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Review

Adaptive Silviculture and Climate Change—A Forced Marriage of the 21st Century?

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Abstract: Climatic changes significantly impact forest ecosystems, inevitably affecting forestry and forest-related industry. Considering that most forests are actively managed, there is a need to define the future risks and set a strategy for forestry and silviculture in a changing world. This review provides insight into the new challenges and opportunities forest management and silviculture face in the coming decades. There is sound recognition of risk factors expected from climate change, yet great uncertainty exists in the predictions of the response of forests to new conditions. Additionally, the stakeholders' interests in the goods and services offered by forests are changing, and this also needs to be taken into account in future forest management. Undoubtedly, the goal of future forestry and silviculture in the 21st century will be primarily to ensure the continuity and sustainability of the forest. Sustainable use of goods and ecosystem services from forests will be directly related to the continuity and sustainability of the forest in the future. Adaptive forest management aims to promote the adaptive capacity of forests to new conditions resulting from climate change. If adaptation efforts are effective, adaptive forest management should be a kind of risk management. There is no one-fits-all strategy for adaptation to uncertain future conditions. Silviculture in the 21st century is expected to be more conducive to adapting forests to changes. Operational silvicultural activities should focus on ensuring the resilience and adaptation of forests to future environmental conditions. Modern silviculture offers activities that fall within the scope of contemporary close-to-nature silviculture practices. However, some of the currently applied practices will require review and modification to be applicable under new conditions. This review also identifies the need to fill knowledge gaps in order to develop more effective and flexible adaptation strategies to foster sustainable forest development and, thus, sustainable forestry.

Keywords: climate change; adaptive silviculture; forest adaptation; adaptation strategies; close-to-nature silviculture; CAS

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1. Introduction

In the *Summary for Policymakers* of the *First Assessment Report* of the IPCC, released for the public in 1990, it was stated that "emissions resulting from human activities are substantially increasing the atmospheric greenhouse gasses (. . .). These increases will enhance the greenhouse effect, resulting in (. . .) warming of the Earth surface" [1]. At that time, the IPCC predicted that the global mean temperature will increase by about 4 °C above pre-industrial times before the end of the 21st century [1]. In the *Summary for Policymakers* of the *Sixth IPCC Assessment Report*, the increase in global surface temperature is projected to continue under all greenhouse gas emission scenarios. It is also expected that global warming of 1.5 °C and 2 °C will be exceeded during the 21st century unless a deep reduction in greenhouse gas emissions occurs [2]. The range in mean global surface temperature at the end of this century is projected to vary between 1.0 °C and 5.7 °C, depending on the emission scenario [2]. Climate change is already affecting all ecosystems on Earth, including forest ecosystems.

Terrestrial ecosystems might face significant consequences mainly due to increasing temperatures and unfavourable changes in the precipitation regime. In the context of climate change (CC), forest ecosystems are one of the most important terrestrial ecosystems on Earth, and they can remove a large amount of carbon from the atmosphere and store it in their biomass and soil [3–6]. So far, the balance between CO_2 captured by plants (photosynthesis) and released back into the atmosphere (respiration and decomposition) is positive (but see [7]). Thus, forests are still assumed to be the most effective carbon sinks among terrestrial ecosystems, storing more than 80% of carbon in the aboveground biomass and more than 70% in soil [6,8]. They are also important because they provide a habitat for approximately 80% of all terrestrial species, playing an important role in maintaining and enhancing biodiversity [9,10].

Trees and forests have an inherent capacity to cope with the gradual environmental changes within which they persist. However, the currently observed changes in the environment resulting from CC—frequently described as historically unprecedented—are so rapid that their adaptation to new conditions might be delayed by decades or centuries and might even be impossible for some species and populations, resulting in their extinction. Certainly, novel forest ecosystems will more likely be different in terms of structure and functionality than the current ones [11,12]. Changes in the structure and functioning of forest ecosystems will force changes in forest management and, therefore, in silviculture [13–18]. Silvicultural practices encompass various approaches used to maintain and/or enhance forest sustainability, multifunctionality, and sustainable use. The certain standardization of silvicultural activities that took place during the 19th and 20th centuries (especially in Europe) often led to a simplification of forest structure, resulting in a reduction in forest multifunctionality. Such management was modelled on intensive agriculture and assumed a high predictability of forest development under relatively constant environmental conditions [19]. However, more than such a concept of silviculture may be required to meet the forestry goals under the observed CC rate.

The multifunctionality of forests and forestry in the 21st century will depend on the continuity of the forest. Continuity, in turn, will be linked to the forest's ability to adapt to new and mostly uncertain environmental conditions. Therefore, increasing the adaptive capacity of forests will be the main goal of silviculture in light of CC [16,17,20–23]. How to adapt our forests to future uncertainty due to CC is a globally pressing question.

There are different approaches in forestry to meet forest adaptation and sometimes they are mutually exclusive [10,24,25]. Strategies differ in their assumptions, actionable recommendations, and the costs of implementing them into practice [24]. For example, it is debatable whether the current paradigm of close-to-nature forest management will be sufficient to adapt our forests to non-analogue habitats or whether a novel adaptive silviculture paradigm with novel activities will take the stage [23,26–28]. Silviculturists have a many options that can be related to specific conditions, such as to meet new social demands related to forests, as was often the case in the past. However, whatever option is chosen, no single practice will work in isolation, and there will be no one-size-fits-all practice or strategy. Actions to adapt forests to CC require a thorough understanding of the drivers of CC and the impacts brought by these changes on organisms, populations, and ecosystems. This also involves the selection of the adaptation mechanism we want to rely on in new conditions. For managed forests, a key action will be to choose the most effective silvicultural measures.

The presented paper is organized as follows:

In Section 2, the main climatic parameters whose changes will have the most noticeable impacts on trees and forest ecosystems are discussed. The information in this chapter is sufficiently general for the reader to learn about their role in the context of their importance for silviculture and forest management. Details regarding the role of these parameters are contained in the cited literature.

In Section 3, the main mechanisms of tree and forest adaptation to changing environmental conditions resulting from CC are presented.

Section 4 provides information on the concept of adaptive forest management in a changing environment.

Section 5 is devoted to adaptation strategies in forestry and Chapter VI describes various activities within the framework of silviculture in the broadest sense, which can result in the adaptation of forests to new conditions and the mitigation of CC by strengthening the mitigation role of forests.

Finally, in Section 6, we point out the uncertainties arising from incomplete knowledge of CC and its impact on silviculture and forestry in the 21st century. We also point out areas that should be considered to reduce the risk of failure in silviculture and forest management failure in the uncertain world of this century.

2. Forests Facing Climate Change—The Role of CO_2, Temperature, Precipitation, and Disturbances

Changes in climatic parameters such as atmospheric CO_2 concentration, temperature, and precipitation affect many aspects of the forest ecosystem. These impacts are both direct and indirect as well as beneficial and adverse. It is expected that the observed changes in climatic parameters will modify the structure and functionality of forest ecosystems by altering genetic structures, tree physiology, tree growth patterns, and competitive interactions [4,18,29–32] (Figure 1).

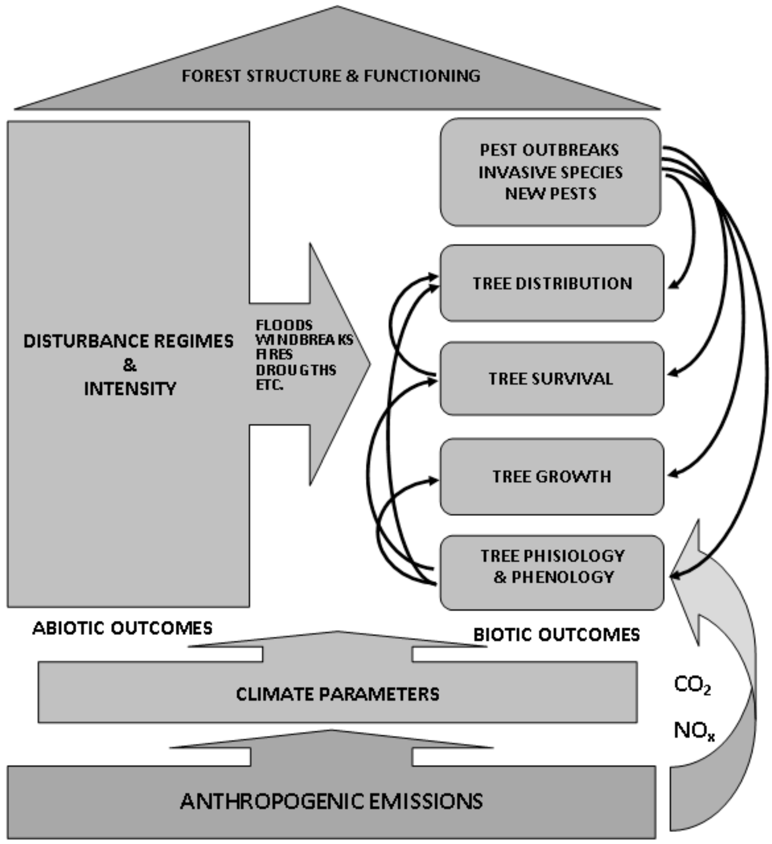

Figure 1. Conceptual diagram of the impact of climate-related parameters on trees and forest structure and functioning.

