



UiT The Arctic University of Norway

Department of Arctic and Marine Biology, Faculty of Biosciences, Fisheries and Economy

Can spruce forest stands be adapted to climate-driven natural disturbances?

The consequential effects of two key disturbance agents and their management in spruce dominated stands under climate change – A review

Carl-Michael Heimo Andersson

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Abstract

The purpose of the thesis is to support the initial stage of the Climate Smart Forestry Norway (CSFN) undertaken by a consortium between NMBU, NIBIO, LUKE (Finland), and Wageningen University & Research, which is a five-year project aimed to assess how Norway's forests are best managed in order to adapt to climate change. As part of the CSFN project a framework for quantifying probability and effects of natural disturbance linked to forest structure and climate change will be developed. Before quantifying probabilities of the main natural disturbances, a literature review on these main disturbance agents is set to begin in 2020, which is going to be supported by this Master project. Extensive damages to Norwegian spruce in Europe after massive outbreaks preceded by windstorms have moved scientists and foresters from trying to control the Eurasian spruce bark beetle to attempt to decipher the reasons behind epidemic populations. Previous literature has uncovered the physiological thresholds behind massive spruce bark beetle outbreaks. But changes in temperature averages, precipitation and human land use throughout Europe have called for different management strategies in the light of the strong coupling of climatic factors and spruce monoculture implementation to spruce bark beetle propagation, by means of direct and indirect effects. The strong interaction of windthrow, acute drought and spruce bark beetle outbreaks resulting in epidemic populations has been synthesized in this review and some of the proposed beetle control tools and landscape-forest stand management strategies from recent frameworks and reviews, such as *Climate Smart Forestry*, are introduced as a potential management solution to dampen the adverse consequences of climate-driven insect disturbances in boreal forests.

Keywords: Natural disturbance agent, Windthrow, Climate Smart Forestry, boreal forest, disturbance regime, Norway spruce *Picea abies* (L.) Karst, Eurasian spruce bark beetle *Ips typographus*

1 Introduction

Climate change has been a focal point in natural sciences for the last three decades. Under most climate change scenarios an increase in frequency of extreme weather events is expected in the boreal region (Mitchell, Lowe et al. 2006). Even though the occurrence of more extreme events is speculative (Benestad 2003), heatwaves with long-lasting drought periods, heavy rainfall and cyclonic storms can have a strong impact on the abiotic disturbance regime, whereas their effect on the interactions of boreal tree species and biotic disturbance agents, fungal or insect, is less clear (Mitchell, Lowe et al. 2006). Norway stands as one of the European countries with an expected increase in cyclonic activity along its coastline, which may significantly alter several natural disturbance regimes in Norway (Benestad 2005, Hanssen-Bauer, Achberger et al. 2005). In addition, warming temperature may not only exacerbate summer heat waves, but cause spring freeze-thaw cycles in Norway to fluctuate even stronger, whilst creating rainy winters which undermine the stability of soils throughout the landscape (Jönsson, Linderson et al. 2004, Benestad 2005, Larsen, Gregersen et al. 2009).

While it is uncertain, how climate change is driving natural disturbances and the distribution of nemoral species, boreal forests and montane forests are likely to experience an increase in natural disturbances perpetrated by xylobiotic insects (Overpeck, Rind et al. 1990). Hereby, temperature increases are key in regulating insect development, allowing them to survive during winter hibernation along with increasing the number of generations in a season (Lange, Økland et al. 2010, Raffa, Aukema et al. 2015, Jakoby, Lischke et al. 2019) and changes in interspecific interactions between host species and insects, as well as their associated enemies (Wermelinger, Epper et al. 2012, Raffa, Aukema et al. 2015). Not only can natural disturbances in the form of biological agents migrate northwards from the hemiboreal boundary line or produce more frequent outbreaks, but disturbance regimes of wind and fire may shift towards increased intensity, severity and shorter intervals between strong disturbances due to a changing climate in Eurasia (Kurz, Apps et al. 1995).

