



Review

What Are Intermediate-Severity Forest Disturbances and Why Are They Important?

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Abstract: The classification of discrete forest disturbance events is usually based on the spatial extent, magnitude, and frequency of the disturbance. Based on these characteristics, disturbances are placed into one of three broad categories, gap-scale, intermediate-severity, or catastrophic disturbance, along the disturbance classification gradient. We contend that our understanding of disturbance processes near the endpoints of the disturbance classification gradient far exceeds that of intermediate-severity events. We hypothesize that intermediate-severity disturbances are more common, and that they are more important drivers of forest ecosystem change than is commonly recognized. Here, we provide a review of intermediate-severity disturbances that includes proposed criteria for categorizing disturbances on the classification gradient. We propose that the canopy opening diameter to height ratio (D:H) be used to delineate gap-scale from intermediate-severity events and that the threshold between intermediate and catastrophic events be based on the influence of residual trees on the composition of the regeneration layer. We also provide examples of intermediate-severity disturbance agents, return intervals for these events, and recommendations for incorporating natural intermediate-severity disturbance patterns in silvicultural systems.

Keywords: disturbance; moderate severity; stand development; structure; succession

1. Introduction

All forest stands are in a state of recovery from prior disturbance [1]. Disturbances modify species composition, the arrangement of biomass and tree ages, and ecosystem functions [2,3]. These events impart informational and material legacies that may be short-lived or perpetual [4]. Disturbances may impact neighborhoods within stands, entire stands, or collections of stands to alter forest and even landscape-level vegetation patterns [5]. Species' responses to natural disturbances have long been used to guide silvicultural systems. In the natural disturbance ecology literature, canopy disturbances are typically classified in the context of the stand by spatial extent, magnitude, and return interval and placed along the disturbance classification gradient into one of three broad categories: Gap-scale disturbances, intermediate-severity disturbances, or catastrophic disturbances [6]. Gap-scale disturbances are caused by the removal of a single canopy tree, a small cluster of trees, or even a large branch from a canopy dominant individual. These disturbances modify microscale biophysical conditions and occur frequently in stands [7–9]. Catastrophic disturbances result from the removal of most all overstory vegetation, serve to regenerate stands, and occur relatively infrequently [10–12]. Between these two endpoints of the disturbance classification gradient exist events classed as intermediate severity.

The scientific understanding of natural gap-scale and catastrophic forest disturbances exceeds that of intermediate-severity events [13–15]. Although many studies have been conducted to document the impacts of intermediate-severity disturbances in forest ecosystems, few have explicitly defined the canopy disturbance events analyzed along the disturbance classification gradient or placed the

studies in the context of intermediate-severity disturbance in general. These studies have made important contributions to their respective subfields, such as fire disturbance or wind disturbance, but a synthesis of intermediate-severity disturbance events is lacking. A confounding factor is that canopy disturbance severity can be measured from a wide range of ecosystem response variables and this complicates making broad generalizations of intermediate-severity disturbances that result from diverse disturbance agents [16]. However, the most basic response variable in forest ecosystems is basal area removed (i.e., tree mortality) [5,17]. By focusing on basal area as the criterion for disturbance severity classification, disturbance severity and disturbance scale (i.e., spatial extent) are directly proportional. A forest disturbance event that removes one canopy tree or a small cluster of individuals would represent a relatively small reduction in basal area, and be small in spatial extent. Conversely, a forest disturbance that removes most all overstory trees in a stand would represent a significant reduction in basal area, and would also occur over a greater extent of the stand. Tree mortality is the common thread in all intermediate-severity disturbance studies, and by restricting our focus to tree mortality, we can make broader generalizations about intermediate-severity disturbance patterns and processes. Our goal is to synthesize information from the disturbance ecology literature to advance our understanding of intermediate-severity disturbance as a category of disturbance. Intermediate-severity disturbances may produce a wide range of residual stand structures, create multi-aged stands, alter successional pathways, and have long lasting legacies. We speculate that intermediate-severity forest disturbances are more common and play more important roles in shaping forest ecosystems than is often recognized. We hope our review of intermediate-severity disturbances will result in a greater understanding of these events, which will ultimately aid forest management planning.

