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Challenges for Uneven-Aged Silviculture in Restoration of Post-Disturbance Forests in Central Europe: A Synthesis

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Abstract: Forest managers are often required to restore forest stands following natural disturbances, a situation that may become more common and more challenging under global change. In parts of Central Europe, particularly in mountain regions dominated by mixed temperate forests, the use of relatively low intensity, uneven-aged silviculture is a common management approach. Because this type of management is based on mimicking less intense disturbances, the restoration of more severe disturbance patches within forested landscapes has received little attention. The goal of this paper is to synthesize research on the restoration of forests damaged by disturbances in temperate forests of Slovenia and neighbouring regions of Central Europe, where uneven-aged silviculture is practiced. Research indicates that active management aimed at favouring mixed uneven-aged forest reduces the risk of disturbance and improves the resilience of stands. Salvage logging may have positive or negative effects on regeneration, much of which is due to the method applied and the quality of work. The most prominent factors that negatively affect restoration are: lack of advanced regeneration and decomposed woody debris, high altitude, steep slopes, dense ground vegetation, and overbrowsing. Planting or sowing should be applied in post-disturbance forests where many negative factors interact and where a high demand for sustainability of forest ecosystem services is present.

Keywords: natural disturbance; advanced regeneration; planting; natural regeneration; uneven-aged silviculture

1. Introduction

The resistance and resilience of forest stands to disturbance are strongly influenced by forest management and the type of silvicultural system used. For example, forest stands managed with uneven-aged silviculture generally create stands with small-scale heterogeneous structure and are thought to be both resistant [1–3] and resilient to disturbance [4–6]. In the context of this paper, the term uneven-aged silviculture refers to a range of silvicultural systems that include single and group selection, irregular shelterwood, and freestyle systems [7–9]. In continental Europe, this type of management, based on a liberal selection of felling regimes within the context of the aforementioned systems, is often called close-to-nature silviculture [9,10]. It has traditionally been used in many alpine countries, particularly in Switzerland, Slovenia, Italy, Austria, and parts of Germany [11–13], and more recently its use has become more widespread [14].

Uneven-aged silviculture employs relatively low intensity and small-scale felling regimes in order to mimic natural forest composition, structures, and processes [10,15]. Given that this type of management mainly mimics natural disturbances on the lower end of the disturbance severity gradient at stand scales (i.e., small tree fall gaps up to moderate severity disturbance events that might remove ca. 30% of the canopy over several hectares), it is not specifically focused on the full range of historic disturbance variability that is present in Central and Southeast Europe, including rare events that damage much larger scales [16]. Traditionally, an important foundation for uneven-aged silviculture was the study of phytosociology and potential natural vegetation (PNV), which describes the expected state of late successional vegetation that would be expected on a given site without human intervention or severe disturbances. PNV served as a guiding principle in setting silvicultural goals, although the concept has received criticism due to the ubiquitous anthropogenic influence on forests in Europe [17]. As the spatiotemporal dynamics of vegetation have become better understood [18], the concept of static PNV has become less useful [19], especially from the perspective of post-disturbance forest restoration. Namely, the interaction of disturbances and environmental change can lead to multiple alternative or novel successional pathways [20,21].

There are several advantages of uneven-aged silviculture in the context of post-disturbance forest restoration. This type of silviculture was developed in several alpine countries as a response to the failure of clear-cut forestry to cultivate ecosystems that are resistant to natural disturbances and soil erosion [22]. Mixed stands are encouraged, which results in a good seed supply of a variety of species [23]. Systematic favouring of scattered broadleaves, which are often of intermediate shade-tolerance, helps ensure the survival of species that are vital for post-disturbance restoration [24]. Facilitating advanced regeneration and intermediate shade-tolerant trees helps maintain a well stocked understory of different species and genotypes. This enables a quick start for restoration after disturbance and delays the development of ground vegetation. Individual trees in uneven-aged forests have a lower height to diameter ratio compared to even-aged forests, since they are released early in the development cycle [2]. This may protect the newly formed forest edge and individual non-damaged trees against future disturbance. There are also several disadvantages of uneven-aged forestry, including the reliance on shade tolerant species (i.e., beech (*Fagus sylvatica* L.), fir (*Abies alba Mill.*)), which can be hampered by the climatic conditions of open areas created by disturbances [25]. Moreover, until recently there was relatively little experience in the planting of large post-disturbance areas [26]. In many countries practicing uneven-aged silviculture, yearly planting areas are small, resulting in poorly developed systems of artificial restocking, with limited capacity for planting and maintaining plantations.

