doi:10.20944/preprints201707.0051.v1

Article

Challenges for uneven-aged silviculture in restoration of post-disturbance forests

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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 within the context of uneven-aged silviculture in the region. 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. We place particular emphasis on the most important biotic and abiotic drivers of post-disturbance regeneration, and use this information to inform silvicultural decisions about applying natural or artificial regeneration in disturbed areas. We conclude with guidelines for restoration silviculture in uneven-aged forest landscapes.

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

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1. Introduction

There is widespread concern that forest disturbance regimes will shift due to climate change, with some regions expected to experience an increase in disturbance frequency and severity [1-3]. The resistance and resilience of forest systems 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 [4-6] and resilient to disturbance [7-9]. 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 [10,11]. Close-to-nature silviculture or continuous cover forestry are synonymous terms. These systems have traditionally been used in many Alpine countries, particularly in Switzerland, Slovenia, Italy, Austria and parts of Germany [12].

Uneven-aged silviculture employs low impact felling regimes in order to mimic natural forest composition, structures and processes [13,14]. Given that this type of management mainly mimics natural disturbances on the lower end of the disturbance severity gradient (i.e. small tree fall gaps up to moderate severity disturbance events), it is not specifically focused on the full range of historic disturbance variability that is present in Central and Southeast Europe [15]. Traditionally, an important foundation for uneven-aged silviculture was potential natural vegetation (PNV), which often served as a guiding principle in setting silvicultural goals, but see [16]. As the spatiotemporal dynamics of vegetation has become better understood [17], the concept of static PNV has become less useful [18], especially from the perspective of post-disturbance forest restoration.

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 [19]. 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 SE Europe [11,20-22].

In the face of these challenges, there are also several advantages of uneven-aged silviculture, particularly 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 traditional clear-cut forestry to cultivate ecosystems that are resistant to natural disturbances and soil erosion [23]. Mixed stands are encouraged, which results in a good seed supply of a variety of species [24]. Systematic favoring of scattered broadleaves, which are often of intermediate shade-tolerance, helps ensure the survival of species that are vital for post-disturbance restoration [25]. Facilitating advance regeneration and intermediate shade-tolerant trees with tree marking and long regeneration periods 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 [5]. 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. fir - *Abies alba* Mill. and beech - *Fagus sylvatica* L.), which can be hampered by the climatic conditions of open areas created by disturbance [26]. Moreover, until recently there was relatively little experience in the planting of large post-disturbance areas [27]. 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 SE Europe. 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 [28]. In early 2014 Slovenia was hit by an ice storm unprecedented in modern history [29]. It damaged about 9,300,000 m^3 of trees, or more than the annual increment of Slovenian forests. The storm was followed by a bark beetle outbreak in the succeeding two years, claiming another half of the annual increment. Similar events have been reported for other countries with a similar silvicultural approach [30-33]. These disturbances triggered a series of studies that provide guidelines for post-disturbance restoration in temperate uneven-aged forest landscapes [34-36]. While disturbance is reported to benefit early successional flora and fauna [37,38], it may retard the fulfillment of some ecosystem services, especially forest protection functions [39]. It can represent a serious financial burden for the forest owner due to the decrease in the value of damaged wood, higher sanitary harvesting costs, delayed regeneration and

 doi:10.20944/preprints201707.0051.v1

thus an extended production period and the possible risk of losing the desired mixture of commercially interesting species [27,40].

The goal of this review is to synthesize studies on forest restoration in Slovenia and neighboring 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 [41], but see [30,35]. Nevertheless, they can inform us about natural processes as well as the possibilities and consequences of non-intervention in managed forests [42]. 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 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 advance 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 advance regeneration prior to mortality of canopy trees [43-47].