Cultural ecosystem services of European boreal forests are well integrated into values of societies in Scandinavia, but imminent climate driven changes in the state of boreal forests are not well communicated and understood amongst the public when changes in recreational possibilities happen slowly. On the other hand, regulating services regarding biotic disturbances are more concretely understood, which may for instance mean pest control by natural enemies which is ensured through sufficient niche diversity in forest community by allowing natural

succession to take place (Wermelinger, Epper et al. 2012). Ecosystem services of boreal forests are essentially manifold but impacted most by natural products are provisioning services as in harvesting products, especially in Northern Europe, which represents the least abstract ecosystem service. Timber and fibre for pulp production or harvesting residues used as biofuel are essential to the forestry industry that produced 11.18 and 10.36 million m³ of industrial roundwood in 2019 and 2020, respectively (excluding harvests for energy and decorative purposes) in Norway (Landbruksdirektoratet 2021), and employs around 70'000 people in Finland (Saarikoski, Jax et al. 2015). Whereas Norway spruce is mainly utilized in the pulp and paper industry, Scots pine is being studied as a potential complement to pulpwood in Norway, and is utilized as wood pellets (Stjørdal 2006, Filbakk, Jirjis et al. 2011). Norway spruce is of high economic importance in forestry industries of Scandinavia (Schlyter, Stjernquist et al. 2006). Moreover, it sums up to 42% of Norway's forests biomass and provides a range of ecosystem services to society because of its importance as an industrially relevant tree species (Breidenbach, Granhus et al. 2020).

Ecological responses in forest ecosystems to extreme weather events can facilitate indirect climate feedbacks (Bonan 2008), which may free stored carbon dioxide through increased decomposition of windthrown trees, possibly leading to changes in species composition and subsequently, forest structure (Overpeck, Rind et al. 1990). Therefore, feedback mechanisms of forest management strategies, and biotic and abiotic disturbance agents such as forest fires, windthrow, insect, root rot and other fungal pathogens need to be considered to ensure ecosystem service provision (Overpeck, Rind et al. 1990, Kurz, Apps et al. 1995, Angelstam and Kuuluvainen 2004, Seidl, Thom et al. 2017).

Natural disturbances are an important component of natural forest dynamics, and many tree species have adapted to ecosystem-specific disturbance regimes (De Grandpré, Waldron et al. 2018). Whereas fire is the predominant natural disturbance in drier boreal forests of Southern Scandinavia, wind and bark beetles next to fungal pathogens are the most significant natural disturbance in the rest of the European boreal forest (Thom and Seidl 2016, Hlásny, Krokene et al. 2019). Natural disturbances impact forest structure and function through their effect on species composition, forest area, age class distribution and ecosystem carbon sequestration (Kurz, Apps et al. 1995, Angelstam and Kuuluvainen 2004, Rich, Frelich et al. 2007). Depending on the severity, intensity, and frequency, strong or extreme disturbances such as storms and massive beetle outbreaks can have long-lasting consequences after stand replacing

mortality. Subsequent successional dynamics come into play and may lead to an altered forest state, altogether (Angelstam and Kuuluvainen 2004).

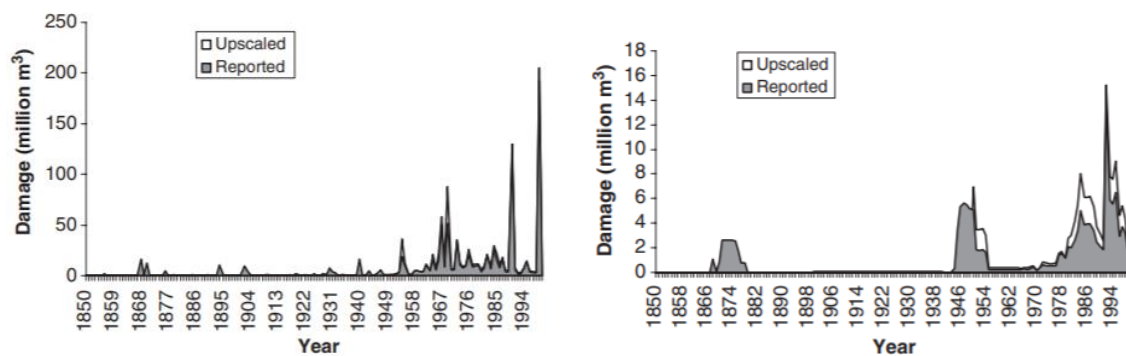


Figure 1: Wood damages from wind (left) and bark beetles (right) in million m³ to European forests from 1850 to 1994, both reported and upscaled. Modified from Schelhaas, Nabuurs et al. (2003).