During the past few decades, a number of large and severe disturbances have occurred in Central and Southeast Europe [27,28]. For example, in the period 1995–2012, sanitary felling constituted thirty percent of the harvest in Slovenia; insects and wind affected larger diameter trees, while snow and ice damaged stands with smaller diameter trees [29]. In early 2014, Slovenia was hit by an ice storm unprecedented in modern history [16]. It damaged about 9,300,000 m^3 of trees (about 110% of the annual increment) across more than 600,000 ha (51%) of Slovenian forests. The storm was followed by a bark beetle outbreak in the succeeding two years, claiming another half of the annual increment. Recent large-scale natural disturbances have been reported for Italy, Germany, Switzerland, the Czech Republic, and Slovakia [30–34]. These disturbances triggered a series of studies that provide guidelines for post-disturbance restoration in temperate uneven-aged forest landscapes [35–38]. While disturbance is reported to benefit early successional flora and fauna [39,40], it may retard the fulfilment of some ecosystem services, especially forest protection functions [41]. It can represent a serious financial burden for the forest owner due to the decrease in the value of damaged wood, high sanitary harvesting costs, delayed regeneration and thus an extended production period and the possible risk of losing the desired mixture of commercially important species [26,42].

Natural disturbances over the last three decades have not only damaged man-made conifer plantations, but also many forests in conversion and natural forests managed with uneven-aged silviculture. In addition to climate change, introduced pests and invasive species also represent a major challenge for uneven-aged silviculture [43]. Indeed, large areas without canopy cover following more severe disturbances may facilitate the spread of introduced species, particularly shade intolerant invasive tree species. Taken together, ongoing global change drivers present new obstacles for uneven-aged silviculture in Central and Southeast Europe [9,14,44,45].

The goal of this study is to synthesize studies on forest restoration in Slovenia and neighbouring countries with similar silviculture after various natural disturbances. We first discuss natural regeneration processes in forest reserves and natural forests. Such areas are typically excluded from post-disturbance intervention [46], although in some places salvage logging was carried out due to the risk of bark-beetle damage [30,36]. Nevertheless, they can inform us about natural processes as well as the possibilities and consequences of non-intervention in managed forests [47]. We then discuss the most important drivers of post-disturbance regeneration, which are important for silvicultural decisions about applying natural or artificial regeneration in affected areas. In the conclusions section, we provide guidelines for restoration silviculture in uneven-aged forest landscapes, indicate open research questions, and discuss future challenges for uneven-aged silviculture amid environmental changes.

2. Post-Disturbance Natural Regeneration in Unmanaged Forests

A number of studies have examined natural regeneration processes in the study region, particularly in old-growth forest reserves where management is not permitted. These reserves allow a unique glimpse into the process of natural regeneration in the absence of forest management practices, such as salvage logging or post-disturbance planting. Most of the forest reserves are located in less accessible mountain regions, where beech or mixed beech-fir forests are the dominant forest types. Like other mesic-temperate forests worldwide, gap-scale disturbances are the primary driver of forest dynamics in the absence of more severe perturbations in these forest types. Consequently, most studies on natural regeneration have focused on the filling of tree fall gaps (i.e., holes in the forest canopy that generally range in size from 10 to 1000 m^2). These studies clearly demonstrate that a bank of advanced regeneration of shade tolerant species, particularly beech and fir, is a common feature of such forests, and that gaps are often filled by individuals already present as advanced regeneration prior to mortality of canopy trees [48–52].

Even after more severe disturbances, such as intermediate severity events that create partial canopy damage (e.g., removal of 10–30% of the canopy in a given stand), the bank of advanced shade tolerant regeneration accelerates succession towards the dominance of these species in the canopy layer [49,53]. Less shade tolerant species that coexist in these forest types, such as *Acer* spp., *Fraxinus* spp., and *Ulmus* spp., tend to recruit in situations where relatively large gaps (e.g., >400 m^2) are formed in areas where advanced regeneration of shade tolerant species is largely absent or less developed [48,53,54].

We know less about natural regeneration following large and severe disturbances in the study region. In some forest ecosystems, such as those prone to severe fires in western North America, there is growing concern that the combination of large-severe disturbances and post-disturbance regeneration exposed to heat and drought may erode the resilience of forests and possibly lead to strong shifts in vegetation structure and composition, such as conversion of forests to grass/shrub systems in extreme cases [55–57]. Under current global warming scenarios, those concerns are likely relevant for any forest system, yet large and severe disturbances are exceptionally rare in the mesic-temperate forests of Slovenia and the surrounding region. Coupled with the scarcity of large areas of unmanaged forests in the region, this limits our ability to understand forest recovery following large and severe disturbances.