Whilst trees and forests have an inherent capacity to deal with a changing environment, the observed changes are historically unprecedented in their magnitude and rate and pose a major threat to their future [8,25,33–35]. The impact of CC on forests will be primarily negative, and a partly beneficial effect may only be expected in northern latitudes, where the relatively short growing season and low temperatures currently limit the growth of trees [36–38]. But, this effect can be transitory [39]. Forests will then be exposed to various stress factors, more of them of extreme intensity [29,40–44]. It should be clearly stated that climate parameters work together, and their impact on forests will be largely synergistic.

Due to numerous simplifications applied in biological and climatic modelling, it might be problematic to provide reliable projections of the future state and dynamics of forests, and they might be subjected to a high level of uncertainty. The average surface temperature and precipitation amount will more likely increase until the end of the 21st century [2]. Although higher precipitation is expected, the precipitation regime will be altered adversely. It is also anticipated that ongoing climate warming will increase the frequency, likelihood, and severity of extreme climate-related events such as droughts, fires, storm winds, floods, and insect outbreaks [45,46]. All these changes in climatic parameters are likely caused by a significant increase in the concentration of CO_2 in the atmosphere [4,40,43,47,48]. Regardless of the cause initiating the climatic changes observed today, these changes are real and tangible.

Certainly, trees and forest ecosystems will respond to CC, but the results of studies dealing with CC impacts on forests are, so far, inconclusive and regionally dependent [3,30,38,49–52]. In addition to incomplete knowledge of how an individual tree responds to change, the response of the entire ecosystem is poorly understood [25]. When developing climate change adaptation strategies in silviculture, it is important to consider the perspective of the individual tree as well as that of the population (stand). The first refers to physiology, phenology, growth, and mortality and the second to species composition of the forest, stand productivity, or tree-to-tree interactions (e.g., [12,53–59]).

2.1. Climate Change from a Tree's Perspective

Due to the complex effects of atmospheric CO_2 concentration, temperature, and precipitation on trees, the detailed response of a single tree to climate change is still to be clarified. Gradual changes in these parameters make it relatively easy for trees to adapt, in contrast to the rate and magnitude of those changes observed today [4,54,60–62]. At the individual level, the mechanism for dealing with the recent shift in bioclimatic variables relies on phenotypic plasticity, whereas a longer perspective requires adaptive change that modifies the fitness-related traits.

2.1.1. Elevated Atmospheric CO_2—Climatic Fertilizer?

A beneficial effect of an elevated atmospheric CO_2 concentration is that it fosters the efficiency of photosynthesis by optimizing photosynthetic carbon acquisition and allocation [32,54,60,63–69]. More effective photosynthesis should lead to higher tree growth and biomass production [29,32,40,54,67,70], but this effect remains species- and biome-specific. Trees have been shown to be most responsive to elevated CO_2 concentrations [71]. The positive effect of CO_2 on tree growth could also result from a better water use efficiency because the elevated CO_2 level plays a certain role in regulating the mechanism of stomata in leaves, reducing stomatal conductance [60] (but, also see [72]). Other processes, e.g., photorespiration and mitochondrial respiration, are also controlled by the CO_2 level, and its increasing concentration decreases both processes, opposite to the temperature effect [32,60]. Better efficiency of photosynthesis and water management due to higher atmospheric CO_2 concentrations are not the only ways this climatic parameter can affect tree performance. The leaf area of individual trees and stands (LAI), the production of tree roots, as well as the growth of fine roots can be stimulated by elevated atmospheric CO_2 concentrations [60,73,74]. However, some recent studies cast doubts on the general and positive relationship between higher CO_2 levels and expected higher tree growth [72,75]. The effect of elevated atmospheric CO_2 on tree performance varies when other environmental factors are considered, e.g., nitrogen, potassium, ozone concentration, soil minerals, water availability, and temperature, as well as factors not related to climate, such as species composition, tree age, or site condition [40,50,54,62,64,68,70,76–80]. Additionally, the complexity of the photosynthesis and biomass acquisition relationships makes upscaling the effect of CO_2 seen at the leaf level to the tree or ecosystem level problematic [81,82]. In the case of trees, their longevity also produces further uncertainty since the effect of CO_2 depends much on the age or ontogenetic stage. The positive effect of CO_2 fertilization on tree growth, which has been observed for several decades, is not necessarily a permanent effect. As trees acclimate to increased CO_2 concentrations in the atmosphere, this effect may disappear [66,72].

2.1.2. Rising Temperature—Climatic Trigger?

Temperature regulates the rate of most biochemical reactions that drive tree growth and other developmental processes [83,84]. Trees can respond to higher temperatures at morpho-anatomical, physiological, and molecular levels, making them less sensitive to certain, but rather minor, changes in temperature. Both photosynthesis and respiration are influenced by temperature. In general, the rates of photosynthesis and respiration increase to the optimal point, beyond which they are inhibited [32,54,60,69,84,85]. The effect of higher temperatures ought to be considered simultaneously with drought, which increases the vapor pressure deficit between the leaves and the atmosphere. A high vapor pressure deficit increases evapotranspiration, which affects biochemical processes by increasing the water loss and the likelihood of cavitation, limiting CO_2 diffusion or triggering a reduction in stomatal conductance [32,69]. Vapor pressure deficit may result in tree mortality [86,87].

In addition to the effect of elevated temperatures on biochemical and physiological processes, there are also effects on tree phenology [4,54,60,88–90]. For example, the timings of budding, leafing, and flowering are susceptible to changing air temperature and CO_2 levels [4,69,89]. Trees growing in higher latitudes will be more exposed to the effects of rising surface temperatures than in the tropics [2]. Cold temperatures, but above the freezing point, allow the satisfaction of the chilling requirements of tree species for rest completion (dormancy) in temperate and boreal zones. Higher spring temperatures will accelerate bud burst and shoot growth. It is assumed that warming of 2–3 °C will hasten bud break; beyond this threshold, the process will be likely delayed due to the lack of fulfilling the chilling requirements of many tree species [54,60]. In such cases, tree growth will be reduced. Increasing temperatures are conducive to extending the growing season in many regions [37,60,88,91]. Whilst this is a positive effect of warming, it may lead to higher frost damage under certain circumstances because the increasing temperature may hasten the dehardening process [92]. Not less important for trees is temperature variability. If the variability is similar to the present one, forest damage might be the same or even lower in warmer climates. However, if the variability increases and winter thaws are more frequent than they currently are, it may cause specific tree injuries.

In general, the role of increasing temperatures in tree growth and development can be positive up to a certain point. However, this effect is modified by other climate-related parameters, e.g., CO_2, drought, or nutrient availability [50,54,60,85,88,93,94]. Whilst the impact of air temperature on plants is most frequently studied, it is still unclear what happens in soil during warming. Soil temperature is extremely significant for tree regeneration, growth, and development, especially in the case of the youngest tree generations. Higher soil temperature affects soil organic matter decomposition and mineralization, altering the functions of roots; this effect depends on many other factors limiting photosynthesis and respiration. Increased soil temperatures, together with other factors (soil water, nutrients, and sunlight), are expected to affect fine root production and mortality [54,95–97].

2.1.3. Water Availability and Precipitation Regime—Almost Pure Threats?

Precipitation, its amount, and temporal regime are climatic parameters whose future projections are less certain than those of temperature. The effect of a changing precipitation regime is twofold: too much rain (floods and waterlogging) as well as too little (droughts) affects trees negatively [4,98–100]. Heavy rains, resulting in floods and waterlogging, cause several physiological disorders due to the deprivation of oxygen in the soil, leading to hypoxia (low concentration of oxygen) or anoxia (lack of oxygen), both negatively impacting tree growth [101]. Additionally, this adverse impact of flooding or waterlogging is related to the production and accumulation of toxic compounds [102]. Reduced oxygen availability is the primary factor affecting the growth, regeneration, and developmental processes under flooding conditions. For example, tree growth limitation is caused by decreased root hydraulic conductivity, which induces shoot desiccation [103], whereas respiration metabolism is affected by an excess of water, frequently leading to tree death [104]. The response of trees to this stressor is species-specific, even sex-specific [105], and depends on the duration of the unfavourable conditions and on the ability of trees to cope with such water stress [69,100]. Floods can also cause physical damage (mechanical injury), leading to reduced root and shoot growth, leaf necrosis, bark damage and the death of individuals. Floods during the active tree growth period can cause more significant physiological and physical damage than those occurring during the dormant season [51,61,69,102].