In Norway, the destructive potential of massive outbreaks of the Eurasian spruce bark beetle *Ips typographus* in Norway has been witnessed during an outbreak in 1971-1981, where close to five million m³ of spruce were killed in south-east Norway (Bakke 1989). Other regions in Scandinavia and Central Europe have experienced similar or worse outbreaks during the 20th and early 21st century (Wichmann and Ravn 2001, Jönsson, Harding et al. 2007). The latest spruce bark beetle outbreak of epidemic proportions in Norway was significantly aided by the extratropical cyclone *Dagmar* in 1987 that caused up to 300'000 m³ of windthrown spruce in Østlandet, Norway (Krokene and Økland 2015). By creating conditions for *Ips typographus* to reach epidemic populations by supplying dead spruce as a resource, storms could have significant impacts in boreal forests (Økland and Berryman 2004). Krokene and Økland (2015) argue that a 100-year record storm may have the potential to fell up to 18 million m³ of forest stands only in Østlandet. Thus, extreme events could aggravate damages to spruce forests even further if high populations of *Ips typographus* persist for several years until resource is depleted. An increasingly strong disturbance regime in boreal forests has been assessed to be favored by a warming climate (Seidl, Schelhaas et al. 2014, Seidl, Thom et al. 2017) by generating an increased risk of more frequent severe storms (Benestad 2005). At what rate the climate induced changes in severe storms or drought periods are underway is unclear, but the strong interaction between massive bark beetle outbreaks after extreme windthrow events has been identified and an increased susceptibility of boreal forests under other forms of extreme weather such as drought hints towards what initial studies are showing could become a concerning trend (Netherer, Panassiti et al. 2019).

The properties of boreal forests to drive biogeophysical cycles and climate forcing make them critical in mitigating climate change (Bonan 2008, Bright, Antón - Fernández et al. 2014) and it provides a range of socioeconomic services (Saarikoski, Jax et al. 2015). This is put forward by the idea of Climate Smart Forestry (CSF), wherein forests can play important roles in maintaining or enhancing global forest carbon stocks, maintaining ecosystem services and adapting forests towards climate change by being managed through redefined silvicultural practices, thus making them more resilient in the process (Verkerk, Costanza et al. 2020).

This review aims to outline past knowledge of two key natural disturbance agents, windthrow and Eurasian spruce bark beetle outbreaks, and their interaction in boreal forest, whilst summarizing what studies have shown of how climate change potentially drives changes in their respective regimes in spruce dominated stands. According to Hlásny, Krokene et al. (2019) an important knowledge gap lies in the synthesis of existing literature on the population dynamics of Norwegian spruce bark beetles and available management strategies to constrain epidemic *Ips typographus* outbreaks. In terms of ecosystem service provision under CSF strategies, this review will attempt to reflect on how these massive outbreaks affect forest managers and other stakeholders.

2 Methods

Google Scholar was screened for peer-reviewed scientific papers addressing the key search words as follows: Natural disturbance, windthrow, (Eurasian) spruce bark beetle *Ips typographus*, Norway spruce *Picea abies*, boreal forest, climate change, drought stress, ecosystem-based approach, climate smart forestry, sustainable forest management, bark beetle epidemic, or outbreak.

For the sake of readability, the Eurasian spruce bark beetle *Ips typographus* will be written as ‘spruce bark beetle’ when other bark beetle species are not clearly stated. In addition, ‘spruce’ will denote Norway spruce *Picea abies* in the thesis. Papers that did not emphasize the hemiboreal boundary line edging boreal forests as well as other biotic disturbances than the Eurasian spruce bark beetle *Ips typographus* were disregarded, unless they included windthrow and the Eurasian spruce bark beetle next to other disturbance agents as their matter of subject. As an example, climate driven effects on the spruce budworm *Choristoneura fumiferana* outbreaks dealing with balsam firs, white and black spruces in North America, were not

included. Over-reaching papers were included if it utilized a methodological approach that could be applied to any ecosystem.

For reasons to limit the scope of the thesis, fire will not be further expanded upon. It is nonetheless important to know of the importance of fire in boreal forests and how it potentially can interact with other natural disturbances whilst undergoing climate driven changes in its regime. One of these potential changes could be a shift detected in conifer forests being dominated by pine instead of spruce in the future, since Scots pine (*Pinus sylvestris*) is found to be well-adapted to fire, which poses the question for forest managers whether to push for spruce monocultures on sites susceptible to *Ips typographus* (Bradshaw, Holmqvist et al. 2000).