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 advance shade tolerant regeneration accelerates succession towards the dominance of these species in the canopy layer [44,48]. Less shade tolerant species that coexist in these forest types, such as maple (*Acer* sp.), ash (*Fraxinus* sp.) and Elm (*Ulmus* sp.), tend to recruit in situations where a relatively large patch of canopy is removed over areas where advance regeneration of shade tolerant species is largely absent or less developed [48,49].

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 N. 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 [50,51]. 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. Some of the largest events for which we have data on regeneration include patches of severe windthrow (> 100 ha) in managed beech-dominated forests that were salvage logged. After a combination of near stand replacing windthrow and salvage logging, results of on-going monitoring suggest large microsite differences in regeneration dynamics, including lower seedling success on south facing sites, providing some indication that future drought could play a role in post-disturbance recovery in the region [52].

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3. Drivers of post-disturbance regeneration dynamics

3.1. Stand structure

Similar to old-growth forests [53,54], initial forest structure in managed forests significantly influences the resistance of the forest ecosystem to disturbance impact as well as its post-disturbance recovery [1,36,55]. Results from studies in Slovenia indicate that mixed uneven-aged forests are more resistant and resilient to disturbance than even-aged spruce (*Picea abies* (L.) H. Karst.) forests with high growing stock and may sooner return to their original state [56-58]. This is similar to other research from Central Europe [4,55,59-61], but see [5]. Understory trees and advance regeneration play a particularly important role in the re-vegetation of open areas (Figure 1). However, there is a risk of damaging advance regeneration during sanitary felling operations [62], but see [63]. Pre-disturbance seedling establishment may not be adequate to ensure successful regeneration. Previous research indicates that on extreme microsites (e.g. sunny, exposed microsites) established regeneration may fail after exposure to open conditions [52,64], particularly if it is composed of shade-tolerant species (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. However, it is important to consider that after logging, especially after thinning, the risk of damage to a stand due to disturbance is increased for a period of 3 to 5 years [65-67]. From this perspective high thinning of stands over entire compartments, e.g. selection thinning following Schädelin [68], 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 situational thinning [69,70] or group thinning [71]. Moreover, due to both geographical setting and meteorological conditions, disturbance often recurs in the same area [54,56,58,59,72,73]. Therefore, frequent silvicultural interventions of moderate intensity [74] and favoring less crop trees [70] may be more preferable than heavy interventions over longer intervals and entire compartments, and special consideration should be given to areas prone to recurrent natural disturbance.

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. [75-77]). In terms of tree regeneration, the Central European literature often demonstrates the clear negative influence of salvage logging on forest recovery following large-scale high severity disturbance in spruce dominated forests [32,37,62,78]. 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. For example, salvage logging did not significantly influence forest recovery following small-scale intermediate severity disturbance in beech dominated stands in Slovenia [82]. 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-disturbance [63]. 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 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 that modify the speed of the recovery.

While the routine practice of salvage logging in the region may not hinder long-term forest development following small-scale disturbance in some forest types, it would be prudent to carefully consider whether salvaging is always justified. There is now overwhelming evidence that a large proportion of forest biodiversity requires dead wood for food and habitat. Recent studies also highlight the unique assemblages of species that require areas with large amounts of sun exposed dead wood [79], conditions created by more severe natural disturbance events. Moreover, salvage operations often remove many live but badly damaged trees, which are otherwise important as canopy cover for regeneration, and also serve as important microhabitats and perches for seed dispersing birds. Therefore, if maintaining biodiversity and other non-timber functions is a management goal, which is often the case in public forest lands, dead and damaged wood should be left on site in some areas (e.g. inaccessible areas where salvage costs are high), or at least partial salvage logging should be considered. This could involve only removing high value logs, while paying particular attention to leave high quality deadwood on site (e.g. both lying and standing snags of large diameter trees of lower economic value). 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 neighboring damaged trees if income is important.

 doi:10.20944/preprints201707.0051.v1

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 [80,81]. This delays post-disturbance forest regeneration [31]. Nonetheless, species whose natural habitat is located at higher altitudes may be favored (e.g. spruce, larch - *Larix decidua* Mill.). Recent studies in Slovenia, which covered a considerable altitudinal range, documented a negative relationship between post-disturbance regeneration success and altitude [52]. Tree species may have on average fewer competitors with increasing attitude, but regeneration development may be retarded by sites with tall herbs or adverse biotic and abiotic factors [83].