In comparison to flooding, the impact of drought and associated water stress dominates the studies dealing with the projected effects of global climatic changes on plants and trees. Drought events can reduce tree growth and increase mortality, decreasing forest productivity at a much wider scale than flooding does. Drought-related tree mortality has been well documented, putting at risk, in particular, gymnosperms [106–108]. Drought stress also affects tree health status, tree physiology (e.g., gas exchange, carbon allocation, carbon balance, and water transport), and phenology (premature leaf senescence) [4,69,91,99,100,108–111].

Drought conditions may lead to carbon starvation and hydraulic dysfunction [60,69,99,112], the result of which is, most likely, the death of an individual tree. The response of drought-prone trees is related to impaired water transport due to xylem cavitation and hydraulic failure [69]. Most tree species and forest communities function within fairly narrow hydraulic safety margins, making all biomes vulnerable to water shortage. The critical point at which xylem embolism develops into hydraulic failure is still unknown [69,112]. Hammond et al. [99] reported that the loss of 80% of hydraulic conductivity likely leads to the death of an individual tree. The risk of hydraulic failure increases with the size of the tree, i.e., taller trees suffer more from drought than smaller trees [113,114]. Tree height has also much to do with drought mortality as xylem regrowth after a drought event takes more time (and resources) in taller trees, leading to tissue carbon starvation and, finally, mortality, which may lag for several seasons [115]. The tree size effect on resistance and resilience to drought can also be species-specific [114].

Drought timing also influences tree performance. Short but severe droughts affect tree growth more than moderate but prolonged ones [69,91]. Rare but severe drought years have rather short-term and reversible effects on tree growth. Long periods of drought usually reduce tree growth for several years or even decades, increasing the probability of tree death [116]. Other factors that are involved in drought-related damages or mortality in trees are the water-use efficiency of species, phenological phase, and habitat, including prevailing climatic conditions or elevation [61,76,79,98,100,109,110,116,117]. The effect of drought on individual trees also depends on the growth performance of the tree in the pre-drought period [117]. Tree height growth is usually limited by mid- and late-season droughts, but tree diameter growth is mainly limited by late-season droughts [60]. In terms of developmental stage, younger forests are more sensitive to drought than old ones [118–120]. The effects of a drought are apparent immediately after or already during its onset. However, the effect of a severe drought can also be observed several years after its occurrence, and the affected trees may be more susceptible to future droughts [116]. The rate of recovery after drought is frequently assumed to be related to a lower resistance to the next extreme event, although this was only observed for gymnosperms [107]. However, slow recovery is not necessarily a sign of a deep function impairment but might be related to structural acclimation induced by drought stress [121]. The tree hydraulic system may respond to drought stress via the formation of smaller xylem conduits, making the hydraulic system less prone to future failures [122].

2.2. Climate Change from the Stand's Perspective

At the community (stand) level, genetic, population, ecological, physiological and phenological processes interact in complex responses to environmental signals. There is considerable evidence that different populations of tree species experiencing different environmental conditions may react divergently to the same factor because of the dissimilarity in their phenotypic and genetic architecture shaped by selection [123,124]. Genotypes and phenotypes interact with the environment; for example, average population fitness may vary among populations as a function of local adaptation [125,126], which is commonly reported for tree species.

Forest ecosystems can respond to any environmental pressure, including CC, according to at least a few different trajectories [25], depending on the composition of the system, internal self-organizing mechanisms, and human intervention, which, by means of adaptive forestry, may alleviate the consequences of CC. The thresholds of the adaptive capacity of forests facing rapid changes have not yet been fully recognized. They can respond to CC in the following ways: they can acclimate (phenotypic plasticity), adapt (evolution), migrate (dispersal and colonization), or die out (locally or regionally) [51,127–129]. None of these possible mechanisms of dealing with CC are mutually exclusive, and each will be important for forest ecosystems, silviculture, forestry, and the human societies that benefit from forest goods and services [4]. Depending on the capacity of species/populations to deal with the stress due to CC, foresters can expect qualitative as well as quantitative changes in forest structure.

2.2.1. Qualitative Changes

For the purpose of this paper, qualitative changes are defined here as being related to changes in tree species ranges, species composition and the relationships among tree species (competitive status change), the emergence of alien and/or invasive species, and, finally, changes at the biodiversity level, which will be the likely consequence of all above-mentioned changes [9,17,51,54,57,127–132]. Generally, tree species distribution has been consistent with latitudinal and altitudinal ecological trends, which indicates a certain dependence of species distribution shifts on climatic conditions and their variability. Because CC scenarios point to climate warming and favourable precipitation levels at higher latitudes, it is expected that the potential expansion of distribution ranges for many tree species will be mostly northward in the Northern Hemisphere [30,38,49,52,93,130,133–135]. Populations in the regions currently experiencing significant warming (e.g., southern Europe) will suffer much more in a warmer and drier future climate than populations currently growing in a milder climate (e.g., mid-latitudes in Europe) [93,133]. Projections of possible changes in the ranges of forest tree species as a response to CC are based on modelling using a variety of models (bioclimatic-envelope, process-based, or dynamic vegetation models) which differ in their reliability. Modern models provide more realistic results than those used decades ago because of the continuous improvement in model hindcast skills. However, they are still not very reliable, because they do not incorporate many biologically important processes relevant to the outcome of the projection made [49,51,127,128,132,136,137]. Additionally, the climatic scenarios used for range predictions suffer from imperfections [138–140]. Climate modelling is largely a simplification of complex physical processes, and downscaling their impacts is still challenging [141,142].

Past range changes prove that migration was almost universal and an efficient response of trees to track their optimal climate. Based on this, the assumption that trees will have a migration capacity in the future was developed (but see [143]). Range expansion requires propagule dispersal throughout the suitable habitat, which enables population establishment and growth. However, many factors and mechanisms interacting in a complex manner are required for this. One of the key determinants of the capacity to migrate is dispersal distance [128], and wind-dispersed tree species will be more likely to expand towards new ecological niches much more easily than trees with heavy seeds [51]. Trees with zoochoric seed dispersal may also perform better during migration. However, other biotic and abiotic variables, such as the fecundity of local populations, landscape configuration of suitable habitats, quality of future habitats and their connectivity, interactions with dispersers, and competitive interactions during and after range expansion, need to be addressed. For example, the connectivity of future habitats is crucial to gene flow, which would help alleviate initial founder effects likely present during colonization. Populations at the leading edge are expected to better cope with CC than those at the trailing edge, although the rate of expansion at the front line may not match that of contraction and trailing edge [144]. Comprehensive reviews about the role of mechanisms and functional traits highly relevant in predictions of the potential change in species distribution of tree species are available in Aubin et al. [132] and Robledo-Arnuncio et al. [145]. The shifts in tree species ranges accelerated by climate change are likely to reorganize forest composition, structure, competitive status of tree species, and intraspecific interactions [4,16,38,52,93,134].

Using niche modelling, Dyderski et al. [52] demonstrated the effects of different CC scenarios on the distribution of the 12 most important tree species in Europe. According to predicted changes in their ranges, tree species were assigned to three groups described by the authors as winners (range expansion), losers (range contraction), and neutral (no change). Potential winners are late-successional tree species (*Abies alba*, *Fagus sylvatica*, *Fraxinus excelsior*, *Quercus robur*, and *Q. petraea*), whereas the early-successional tree species (*Pinus sylvestris*, *Betula pendula*, *Larix decidua*, and *Picea abies*) are suggested to be the losers. Kasper et al. [76] reported the possible replacement of mesic European beech forests with more thermophilic oak forests in western Romania. Another study [146] instead confirmed the status of losers in the case of European beech (*Fagus sylvatica*) and Norway spruce, (*Picea abies*), which are expected to lose large parts of their modern areas. Elms (*Ulmus* spp.) are among the winners of projected CC because they show significant potential to increase their distribution range towards higher latitudes. Koch et al. [144] predicted that Norway spruce, silver fir (*Abies alba*), and European beech facing CC will retreat their occurrence significantly. Tree species such as wild service tree (*Sorbus torminalis*), European white elm (*Ulmus laevis*), and hornbeam (*Carpinus betulus*) will expand their distribution across various CC scenarios.