Papers were included that utilize climate scenarios based on “business as usual” simulation models (Seidl, Rammer et al. 2008), such as scenarios portrayed in the previous IPCC assessment reports (Pachauri, Allen et al. 2014) for the 21st century. The criteria to select papers assessing damage risk from bark beetle disturbance were based on well-studied physiological thresholds (Wermelinger and Seifert 1999) for *Ips typographus* development; sum of degree days above threshold temperature (8.3 °C), development optimum (30.4 °C) and limit (>38.9 °C). Additionally, flight activity as in swarming requires a minimum temperature threshold of 16.5°C, optimum between 22 and 26 °C and upper limit of 30°C (Lobinger 1994), and initiation of facultative diapause at daylengths less than 15 hours (Økland, Netherer et al. 2015).

To assess the effect of climate change on natural disturbances in boreal forests, the definition of boreal forests included hemiboreal as well as montane forests, due to their species distributions and associated adaptations to similar climatic conditions (Angelstam and Kuuluvainen 2004). This definition encompasses boreal forests, principally focusing on Scandinavia and Eurasia. North American boreal forests are also of interest for the purpose of understanding disturbance regimes, but less for historic disturbance data, due to the different climatic systems and biotic disturbance agents. Furthermore, spruce stands grown outside of their natural range such as in Central Europe are of great interest and relevance, not only due to the socio-ecologic impact and management implications, but also due to their increased susceptibility to climate induced bark beetle outbreaks (Hlásny, Mátyás et al. 2014). For the purpose of investigating climate driven effects on natural disturbances in boreal forests, a distinction should be made between unmanaged mixed stands and intensely managed forest stands, while in Northern Scandinavia both are practically dominated by one or two tree species,

Norway spruce *Picea abies* and Scots pine *Pinus sylvestris*, respectively, with the northernmost parts of Fennoscandia transitioning towards downy birch *Betula pubescens*.

The objective of CSF is to provide guidance to forest managers to improve forest resilience against natural disturbances and climate change. One of the key tools that forest managers can use towards this goal is to modify forest structure (Verkerk, Costanza et al. 2020). Therefore, a secondary aspect of the thesis will be linking two key disturbances, bark beetles and wind, to boreal forest structure (Verkerk, Costanza et al. 2020).

The selected papers ranged from years 1977 to 2021. Previous reviews (Sousa 1984, Kuuluvainen 1994, Ulanova 2000, Angelstam and Kuuluvainen 2004, Wermelinger 2004, Schlyter, Stjernquist et al. 2006, Turner 2010, Kausrud, Økland et al. 2012, Mitchell 2013, Økland, Netherer et al. 2015, Díaz-Yáñez, Mola-Yudego et al. 2016, Seidl, Thom et al. 2017, Valta, Lehtonen et al. 2019, Venäläinen, Lehtonen et al. 2020) and studies based on global climate models, historical as well as paleoclimatic and fossil pollen data were part of the literature, with key knowledge gaps focusing on consequential effects of climate change on natural disturbances, disturbance regimes and their links to forest structure dynamics, were reviewed. The approaches for model use included estimations through simple analytical models for equilibrium dynamics and simulation models, which aid in answering what type of structures prevail under historical or natural dynamics (Bradshaw, Holmqvist et al. 2000).

To pursue the task of reviewing this subject matter, the following questions serve as a guideline: (1) How have wind and bark beetle disturbances affected Scandinavia's forests historically under boreal conditions? (2) What is the current state knowledge on the climate driven effect on these disturbances? (3) How do forest structure and successional dynamics interact with disturbance mitigation or exacerbation? (4) How do the main management methods compare when assessing the differences in damages caused by *Ips typographus* outbreaks and the potential consequences for Norwegian forests?

3 Natural disturbances in boreal forests

3.1 Disturbance regimes

Natural disturbances serve a vital purpose to boreal forests. Through creating gap dynamics within stands of forests, they drive niche construction for shade-intolerant plants and a variety of associated animal life, diversification of age classes and thus enhancing the vitality of forests (Angelstam and Kuuluvainen 2004, De Grandpré, Waldron et al. 2018). Each stand of forest

has its own ecosystem-specific disturbance regime (Fig. 1), which brings forth site-specific adaptations to its respective disturbance regime (Sousa 1984, Gutschick and BassiriRad 2003). This begs the questions, whether climate change may cause a discrepancy with boreal forest communities not being sufficiently adapted to a stark increase in natural disturbance frequency or severity due to climate change, and thus be stressed with an offset time lag between changes in disturbance regimes and consequent adaptations or acclimatization?