2. What Are Intermediate-Severity Disturbances?

A central, but as of yet unanswered, question is at what point does a canopy disturbance event cross the threshold from gap scale to intermediate severity or likewise, from intermediate severity to catastrophic [18]. In theory, all forest disturbances that exceed the definition of a canopy gap, but are not stand replacing (i.e., catastrophic) would be considered intermediate-severity events [19]. The endpoints on the disturbance classification gradient represent a large range as canopy gaps usually involve the death of only one or a small group of trees and catastrophic events involve the removal of most all overstory stems [6,8]. Thus, the majority of the disturbance classification gradient would actually be within the intermediate-severity disturbance category (Figure 1).

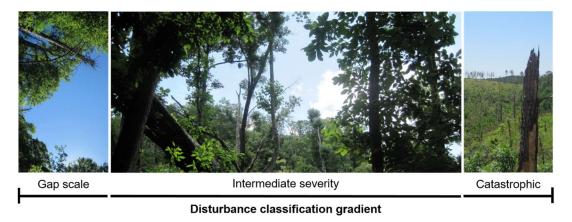


Figure 1. Forest disturbance classification gradient based on spatial extent, magnitude, and frequency of discrete disturbance events (adapted from Hart [9]). Basal area removed increases from left to right.

2.1. Gap to Intermediate Disturbances

Although it is straightforward to assume the void created by the death of a single canopy tree would be classified as gap-scale disturbance, this classification becomes less clear as the

number of canopy trees removed increases. The most common approach has been to set upper size limits for the classification of canopy gaps to separate gaps from intermediate-severity events. For example, Schliemann and Bockheim [20] suggested that maximum gap size should be 1000 m². Similarly, Yamamoto [8] stated that canopy gaps were typically less than 1000 m² in extent. However, some researchers have categorized disturbances beyond 1000 m² as gap-scale events (e.g., References [21–24]). In contrast, many studies have reported maximum gap sizes of less than 500 m² (e.g., References [25–29]). Because of variability in forest structure and species composition, we propose that it is best to use a metric that includes height of surrounding vegetation rather than a static size threshold to delineate gap-scale from intermediate-severity disturbances. Although it would be simple to state that all events larger than a pre-determined threshold would be too large to be classed as canopy gaps, disturbance extent should be scaled in relation to the size of the organisms that dominate the ecosystem (i.e., the trees). We propose that gaps are context specific and upper size thresholds vary by stand characteristics, primarily by tree density and tree height.

The diameter of the gap (often an average of the length, which is the longest distance from gap edge to gap edge, and the width, which is the longest distance perpendicular to the length) in relation to the mean height of canopy trees surrounding the gap (D:H), has been reported by some authors; and we contend this is the best criterion to classify canopy disturbances that fall near the gap scale-intermediate severity boundary. At present, there is no universally accepted D:H threshold to separate gap-scale from intermediate-severity canopy disturbance events. Reported D:H ratios vary by forest type. For example, Richards and Hart [30] reported mean D:H of 0.5 in mixed Quercus stands in the southeastern USA. Similar D:H values were reported by Kneeshaw and Bergeron [31] in boreal stands in Quebec, Canada and by Spies et al. [32] in Pseudotsuga menziesii (Mirb.) Franco-Tsuga heterophylla (Raf.) Sarg. stands in Oregon and Washington, USA. Runkle [7], a pioneer of canopy gap research in temperate forests, stated that D:H values of canopy gaps in temperate hardwood stands were typically <1.0. We suggest that D:H values are needed from more forest types before a universal D:H value to delineate gap-scale from intermediate-severity disturbance can be established. Nonetheless, we suggest that D:H of 2.0 serve as a starting point and stress that this value may be adjusted based on forest type and the range of values reported from canopy disturbances [33,34]. This value corresponds to the threshold between medium and large gaps proposed by Zhu et al. [18]. Zhu et al. [18] analyzed the impact of canopy trees surrounding gaps on growth of shade intolerant tree species within gaps. Specifically, they analyzed shadow length of gap perimeter trees at local noon during the growing season and photosynthetically active radiation in the gap and proposed that a D:H of 2.0 separate medium from large canopy gaps.