3. Drivers of Post-Disturbance Regeneration Dynamics

3.1. Stand Structure

Similar to old-growth forests [58,59], initial forest structure in managed forests significantly influences the resistance of the forest ecosystem to disturbance impact as well as its post-disturbance recovery [38,60–63]. Results from many studies in Europe indicate that mixed uneven-aged forests are more resistant to disturbance and may sooner return to their original state than monospecific even-aged forests [1,61,64–66]. There are several tree and stand characteristics in a structurally complex arrangement that improve their resistance to disturbance in comparison with even-aged forests. Individual trees are resistant due to several special features, including a low height/diameter ratio, and distinct wood properties, tree architecture, and root patterns that result from gradual release and conditions created by uneven aged structures [2], potentially enhanced vitally as a consequence of slow growth and strong selection during the juvenile phase [67–69]. Uneven-aged stands are resistant due to the intrinsic heterogeneous environment which enables coexistence of different tree species and tree stages [6]. Further, roughness of the canopy layer may decrease the impact of wind, while young tree cohorts are protected against different abiotic disturbances by mature trees. Additionally, management intervals in uneven-aged forests are often short and focused on favouring vitality and species diversity [24], which provides for more resistant stands. However, some reviews indicate that there are many confounding factors and research results comparing even-aged and uneven-aged forests are inconsistent [70,71].

Following a disturbance in uneven-aged stands, much of the pre-disturbance compositional and structural diversity is typically left intact and these legacies improve forest recovery (Figure 1); for an overview see [6]. Similar post-disturbance patterns were documented in Slovenia [72–74]. However, the advantages of uneven-aged stands may hold within the certain thresholds imposed by the site and disturbance severity [2]. Furthermore, comparisons between uneven-aged and even-aged forest in Central Europe are difficult due to deficiency of younger stages of even-aged stands, thus more experimental research would be warranted.

Understory trees and advanced regeneration play a particularly important role in the re-vegetation of open areas (Table 1). However, there is a risk of damaging advanced regeneration during salvage operations [33], yet this is not always the case [75]. In many cases in uneven-aged forests, the density of advanced regeneration was not adequate to ensure successful stand recovery. Previous research indicates that on extreme microsites (e.g., sunny, exposed microsites) established regeneration may fail after exposure to open conditions [21,76], particularly if it is composed of shade-tolerant species (silver fir, beech).

Overall, regular uneven-aged management will help perpetuate well-structured and mixed forest stands and lessen the impact of disturbance and increase the ability of the forest to recover [24]. Regular silvicultural interventions (5–7 years) of moderate intensity (<100 $m^3 \cdot ha^{-1}$) decrease disturbance risk in uneven-aged stands [1]. However, it is important to consider that after logging risk of damage to a stand due to disturbance is increased. This is especially true for thinning, where risk of snow, ice, and storm damage is increased for a period of 3 to 5 years [77–79]. From this perspective, high thinning of even-aged post-disturbance stands (e.g., selection thinning following [80]) may lead to lower collective stability and thus higher risks. Therefore, it seems more appropriate to apply other types of thinning that have less influence on the collective stability of the stand, such as situation thinning [81,82] or group thinning [83]. Moreover, due to both geographical setting and meteorological conditions, disturbance often recurs in the same area [59,64,84,85]. Therefore, stands prone to recurrent natural disturbances should be given special consideration. In such circumstances, heavy uniform interventions over longer intervals and entire compartments would not be recommended. The preferred intervention may include frequent silvicultural interventions (<10 years) of moderate intensity (one or two closest competitors) [86,87], and only about 100 crop trees ha^{-1}, depending on the species, when thinning in more even-aged patches [81,82].

Pre-disturbance risk management may include the following treatments: regeneration fellings adapted to the ecology of tree species and the prevalent disturbance regime; favouring of rare, especially light demanding tree species, advanced regeneration, and subcanopy tree layer; accelerated conversion of high risk stands; increasing resistance of individual trees and stands to biotic and abiotic stress though selection of crop trees and density regulation [6,14,24,60].

Figure 1. Uneven-aged managed forest stand in the Dinaric region of Slovenia immediately after a severe storm in 2004 that removed most of the canopy layer. The well-developed understory layer was largely undamaged, and serves an important role in forest recovery.

3.2. Salvage Logging

Salvage logging is a routine practice after natural disturbance in Slovenia and elsewhere in Central Europe. The potential negative effects of salvage logging on forest recovery, ecosystem function, and biodiversity have often been highlighted in the literature (e.g., [88–90]). In terms of tree regeneration, the Central European literature often demonstrates a negative influence of salvage logging on forest recovery following large-scale high severity disturbance in spruce (*Picea abies* (L.) H. Karst.)-dominated forests [32,33,39,91] (Table 1). In other forest types in the region, it is less clear whether salvage logging hinders natural regeneration, particularly in broadleaf forests damaged by moderate severity disturbance [92]. Because these forests often have a well-developed bank of advanced regeneration, salvage machinery and removal of logs would be expected to damage this regeneration layer and hinder forest recovery. Other negative effects, such as soil compaction or erosion and loss of litter, could also hinder the establishment of new regeneration. On the other hand, salvage logging may provide a favourable seedbed for germination and suppress competing ground vegetation [26,37,38,93]. It is also important to consider that the impact of salvage logging depends on the type of harvesting and skidding (i.e., cable crane or tractor) that is used during salvage operations, as well as the density of forest roads and the quality of work during the salvage [94]. In a comparative study in mountain forests in Slovenia, for example, tractor skidding caused substantially more damage to advanced regeneration compared to cable crane skidding [95]. Salvage logging did not significantly influence forest recovery following small-scale intermediate severity disturbances in beech dominated stands in Slovenia, but the majority of sites (five out of eight) were harvested with a cable crane [92]. Similarly, salvage logging of windthrow gaps in Swiss forests (various mixtures of beech, fir, and spruce) had little influence on forest recovery 20 years post disturbances [75].