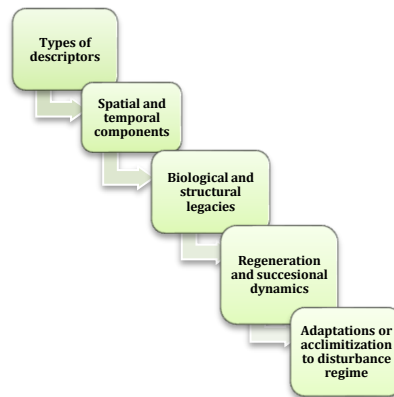


Figure 2: Layout of disturbance regimes. Descriptors can be used in disturbance ecology to describe natural disturbances. According to Jentsch (2007) these descriptors include temporal characteristics (such as frequency, duration, and seasonality), spatial characteristics (such as patch size, shape, and distribution), magnitude (or intensity), severity, specificity (to species, size, or age classes), and interactions of natural disturbances. In boreal forests spatiotemporal descriptors may determine the forest structure, whereas intensity and severity may e.g. determine microsite creation through differences in soil disturbance, thus influencing succession of a disturbed forest stand (Angelstam and Kuuluvainen 2004).

In boreal forests, the main natural disturbances include agents such as fire, windthrow, bark beetles, root rot and some fungal pathogens (Climate Smart Forestry Norway project description, 2020). Fire is the dominating natural disturbance in boreal forests (Thom and Seidl 2016), particularly in drier Southern forests of Scandinavia, with the most recent extreme fire in 2018 burning up a large part of forests in Southern Sweden. Fire differs from windthrow and bark beetle outbreaks in its spatial-temporal characteristics. Foremost, fire is mainly driven by long-lasting drought and an increased amount of undergrowth to fuel burning and increase connectivity of individual fires, which may then erupt into massive regional outbreaks. The function of deadwood production is another characteristic that differs in wind disturbances in relation to the disturbance agents in the boreal forest such as drought and forest fires. What is left after a natural disturbance event are biological legacies which are generally important for the regeneration and succession patterns of the forest stand (Angelstam and Kuuluvainen 2004).

Disturbances initiate regeneration and succession after disturbance events where the forest stand undergoes more or less distinct developmental stages (Angelstam and Kuuluvainen 2004). These represent structural components as well as age distributions of the canopy trees,

shrub undergrowth and regeneration of trees. Depending on the spatial scale of damage from the disturbance event, the regime that follows is initiated from each stand individually, with an extreme disturbance event having the potential of restoring complete stands to their initial phase. Hereby, a stand-replacing disturbance event is rarely the complete destruction of mature trees, as most likely core groups remain with the ability of initiating succession (Angelstam and Kuuluvainen 2004). This leaves to argue that monocultures are manipulated in their structure as well as dead wood and species distribution, which drives the resurgence of desired forest components such as specific stem density (Burton, Messier et al. 2003). However, this manipulation may also entail changes in the decomposition dynamics, soil properties, as well as insect and fungal community assembly. By attributing the stand with a homogenous structure, the risk of stand-replacing windthrow, fire or massive insect outbreak may be increased, whereas remnant structural traits of a varied age composition of the disturbed forest may aid in successional development of the stand and offer elasticity to disturbances. Moreover, climate change is likely to lead to an ‘asymmetry of rate of change’ in boreal forests, where rapidly changing environmental conditions lead to failure of succession or regeneration because of inaptitude to cope with extreme natural disturbances due to missing natural forests or old growth characteristics (Kurz, Apps et al. 1995). The spatial components of the other types of disturbances are followed up on in the next chapter.

An important component of disturbance regimes is the intensity, which according to Turner (2010) is an intrinsic characteristic of a disturbance event whereas the disturbance severity stands for a measure of its ecological effect (Rich, Frelich et al. 2007, De Grandpré, Waldron et al. 2018). The severity of a disturbance is determining from what developmental stage a stand is regenerating from with the proportion of woody debris, broken branches, uprooting and soil disturbances all factoring into the severity paradigm (Angelstam and Andersson 1997, Gutschick and BassiriRad 2003, Roberts 2004, De Grandpré, Waldron et al. 2018).

Disturbance regimes for forests form a continuum, where three main post-disturbance dynamics may set in simultaneously (Angelstam and Kuuluvainen 2004), which are (1) Succession with stand development after stand-replacing disturbance, (2) Cohort dynamics following partial disturbances and (3) Gap dynamics after mortality of a single tree or small group of trees. Whereas (1) and (2) are characteristic for intermediate to severe disturbances in boreal forests, namely fire and wind, gap dynamics can be associated to small-scale biotic and autogenic disturbances operating at the scale of individual trees and tree groups (Kuuluvainen 1994, Kuuluvainen, Syrjänen et al. 1998, Angelstam and Kuuluvainen 2004), albeit the latter holds

up under normal or endemic conditions and most likely not during epidemic spruce bark beetle outbreaks.