Climate change favours the spread of alien and invasive species, also among tree species [4,33,52,144,146]. The chance for alien species to colonize new areas will result from the loss of ecological niches by the hitherto dominant native tree species. An increasing number of studies report the suitability of different non-native tree species for European forests and forestry [147,148]. A dozen non-native tree species have the potential to be alternatives to native tree species in Europe, replacing species that are endangered in warmer and drier climates. Some of them, e.g., Douglas fir (*Pseudotsuga menziesii*), red oak (*Quercus rubra*), giant fir (*Abies grandis*), black locust (*Robinia pseudoacacia*), and red cedar (*Thuja plicata*), have already adapted to the planting region. Moreover, Douglas fir, red oak, and black locust are promising tree species for forestry, whereas giant fir, sweet chestnut (*Castanea sativa*), Turkey oak (*Quercus cerris*), and Japanese larch (*Larix kaempferi*) are of minor importance [33,52,146–152]. Given that the natural process of species migration is a long-term process, the intentional introduction of alien species into new areas is primarily discussed in the frame of the assisted migration concept [153,154]. However, the wide introduction of alien tree species to forestry must be preceded with a sound evaluation of their suitability and potential damage to the native flora and fauna [33,139,146,151,152]. In some regions, the introduction of alien species that show good adaptation to the local climate can mitigate the adverse effects of CC on biodiversity. For example, a recent study showed that an admixture of Douglas fir may modify the impacts of herbivores and pathogens on European beech, enhancing the survival and growth of seedlings and mature trees of this species [148].

According to IPCC reports, CC is a major threat to biodiversity in the 21st century due to potential species extinctions. Forest biodiversity is also highly impacted [155–157]. The loss of certain tree species means the loss of many other organisms because forest ecosystems are the most important reservoirs of terrestrial biodiversity. According to

Aitken et al. [127], under a moderate CC scenario, 3–38% of plant species may become extinct by 2050. In the absence of migration and adaptation, about 60% of tree species that are well protected today in situ will be threatened due to CC. Migration alone might decrease the losses by 30–50%, whereas adaptation can result in a 20% decrease. If both processes could work simultaneously, only 15% of species would be at risk [127,158]. Milad et al. [133] noted that the past strategies for nature conservation should be revised, and new strategies must be developed to ensure the persistence of the species within novel environmental conditions. As Urban [159] noted, the extinction rate will depend on the CC scenario being realized. Accordingly, it may increase from 2.8% (present) to 5.2% at a 2 °C increase of the mean global temperature or will reach the level of 8.5% in case of a rise by 3 °C. The extinction rate will probably vary geographically—the lowest rates are expected for North America and Europe (5% and 6%, respectively) and the highest in South America (23%) [159]. The expected loss of forest biodiversity will pose a challenge for conservation managers and naturalists.

2.2.2. Quantitative Changes

Quantitative changes mean changes in forest productivity and economic value. Quantitative changes referring to forest productivity may be positive [4,60,160]. The major climate variables influencing forest productivity are precipitation, temperature, and droughts [4,54,161]. The relationships between climate change and forest productivity are further complicated by the simultaneous effects of several other factors (e.g., species mixing effect or nutrients) [94,162,163]. Evaluating the combined effects of these factors on forest productivity is still challenging, and reliable predictions of change in forest productivity lack complexity and suffer from uncertainty [50,54,67]. As climatic changes are assumed to be different in different climatic zones, their impact on forest productivity will also be sensitive to geographical variation. It is expected that boreal forests will benefit the most in terms of climate warming due to removing the temperature-related environmental constraints [4,38,50,134,164], whereas temperate forests (at mid-latitudes) will show larger spatial variability. Forest productivity in the northern part of this zone will benefit more than that in the southern part [4,30,93]. However, wood production is expected to decline in regions that will suffer from water deficits, low temperatures, and low nitrogen deposition, which will overshadow the possible CO_2 fertilisation effect. Many studies show that drought periods, especially severe ones, as well as other extreme events will exert the greatest negative impact on forest productivity [79,98,106,109,116].

Enhanced forest growth attributed to CC (higher temperatures and CO_2 concentrations and an growing season) was reported by McMahon et al. [162] and Fang et al. [163] across many forest types. The authors stated that the change in forest growth was significantly higher than that due to natural forces. The growth response to CC is also species-specific. Peltola et al. [164] reported a steady increase in the mean volume of growing stock towards the end of the 21st century in Finland, and the northern part of Finland will benefit more (+53%) than the southern one (+13%). Towards the end of the century, Norway spruce and Scots pine will lose their share in growing stock, especially in the southern part of Finland (spruce more than pine), whereas the share of birch will increase throughout the century. Pretzsch et al. [56] presented the results of a comprehensive study on the forest stand growth dynamics in central Europe in the context of CC (expressed by increased CO_2 concentration, *N*-deposition, and rising temperatures) over more than a century (since 1870). They found that, when forest stands were exposed to CC in the 20th century, the most important European tree species (*Picea abies* and *Fagus sylvatica*) exhibited significantly faster tree growth (+32% and +77%, respectively), stand volume growth (+10% and +30%, respectively) and standing stock accumulation (+6% and +7%, respectively) in 2000 than in 1960. The authors also found that stands growing on better (more fertile) sites exhibited greater stand productivity compared to those on poor sites. Sigurdsson et al. [165] reported that, at low nutrient availability, the growth response to the elevated CO_2 level is expected to be restricted.

The economic value of the forests results from both species composition changes and forest productivity changes due to the potential replacement of economically important species by species of minor economic value. The most comprehensive study to date on the impact of CC on the economic value of the European forest was provided by Hanewinkel et al. [134]. The authors projected that the most economically important tree species will lose their current natural range (Norway spruce and Scots pine) and/or will shift northward (European beech and oaks), regardless of the climate scenario. Norway spruce is expected to lose approximately 43–60% of its current range until the end of the century, depending on the climate scenario. Scots pine (together with *Pinus nigra*) will also retreat to the north of Europe, and the contraction of its range is expected to be at the level of 57–72% of its current range by 2100. In the case of deciduous species (beech and oaks), the situation seems better; however, their distribution range is also expected to shift northward until the end of the 21st century. Currently, economically important oak species (*Q. robur* and *Q. petraea*) will benefit from CC much less than Mediterranean oaks (*Q. cerris, Q. ilex, Q. freinetto, Q. suber,* and *Q. pyreneica*), which are assumed to be the biggest beneficiaries of change. Mediterranean oaks will significantly increase (several times compared to 2010) their share in the European forests over the century. It is anticipated that, by 2100, up to 60% of European forests (with a mean of 34%) will be suitable only for Mediterranean oak forest types. However, these oak species are of low economic value nowadays, and it is, therefore, expected that the value of European forests will decrease significantly by 2100 [134].

2.2.3. Disturbances and Extremes—Climate Plagues

Natural disturbances (wildfires, floods, windthrows, and pest outbreaks) are the integral drivers of forest dynamics. As discrete events, they modify the forest structure, composition, and functions. Small-scale disturbances (e.g., the death of a single or a few trees) increase the heterogeneity of the ecosystem by creating a mosaic of habitats suitable for different organisms, increasing overall biodiversity [43,48,60,166–170]. Heterogeneity and diversity support healthy and resilient forest ecosystems, which may provide multiple services to humans. However, climate change can influence the spatiotemporal characteristic of disturbances, altering their known patterns [171,172]. Whilst the nature of discrete natural disturbances has been mimicked in silvicultural systems for decades, large-scale disturbances can be challenging for silviculture [173].

The observed pace and magnitude of CC are major factors triggering the frequency and severity of disturbances and extreme events, especially of a large-scale nature (but, see [174]). Whilst the prediction of extreme events is highly uncertain due to their high variability across space and time, the IPCC, in its *Sixth Assessment Report*, stated a *medium* (fire and floods) to *high confidence* (heatwaves and droughts) [2] that climate change will lead to more frequent and more severe events on the global scale [4,37,41,43,48,175–181]. If these predictions prove accurate, future extreme disturbances will significantly affect forests in the next decades of the 21st century.

Large-scale disturbances are responsible for significant forest damage, resulting in economic losses in the forestry sector. In Europe, forests are most intensively managed, and abiotic disturbances are the most important cause of damage. For instance, storms are responsible for 53%, fire for 16%, and snow for only 3% of the total damage. Biotic disturbance agents cause 16% of the damage, and insect-related disturbances (bark beetle outbreaks) are the most common ones and have great impacts [124]. In 1999, for instance, severe storms damaged European forests, impacting approximately 180 million m^3 of wood [124]. Running [178], Seidl et al. [43], and Forzieri et al. [171] claim that disturbances such as fires, droughts, and insect outbreaks are expected to be facilitated by a warmer and drier climate, whereas a warmer but wetter climate will favour wind- and pathogen-related disturbances.

Temperature-related disturbances (e.g., heatwaves and droughts) will be more significant in boreal and temperate forests than in the tropics, whereas water-related disturbances show the opposite trend. In the future, wind, drought, and insect disturbances will be more frequent than snow-related ones [37,43]. It is also acknowledged that regions experiencing extreme droughts today (e.g., the Mediterranean zone) will suffer even more from wildfires in the future [182]. However, as noted by Flannigan et al. [183], the influence of climate change on fire intensity may be a secondary effect. Changes to the fire regime may be due to decreased fuel moisture, increased fuel load, increased wind speed, or a combination of any of these factors.