A number of factors likely come into play with regard to the influence of salvage logging on forest recovery in Central Europe, such as the type and intensity of salvage logging, availability of and distance to seed sources, ability of seedlings to regenerate on the forest floor (as opposed to nurse logs), the presence of an existing seedling-sapling bank, and site conditions (productivity) that modify the speed of the recovery. The case of salvage logging following ice and snow disturbances requires specific mention. Both of these disturbance agents are relatively common in the region; a common damage type following these events is bending of broadleaf trees, which often remain alive and resprout vigorously (Figure 2). In such cases, crop trees should be released from neighbouring damaged trees in spite of high costs. Finally, it is important to note that although salvage logging may not hinder the long-term recovery of some forest types, the routine practice of removing dead and damaged wood has important consequences for biodiversity dependent on such post-disturbance conditions [89,90].

Figure 2. Broadleaved pole stands damaged by wet snow in southeast Slovenia in October 2012. The figure depicts vigorous re-sprouting of bent beech poles in summer 2015, which will reduce the future commercial value of the stand.

3.3. Aspect, Slope Inclination, and Altitude

Aspect, slope inclination, and altitude are mutually related modifiers of primary ecological factors. With increasing altitude, the vegetation period shortens, climatic extremes increase, ecological differences among microsites become more pronounced, and growth and seed production decrease [96,97]. This delays post-disturbance forest regeneration [31,37]. Nonetheless, species whose natural habitat is located at higher altitudes may be favoured (e.g., spruce, larch). Recent studies in Slovenia, which covered a considerable altitudinal range, documented a negative relationship between post-disturbance regeneration success and altitude [76,92]. Tree species may have on average fewer competitors with increasing altitude, but regeneration development may be delayed due to lower tree species diversity, shorter vegetation period, adverse biotic and abiotic factors, and on sites with tall-herb vegetation [98].

With increasing altitude and slope inclination, differences in aspect become more ecologically important. Southern aspects are prone to organic matter accumulation and drying out, and they experience greater microclimatic variability [97,99]. Studies from Slovenia suggest that, on average, southerly exposed microsites delay tree regeneration [92,100], but this may change for cold-intolerant species (e.g., silver fir) and at higher altitudes [73]. Near the timberline southern aspects may possess better thermal conditions for growth, causing early snowmelt and thus lowering the risk of seedlings developing fungal diseases [96].

Besides its influence on aspect, slope inclination influences snow and water movement as well as erosion and may therefore negatively influence regeneration dynamics [96,101,102]. In such conditions, special microsites may prove favourable (e.g., vicinity of stumps, root plates, downed wood). Slope inclination accelerates erosion processes and surface water runoff, impedes seedling establishment, and exacerbates the microclimatic extremes on microsites [101,102]. Slope inclination was not a major influential factor in studies in Slovenia. It was positively associated with the density of light-demanding species [76] and negatively associated with the density of spruce [73], fir, and beech [103]. However, disturbed areas in Slovenia did not encompass extremely steep slopes.

3.4. Seed Trees and Proximity of Forest Edge

Microsites near the forest edge within disturbance-induced openings are characterized by a transitional microclimate between the forest interior and open areas and are also near seed sources, making them favourable for regeneration [35,101,104,105], (Table 1). This has been confirmed in several studies of post-disturbance regeneration in Slovenia [21,73,76,103,106]. In the context of species groups this was especially significant for anemochorous (non-pioneer) species, while pioneers were more successful further from the forest edge (e.g., at least one tree height). In a study by Rozman et al. [21], the density of zoochorous species was not related to distance to the forest edge. It seems from field observation that they were more related to the remnants of the pre-disturbance trees and shrubs, where seed dispersing birds and small mammals can rest (perches) and hide (cf. [107]). Removing tree residuals and shrubs (e.g., for easier planting) may have a negative effect on the encroachment of zoochorous species.