3.2 Spatial component and structural legacies

An important aspect of the structural component of natural disturbances, next to extreme events that make way for complete stand succession and regeneration, or die-offs, is the gap-dynamic of forest stands, which creates two types of age distributions, according to Dyrenkov (1984). These include even and patchy spatial tree age distributions, which can be associated with smaller and larger gap sizes, respectively. But as Angelstam and Kuuluvainen (2004) argue, each of the three dynamics associated to disturbance regimes affect the probability of occurrence of one another – “Therefore disturbances may also appear as mixed patterns in different time and space scales”. Angelstam and Kuuluvainen (2004) and Syrjänen, Kalliola et al. (1994) conclude that on wet spruce-dominated sites gap dynamics should dominate, however, severe stand-replacing disturbance events may befall this forest type periodically, and initiate cohort dynamics.

Regarding the dynamics of regeneration and succession after windthrow, catastrophic large-scale windthrows are considered at landscape and associated to secondary succession (Angelstam and Kuuluvainen 2004). Single or multiple smaller events affecting the forest community are associated to gap phase while individual tree fall is associated to micro-succession dynamics (Ulanova 2000). Windthrow is, parallel to succession, a continuous process, where the time when an event occurred is hard to determine, due to the mechanism of damage and the scale. Furthermore, a lag of tree mortality may be expected, as windthrow does not necessarily kill trees instantly, but break off significant parts of the tree or weaken it to an irreversible point, where death sets in after a few months to years. This makes point assessments of stand damage difficult to estimate within fixed time intervals (De Grandpré, Waldron et al. 2018). The mechanisms of damages can lead to patch spreading, where trees at edge of stand are exposed and may open up further points of attack for wind to penetrate.

A question that remains is, whether structural changes derived from climate change driven disturbances lead to functional disparity. Biome shifts may take very long in comparison with climate effects in disturbance regimes. The effect of climate driven disturbance regimes on succession patterns may thus bring structural novelties on a short time scale within the forest community. Therefore, changes brought on by climate warming in the functional diversity of unevenly aged natural spruce stands may have severe consequences for ecosystem services of

the boreal forest, whereas unevenly aged forests owning higher niche diversity are able to promote succession by supplying seeds to small scale disturbed areas where younger trees cannot (Kuuluvainen 1994, Angelstam and Kuuluvainen 2004, Lehnert, Bässler et al. 2013).

4 Norway spruce *Picea abies*

Picea abies (Linnaeus) Karsten 1881, or as it is commonly referred to, Norway spruce, is the most economically important tree species in Scandinavia with vast proportions of spruce dominated stands throughout Fennoscandia (Bradshaw, Holmqvist et al. 2000, Angelstam and Kuuluvainen 2004). Norwegian spruce is found on many sites throughout Scandinavia, but mesic sites have shown it to proliferate into stands dominated by this species (Angelstam and Kuuluvainen 2004).