For windthrows, it is generally hard to obtain reliable predictions since the modelling of storms and strong winds is difficult due to the largely stochastic nature of these events. Recent simulation studies have shown only a slight upward trend (up to a 2% increase) for boreal forests in the future. The slightly higher incidence of wind disturbance in northern forests can be attributed to the accelerated melting of permafrost [37].

Synergistic effects of different climatic variables of extreme value can be supportive of insect outbreaks. A warmer climate, together with prolonged drought periods, will make pests more active in the future, causing more significant damage in forests [41,136,184–187]. In addition to the assumed increased activity and damage by native pests, invasive insects can pose a serious threat to forest ecosystems around the world. Climate change may also increase the fitness of various fungal pathogens that do not manifest a significant role today but that, as a result of weakened trees due to stress factors, can cause epidemics, leading to significant losses [172,188–190]. Climate change can alter pathogens' life cycles, sporulation, and dispersal, together with the health conditions of host plants, making some pathogens more infectious than they are now. Changes in the precipitation regime can, for example, promote the occurrence of the pathogens responsible for needle disease. For example, increased mean winter temperatures, seasonal precipitation shifts, and heavy rainfalls promote *Phytophthora* ssp. occurrence. Thus, an increase in root rot caused by these species is expected in a warmer but wetter climate [188]. In the case of *Armillaria* ssp., one of the most destructive pathogens in European forests, CC is also expected to increase their activity and modify the growth of rhizomorphs, which increases the susceptibility of trees to these pathogens. In this case, a warmer and drier climate will be more beneficial for it [188,191,192]. As with insects, the migration of pathogens toward new regions with suitable climate conditions can contribute to increased forest damage.

3. Mechanisms of Forest Response to Climate Change

Environmental changes resulting from global climatic changes alter the growth, survival, and regeneration of forest tree species, ultimately affecting the stability and long-term persistence of forests. The functional traits (morphological, biochemical, genetic, physiological, structural, phenological, and behavioural characteristics) of tree species are fundamental for their responsive capacity to cope with novel climates [132,193,194]. The response of trees to CC involves phenotypic plasticity and adaptive evolution, and the role of these two mechanisms is widely discussed [54,127,195,196].

3.1. Phenotypic Plasticity—A Property of Individuals to Survive

The persistence of forest ecosystems under climate warming depends on the adjustments of functional traits (morphological and physiological), described as phenotypic plasticity (PP) [51,126,196–200]. This term is defined as the ability of a single genotype to produce different phenotypes under different environmental conditions, resulting in similar or higher fitness (survival and reproduction) compared to that without a phenotypic response to these changing conditions [51,126,199]. A facultative and reversible form of plasticity is acclimation, which alters short-term physiological processes in response to environmental variation. Other forms of plasticity are developmental plasticity, environmental induction, inducible defence, maternal effects, and epigenetics. The phenotypic response involves the proper signalling pathways that detect environmental change and transmit the signal to selected regions of the genome to modify gene expression, which can be tracked via changes in the transcriptome and proteome. Phenotypic plasticity, which is a fast-working process, is perceived to be the crucial mechanism for tree species performance and survival in rapidly changing environments [127,197]. Phenotypic plasticity has already been shown to be important for tree performance and survival in changing conditions [198,200].

A few remarks should, however, be made about the limitations of phenotypic plasticity in an effective form of CC mitigation. First, PP can be adaptive, neutral, or maladaptive, and it is extremely difficult to assess and predict the outcome of the plastic response under natural conditions [196,201]. Also, fitness-related traits are under strong selection and should, thus, be limited in their plasticity. Second, adaptation to new conditions rarely involves a single trait but rather a set of traits. Some functional traits may have greater plasticity than others, and different functional traits may also exhibit different plasticity to different stress factors. The situation complicates the complex genetic architecture of functional traits—polygenic inheritance (many genes encode a single trait) and pleiotropy (one gene is involved in different biochemical pathways). Third, different individuals within a population may exhibit different plasticity, and, therefore, the response of the entire population may vary. Considerable variability in plastic responses among populations has been reported [126]. Finally, PP may include a maladaptive reaction to altered conditions because new phenotypes are of reduced fitness or are further away from the new adaptive peak. However, in this case, a maladaptive plastic response may act toward favouring the genetic adaptive response [202].

Whilst plasticity is seen as a rapid response of the species to an altered environment, it is possible, however, that it may retard evolutionary adaptation to novel conditions because it modifies genotype selection [196,200,203]. The question of whether PP will promote or retard the evolutionary rate of species response to CC is still discussed [159,202,203]. Another interesting question is to what extent plasticity can be selected since it is under genetic control and mirrors past selection [203].

3.2. Local Adaptation—Adaptive Evolution at Local Scale

Local adaptation (LA) is when populations attain higher relative fitness in the local site compared to other sites and non-local populations. In the results of natural selection, new genotypes better match the home site conditions. Different selective factors may result in LA, including ongoing CC that transforms habitats [51,203,204]. However, in contrast to PP, evolutionary adaptation is a much slower mechanism and requires high genetic diversity to be present in natural populations.

The potential for trees to respond to natural selection (and, thus, adaptation) depends on the effective population size, *Ne* [204]. It is defined as the size of the idealised Wright–Fisher population that would experience the same number of random fluctuations (genetic drift) at neutral loci or same amount of inbreeding as the population under study. Simplified, *Ne* quantifies the loss in genetic diversity from generation to generation. Population size is important because it controls the effectiveness of selection (natural and artificial) in such a way that the decrease in population size decreases the response to selection and, thus, the adaptive potential [204,205]. Studies show that *Ne* is often 1/2–1/10 of the census population size, but it may be even smaller. Generally, forest trees are assumed to have a high *Ne* due to their wide distributional ranges, predominantly outcrossed mating system, and high gene flow, which all boost genetic diversity, crucial for adaptability [204–206].

Evolutionary adaptation requires changes in allele frequencies from generation to generation. Trees are long-lived organisms with an extended juvenile phase [206]. Consequently, there are some doubts regarding the pace of evolutionary change reachable for tree species in the context of the experienced velocity of CC. Nevertheless, the examples of rapid evolution in invasive tree species deliver some clues about the feasibility of adaptation through the evolution of forest trees [207].

Theoretically, the rise in local adaptation could be constrained by gene flow, which is exceptionally high and covers long distances in tree species. Whilst extensive gene flow (via pollen and seeds) is perceived positively in the case of tackling CC via migration, it could inhibit evolutionary adaptation due to maladapted genotypes. Genomic studies, provenance trials, and transplant experiments prove the ubiquity of LA among forest tree species [124,208,209]. The apparently opposing relationship between LA and high gene flow in trees has not yet been fully understood. However, the particular genomic architecture of trees, i.e., polygenic inheritance of traits and the emergence of few but more tightly linked loci of larger-effect-size alleles, occurring under relatively strong selection, is a favoured hypothesis [209,210].

Besides divergent natural selection and gene flow, interspecific hybridisation, naturally occurring among many tree species (e.g., *Quercus* ssp., *Populus* ssp., *Abies* ssp., *Pinus* ssp., or *Picea* ssp.), is currently considered a possible factor accelerating the needed evolutionary shift [51,154,211]. Due to adaptive introgression, new alleles required in novel conditions could mitigate the adverse effects of CC. Transgressive segregation, the result of introgression and selection, can lead to the emergence of individuals that will have their phenotypes outside of the range of the parental individuals [127]. Recently, adaptive introgression from *Q. robur* has been proposed as the possible driver of the adaptation of *Q. petraea* populations to higher elevations and wetter climates [208]. Hybridisation between *Fagus sylvatica* and *F. orientalis*, the latter growing under much harsher climatic conditions in southern Europe and West Asia, is being discussed as a possible scenario to accelerate the adaptive evolution of European beech, which suffers from drought-induced mortality [211]. From a wider perspective, adaptive hybridisation represents the concept of assisted gene flow, which helps push forward the adaptation to novel conditions resulting from CC. Besides the interspecific level, it might also be applied to the intraspecific level, i.e., by hybridising populations of the same species but that have been adapted to divergent habitat conditions. However, some caveats need to be considered, such as inbreeding depression, that may disrupt beneficial clusters of loci, leading to decreasing fitness of hybrids not only to novel climatic factors but also regarding non-targeted traits [212].

4. General Concept of Adaptation Facing Uncertainty and Risk

Adaptation means "adjustments in natural or human systems in response to actual or expected climatic stimuli or their effects, which moderates harm or exploits beneficial opportunities" [4]. Adaptation to CC is recognised as a management strategy aimed at adjustments in ecological, social, and economic systems in response to the effects of changes in the Earth's climate system [213,214]. Adaptation, in general, can be reactive, anticipatory, autonomous, or planned. Biological adaptation is autonomous and reactive, meaning that it is not a conscious response to CC but is triggered by it. Autonomous ecosystem adaptation may be understood as the capacity of the ecosystem to adapt naturally to environmental changes, thus without deliberate and planned actions. Planned adaptation, in contrast, is the result of a deliberate decision based on the awareness that action is required to maintain or achieve a desired state of the system [215]. Whilst expected changes in environmental conditions due to CC may be poorly understood, planned and anticipatory adaptation can be fraught with the risk of failure [4].