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 [84,85] cf.[81]. Studies from Slovenia suggest that on average southerly exposed microsites delay tree regeneration [86,87], but this may change for cold-intolerant species (e.g. fir) and at higher altitudes [57]. 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 [80].

Besides its influence on aspect, slope inclination influences snow and water movement as well as erosion and may therefore negatively influence regeneration dynamics [80,88,89]. In such conditions, safe sites may prove favorable (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 [88,89]. Slope inclination was not a major influential factor in studies in Slovenia. It was positively associated with the density of light-demanding species [87] and negatively associated with the density of spruce [57], fir and beech [90]. 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 (Figure 3), making them favorable for regeneration [34,88,91,92]. This has been confirmed in several studies of post-disturbance regeneration in Slovenia [57,64,87,90,93]. In the context of species groups

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this was especially significant for anemochorous species, while pioneers were more successful further from the forest edge (e.g. at least one tree height). Zoochorous species were more dependent on the remnants of the original vegetation and shrubs, where seed dispersing birds and small mammals can rest (perches) and hide. Removing tree residuals and shrubs (e.g. for easier planting) may have a negative effect on the encroachment of zoochorous species. The association between the forest edge and newly established seedlings may be blurred by the presence of pre-disturbance early established seedlings, which may be erroneously regarded as post-disturbance regeneration during inventories.

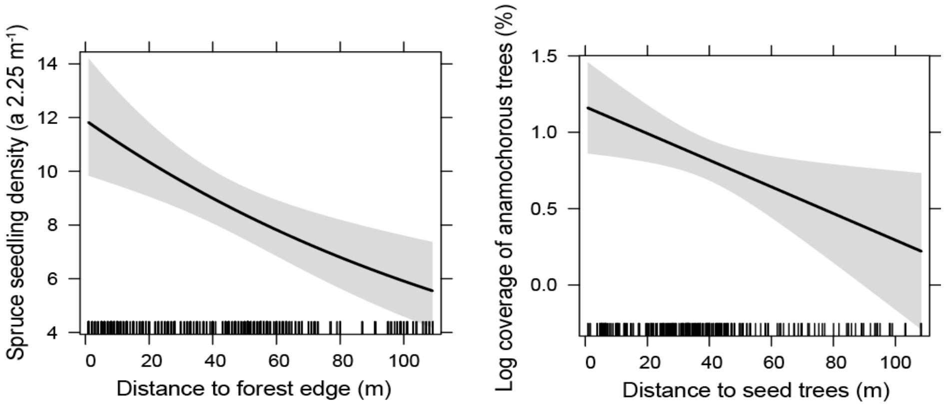

Figure 3. Predicted spruce seedling density (left) and coverage of anemochorous trees (right) with 95% confidence intervals (grey area) as a function of distance to the forest edge (composed mostly of spruce) or distance to conspecific seed trees. Predicted values are from multivariate regression models, thus accounting for other variables in the model (modified after [64]). Coverage of anemochorous species ranges from approximately 2 to 16%.

3.5. Microsite variability

After disturbance 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 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 may be greater than that of regular regeneration fellings [38,94,95]. 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. While higher regeneration success on pits 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 [96,97], but see [98], on mineral soil and decomposed deadwood [31,34,89,99-101]. 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 4), which may delay regeneration [27,102].

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 [64,87]. 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 [64,87].

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 seedling abundance [57,64,90]. This is often not the case for spruce and fir,

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which during controlled or natural regeneration in mixed forests often choose regeneration niches on more rocky sites, where they can more easily compete with ground vegetation and broadleaves [103,104].

