interest is on or near the leading edge of a different forest biome with largely different species composition. This frame is likely to occur near trailing edges for temperature and moisture tolerance for all of the foundational tree species. Ecosystem legacies are overwhelmed in areas with low landscape diversity and moderate magnitudes of climate change; or perhaps in the middle of the biome or tree species ranges there is high magnitude climate change combined with low landscape diversity. Continuous forest may still occur, but given the expected magnitude of climate change, transition among forest types or biomes is likely; therefore resilience debt is high. Examples expected to occur include boreal to temperate forest transition in the southern boreal forest [32], or mesic forest to dry forest transition in mesophied oak forests of the northeastern U.S. [33]. Many examples of boreal forests that underwent a Frame 3-type transition to temperate sugar maple (*Acer saccharum* Marshall) forests as climate warmed during the Holocene exist in the western Great Lakes region of Minnesota, Wisconsin, and Michigan, USA [34] (Figure 4 D). Major management strategies include facilitating the expansion of leading edge species that are currently in low abundance, but likely to become the new dominant species, and assisted migration of those tree species in equatorward locations that have poor dispersal abilities [6,24]. In diverse landscapes it may also be possible to identify locations with refugium characteristics and enhance resilience of stands of existing tree species in those locations [26].

Frame 4, *forest loss.* When climate change is of sufficient magnitude that a biome shift occurs, there can be a transition from forest to non-forest biome. The landscape of interest is on the trailing edges of a forest biome and all foundational tree species, although there may remain small refugial locations for trees in landscapes with high diversity. This frame is likely to occur in areas near the trailing edge of a biome under a scenario with low-to-moderate magnitude of climate change, or perhaps mid-biome locations for high magnitudes of climate change. This would include boreal or temperate forest transition to savannas or grasslands due to change in annual water balance—increasing evaporation to precipitation ratio from a positive to negative balance [35,36], as has happened during the mid-Holocene in areas currently dominated by prairie in western Minnesota [37] (Figure 4E). Generally, water balance determines forest versus grassland and temperature determines boreal versus temperate forest [32,35]. However, species diversity can also determine where biome lines are—for example tree lines are at lower elevations on islands than mainlands, partly due to lower tree species richness, so that it is less likely that a species will be present on a given island that can tolerate cold conditions [38]. Resilience debt is extremely high, and ecosystem forest legacies are totally overwhelmed by changing climate. Management options include facilitation of species from the new biome, and considering whether maintaining forest cover is important enough to establish a Frame 5 scenario.

Frame 5, *planted novel ecosystems.* Novel ecosystems may be intentionally established to maintain a forest biome, albeit of non-native or even bioengineered species adapted to the altered climate. This transformational adaptation strategy introduces a high degree of novelty where ecosystem legacies have been overwhelmed. By planting, regeneration constraints can be overcome as a novel forest will develop as long as growing conditions are amenable. This facilitation strategy [6] provides a gentle trajectory rather than an abrupt loss of ecosystem services from the forest. It may, however, be a relatively short-term respite in areas expected to undergo even more change in climate [39,40].

6. Forest Readiness for Climate Change

The frame in which a given forest sits provides a vision for feasible management options during the 21st century. By identifying the appropriate frame, we can begin to answer the questions of "What change will we try to be ready for?" and "When should we begin?" These questions apply to both ongoing forest management [41] and to restoration of degraded forests [5,42]. Forest managers need to know what thresholds will trigger each of these frames. Getting to the appropriate frame for a given forest landscape requires access to information including an understanding of scenarios for projected climate change from general circulation models (GCMs), how climate interacts with landscape features, and how the tree species and forests will respond to the projected changes. While GCMs are improving in skill and resolution, their spatial resolution is still inadequate for stand- and landscape-level planning, and therefore most studies use a range of GCMs (including those which run relatively warm and dry or cool and wet) to bracket the range of possibilities [43]. Models of tree species' future ranges, future responses of the forest landscape via models such as LANDIS, and studies of factors that determine biome boundaries for a given climate scenario can help determine which frame is appropriate for a given forest and climate scenario [29,32–34,43,44].