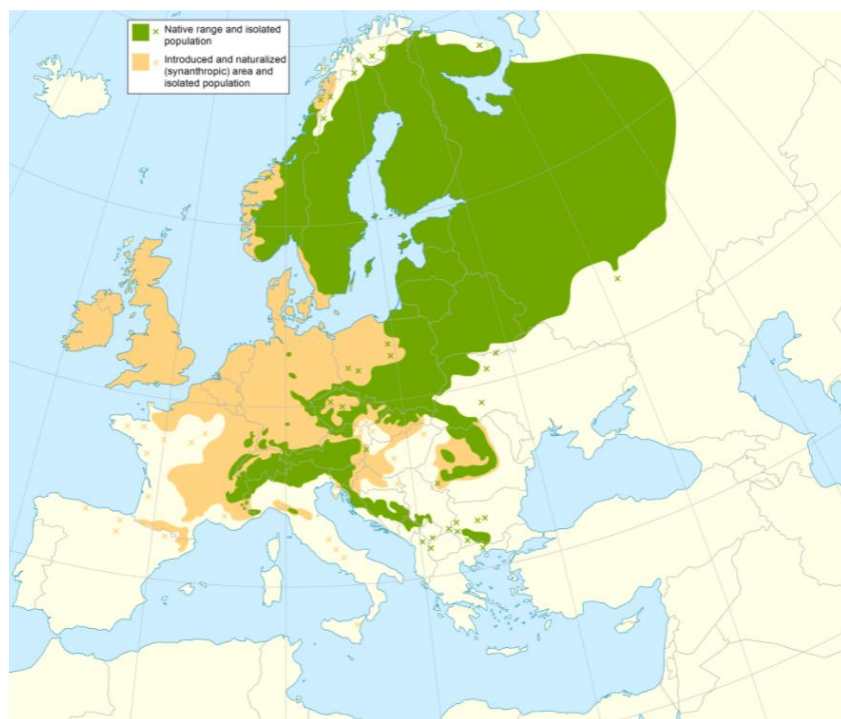


Figure 3: Distribution of native and introduced and consequently naturalized ranges of Norway spruce *Picea abies* (L.) Karst in Europe (The European Commission's science and knowledge service 2017).

Norway spruce has established itself within most of Scandinavia after the last ice age (Bradshaw, Holmqvist et al. 2000). The natural and potential ranges for Norway spruce have since then trailed climate change more accurately than was thought to be limited by seed dispersal, implying that climate change enabled spruce to establish itself faster into Northern areas, only about a hundred years after conditions were right. Bradshaw, Holmqvist et al. (2000) continue stating that “short-term climatic variation can lead to significant range adjustments, with consequences for practical forestry”. Due to increasing climate-driven disturbances, increased necessary efforts may be generated for silviculture of spruce stands to reach mature

ages outside their optimal climatic ranges of Scandinavia, Russia, and the mountainous spruce forests of Central and Eastern Europe. Studies have shown Norway spruce to reach maximum ages of 400-600 years, with the oldest recorded trees ranging between 500 and 600 years in Fennoscandia (Castagneri, Storaunet et al. 2013). Unexpectedly, growth rates studied in these old individuals were not being directly linked to age on wet mesic sites, but rather to size, site specific conditions with environmental constraints and based on species specific parameters such as shade tolerance, establishment rates and sprouting potential. With spruce ranging outside its natural habitats, environmental constraints and species specific growth properties may thus declare it an increasingly demanding species to successfully harvest outside of the boreal forest belt (Hari and Kulmala 2008).

When succession dynamics are initiated after an intermediate to severe disturbance event in a mixed stand, spruce first starts to establish itself during the developmental stage of a middle-aged forest. Here the stand is aged between 60 to 100 years, during which spruce may gradually replace species like *Populus* and *Betula*, due to its shade tolerance, but the light demanding deciduous species may dominate until later stages if the site is favorable, as they will utilize available resources faster (Angelstam and Kuuluvainen 2004). Spruce reaching ages older than about 80 years are of ecological importance in the boreal forest, where through senescence and natural disturbances gaps are created in canopy and undergrowth that, depending on site conditions, reveal niches for specialized species and early successional stages (Svensson and Jeglum 2001, Castagneri, Storaunet et al. 2013).

Picea abies has developed adaptations towards the Eurasian spruce bark beetle (Økland, Netherer et al. 2015), owing chemical defenses from secondary metabolites, considering stands of Northern Europe and Eurasia. Its hardiness towards frost and sub-zero temperatures, may be an interplay between acclimatization and adaptation to the climate of open areas in boreal conditions. However, its shallow root systems (Schlyter, Stjernquist et al. 2006) do not provide an effective defense against windthrow for mature trees that have reached a vulnerable diameter to height ratio (Rich, Frelich et al. 2007), which is further exacerbated by the absence of frozen topsoil and low snow conditions (Díaz-Yáñez, Mola-Yudego et al. 2017) and may lead to increased uprooting under a warmed climate (Díaz-Yáñez, Mola-Yudego et al. 2017).

The selection of its host tree of *Ips typographus* is met by a multifaceted adaptation by Norwegian spruce, more so than any other natural disturbance the Norwegian spruce faces. As their first response trees under attack secrete preformed resin as local wound reactions and

following continuous attacks spruce trees can shift to systemic changes in their physiology to combat these advanced attacks (Wermelinger 2004). However, high densities of beetles and preceding drought may diminish a tree's capacity to overcome an attack (Henschke, Netherer et al. , Führer, Lindenthal et al. 1997, Netherer, Pennerstorfer et al. 2018, Netherer, Panassiti et al. 2019). By adding to changes in natural disturbance regimes, climate change may also add to a dilemma for forest managers with the economically important species of spruce producing lower quality of salvaged timber, all the while decreasing the vitality in both managed and semi-natural stands, pushing for changes in species distribution (Seidl, Rammer et al. 2008).