It is imperative to note that gap size or even D:H of canopy disturbances cannot be used alone to classify a forest disturbance event. Discrete disturbance events are classified in the context of the forest stand. Therefore, a high frequency of relatively small canopy gaps may actually constitute an intermediate-severity disturbance, if gap creation exceeds the background gap formation rate. For example, in mixed hardwood stands of the eastern USA, the canopy gap formation rate is typically 0.5%–2.0% per year [7,22]. Thus, the average time between natural canopy disturbances for a given location within a stand is 50–200 years [7]. The creation of even small canopy gaps above the background formation rate would, at the stand scale, be an intermediate-severity disturbance event.

2.2. Intermediate to Catastrophic Disturbances

Literature concerning the threshold separating intermediate-severity and catastrophic disturbances is not as well developed as that for upper limits of canopy gap size. By definition, catastrophic disturbances remove most all overstory vegetation. At what point is residual tree density or residual basal area high enough that the event is not catastrophic, but actually intermediate in severity? We suggest this threshold should correspond to the point when residual trees have an impact on biophysical conditions such that regeneration patterns are altered from what would occur following the removal of the entire overstory. After a catastrophic disturbance, light intensity, surface

temperature, evaporation rates, and light quality increase. As the number of residual trees or amount of residual basal area (corresponding to residual overstory) increases, the change in light intensity, evapotranspiration rates, and diurnal temperature variation is lessened [34]. Our proposed criterion is consistent with the seed tree regeneration method. The seed tree method is an even aged regeneration method that removes most mature trees in one entry, similar to a clearcut. The difference is that some residual, mature trees are left singly or in groups throughout the harvested area to supply seed for natural regeneration, but the residual cover of seed trees does not modify the physical environment more than what would have been created by a clearcut [35]. When residual trees are sufficient in density or basal area to impact conditions in the regeneration layer, the entry would not be categorized as a seed tree, but rather as a shelterwood. The number and spatial configuration of the seed trees varies by forest type and site conditions. However, most seed tree cutting retains 5–30 mature trees ha⁻¹ [34]. In western North America, as few as 7 seed trees ha⁻¹ are often retained for *Larix occidentalis* Nutt. and as many as 20 for Pseudotsuga menziesii [36,37]. In Pinus echinata Mill. stands in the southeastern USA, as many as 124 seeds trees ha⁻¹ may be retained when diameter at breast height averages ca. 25 cm (ca. 6 m^2 basal area ha^{-1}) and in *Pinus taeda* L. and *Pinus elliottii* Engelm. stands ca. 74 seed trees may be retained [38]. We propose this silvicultural distinction, which is based on the regeneration requirements of desired species, is also appropriate for the classification of natural canopy disturbances, because it is based on the influence of tree mortality on successional and developmental pathways.

Therefore, we propose that the boundary between gap-scale and intermediate-severity disturbances be canopy openings with a D:H of >2.0 and at the stand scale to be less than the background mortality rate. We note that light is not the only factor that influences gap dynamics [39–41], but D:H is appropriate for other noted factors of gap-scale processes. D:H is increasingly used to guide silvicultural systems to achieve desired stand conditions [34,42]. Therefore, using canopy opening D:H may help unify disturbance categorization with silviculture terminology and practice. We propose that the boundary between intermediate-severity and catastrophic events be set to the point at which residual stems influence regeneration patterns. This criterion is also consistent with silvicultural classification. We propose these as starting points and hope that our suggestions will be modified as more quantitative data become available.