The key for assessing readiness is to examine the interactions of the appropriate frame with ecological resilience and landscape diversity in a given forest (Table 1). Ecological resilience levels are highest in the upper left cell of Table 1 (Frame 1, continuous second growth), and become lower moving down the rows from Frame 1 to Frame 4 or across columns from continuous 2nd growth to planted forests. Within each cell, resilience levels are as high or higher for high landscape diversity (right side of each cell) as compared to low landscape diversity (left side of each cell). Note that resilience debt has the opposite pattern; e.g., low levels in the upper left mean that it is unlikely that routine disturbances will suddenly cause a large change in forest composition. Management for resistance is feasible in the very high and high resilience cases of Table 1, while resilience management strategies (incremental and anticipatory) are feasible in the medium cases. These two management strategies are futile in low resilience cases, where facilitation of a novel ecosystem, possibly including assisted migration of species from leading edges of the nearest equatorward forest type or biome may be necessary, and in flat landscapes large geographical distances may be involved [31].

Table 1. Forest resilience levels by frame and forest legacy type. Each cell shows the two levels of forest resilience to climate change: for high (left) and low (right) levels of landscape diversity. Resilience depends on ecosystem legacy/memory and resilience debt as explained in the text. Frame 5 is not considered here, since such forest by definition would be planted in the future using non-native species or bioengineered native species that do not fit within any of the legacy types shown here.

Resilience Frame	**Secondary Forest Legacy Type**			
	Continuous 2nd Growth	**Non-Continuous**	**Non-Continuous Novel**	**Planted**
Frame 1	Very high/Very high	High/High	High/Medium	Variable [1]
Frame 2	High/Medium	Medium/Medium	Medium/Medium	Variable [1]
Frame 3	Medium/Low	Medium/Low	Low/Low	Variable [1]
Frame 4	Low/Low	Low/Low	Low/Low	Low/Low

[1] Currently existing planted forests could have the levels of non-continuous or non-continuous novel legacy types, depending on their species composition.

Future tree species richness will be a balance between loss of trailing edge and gain of leading edge species, which will be unique at landscape and/or ecoregion scales, because of variations in magnitude of climate change, landscape diversity and ecosystem legacies across forested biomes. Managers need analyses of which foundational tree species in their forest will or will not have their environmental tolerances exceeded in the most likely climate change scenario several decades into the future. Such analyses may take into account the unique aspects of tree ranges and relationship to climate—each species responds to a different set of variables [43], rather than simple climate envelope models.

Studies of microclimatic differences across topographical features and how these relate to persistence of individual tree species are lacking at this time. However, another perspective on tree species comes from examining regional climate gradients in a space for time substitution, to see which foundational tree species can tolerate the driest/warmest conditions likely to occur as the climate warms. In other words, locating equatorward sites with summer climates analogous to future climates projected for a given forest, followed by collecting data on tree species at the analog site and their relationships to landscape diversity. For example, for locations in the southern boreal forest, which boreal tree species persist the farthest along a southwards climate gradient? For locations near the trailing edge of forests near grassland boundaries, which tree species persist farthest along the climate gradient from forest to grassland?

Management strategies are quite different for trailing edge versus leading edge species. We expect species near the trailing edge of the range to contract to smaller spatial niches in the landscape, or to disappear altogether from landscapes with low landscape diversity. Managers can look for occurrences of and possibly facilitate expansion of outliers of species at the leading edges of their ranges.

Management can potentially create diversity of stand ages and tree species, even in landscapes with low landscape diversity, thus manipulating the ecosystem legacies to reap some of the resilience benefits of a landscape with high natural diversity [21]. A mixture of species with different levels of drought and heat tolerance could lead to maximum productivity in a warming climate at landscape and stand spatial scales, even with the expectation for more wind storms. Tolerance of more frequent high wind occurrences depends not only on species, but also age/size class within species, with late-successional species and smaller individuals more tolerant of high winds [45]. Small patches of tree species near the leading edge of their range could be placed throughout the landscape so that they can expand on their own as the climate warms.

Spatial variability across scales, from ecoregion through landscape, stand, individual tree and micro-topography, all contribute to ecosystem memory and forest resilience [2]. Within stand structural diversity, standing and downed woody debris, and micro-topographical features such as tip-up mounds, are important because microsites are important for germination of most species [21]. Very large material legacies, in terms of coarse woody debris and snags, can be created by climate change as poorly adapted tree species decline and die, but much of the information legacy would be rendered useless, although what remains could be magnified as a management strategy.