Table 1. Synthesis table showing the relationship between driving factors and post-disturbance regeneration success from published literature. The table covers mostly temperate European mountains, with a focus on beech, mixed mountain, and spruce forests, with some comparable studies from North and Eastern Europe. The most frequent species in the regeneration layer was spruce. Mixed denotes that a given factor was tested, but its effects were either non-consistent or non-significant.

Drivers of Post-Disturbance Regeneration Dynamics	Effect on Overall Regeneration Success (Density, Coverage, Mixture)		
Presence or increasing factor intensity	Positive	Mixed	Negative
Salvage logging	[26,37,38,93]	[31,75,92,108]	[32–34,36,39,63,109–111]
Pre-storm regeneration	[32,34,36,60,63,73,109,110]	[26,37] sparsely developed	
Nurse seedlings/growth in clusters	[63,112,113]	[111]	
Altitude		[75]	[26,31,37,76,92,113]
Slope inclination	[113]	[76]	[73,96,101–103]
Aspect—sun exposed sites	[73,113]		[21,37,76,100]
Rockiness	[113]		[21,73,103]
Acidic soil			[75,114]
Disturbed soil	[40,76,115,116]		[39,101]
Elevated microsites, mounds, stumps	[35,76,92,102,110,113,117–119]		[26,93]
Ground vegetation cover		[73,76] not negative on extreme sites	[21,39,40,75,105,110,113–115,119–121]
Shrub coverage	[73,92]		
Decayed logs as seedbed (spruce, fir) and shelter	[33–35,39,63,105,110,113,121]		[21,34,73,76,92,103,110] for poorly decomposed CWD in woodpiles
Snags	[32,36,39,63,120]		
Distance to forest edge for non-pioneer tree species: seed source, forest climate			[21,34,35,73,76,101,103,105,106,114,115]
Distance to seed trees			[21,60,76,115]
Browsing		[113,122,123]	[21,34,35,60,73,76,103,105,106,115,119,124]

3.5. Microsite Variability

After disturbances, the overall conditions for regeneration are demanding due to the vigorous successional development of competing ground vegetation and the extreme climatic conditions of open non-forested areas. Special microsites (e.g., pit and mound topography, exposed mineral soil) may slow down the development of ground vegetation or mitigate the ecological extremes of the non-forest climate. Thus, the importance of microsites for post-disturbance regeneration of weaker competitor species may be greater than that of regular regeneration fellings, where light incidence is controlled [40,108,119]. Any attempt to generalize should therefore carefully address these factors.

Microsite variability with pre- and post-disturbance features (micro-relief, treefall pits and mounds, disturbed soil, woody debris) in general may have different effects depending on the ecological setting (Table 1). While higher regeneration success on mounds would be expected on steep southern aspects, the same would not be the case on waterlogged soils. In average conditions regeneration is more successful on elevated positions (e.g., near stumps) and stabilized treefall mounds [117,118], although some researchers found higher small seedling densities in pits [26,93]. Higher regeneration densities are reported also for mineral soil and decomposed deadwood [31,35,102,116,125,126]. The advantage of these sites for regeneration is less competition from ground vegetation, less exposure to browsing, and special nutrient status on mineral soils exposed by upthrown root plates or salvage logging. However, pit-and-mound microsites may initially suffer from erosion (Figure 3), which may delay regeneration [26,30,127].

In studies carried out in Slovenia on post-disturbance regeneration, disturbed (by logging or treefall) and elevated microsites (near stumps) experienced lower initial ground vegetation coverage and were associated with higher regeneration densities [21,76]. Older observational studies also indicated better regeneration in sinkholes within flat meso-relief and micro-depressions within southern exposed slopes, but we found only indirect evidence for this in recent studies [21,76].

In Slovenia, forest sites on carbonate bedrock are widespread. In the event of natural disturbance, they are often subject to severe erosion. Most research indicated a negative association between rockiness and broad-leaved tree seedling abundance [21,73,103], which may be due to reductions in microsite availability or drought. This is often not the case for spruce and fir, which tend to be more successful on more rocky microsites in mixed forests, where they can avoid competition from ground vegetation and broadleaves [128,129].

Figure 3. Over the long term, treefall pit-and-mounds facilitate tree diversity through enhancing microsite topography and soil variability. However, for the first few years, regeneration may be delayed by erosion.

3.6. Ground Vegetation

Ground vegetation may have positive and negative effects on tree regeneration in open areas. Most studies have highlighted its negative role as a competitor for growing space and resources (Table 1; Figure 4). This was suggested from research on gaps in managed forests [130,131] and in large openings created by disturbance [21,35,40,75,105,110]. On the other hand, post-disturbance ground vegetation conserves nutrients on site by the intensive use of resources and exuberant growth [132,133], prevents erosion [134], and may facilitate tree regeneration by acting as nurse plants preventing seeds from getting washed away and providing less severe environmental conditions [135]. Most recent studies of post-disturbance regeneration in Slovenia have indicated a negative association between seedling density and ground vegetation [21,121], especially on sites with already established ground vegetation and pre-disturbance regeneration. On some extreme sites with poorly developed advanced regeneration, ground vegetation was not negatively related to seedling establishment [73,76]. It seems that in the initial years after disturbance, facilitation or neutrality are more important than competition cf. [136]. On extreme sites, otherwise competing species may temporarily function as nurse plants [130]. However, after establishment, further seedling development is hampered by dense ground vegetation cover.