Figure 4. 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 (Figure 5). This was suggested from research of gaps in managed forests [105,106] and in large openings created by disturbance [34,38,63,64,92,107]. On the other hand, post-disturbance ground vegetation conserves nutrients [108,109], prevents erosion [110] and may facilitate tree regeneration by acting as nurse plants [111]. Most recent studies of post-disturbance regeneration in Slovenia indicated a negative association between seedling density and ground vegetation, especially on less extreme sites with already established ground vegetation and pre-disturbance regeneration [57,64,87,112]. On some extreme sites with poorly developed advance regeneration, ground vegetation was not negatively related to seedling establishment [87]. It seems that in the initial years after disturbance, facilitation or neutrality are more important than competition [113]. On extreme sites otherwise competing species may function as nurse plants [105]. However, after establishment further seedling development is favored by less dense ground vegetation cover.

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Figure 5. 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 [114]. In open areas with abundant resources, younger and generally more palatable plants are abundant. Therefore, deer may substantially hinder the development of forest succession [34]. Other studies suggests that the faster growth of seedlings ("escape strategy" sensu [115]) within large clearings and the abundance of other food resources may positively influence forest succession, but see [116]. Research results from Slovenia are more closely aligned with the former findings. This may be the result of high overall game densities in Slovenia and particularly high densities in some research areas. For example, in the Kocevje region the current red deer density is approximately 13 deer km−2 [117]. 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 (Figure 6)[64]. Moreover, in areas with lower deer densities, spruce was favored by browsing [57,90,93], and dominant naturally regenerated and planted seedlings other than spruce had a significantly higher survival rate if unbrowsed [52,87]. 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 [1,55,56]. 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 [118,119] 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 [120-123]. This is particularly a problem for post-disturbance regeneration where saplings are unevenly distributed and their density is low [36,38,95]. In areas with high deer densities, as is the case in most of Slovenia [124], browsing should be carefully monitored with regular inspection of selected seedlings,

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monitoring of browsing with deer exlosures, and culling measures should be implemented if needed.

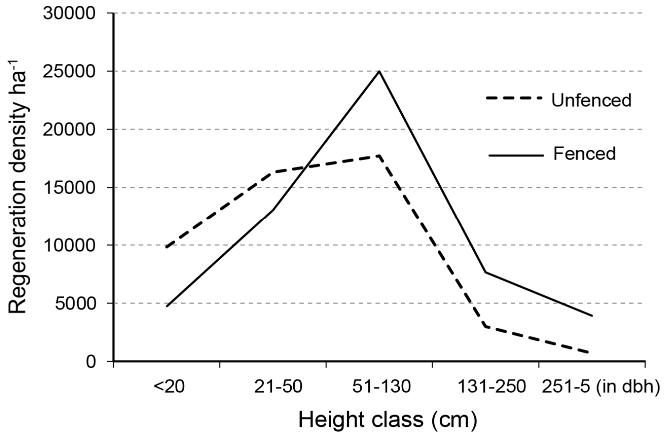

Figure 6. Regeneration density of all woody species according to height class and presence of fencing ten years after bark beetle outbreak [125]

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 [126]. Salvage logging may severely deplete the amount of CWD [37]. However, CWD is usually more abundant after disturbance than under gradual regeneration felling [38,63]. CWD represents a seedbed for spruce and fir [99,127]. Decomposed CWD is required for seedling survival [107,128], but it is not available immediately after windthrow. 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, while positive effects include preventing erosion [31], facilitating development of safe sites for regeneration [89] and protecting seedlings against browsing and competing vegetation [129]; but see [107]. In most post-disturbance regeneration studies in Slovenia, CWD was negatively associated with seedling density and coverage [57,64,87,90,93]. 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 [112].