3. What Causes Intermediate-Severity Disturbances?

Intermediate-severity disturbances are caused by a range of biotic and abiotic disturbance agents (Table 1). We acknowledge that a relatively large body of literature exists for most specific agents. However, we suspect that most in the disturbance ecology community are well versed in the literature related to the disturbance agents they study, but may be relatively unaware of other agents that also result in intermediate-severity disturbances. Our goal is to highlight some of these disturbance agents, and provide a framework to synthesize information from different disturbance processes to advance our understanding of intermediate-severity events. Natural biotic disturbance agents that may result in intermediate-severity disturbances include insect outbreaks and pathogens [43]. Castanea dentata (Marshall) Borkh. was abundant throughout the eastern USA in the early 1900s. The species was a common canopy tree, and in some stands represented over 40% of the basal area [44]. By the mid-1900s, the species was functionally extinct, because of the introduction and spread of Cryphonectria parasitica (Murrill) Barr [45]. The loss of C. dentata in a short period from stands where it was dominant resulted in an intermediate-severity disturbance event and is evident today in species composition and stand and age structure of stands where the species once occurred [46,47]. A similar story is currently unfolding with Tsuga Canadensis (L.) Carrière. This species once spanned from southern Quebec and Ontario, Canada southward along the Appalachian Highlands into Georgia and Alabama, USA. The species was dominant especially in riparian zones and protected coves and could form almost pure stands. Tsuga canadesis is currently facing an extinction threat by Adelges tsugae Annand. The species has already been lost from stands throughout the core of its range and the level of mortality in many of these stands constitutes intermediate-severity disturbance. Periodic Dendroctonus ponderosae

Hopkins outbreaks have maintained stand structural complexity in *Pinus contorta* Douglas ex Loudon stands [48,49]. Other examples of pathogen and pest-induced intermediate-severity disturbances include *Ceratocystis platani* Engelbrecht & Harrington [50], *Choristoneura freemani* Razowski [51], *Agrilus planipennis* Fairmaire [52,53], and *Cryptococcus fagisuga* Lindinger-*Nectria coccinea* var. *faginata* M.L. Lohman, A.M.J. Watson & Ayers [54].

Table 1. Examples of studies that have investigated intermediate-severity forest disturbances from a variety of disturbance agents.

Disturbance Agent	Location	Forest Type	Citation
Drought	Arizona, USA	Pinus edulis EngelmJuniperus monosperma (Engelm.) Sarg.	Mueller et al., 2005 [55]
Drought	North Carolina, USA	Mixed Quercus	Elliot and Swank 1994 [56]
Flood	Illinois, USA	Mixed Quercus	Cosgriff et al., 2007 [57]
Flood	Tochigi, Japan	Quercus mongolica Fisch. ex Ledeb.	Sakai et al., 1999 [58]
Ice storm	Connecticut, USA	Quercus rubra L.	Covey et al., 2015 [59]
Ice storm	Missouri, USA	Quercus alba LQuercus rubra	Rebertus et al., 1997 [60]
Ice storm	Ohio, USA	Mixed Quercus-Carya	Turcotte et al., 2012 [61]
Ice storm	Virginia, USA	Quercus prinus L.	Lafon 2006 [62]
Ice storm	Virginia, USA	Mixed Quercus	Whitney and Johnson 1984 [63]
Insect outbreak	Alberta, Canada	Pinus contorta	McIntosh and Macdonald 2013 [64]
Insect outbreak	British Columbia, Canada	Pinus contorta	Axelson et al., 2010 [48]
Insect outbreak	Pennsylvania, USA	Mixed Quercus	Fajvan and Wood 1996 [65]
Insect outbreak	Wyoming, USA	Pinus contorta	Kayes and Tinker 2012 [66]
Landslide	Miyagi, Japan	Fagus crenata Blume	Seiwa et al., 2013 [67]
Landslide	Oregon, USA	Psuedotsuga menziesii	Miles and Swanson 1986 [68]
Mixed-severity fire	Arizona, USA	Mixed Picea-Abies	Fulè et al., 2013 [69]
Mixed-severity fire	California, USA	Psuedotsuga menziesii	Taylor and Skinner 1998 [70]
Mixed-severity fire	South Dakota, USA	Pinus ponderosa Lawson & C. Lawson	Lentile et al., 2005 [71]
Pathogen	Hawaii, USA	Metrosideros polymorpha Gaudich.	Mortenson et al., 2016 [72]
Pathogen	North Carolina, USA	Mixed Quercus	Keever 1953 [44]
Wind event	Alabama, USA	Mixed Quercus	Cox et al., 2016 [73]
Wind event	Illinois, USA	Mixed Quercus	Holzmueller et al., 2012 [74]
Wind event	Jeju-do, South Korea	Quercus mongolica	Altman et al., 2013 [75]
Wind event	Oklahoma, USA	Quercus marilandica MünchhQuercus stellata Wangenh.	Myster and Malahy 2010 [76]
Wind event	Slovenia	Fagus sylvatica LAbies alba Mill.	Nagel and Diaci 2006 [77]
Wind event	Wisconsin, USA	Acer-Tsuga-Betula	Hanson and Lorimer 2007 [14]