Many adaptation measures focus on reducing system (e.g., forest) vulnerabilities or enhancing the potential benefits of change. In the case of forestry, adaptation aims to decreasing forest vulnerability or enhancing forest stability (resilience and resistance) in anticipation of expected changes, e.g., due to CC. Forest vulnerability can be defined as the predisposition of the forest to be adversely impacted by a change and can be determined via two elements: (1) exposure; (2) sensitivity and adaptive capacity [4].

Adaptive forest management (AFM) can be defined as activities aimed at preserving and developing the functionality of forests as a condition for meeting future demands for forest goods and services [33,216]. If the forest ecosystems adapt autonomously in an acceptable way, foresters will not have to work against the impacts of CC. Thus, they will employ currently existing adaptive measures. However, the pace of environmental transformations imposed by CC and the challenges that will emerge convince us that adaptation in forestry should be planned. This type of adaptation requires new or modified procedures (tools and actions), which implies an awareness of the new environmental boundary conditions. This requires not only novel silvicultural guidelines but also new legislative and organisational approaches [217]. Adaptation in forestry includes wide issues related to site, ecology, risk and uncertainty, forest products and markets, gaps in professional training, the balance between national and international aspects of forestry, as well as human and social dimensions [217]. The most important adaptation measures in the context of silviculture appear to be those that take into account changing habitat conditions (site), the ecology of forest tree species, and the risk (or uncertainty) associated with the impact of projected changes on the response of trees and the forest. Most current actions implemented on the basis of incomplete knowledge of the impact of CC on forest ecosystems will likely involve some risk of failure. Therefore, it is widely accepted that AFM should be more or less similar to risk management [15,33,153,217]. One approach to risk management in the context of forest ecosystems is managing the forest as complex adaptive systems, which aims at increasing the adaptive capacity of the systems in the face of increasing uncertainty (risk) due to CC [19,21,34,218–220].

The basis for searching for the optimal adaptation strategies in forestry stems from the assumption that today's forests are poorly adapted to future environmental conditions resulting from ongoing CC [221]. Despite the known shortcomings in CC modelling and the ambiguity of CC scenarios, foresters should take action now. Whilst the change in the means of bioclimatic variables should not be a problem for adaptation, the amplitude of such changes will be significant for the persistence of the forest ecosystem. The reasons for the need for AFM are also related to the presumed negative effects of CC, potentially affecting forest ecosystem health, threatening forest stability, and involving a myriad of socio-ecological benefits [33,153,221,222]. Adaptive management will also help to enhance the role of forests in mitigating CC by increasing carbon sequestration and permanent carbon fixation in biomass and forest soil [8,223,224].

5. Strategies of Adaptive Forest Management

In general, AFM aims to decrease the vulnerability of today's forests to achieve the following: (1) increase the resistance of the forests to change; (2) increase (promote) resilience to change; (3) enable the forest to react to change. All this is to ensure the forests' continuity and their sustainable capacity to meet the needs of society in terms of goods and services in the uncertain future [33,153,225]. This means that AFM should allow the forest to cope with unfavourable abiotic (wind, fire, snow, flood, frost damage, and drought) and biotic (insects, pathogens, and invasive species) factors threatening their stability and functionality. Some problems with how to obtain resistant managed forests may arise due to indirect and yet-to-be-recognised effects of climate changes or their lagged effect on the forests. Consequently, such management will require more intensive actions than we currently suppose. Moreover, significant investments in treatments might be needed. Intensive management efforts to maintain the forest are recommended for forests with high sensitivity to potential changes (e.g., forests of simplified structure and maladapted tree species, among others). Low-sensitivity forests (e.g., selection forests and structural forests) are more likely to cope with change without intensive efforts [153]. However, risk-based adaptive management includes the probability of failure, which, in turn, may result in the loss of the whole forest ecosystem. Management for resilience means actions to promote forests capable of absorbing, reorganizing, and recovering after stress impact [153,226]. Frequently, management for resilience means simultaneous management for resistance and these two are complementary. Enabling the forest to respond adaptively to change means a change in accommodation rather than resistance to change. All treatments should mimic, assist, or enable natural processes (e.g., seed dispersal, colonisation, mortality, and migration) to encourage gradual adaptation to change. Adaptive forest management, and, thus, adaptive silviculture, should be dynamic, which means that all decisions made and their effects are continuously monitored to ensure the persistence of the multifunctionality of the forest [18,33]. Moreover, adaptive forest management should integrate CC into all facets of theoretical and practical forestry [217].

Adaptation in silviculture may be achieved by keeping or changing the forest structure and composition, depending on the state of the system. Three different strategies for forest adaptation can be indicated: conservative (maintaining the present forest structures), active, and passive adaptation [33]. They are different in their assumptions about their application and potential effects on forest ecosystems (Figure 2).

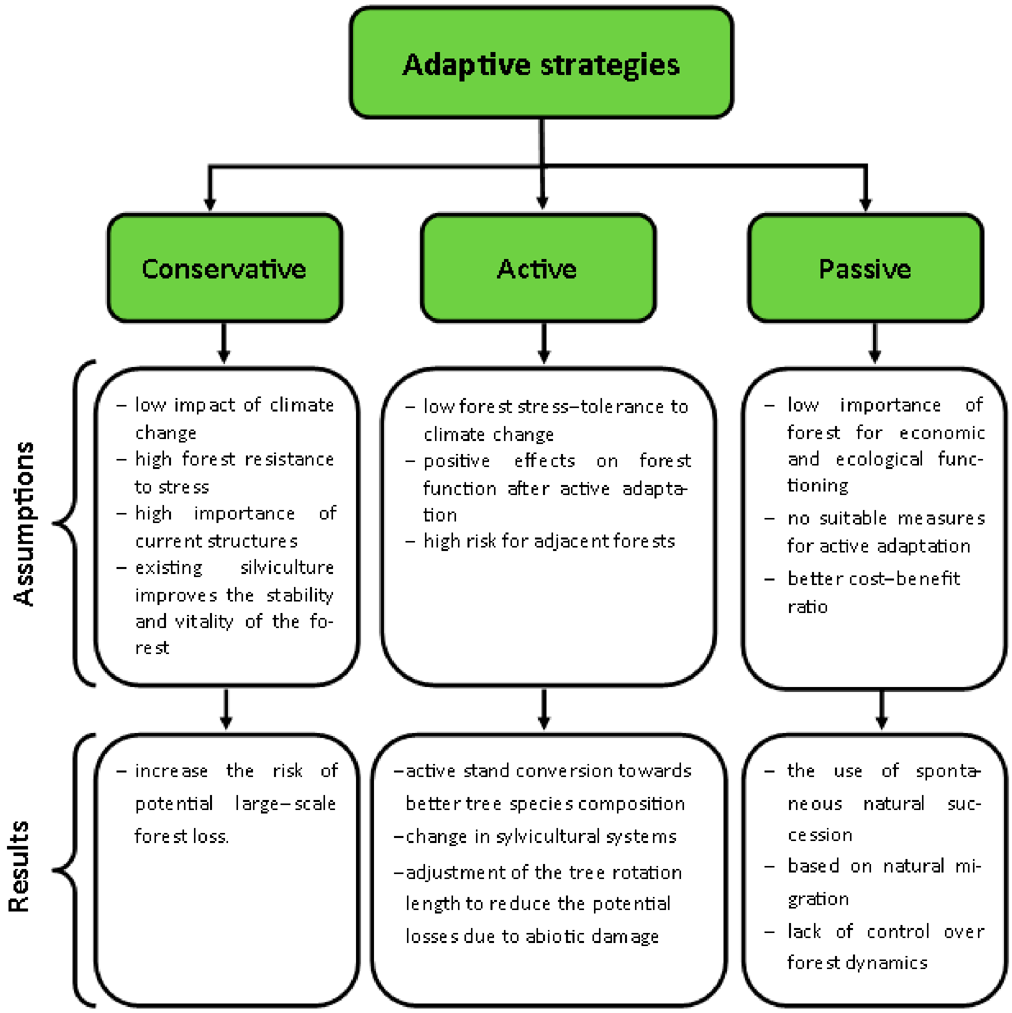

Figure 2. Assumptions and consequences of different forest management strategies (based on [33]).