4. Secondary succession versus artificial regeneration

Until the large-scale disturbances of the late 20th century in Europe (e.g. 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 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 4,000 ha-1 in 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 [30,35,38] as well as controlled experiments comparing natural and artificial regeneration [27,31]. 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 advance

 doi:10.20944/preprints201707.0051.v1

regeneration, long distances to the forest edge and/or seed trees, extreme geomorphological features (e.g. steep slopes, southern aspects, high altitudes) and abundant ground vegetation. 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 [130] 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, e.g. financial, socio-economic (interest of the forest owner) or technological (bottlenecks in the production of seedlings).

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 [131,132]. 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 advance 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 [27,31], which were taller and more evenly distributed [36]. 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 [37,38,62,133].

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 [58,134]. 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 declined. 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 [64,87,90]. 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, but planting success is often not satisfactory (Figure 7). Some shade-tolerant advance regeneration declined in post-disturbance areas [87,90]. Regarding fir this may be attributed to browsing [57]; however, in an experimental study, the decline was also observed in fenced areas [64].

Direct seeding is rarely applied as a measure of artificial regeneration in temperate forests [131,132]. This is particularly true for post-disturbance revegetation due to dense ground vegetation and slow development of sown seedlings [91]. In Slovenia the share of sowing in artificial reforestation declined after WWII. However, sowing has proved very successful in the restoration of post-fire areas in the sub-Mediterranean region [135]. Recent studies in Slovenia [93,136] indicated that direct seeding has potential as a restocking practice following large-scale windthrow, and that direct-sown broadleaves may experience higher survivorship compared to planting. The development of sown seedlings closely resembles natural processes, which results in undisturbed root development. Although direct seeding requires preparation of forest soils and repetitive mowing of ground vegetation, the cost is 30 percent to 50 percent lower than that of planting [137].

 doi:10.20944/preprints201707.0051.v1

Figure 7. 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.

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 [113,138]. However, recent research in Slovenia suggests that these measures may also drastically decrease the potential of naturally regenerated seedlings within young plantations [87]. 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 oak, maple, elm, wild service tree and wild cherry. 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 [27,36]. 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 favored with silvicultural measures. This could be done simultaneously with tending of planted saplings, reducing tending costs. 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 tending to accelerate conversion to a protection or commercial forest. Often, intermediate and light-demanding crop trees need to be released from competition [139]. However, some pioneers, such as goat willow (*Salix caprea* L.), are weak, relatively short-lived competitors and therefore do not need to be removed, although a traditional silvicultural prescription may require this [90]. On the other hand, birch (*Betula pendula* Roth) much more effectively restrains climax tree species [86] 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 [140]. Therefore, tending should focus on maximum 100 valuable crop trees according to the silvicultural goals per hectare, and crop trees should be favored only if needed [141,142]. Due to the lower tree density, the intensity of crop tree crown release should be moderate when compared to regular tending of undisturbed forests [143].

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 advance 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. Many studies confirm that non-intervention should be encouraged in commercial forests provided certain conditions are met: no profit for the forest owner from salvaging operations, no need for protection functions or protection of forest visitors and no forest health concerns.

While in the past most forests affected by disturbances were artificially regenerated, more recent research suggests that natural regeneration is often sufficient. Many factors positively affect natural recovery, most prominently presence of advanced regeneration and seed tress, proximity to forest edge, less developed ground vegetation 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 favored. For example, the success of natural regeneration may be improved by mowing of competing ground vegetation, and artificial regeneration can be enhanced by planting on selected favorable 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. 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. Most contemporary studies were carried out as retrospective studies and thus exhibit high variability of data and sometimes confounding of sites and treatments. Due to 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.

Acknowledgments: This work was supported by the Slovenian Research Agency (ARRS) Programme group P-0059.

Author Contributions:

Literature overview: all authors; manuscript drafting: all authors.

Conflicts of Interest: The authors declare no conflict of interest.

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