Natural abiotic disturbance agents that cause intermediate-severity disturbance include low intensity tornadoes, floods, ice storms, mixed-severity fires, and landslides. Low intensity tornadoes and other strong wind events, such as derechos, often remove canopy trees [73,78] and result in intermediate levels of damage [14,15,19,79-81]. Flooding may result in intermediate-severity disturbances [57,58] as species that occupy floodplains vary in their tolerance of submersion, and prolonged inundation may result in mortality of the relatively more flood sensitive species [82]. Ice or glaze storms may also result in intermediate-severity disturbance [60,62,63]. Ice loading often removes canopy trees and patterns of mortality may be caused by topographic factors or species-specific characteristics [83]. A wide range of structures may result from mixed-severity fires (more importantly from the mixed-severity fire regime). Individual mixed-severity fires typically include patches that sustained high, moderate, and low severity fire, as well as patches that went unburned [84]. This pattern of mortality across the landscape may foster the development of biologically diverse communities and complex stand and age structures [48,85,86]. Landslides, which are common in some regions, can also result in intermediate-severity disturbance [68,87]. For example, the remnants of Hurricane Camille in 1969 triggered 5377 documented landslides (mainly in the form of debris flows) in the Appalachian Highlands of Virginia and West Virginia [88].

In some cases, intermediate-severity disturbances may interact with subsequent disturbances to produce compound effects that delay or alter forest recovery trajectories [89]. In a Rocky Mountain *Pseudotsuga menziesii* forest, in Wyoming, USA, Harvey et al. [90] attributed reduced post-fire regeneration density to a *Dendroctonus pseudotsugae* outbreak, 4–13 years before the fire. By preferentially killing mature, cone-producing trees throughout the forest, the intermediate-severity *D. pseudotsugae* outbreak reduced the available seed source for post-fire regeneration, thereby negatively

impacting forest resilience. In a *Pinus contorta* forest in central Oregon, USA, intermediate-severity *Arceuthobium americanum* Nutt. ex Engelm. infection was associated with delayed forest development 21–28 years after a *Dendroctonus ponderosae* outbreak [91]. Although pre-outbreak *A. americanum* severity was not quantified, it is likely that by killing canopy trees, the *D. ponderosae* outbreak facilitated the spread of *A. americanum*, which restricted residual trees from recruiting to higher forest strata. Thus, multiple interacting disturbances may impact forest succession and development in ways that are distinct from isolated disturbance events, and it is important to consider the impacts of intermediate-severity disturbances in the context of other disturbances.

Spatial patterns of mortality and residual trees of intermediate-severity disturbances can typically be classified as uniform, patch, or linear [6,92] (Figure 2). Derechos and ice storms may remove the largest and most dominant canopy trees throughout a stand resulting in a uniform pattern [83,93]. Species-specific mortality agents could result in uniform or patch patterns depending on the spatial distribution of the susceptible species. Tornadoes and floods often result in linear patterns of mortality through a stand corresponding to the storm track or the stream corridor [45]. These events may result in complete mortality of overstory individuals so that they are catastrophic at local scales, but intermediate in severity at the stand scale. The spatial patterns of residual trees may influence the developmental and successional pathways following intermediate-severity disturbance [92].