Figure 4. Competing grass (*Avenella flexuosa* (L.) Drejer) inhibits the natural regeneration on a steep, southern slope of Črnivec nine years after windthrow (upper images). Thick ground vegetation at mid (lower left) and lower slope (lower right) positions with deep and moist soils also hinder natural regeneration.

3.7. Browsing

Research results regarding the effects of browsing on post-disturbance revegetation have been inconsistent. Some research indicates that deer tend to concentrate in stands damaged by natural disturbance due to increased food and shelter resources [137]. In open areas with abundant resources, younger and generally more palatable plants are abundant. Therefore, deer may substantially hinder the development of forest succession [35]. Other studies suggest that the faster growth of seedlings ("escape strategy" sensu [138]) within large clearings and the abundance of other food resources may positively influence forest succession, although this was not confirmed in an experimental study by [122] (Table 1). Research results from Slovenia are more closely aligned with findings pointing towards adverse influences. This may be the result of high overall game densities in Slovenia and particularly high densities in some research areas. For example, in the Kočevje region the current red deer density is approximately 13 deer·km^{-2} [139]. After a large-scale bark beetle outbreak in this area, broadleaves had a significantly greater density, coverage, and height within fences, while spruce displayed the same pattern in unfenced areas [21]. Moreover, in areas with lower deer densities, spruce was favoured by browsing [73,103,106], and dominant naturally regenerated and planted seedlings other than spruce had a significantly higher survival rate if unbrowsed [76]. In the original stands within the research areas, the proportion of spruce was well above natural conditions. Therefore, silvicultural objectives targeted a reduction in the proportion of spruce due to the increased susceptibility of modified stands to climate change and disturbance (cf. [61,62,72]). However, without fencing or individual protection of broadleaves such objectives seem unrealistic. A more probable scenario resulting from overbrowsing is a long-term alternative ecosystem state [140,141] dominated by spruce. Moreover, overbrowsing can also decrease the commercial value of future stands, since it increases undesirable seedling growth patterns (e.g., multi-trunking, stem forking) and stem decay [142–145]. This is particularly a problem for post-disturbance regeneration where saplings are unevenly distributed and their density is low [38,40,109,119]. In areas with high deer densities, as is the case in most of Slovenia [146], browsing should be carefully monitored with regular inspection of selected seedlings, monitoring of browsing with deer exclosures, and culling measures should be implemented if needed.

3.8. Coarse Woody Debris

Another feature of disturbance is the input of coarse woody debris (CWD), which influences the microclimate as well as water and nutrient regimes [147]. Salvage logging may severely deplete the amount of CWD [39]. However, CWD is usually more abundant after disturbance than under gradual regeneration felling [40,75]. CWD represents a seedbed for spruce and fir [125,148]. Decomposed CWD strongly facilitates seedling survival [110,149], but it is not available immediately after windthrow (Table 1). Thus, only some of the effects of CWD on post-disturbance regeneration are relevant. CWD has a temporary negative effect when it occupies microsites potentially suitable for regeneration [34], while positive effects include preventing erosion [31], facilitating development of safe sites for regeneration [102], and protecting seedlings against browsing and competing vegetation [150]; the latter was not confirmed in all studies where it was examined [110]. In most post-disturbance regeneration studies in Slovenia, CWD was negatively associated with seedling density and coverage [21,73,76,92,103,106]. This was probably due to the prevalence of poorly decomposed CWD in these studies. In contrast, a study of post-windthrow regeneration in a forest reserve with existing decaying CWD indicated its importance for spruce regeneration [121].

4. Secondary Succession versus Artificial Regeneration

Until the large-scale disturbances of the late 20th century in Europe (e.g., storms Vivian, Wiebke, Lothar, Martin) salvage logging and planting were the most common restoration measures, and this was also the case in countries with prevalent uneven-aged silviculture. Spruce was the most frequently planted species due to its high survival rate and economic value. Planting densities were initially relatively high at about 10,000 seedlings ha^{-1} after WWII and gradually declined to 4000 ha^{-1} in the 1980s. Such densities inhibited the establishment of naturally regenerated seedlings. Moreover, most spontaneously developed regeneration was removed by regular mowing of competing ground vegetation around planted seedlings for the first few years after planting.