Continuous secondary forests are in relatively good shape to adapt to low to moderate magnitudes of climate change such as would occur with climate change scenarios with reduced greenhouse gas emissions, while no forest type is likely to adapt to the 'business as usual' climate scenario, since the magnitude of warming would exceed the temperature differences across the ranges of most tree species and biomes [21]. In addition, the ability of high landscape diversity and strong environmental memory to buffer forests is probably limited to Frames 1 and 2.

Examples of forests with large spatial extents that have the landscape and legacy characteristics needed to adapt to Frames 1 and 2, but not 3 or 4, include sugar maple-dominated northern hardwoods in the Great Lakes region of the U.S. and southern boreal forests in Canada and Scandinavia. Both would undergo moderate changes in composition while retaining most of their current native tree species (Frame 2) if the climate warmed by 1–2 °C, but are close enough to the prairie-forest border and temperate deciduous forest, respectively, so that they will likely transition to prairie (Frame 4) or temperate deciduous forests (Frame 3), respectively, for a business as usual climate change scenario with 3–4 °C warming [32,33,46]. Research is underway in this area to determine what the best species are for facilitating expansion of leading edge species for Frame 2 or 3 scenarios or establishing novel forests for a Frame 5 scenario. In addition, planting species that could potentially persist on poleward (north) slopes in areas with high landscape diversity is underway [44,47,48].

In contrast, plantations of Norway spruce (*Picea abies* (L.) H. Karst) and Scots pine (*Pinus sylvestris* L.) in Europe, and red pine (*Pinus resinosa* Aiton) in eastern North America are not ready for climate change for several reasons. The species were frequently placed in off-site locations, resulting in unstable stands in the face of windstorms and periodic drought. Today many of these locations would be considered trailing edges that are out of range given the incoming climates [43]. Species near dry range limits are more affected by droughts than in the middle of species ranges [49], while fungal diseases and insect outbreaks are increasingly common in areas with climates that are becoming warmer and wetter [50]. Other factors include lack of structural and species diversity in the understory.

A final point regarding transient dynamics of the forest—note that only Frame 1 has a stable endpoint similar to that which managers have been used to in the past, and it is only likely to occur with dramatically reduced greenhouse gas emissions. In the other frames all management activities will be directed at shepherding ecosystem change with transient dynamics for the duration of the 21st century. Given the expected non-equilibrium dynamics, management will be dominated by new trajectories of successional dynamics and novel disturbance regimes in addition to traditional stand growth and yield [51]. Furthermore, multiple factors are also chipping away at resilience of secondary forests in many places, such as heavy ungulate browsing, earthworm invasions, and invasive tree pests and diseases [46,52].

7. Conclusions

Interactions among magnitude of climate change, ecosystem legacies, and landscape diversity may determine whether forests will change little, with small relative shifts in abundance among species, have major shifts among species, shift to mostly new tree species, or shift to a non-forest biome. These interactions are complex, however, we have attempted to provide a conceptual way for forest managers to view future change in their area. A combination of downscaled climate models and assessment of the legacy and landscape status of forests is needed to make use of the conceptual scheme and types of changes that can be expected.

Paleoecological evidence shows that Frame 3 and Frame 4 shifts occurred in boreal and temperate forests during the mid-Holocene in response to climate changes similar in magnitude to those projected by the late 21st century for business as usual greenhouse gas emissions scenarios, while field studies show that forests are beginning to experience Frame 2 and Frame 3 responses due to climate change that has already occurred. Unless major reductions in carbon emissions occur soon, climate change is likely to overwhelm the capacity of ecosystem legacies and landscape diversity to buffer forest response—scenarios outlined by our Frames 3 and 4—setting forests on a course of transient dynamics leading to vastly different vegetation, or forcing the establishment of novel planted forests as in Frame 5.