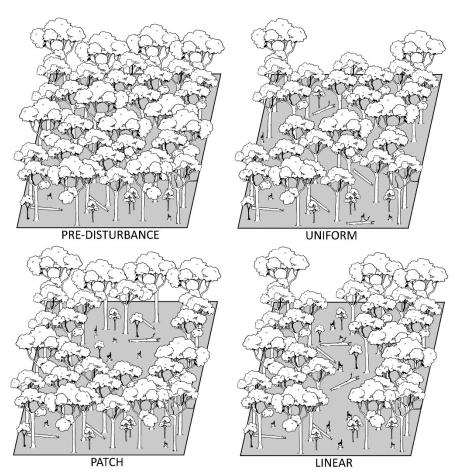


Figure 2. Spatial patterns of mortality and residual trees after intermediate-severity disturbance. The pre-disturbance condition represents a mature, deciduous broadleaf dominated stand prior to intermediate-severity disturbance. In the uniform pattern, canopy trees were removed relatively evenly throughout. The patch pattern shows clustered mortality and the linear pattern shows stems removed in a strip. In each disturbance pattern depicted, seven canopy trees (ca. 25% reduction in canopy tree density from the pre-disturbance depiction) were removed.

4. How Frequent Are Intermediate-Severity Disturbances?

An important component of the forest disturbance regime is the return interval of disturbances by severity. Quantification of the disturbance regime is often based on retrospective investigations. A common method to reconstruct and classify forest disturbance regimes is through the use of tree-ring analysis. Disturbance history reconstructions using tree-ring records and forest inventory data (especially tree age data) have been conducted in stands across a wide range of forest types. Although variability exists by forest type and region, studies generally show that stands are impacted by (i.e., have a history of) intermediate-severity disturbances at intervals shorter than the lifespans of dominant species. In fact, in many forest types, more than one intermediate-severity disturbance is likely to occur during the lifespan of the dominant trees. In Quercus stands of the eastern USA for example, the return interval of intermediate-severity disturbance events based on tree-ring records has been found to range from 20–50 years [94–100]. An intermediate-severity disturbance return interval of ca. 50 years was reported from a 100 ha plot in a *Picea abies* stand in Slovakia [101] and ca. 65 years from a 20 ha plot in a *P. abies* stand in the Czech Republic [102]. Intermediate-severity disturbance return intervals of 20-30 years [103], 20-80 years [104], and 40 years [105] have been reported for Fagus sylvatica dominated stands in Austria, Slovenia, and the Czech Republic, respectively. In a Pinus strobus L.-Tsuga canadensis stand in Massachusetts, USA, an intermediate-severity disturbance return interval of ca. 40 years was reported by Abrams et al. [106]. Axelson et al. [107] found the mean return interval of Dendroctonus ponderosae outbreaks to be 36 years across three Pinus contorta stands in British Columbia, Canada. Similarly, Fraver et al. [108] and Boulanger et al. [109] reported return intervals of Choristoneura fumiferana Clemens outbreaks to be 67 years in Maine, USA and ca. 40 years in Quebec, Canada, respectively. In seasonal dry evergreen stands in Thailand, Baker et al. [110] documented return intervals of intermediate-severity disturbance of 20-60 years.

These tree-ring based disturbance history reconstructions and plot data demonstrate that intermediate-severity disturbances are relatively common. Based on the return intervals that have been reported from these retrospective studies, most forest stands will experience at least one intermediate-severity disturbance between stand initiation and a catastrophic disturbance event. Indeed, it might be that most stands will actually experience two or more such events. We hypothesize that intermediate-severity forest disturbance events are more common than is often recognized, and their influence as a driver of species composition, stand structure, and ecosystem function is underappreciated.

5. How May These Events Influence Our Management?

Forest managers are increasingly tasked with developing plans to increase native forest diversity, enhance structural complexity, and promote ecosystem resilience [111]. Silvicultural systems that are patterned after natural disturbance process may be utilized to achieve these goals [112,113]. A deeper appreciation and understanding of intermediate-severity disturbances and the impacts these events have on species composition and stand structure, should aid in development of natural disturbance-based silvicultural systems. Increasingly, forest ecosystems are undergoing changes in species composition, structure, and function as a result of climate change, disturbance regime alteration, nitrogen deposition, fragmentation, invasive species, and other anthropogenic pressures, as well as the interactions of these factors [114–116]. Accordingly, ecological resilience has become a major focus of forest management, science, and policy [117-119]. A mechanistic understanding of intermediate-severity disturbances as drivers of forest ecosystem change is essential for the development of systems that are patterned after natural disturbance processes to meet management goals. For example, we may develop a silvicultural entry that approximates the spatial extent and spatial configuration of a natural intermediate-severity disturbance event. In the silvicultural system, time between entries may be based on the return interval of intermediate-severity disturbances in that forest type and region. Intermediate-severity disturbances result in a wide range of stand structures

and alter developmental pathways [15,92,120,121], and thus, provide wide flexibility to forest managers for incorporation into management plans.