Disturbances of the late 20th century in Central and Southeast Europe prompted the installation of many research plots in areas designated for natural regeneration [30,36,40] as well as controlled experiments comparing natural and artificial regeneration [26,31]. These studies indicated the potential and limitations of natural regeneration following large-scale disturbance. When summarizing the influential ecological factors outlined in the previous section, it seems that the most important limiting factors for natural regeneration of post-disturbance areas are sparse advanced regeneration, long distances to the forest edge and/or seed trees, lack of decomposed CWD, extreme geomorphological features (e.g., steep slopes, southern aspects, high altitudes), abundant ground vegetation, and overbrowsing (Table 1). Therefore, the decision on the type of restoration should take into account the presence and intensity of these limiting factors. The inclusion of other influential management factors such as available infrastructure, site quality, and size of the area could also inform the decision-making process. The same approach could also be applied for prioritizing planting [151] if areas are too extensive to be replanted in a few years. However, there may be other constraints influencing the decision on the type of restoration, for example, financial, socio-economic (interest of the forest owner), or technological (bottlenecks in the production of seedlings) constraints.

When deciding between natural and artificial regeneration it is reasonable to also consider the general advantages and disadvantages of planting vs. natural regeneration; for example, natural regeneration may result in slower forest restoration, but better root development, as well as an optimal match between the ecotype and site [152,153]. Even when forest stands managed by uneven-aged silviculture are completely damaged by disturbance, conditions are still more conducive for post-disturbance natural regeneration than those in areas under clear-cut management (Figure 1). These include primarily mixed stands with specially tended seed trees within the non-damaged forest matrix, omnipresent advanced regeneration, and small and intermediate trees. Long-term regeneration research in mountain windthrow areas in Switzerland and Germany indicated about 10 years of advantage for planted seedlings [26,31], which were taller and more evenly distributed [38]. Open areas are an opportunity for light-demanding species, especially pioneers, while the development of shade-tolerant species may be retarded due to lack of seed trees, adverse climate conditions, and competing ground vegetation [33,39,40,154].

Studies that compared the success of artificial and natural regeneration after large-scale windthrows in 1984 in the alpine region of Slovenia indicated small differences between stand structure two decades after restoration [74,155]. While naturally developed stands consisted of a higher proportion of pioneer and deciduous trees in general, plantations were more dominated by spruce, and planted larch saplings completely failed. Based on the results, the authors proposed more reliance on natural regeneration and targeted planting in clusters on selected sites with low probability of natural regeneration. In most comparative studies of natural vs. artificial regeneration of more recently disturbed forests in Slovenia, planted seedlings were more dense, taller, covered more of the open area, and were significantly less hindered by ground vegetation than naturally regenerated seedlings due to regular mowing of competing vegetation [21,76,103]. More commercially interesting species were represented in the composition of planted seedling, but these species may not be part of the natural vegetation community. Therefore, spruce is being increasingly replaced by broadleaves, yet success is often not satisfactory (Figure 5). Some shade-tolerant advanced regeneration declined in post-disturbance areas [25,76,103]. Regarding silver fir, this may be attributed to browsing [73]; however, in an experimental study, the decline was also observed in fenced areas [21].

Figure 5. Sycamore maple (*Acer pseudoplatanus* L.) is often used as a substitute for spruce in plantations for post-disturbance forest restoration. Its mortality is considerably higher than that of spruce despite expensive protection of maple against browsing and competing ground vegetation. Note the browsing damage to the sapling in the image.

Direct seeding is rarely applied as a measure of artificial regeneration in temperate forests [152,153]. This is particularly true for post-disturbance revegetation due to dense ground vegetation and slow development of sown seedlings [104]. In Slovenia, the share of sowing in artificial reforestation declined after WWII. However, sowing of black pine (*Pinus nigra* J.F.Arnold) has proved very successful in the restoration of post-fire areas in the sub-Mediterranean region [156]. Recent studies in Slovenia [106,157] indicated that direct seeding has potential as a restocking practice following large-scale windthrow, and that direct-sown broadleaves may experience higher survival compared to planting. The development of sown seedlings closely resembles natural processes, which results in undisturbed root development. Although direct seeding requires site preparation and repetitive mowing of ground vegetation, the cost is 30 percent to 50 percent lower than that of planting [158].