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References

1. Nikinmaa, L.; Lindner, M.; Cantarello, E.; Jump, A.; Seidl, R.; Winkel, G.; Muys, B. Reviewing the use of resilience concepts in forest sciences. *Curr. Rep.* **2020**, *7*, 1–20. [CrossRef]
2. Johnstone, J.F.; Allen, C.D.; Franklin, J.F.; Frelich, L.E.; Harvey, B.J.; Higuera, P.E.; Mack, M.C.; Meentemeyer, R.K.; Metz, M.R.; Perry, G.L.W.; et al. Changing disturbance regimes, ecological memory and forest resilience. *Front. Ecol. Environ.* **2016**, *14*, 369–378. [CrossRef]
3. Frelich, L.E. Forest dynamics. *F1000Research* **2016**, *5*, 183. [CrossRef]
4. Jõgiste, K.; Korjus, H.; Stanturf, J.A.; Frelich, L.E.; Baders, E.; Donis, J.; Jansons, A.; Kangur, A.; Köster, K.; Laarmann, D.; et al. Hemi-boreal forest: Natural disturbances and the importance of ecosystem legacies to management. *Ecosphere* **2017**, *8*, e01706. [CrossRef]
5. Stanturf, J.A. Future landscapes: Opportunities and challenges. *New For.* **2015**, *46*, 615–644. [CrossRef]
6. Millar, C.I.; Stephenson, N.L.; Stephens, S.L. Climate change and forests of the future: Managing in the face of uncertainty. *Ecol. Appl.* **2007**, *17*, 2145–2151. [CrossRef]
7. Jandl, R.; Spathelf, P.; Bolte, A.; Prescott, C.E. Forest adaptation to climate change—Is non-management an option? *Ann. For. Sci.* **2019**, *76*, 48. [CrossRef]
8. Millar, C.I.; Stephenson, N.L. Temperate forest health in an era of emerging megadisturbance. *Science* **2015**, *349*, 823–826. [CrossRef]

9. Chazdon, R.L.; Brancalion, P.H.; Laestadius, L.; Bennett-Curry, A.; Buckingham, K.; Kumar, C.; Moll-Rocek, J.; Vieira, I.C.G.; Wilson, S.J. When is a forest a forest? Forest concepts and definitions in the era of forest and landscape restoration. *Ambio* **2016**, *45*, 538–550. [CrossRef]
10. Putz, F.E.; Redford, K.H. The importance of defining 'forest': Tropical forest degradation, deforestation, long-term phase shifts, and further transitions. *Biotropica* **2010**, *4*, 10–20. [CrossRef]
11. van Noordwijk, M.; Suyamto, D.A.; Lusiana, B.; Ekadinata, A.; Hairiah, K. Facilitating agroforestation of landscapes for sustainable benefits: Tradeoffs between carbon stocks and local development benefits in Indonesia according to the FALLOW model. *Agric. Ecosyst. Environ.* **2008**, *126*, 98–112. [CrossRef]
12. Zomer, R.J.; Neufeldt, H.; Xu, J.; Ahrends, A.; Bossio, D.; Trabucco, A.; van Noordwijk, M.; Wang, M. Global tree cover and biomass carbon on agricultural land: The contribution of agroforestry to global and national carbon budgets. *Sci. Rep.* **2016**, *6*, 29987. [CrossRef] [PubMed]
13. Chokkalingam, U.; De Jong, W. Secondary forest: A working definition and typology. *Int. For. Rev.* **2001**, *3*, 19–26.
14. Holling, C.S. Resilience and stability of ecological systems. *Ann. Rev. Ecol. Syst.* **1973**, *4*, 1–23. [CrossRef]
15. Folke, C.; Carpenter, S.; Elmqvist, T.; Gunderson, L.; Holling, C.S.; Walker, B. Resilience and sustainable development: Building adaptive capacity in a world of transformations. *AMBIO* **2002**, *31*, 437–440. [CrossRef]
16. Walker, B.; Holling, C.S.; Carpenter, S.; Kinzig, A. Resilience, adaptability and transformability in social–ecological systems. *Ecol. Soc.* **2004**, *9*, 5. [CrossRef]