Intermediate-severity disturbances typically increase stand-level structural complexity through coarse woody debris inputs, creation of canopy voids, alteration of the seedbed, and changes in the light regime [14,15,73,80,121,122]. Importantly, intermediate-severity disturbances often result in multi-aged stands [123]. O'Hara and Ramage [124] argued that multiple age classes in a stand provide different levels of adaptations to stresses that enhances resiliency in multi-aged stands. Multi-aged silvicultural systems, including those patterned after natural intermediate-severity disturbance, should be part of our efforts to increase resistance and resilience in forest ecosystems to future, including novel, stressors [123,125].

Silvicultural systems that approximate the impacts of natural intermediate-severity disturbance are being used in some forest types. For example, in the northeastern USA, irregular shelterwoods have been implemented to increase structural heterogeneity [126], such as may be caused by infrequent windstorms in the region [127]. One variant of the irregular shelterwood system is the irregular group shelterwood with reserves. This system uses shelterwood regeneration in patches within the stand, rather than uniformly, and retains reserve trees in the openings after they are regenerated [126]. In these systems, structure varies spatially through the treated stands. In the Pacific Northwest region of North America, retention systems that maintain sufficient canopy coverage to have forest or residual tree influences over the majority of the harvested area, and retain live and dead trees of varying sizes and canopy classes are becoming increasingly popular [128–130]. Both group and dispersed retention may be analogous to the impacts of natural intermediate-severity disturbances.

We understand that silvicultural systems that mimic the effects of intermediate-severity disturbance are not a panacea and not appropriate in all forest management scenarios. However, we encourage forest managers to consider intermediate-severity disturbances in their management plans and long-range forecasts. For most forest types and in most regions, intermediate-severity disturbances will occur in the life of a stand. These events should be anticipated so that the response can be more organized, more efficient, and less reactive [131]. Such anticipation will become increasingly important as disturbance regimes shift in accord with changing climates and other anthropogenic forces. Some decisions, such as salvage harvesting, must often be made quickly after intermediate-severity disturbance and anticipating these events would greatly aid the ability of managers to make sound decisions for the long-term sustainability of impacted forest ecosystems.

6. Conclusions

Intermediate-severity disturbances are those that are greater in extent than gap-scale disturbances and more localized than stand replacing events. Therefore, intermediate-severity disturbances represent disproportionate space along the disturbance classification gradient. We contend the best approach to delineate gap-scale from intermediate-severity events is to use the canopy opening D:H, and we recommend a D:H of 2.0 as a starting point for this threshold, while acknowledging this value may be adjusted by forest type and as new information becomes available. We recommend that the division between intermediate-severity events and catastrophic events, should be the point when residual tree density or basal area influences the regeneration layer by altering abiotic site conditions differently from what would occur after complete, or near complete, overstory removal. A variety of agents may result in intermediate disturbance and importantly, interactions of different disturbance agents (e.g., insect outbreaks and fire) may result in intermediate levels of forest disturbance [107]. The return intervals of intermediate-severity disturbance vary by forest type and region, but disturbance history reconstructions demonstrate that these events occur at intervals of 20 to 80 years [104,110]. Therefore, we suggest that most stands will experience an intermediate-severity event between stand initiation and a stand replacing disturbance. We speculate that intermediate-severity disturbances are more common and more important drivers of forest ecosystem change than is typically recognized and we call for more research into intermediate-severity

disturbance, especially with regard to the impacts of these events on successional and developmental pathways [92]. Intermediate-severity disturbance patterns may be incorporated into silvicultural systems, and this may become more important as management goals increasingly include promotion of intra-stand heterogeneity [111,129].

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