Active adaptation includes different silvicultural treatments, e.g., tending, thinning, and regeneration, but also should allow so-called assisted migration in case of non-native tree species or provenances. It is assumed that these treatments will result in better effects than those achieved by natural forces alone. The disadvantage of this strategy is the higher input effort (costs). In contrast, the passive adaptation strategy is based on natural succession and natural migration of tree species; inputs are minimal, but this method allows for potential ecosystem losses due to disturbances caused by various factors (e.g., pests, wind, and fire). The conservative strategy (called *business as usual*) assumes that the current management procedures are sufficient to adapt the present forests to change, but, as in the passive strategy, the potential losses should be considered in the context of intense changes.

6. Silviculture—Actionable Activities in the 21st Century

Silviculture has evolved throughout history in response to changes mainly related to the owners' as well as the public's perceptions of the forest. The changing needs of society have transformed management practices and have led to the creation of structurally complex stands or a wider use of natural processes in the management of forest resources. Initially, the forest was treated as a kind of timber "factory"; over time, more attention has been paid to the non-productive functions of forests [19]. To face the changing needs arising from various socio-economic transformations, forest managers have developed procedures to ensure that these expectations are met. Until a few decades ago, silvicultural planning and forest management were governed by the assumption that habitat (climatic) conditions are relatively stable or change slightly, which made it easier for foresters to plan and manage forest resources. Thus, in the past, foresters operated in a predictable manner, resulting from the predictable development of the forest over a long period of time (e.g., the production cycle). Such a perception of forest management is questionable, and it is often pointed out that it might be neither effective nor rational in the light of the observed global changes due to climate warming [15,18,34,213,220,227,228].

In the 21st century, changes in silvicultural actions are needed. Modifying and reassessing silvicultural practices to ensure forest continuity and sustainable use of forests will be a major challenge for foresters and forest owners [19,33,228]. Although it is expected that there will be no one-fits-all solution in the face of global changes, some general principles of adaptive silviculture can be identified [13–15,21,25,26,153,225,228]. In general, for adaptation efforts to be effective, it is necessary to properly identify the risk factors, determine the forest's vulnerability (exposure and sensitivity and adaptive capacity) to the factor, and plan current and future actions to reduce that vulnerability to the defined factor together with monitoring of their effects (Figure 3).

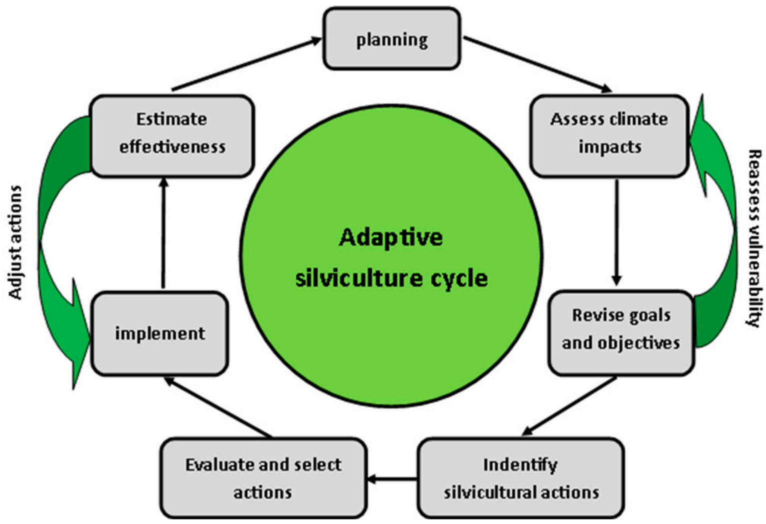

Figure 3. Dynamic adaptive silviculture cycle.

In forestry, the active and planned adaptation strategy appears to be the most effective and rational one. Silvicultural activities are part of such a strategy that fosters forest adaptation to novel and uncertain future conditions [25]. Silviculture has many tools to prevent the adverse impacts of CC. Modification of the harvest cutting system, species composition modifications, selection of tree species and provenances better adapted to anticipated changes, regeneration and afforestation approaches, thinning treatment modifications, and the choice of the length of the rotation cycle are among the most promising tools to foster forest adaptation to change [13,15,21,135,213,225,228].

Despite the still high uncertainty of CC projections and the even higher uncertainty related to responses of forest ecosystems to these changes, the general principles of adaptive silviculture should be in line with increasing species and structural diversity, maintaining or increasing genetic diversity, supporting the stability of individual trees, converting high-risk stands, and keeping low-level stand growing stock [15]. These goals are achievable through various silvicultural practices [9].

6.1. Heterogeneous Species Composition

Enriching the species composition of forests contributes to their better adaptation to change as different tree species are characterised by different levels of sensitivity (tolerance) to changes in various climatic and site parameters [15,225,228]. Multispecies forests fulfil the postulate of ecological insurance by spreading the potential risks due to CC much better than monocultures. Such forests better cope with, for example, pest outbreaks, which are most often species-specific [229]. The selection of tree species or species functional groups should be based on knowledge of their functional traits, e.g., tolerance to drought and higher temperatures and ability to re-sprout after disturbance, among others, which are largely responsible for the adaptive capacity of the species to perturbations [194,228,230]. When dealing with water stress resulting from drought periods, the benefits of multispecies forests are still discussed [231–235]. There are good examples of the benefits of species mixing compared to monocultures [236,237]. Pretzsch et al. [238] indicated that Norway spruce growing in pure stands showed the lowest resistance but better resilience (quicker recovery after drought period). Opposite to spruce, oak and beech were more resistant but less resilient. In mixed stands, spruce and oak performed similarly to pure stands, but beech was significantly more resistant and resilient in mixed stands than in monocultures. The increase in the resilience of mixed forests is greater for the conifer-broadleaved admixtures than for the broadleaved–broadleaved combinations [59,233]. Both mixture combinations showed better resilience to water stress than monocultures. Mixed forests also frequently show higher productivity, which can help mitigate potential economic losses in forestry due to changes in the share of tree species with different economic values [231,239,240]. However, the mixing effect on forest productivity should be further recognised in terms of the tree species, site condition, and stress factors (e.g., [241]). Different silvicultural actions can be recommended to fulfil this principle, e.g., the use of different silvicultural systems (selection, irregular shelterwood, and shelterwood systems), artificial planting (less-sensitive species or provenances), as well as the promotion of natural regeneration and assisted migration (non-native tree species or provenances). In more fertile sites, intensive thinning treatments may enhance the growth of understory (shade-tolerant) species. Importantly, to promote the regeneration of different tree species, the population of large herbivores must be effectively controlled, which is equally important for adaptation today.

6.2. Structurally Complex Forests

Promoting multispecies forests is in line with the principle of creating structurally complex forests. A species-specific growth pattern promotes tree size (diameter and height) inequality in a forest, which is better suited to change than even-sized stands. Structurally complex forests cope better with different adverse climate-related factors, such as pest outbreaks and pathogen diseases, water stress, and fire- and wind-related extremes, as trees of different sizes show different levels of sensitivity to stress factors (e.g., [131]). For example, greater variation in tree height leads to a decrease in the average stand height, making such stands less sensitive to wind-related disturbances [13,33]. The implementation of selection single or group cutting, as well as irregular shelterwood cutting, resulting in gaps in the stand canopy and enables the occurrence and growth of trees of different generations. Better growth conditions for understory individuals are also ensured by more intensive thinning operations [13,33,225,242–244]. Structurally complex forests can also be shaped via selective thinning or thinning from above, in which individuals of good health status are maintained regardless of the stand layer in which they occur. Structurally complex forests can also be achieved via variable density thinnings. In monocultures, underplanting of tree species and shrubs is recommended to structurally diversify such stands (e.g., [242–244]). It is worth keeping in mind, however, that multi-layered forests are potentially more susceptible to intense fires than single-layered ones; therefore, in regions where wildfires are common, this approach should be practised carefully, with a thorough recognition of the fire risk.

6.3. Increase Genetic Diversity

The adaptive capacity of trees and forests largely depends on the genetic diversity. A common practice in forestry is to rely on the natural abilities of trees to cope with a changing environment [15,127,245,246]. The use of cutting systems that promote natural and artificial regeneration, retaining old trees during harvesting or trees of poor quality but vital during thinning treatments, can increase the natural genetic diversity of the stand. Also, extending the rotation cycle in the case of certain managed forests can be worth considering [15]. In light of unprecedented CC, special attention should be paid to assisted migration, concerning not only tree species but also provenances [60,149,213,245,246]. Higher genetic diversity in the forest can also be achieved by changing the selection criteria during thinning treatments [13,247,248]. Currently, selection criteria take into consideration traits relevant to timber production, which may reduce the genetic variability of the stand and, thus, its adaptation to novel environmental conditions [15,249].