17. Pimm, S.L. The complexity and stability of ecosystems. *Nature* **1984**, *307*, 321–326. [CrossRef]
18. Stanturf, J.A.; Frelich, L.; Donoso, P.J.; Kuuluvainen, T. Advances in managing and monitoring natural hazards and forest disturbances. In *Achieving Sustainable Management of Boreal and Temperate Forests*; Stanturf, J., Ed.; Burleigh Dodds Science Publishing: Cambridge, UK, 2020; pp. 627–716.
19. Folke, C.; Carpenter, S.R.; Walker, B.; Scheffer, M.; Chapin, T.; Rockström, J. Resilience thinking: Integrating resilience, adaptability and transformability. *Ecol. Soc.* **2010**, *15*, 20. [CrossRef]
20. Peterson, G.D. Contagious disturbance, ecological memory, and the emergence of landscape pattern. *Ecosystems* **2002**, *5*, 329–338. [CrossRef]
21. Webster, C.R.; Dickinson, Y.L.; Burton, J.I.; Frelich, L.E.; Jenkins, M.A.; Kern, C.C.; Raymond, P.; Saunders, M.R.; Walters, M.B.; Willis, J.L. Tamm Review: Promoting and maintaining diversity in contemporary hardwood forests: Confronting contemporary drivers of change and the loss of ecological memory. *For. Ecol. Manag.* **2018**, *421*, 98–108. [CrossRef]
22. DiMarco, M.; Ferrier, S.; Harwood, T.D.; Hoskins, A.J.; Watson, J.E.M. Wilderness areas halve the extinction risk of terrestrial biodiversity. *Nature* **2019**, *573*, 582–585. [CrossRef] [PubMed]
23. Jõgiste, K.; Frelich, L.E.; Laarmann, D.; Baders, E.; Donis, J.; Jansons, A.; Kangur, A.; Korjus, H.; Köster, K.; Kusmin, J.; et al. Imprints of management history on hemiboreal forest ecosystems in the Baltic States. *Ecosphere* **2018**, *9*, e02503. [CrossRef]
24. Anderson, M.G.; Clark, M.; Sheldon, A.O. Estimating climate resilience for conservation across geophysical settings. *Conserv. Biol.* **2014**, *28*, 959–970. [CrossRef] [PubMed]
25. Loreau, M.; Mouquet, N.; Gonzalez, A. Biodiversity as spatial insurance in heterogeneous landscapes. *Proc. Natl. Acad. Sci. USA* **2003**, *100*, 12765–12770. [CrossRef] [PubMed]
26. Stralberg, D.; Arsenault, J.L.; Baltzer, Q.E.; Barber, E.M.; Bayne, Y.; Boulanger, C.D.; Brown, H.A.; Cooke, K.; Devito, J.; Edwards, J.; et al. Climate-change refugia in Boreal North America: What, where, and for how long? *Front. Ecol. Environ.* **2020**, *18*, 261–270. [CrossRef]
27. Lawler, J.J.; Ackerly, D.D.; Albano, C.M.; Anderson, M.G.; Dobrowski, S.C.; Gill, J.L.; Heller, N.E.; Pressey, R.L.; Sanderson, E.W.; Weiss, S.B. The theory behind, and challenges of, conserving nature's stage in a time of rapid change. *Conserv. Biol.* **2015**, *29*, 618–629. [CrossRef]
28. Twedt, D.J. Stand development on reforested bottomlands in the Mississippi Alluvial Valley. *Plant Ecol.* **2004**, *172*, 251–263. [CrossRef]
29. Stanturf, J.A.; Vance, E.D.; Fox, T.R.; Kirst, M. Eucalyptus beyond its native range: Environmental issues in exotic bioenergy plantations. *Int. J. For. Res.* **2013**, *5*, 463030. [CrossRef]
30. Johnstone, J.F.; Chapin, F.S., III; Hollingsworth, T.N.; Mack, M.C.; Romanovsky, V.; Turetsky, M. Fire, climate change, and forest resilience in interior Alaska. *Can. J. For. Res.* **2010**, *40*, 1302–1312. [CrossRef]
31. Williams, M.I.; Dumroese, R.K. Preparing for climate change: Forestry and assisted migration. *J. For.* **2013**, *114*, 287–297. [CrossRef]