5. Silvicultural Interventions

Silvicultural operations that accompany planting, such as site preparation for planting or direct seeding, mowing of competing vegetation surrounding seedlings, and maintenance of protection tubes, improve planted seedling survival [136,159]. However, recent research in Slovenia has indicated that these measures may also drastically decrease the potential of naturally regenerated seedlings within young plantations [76]. Volunteer seedlings are often unwanted, since they may not be commercially interesting or may even be comprised of invasive species. Nevertheless, in the more natural forests of Central Europe, they often consist of economically valuable intermediate and light-demanding species such as oaks (*Quercus* spp.), maples, elms, wild service tree (*Sorbus torminalis* (L.) Crantz), and wild cherry (*Prunus avium* L.). While mowing of competing ground vegetation around planted seedlings is performed on a routine basis, it is rarely done for a naturally regenerated seedling or a sown seedling. It is very likely that this approach would help improve the spatial distribution of seedlings, which is one of the major shortcomings of natural regeneration following disturbance [26,38]. This would require additional training of forest workers so that they could identify target species. Selected naturally regenerated saplings for tending should be permanently marked with poles and favoured with silvicultural measures. This could be done simultaneously with tending of planted saplings, reducing tending costs [76]. The same applies for sites where direct seeding is planned. Site preparation for direct seeding is necessary, but the subsequent mowing of ground vegetation is not considered to be equally important.

Spontaneously developed young stands may require early cleaning and thinning to accelerate conversion to a commercial forest or a forest that protects against natural hazards. Often, intermediate and light-demanding crop trees need to be released from competition [160]. However, some pioneers, such as willow, are weak, relatively short-lived competitors and therefore do not need to be removed, although a traditional silvicultural prescription may require this [103]. On the other hand, birch (*Betula pendula* Roth) much more effectively restrains climax tree species [100] and often needs to be removed during later successional stages, if not selected as a crop tree. Natural stands that develop on disturbed areas are horizontally and vertically irregular and sparsely stocked [111]. For this reason, and for retaining collective stability in post-disturbance young stands, situational tending [81] may be a better approach than traditional tending with high densities of crop trees. Situational tending focuses on ca. 100 of the most valuable crop trees per hectare depending on the species, and they are favoured only if needed [161,162]. Due to the lower tree density, the intensity of crop tree crown release should be moderate when compared to regular tending of undisturbed forests [163].

6. Conclusions

Research in old-growth forests and forest reserves has repeatedly confirmed that after small-scale natural disturbance natural regeneration is relatively fast, mainly due to the presence of advanced regeneration. Moreover, biological legacies such as veteran trees, damaged trees, treefall pit and mound topography, and microsites with more light are necessary for the long-term survival of intermediate and light-demanding species. Salvage logging may deplete damaged stands of biological legacies and damage advanced regeneration on the one hand, while on the other hand it may favour natural regeneration by providing special microsites for seedling establishment and restraining growth of competing ground vegetation. The impact of salvage logging on erosion and regeneration is strongly associated with the type of harvesting and the allowed procedures during the salvage. Thus, decisions on the application of salvage logging should be based on careful optimization of ecological, silvicultural, forest health, technological, and economic issues.

While in the past most forests affected by larger and more intensive disturbances were artificially regenerated, more recent research suggests that natural regeneration is often sufficient. Many factors positively affect natural recovery, most prominently (Table 1) presence of advanced regeneration and seed trees, proximity to forest edge, less developed ground vegetation, decomposed CWD, tolerable deer browsing, and less extreme geomorphological features. Thus, the decisions regarding the use of natural or artificial regeneration should be adapted to the conditions of an individual site. In situations where several negative factors interact or there is a need for fast forest recovery (e.g., forests with direct protection function) artificial regeneration is preferred. Often, both types of regeneration may be combined and favoured. For example, the success of natural regeneration may be improved by mowing of competing ground vegetation, and artificial regeneration can be planted on selected favourable microsites, in clusters or by direct seeding. Naturally regenerated seedlings among planted seedlings represent an important, but often overlooked, opportunity for forest restoration. Overall, there are more possibilities in the context of uneven-aged forest landscapes for restoration than previously thought.

A substantial body of research regarding successional development following natural disturbance suggests a higher resilience of uneven-aged stands. Therefore, the silvicultural systems oriented towards uneven-aged stand structures will continue to be important in Central Europe. Due to the rise of extreme climatic events, it seems reasonable to accelerate gradual conversion of even-aged monospecific stands and favour active forest management to reduce risk of disturbance. Moreover, the conversion of post-disturbance even-aged stands to uneven-aged stands may be a meaningful management strategy. This can be facilitated through the great structural diversity of post-disturbance stands and novel thinning approaches, such as situational and group thinning.

On-going global changes are setting new challenges for the uneven-aged silviculture. Further research is warranted on a number of areas, including: how to compensate for the decline of spruce and other tree species severely threatened by insects or diseases (e.g., European ash dieback); to what extent to take into account introduced but non-invasive tree species; whether to continue using local provenances or consider assisted migration for restoration planting. Most contemporary studies were carried out as retrospective studies and thus exhibit high variability of data and sometimes confounding of factors, and treatments are often not randomly assigned to sites. Due to the high complexity of successional development and many possible treatments it would be beneficial to start joint international concerted experimental studies, which may facilitate improvement of restoration strategies.

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