6.4. Increase Tree and Stand Stability

In the context of increasing stand stability (resistance and resilience), recommended silvicultural measures should reduce the vulnerability of current forests to various climate-related stressors. Different tree species exhibit different levels of sensitivity to stress factors; therefore, it makes sense to promote regeneration cuts (management systems) that allow the regeneration of different tree species. Thinning treatments diversifying the forest structure (e.g., selective thinning or thinning from above) may increase the resistance of a stand to biotic and abiotic stressors [250]. More intense thinning treatments promote greater tapering of trees, which makes them more resistant to wind. Whilst dense managed stands are more susceptible to insect and pathogen attacks, increasing thinning intensities make them less prone to these damage factors. Less competition among trees, resulting from wider initial spacing, adequate vegetation management, and more intensive thinning, can lead to higher vigour in the remaining trees, making them less susceptible to biotic and abiotic stresses. The removal of dying and dead trees as a potential source of infections may be another measure worth considering as part of silvicultural treatments to enhance stand resistance in general.

6.5. Limited Growing Stock

A low-level growing stock is consistent with reducing the potential economic losses caused by CC-related factors, especially by storms and wildfires. The higher the density of trees, the greater the risk of wildfire due to higher fuel loads. The threat of wind damage increases with stand age and height. In regions where water stress will limit forest productivity, maintaining a lower growing stock will mitigate losses due to drought [15]. Shortened rotation cycles, intensive thinning treatments, reduced initial tree density, and a diverse species composition are adaptive silvicultural treatments that work in line with reducing potential climate-induced damage and losses.

As can be seen from the above, the principles of adaptive management and corresponding silvicultural activities are hardly new to foresters. Some of them are embedded in the current close-to-nature forestry paradigm [9,15]. However, growing concerns about the sustainability of today's forests in a changing world, as well as growing awareness among foresters, forest owners, scientists, and the public of the consequences of these changes, has fed the need to take more steps to increase the adaptive potential of our forests to unpredictable changes. This has contributed to the emergence of a new approach in forest management, in which the primary silvicultural goal will be to promote the functional complexity of the forest as the prerequisite for achieving forest management goals in a changing world. Increased general awareness of the threats to forest ecosystems from climate change has resulted in the development of a new approach to forest management that considers the forest as a complex adaptive system [19,21,218].

6.6. Complex Adaptive System (CAS) Approach in Silviculture

Observed changes in the environment might lead to the establishment of non-analogue environmental conditions to which forests should adapt. Increasing forest adaptation to novel conditions will require a more holistic silviculture approach [19,21,34,218,219,228,251]. The forest ecosystem is an excellent example of CAS, consisting not only of a single element (e.g., trees) but also of other elements, biotic and abiotic ones, that interact with each other in both linear and nonlinear ways at multiple hierarchical scales, with positive and negative feedback loops (Figure 4) [34,228,251]. This suggests that the response of the forest ecosystem to rapid changes in environmental conditions is not highly predictable, especially in terms of biomass productivity, species composition, or stand structure [19].

Figure 4. Properties of forest ecosystem viewed as a complex adaptive system (CAS).

The adaptation of a forest ecosystem to a changing environment is driven by system internal processes through changes in components, cross-scale interactions, and self-organisation processes [220,228]. Thus, adaptive silvicultural actions aiming at adaptation to external non-analogue conditions should focus on three characteristics specific to CAS: diversity in composition and structure at multiple scales, cross-scale interactions, and self-organisation processes (Table 1).

Table 1. Principles and actionable activities in CAS approach in forest management.

Principle	Silvicultural Actions Supporting the Principle of CAS Approach
Promotion of species and structural diversity	- Selection cuttings and irregular shelterwood cuttings; - Retention of large and old trees; - Establish mixed forests (increase functional diversity); - Selective, crown, and variable density planting and thinning; - Natural regeneration; - Assistance in species and provenance migration; - Rational wildlife management.

Table 1. *Cont.*

Principle	Silvicultural Actions Supporting the Principle of CAS Approach
Promotion of hierarchical interactions	- Selection cuttings and irregular shelterwood cuttings; - Establish mixed forests (increase functional diversity); - Selective, crown, and variable density planting and thinning; - Retention of large and old trees; - Underplanting.
Promotion of self-organisation	- Selection cuttings and irregular shelterwood cuttings; - Establish mixed forests (increase functional diversity); - Variable density planting and thinning; - Reduce salvage logging (ecosystem legacy).

The encouragement of species and structural diversity is based on the assumption that higher diversity leads to more possible developmental trajectories and, thus, increases the probability that at least one pathway will be successful in maintaining the forest and its services [228]. In the context of diversity, the diversity in functional traits (e.g., drought tolerance, water use efficiency, and the ability to re-sprout) is much more important than simple diversity in terms of the number of taxa. This is because functional traits are responsible for the functioning of the system. The promotion of relationships among different scales (temporal, spatial, and organisational) is based on the assumption that a high diversity of interactions and feedbacks (positive and negative) among scales will allow more internal processes to take place, even after a disturbance. The assumption behind this is that not only the diversity of components of the system is important for adaptation but that the diversity in interactions among these elements is no less important. Encouraging ecosystem adaptation through self-organisational processes takes into account not only focusing on simply species diversity or the diversity of interactions but also pays attention to a diversity that ensures the persistence of ecosystem self-organisational processes [19,228].

Therefore, CAS-compliant management should not only focus on emphasising species diversity and interactions but also on the kind of diversity that is particularly conducive to ecosystem self-organisation. In this context, the ecosystem can follow many potential paths, and the use of self-organisation processes allows the selection of the path that best suits the current conditions [229]. This principle of using natural processes to reduce human interventions corresponds to the principle of biological automation, emphasised in modern close-to-nature silviculture. It should potentially be applied in a phase of stand initiation as well as after disturbance when natural self-organisation processes ensure forest regeneration in various ways. In older forests, leaving dead wood and preserving old trees of different species also promotes self-organisation by providing so-called safe places for regeneration, seed banks, or ecological niches for other organisms [229]. As one might expect, the same silvicultural actions may work in accordance with all three guidelines.

As indicated above, modern silviculture, especially close-to-nature silviculture, has several features that promote the resistance of forests as well as their resilience and adaptation to new environmental conditions. These measures have been successfully implemented in practice for years. However, they may not be effective in the face of a rapidly advancing CC. In the diversification of ecological risks through the diversification of stand structure, the use of full genetic variability, regardless of changes, will be a kind of insurance policy, a sure hedge against losses under the uncertain conditions of the future.

7. Looking Ahead—Making the Uncertain Future More Certain

There is no doubt that Earth's climate has changed, is changing, and will continue to change. Despite our increasing knowledge of the complexity of the climate system, our more complete recognition of the interrelationships among the elements of this chaotic system and the fact that we know more and more about the adaptive capacity of species, populations, and entire ecosystems, we still need to be aware of the fact that the science (climate, ecology, and response ecology science) is not settled. Incomplete knowledge is always linked to uncertainty and, thus, the risk of decisions made on the basis of current knowledge. Being aware of this, we should remember that unpredictability and uncertainty are inherent in the future, and silviculture and forestry are no exceptions. In the context of forestry, uncertainty is related to the following: (1) uncertainty in the magnitude and rate of CC; (2) uncertainty related to the impact of these changes on forests; (3) uncertainty in the responses of forest ecosystems to change.

Silviculture and forest management have been adapting to new realities throughout their history due to changing public and forest owners' perceptions of the forest. In the 21st century, the most important goal of silviculturists will be to ensure the sustainability of the forest ecosystem in the presence of increasing threats to forests from CC. Maintaining forests that are resilient, resistant, and adaptable to change will be the most important challenge for foresters in the 21st century. The first two are within the context of forest stability. The looming question is how to deal with stability in the face of prolonged droughts, fires, insect gradations, or invasive species. Currently available procedures aimed at increasing forest stability in the face of these factors may not be effective in the case of their permanent co-occurrence. Some of the current silvicultural procedures in the context of forest stability should be re-evaluated under conditions of simultaneous and prolonged exposure to various stress factors. However, it seems that silvicultural practices aimed at spreading the ecological risk (within a broad frame of close-to-nature silviculture) will, nevertheless, be effective against climate stress. At least, it is our hope that they are.

To make the assumptions a reality, some scientific efforts should be made to fill some knowledge gaps within some areas of interest, with emphasis on the following issues:

- What functional traits of different tree species determine their adaptation to novel environmental conditions caused by CC?
- What is the relative role of phenotypic plasticity and adaptive evolution in the adaptation of different forest tree species to a warming climate?
- What are the long-term effects of elevated concentrations of atmospheric CO_2, rising temperatures, and frequent droughts on the physiology, phenology, and growth of different forest tree species?
- What is the role of climate-related disturbances in forest adaptation to a warmer and drier climate?
- How might CC alter the relationships among tree species and what is the impact of the altered competitive relationships on forest adaptation to novel conditions?
- What is the role of forest structural diversity in forest adaptation?
- Additionally, efforts to identify the suitability of the use of non-native tree species in future forestry need to be continued, and the resulting biological and ecological threats and opportunities in the face of projected CC scenarios need to be recognized.

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