32. Fisichelli, N.A.; Frelich, L.E.; Reich, P.B. Temperate tree expansion into adjacent boreal forest patches facilitated by warmer temperatures. *Ecography* **2014**, *37*, 152–161. [CrossRef]
33. Frelich, L.E.; Peterson, D.W.; Reich, P.B. The changing role of fire in mediating the relationships among oaks, grasslands, mesic temperate forests and boreal forests in the Lake States. *J. Sustain. For.* **2017**, *36*, 421–432. [CrossRef]
34. Davis, M.B.; Douglas, C.; Calcote, R.; Cole, K.L.; Winkler, M.G.; Flakne, R. Holocene climate in the western Great Lakes national parks and lakeshores: Implications for future climate change. *Conserv. Biol.* **2000**, *14*, 968–983. [CrossRef]
35. Hogg, E.H. Climate and the southern limit of the western Canadian boreal forest. *Can. J. For. Res.* **1994**, *24*, 1835–1845. [CrossRef]
36. Danz, N.P.; Reich, P.B.; Frelich, L.E.; Niemi, G.J. Vegetation controls vary across space and spatial scale in a historic grassland-forest biome boundary. *Ecography* **2011**, *32*, 402–414. [CrossRef]
37. Nelson, D.M.; Hu, F.S. Patterns and drivers of Holocene vegetational change near the prairie-forest ecotone in Minnesota: Revisiting McAndrews' transect. *New Phytol.* **2008**, *179*, 449–459. [CrossRef] [PubMed]
38. Karger, D.N.; Kessler, M.; Conrad, O.; Weigelt, P.; Kreft, H.; König, C.; Zimmermann, N.E. Why tree lines are lower on islands—Climatic and biogeographic effectshold the answer. *Glob. Chang. Biol.* **2019**, *28*, 839–850.
39. Williams, J.W.; Jackson, S.T. Novel climates, no-analog communities, and ecological surprises. *Front. Ecol. Environ.* **2007**, *5*, 475–482. [CrossRef]
40. Williams, J.W.; Jackson, S.T.; Kutzbach, J.E. Projected distributions of novel and disappearing climates by 2100 AD. *Proc. Natl. Acad. Sci. USA* **2007**, *104*, 5738–5742. [CrossRef]
41. Spathelf, P.; Stanturf, J.; Kleine, M.; Jandl, R.; Chiatante, D.; Bolte, A. Adaptive measures: Integrating adaptive forest management and forest landscape restoration. *Ann. For. Sci.* **2018**, *75*, 55. [CrossRef]
42. Stanturf, J.; Palik, B.; Dumroese, R.K. Contemporary forest restoration: A review emphasizing function. *For. Ecol. Manag.* **2014**, *331*, 292–323. [CrossRef]
43. Dyderski, M.K.; Paz, S.; Frelich, L.E.; Jagodzinski, A.M. How much does climate change threaten European forest tree species distributions? *Glob. Chang. Biol.* **2018**, *24*, 1150–1163. [CrossRef] [PubMed]
44. Ravenscroft, C.; Scheller, R.M.; Mladenoff, D.J.; White, M.A. Forest restoration in a mixed ownership landscape under climate change. *Ecol. Appl.* **2010**, *20*, 327–346. [CrossRef] [PubMed]
45. Rich, R.L.; Frelich, L.E.; Reich, P.B. Wind-throw mortality in the southern boreal forest: Effects of species, diameter and stand age. *J. Ecol.* **2007**, *95*, 1261–1273. [CrossRef]
46. Frelich, L.E.; Reich, P.B. Will environmental changes reinforce the impact of global warming on the prairie-forest border of central North America? *Front. Ecol. Environ.* **2010**, *8*, 371–378. [CrossRef]
47. Muller, J.J.; Nagel, L.M.; Palik, B.J. Forest adaptation strategies aimed at climate change: Assessing the performance of future climate adapted tree species in a northern Minnesota pine ecosystem. *For. Ecol. Manag.* **2019**, *451*, 117539. [CrossRef]
48. White, M.A.; Cornett, M.W.; Frerker, K.; Etterson, J.R. Partnerships to take on climate change: Adaptation forestry and conifer strongholds projects in the northwoods, Minnesota. *J. For.* **2020**, *118*, 219–232. [CrossRef]
49. Anderegg, W.R.; Anderegg, L.D.L.; Kerr, K.L.; Trugman, A.T. Widepread drought-induced tree mortality at dry range edges indicates that climate stress exceeds species' compensating mechanisms. *Glob. Chang. Biol.* **2019**, *25*, 3793–3802. [CrossRef]
50. Hlásny, T.; Krokene, P.; Liebhold, A.; Montagné-Huck, C.; Müller, J.; Qin, H.; Raffa, K.; Schelhaas, M.-J.; Seidl, R.; Svoboda, M.; et al. Living with bark beetles: Impacts, outlook and management options. *From Sci. Policy 8* **2019**, 53. [CrossRef]
51. Wilson, D.C.; Morin, R.; Frelich, L.E.; Ek, A.R. Monitoring Disturbance Intervals in Forests: A Case Study of Increasing Forest Disturbance in Minnesota. *Ann. For. Sci.* **2019**, 76–78. [CrossRef]
52. Roy, B.A.; Alexander, H.M.; Davidson, J.; Campbell, F.T.; Burdon, J.J.; Sniezko, R.; Brasier, C. Increasing forest loss worldwide from invasive pests requires new trade regulations. *Front. Ecol. Environ.* **2014**, *12*, 457–465. [CrossRef]