5 Eurasian spruce bark beetle *Ips typographus*

5.1 Ecology

The Eurasian spruce bark beetle *Ips typographus* is one of the most influential bark beetle species considering Norwegian spruce *Picea abies* in Europe. Found throughout Europe and in most of Russia, these bark beetles both infest managed and natural spruce stands. The Eurasian spruce bark beetle poses a destructive threat during massive outbreaks, although under regular conditions it does not pose risk to healthy trees, but rather initiates biological degradation of weakened or dead trees, and turns over substrate for other species that share its ecosystem. Even though biodiversity is enhanced through this function, the preference of *Ips typographus* to target healthy mature spruce trees during outbreaks increases the economic impact of its damage (Müller, Bußler et al. 2008).

The life cycle of the Eurasian spruce bark beetle consists of three life stages – larvae, pupae, and the adult stage. The complete development is necessary to survive the cold winters of temperate and boreal Scandinavia during which the beetles hibernate (Lange, Økland et al. 2006). Although the hibernation is found to take place in host trees close to a beetle's brood tree, they possess excellent flight dispersal capabilities (Wermelinger 2004). After the spruce bark beetle adults emerge from their brood trees, dispersing pioneer beetles bore through the bark of their host tree where they excavate nuptial chambers and secrete aggregation hormones to attract their conspecifics. Males mate with one to four females, and consequently maternal galleries are dug out by the females, who lay their eggs along the outward channels where the emerging larvae can feed in the phloem.



Figure 4: The white pupae (along with the larvae) cannot overwinter, whereas adult *Ips typographus* may hibernate in dead and windthrown trees or tree branches (Pouttu and Annala 2010).

As spruce bark beetles are endemic to most coniferous forests in Europe they are preyed on by a range of natural enemies; most notably the ant beetle *Thanasimus formicarius*, which preys on adult beetles and, depending on the host tree, other predatory flies, larvae, and wasps that favor the larval stages of the spruce bark beetle (Wermelinger 2004, Økland, Netherer et al. 2015). Insect predators are likely to have similar climate driven population dynamics to spruce bark beetles, albeit under different climatic thresholds, including a delayed response of parasitoid species to host densities (Økland, Netherer et al. 2015). The responses of bark beetle predators to management actions against *Ips typographus* remain uncertain and future research should include their responses in ecosystem-based approaches to forest management. Although the Eurasian spruce bark beetle highly favors Norwegian spruce they have been observed to infest other tree species, but mostly on the level of individual trees and not during outbreaks (Wichmann and Ravn 2001, Zhang and Schlyter 2003).

5.2 Disturbance regimes of endemic and epidemic populations

Severe outbreaks (epidemic population) encompass differing disturbance regimes than low population infestations (endemic population) (Kausrud, Økland et al. 2012, Vega and Hofstetter 2014). Norway spruce bark beetle outbreaks have happened several times throughout Europe, but the most severe outbreaks have occurred after heavy storms, leading to a steep increase in windthrown trees that are often uprooted and either heavily damaged or dead. These can serve

as a “springboard” and host a generation that emerges the following spring when temperature thresholds permit it (Wermelinger and Seifert 1999, Lange, Økland et al. 2006).

An important aspect to determine if an outbreak will happen seems to be the intraspecific competition within brood trees, which according to Anderbrant, Schlyter et al. (1985), Anderbrant (1990) may affect the beetles behavior. At low quantities of windthrown and decaying trees beetles are likely to compete for breeding ground which may be lowered with windthrown trees after heavy storm events. The low population densities within each brood tree benefit the development of the new generation (Fahse and Heurich 2011, Kärvemo, Van Boeckel et al. 2014), and thus the emerging generation can be monumental (Heurich 2009). After the generation of beetles emerges from the high proportion of windthrown brood trees, and led by pioneer beetles secreting attraction pheromones, competition for hosts forces them to attack living spruces (Wermelinger 2004, Økland, Netherer et al. 2015) instead of only decaying ones under normal circumstances. Additionally, many more of the living spruces serve as susceptible host trees, on one hand due to preceding drought that may have weakened many of the otherwise healthy mature spruces, but on the other hand, due to higher population densities that swarm out to infest neighboring tree stands and are able to overcome the trees defenses (Økland, Netherer et al. 2015). The differences between disturbance regimes of endemic and epidemic populations and their dynamics, the bimodal population dynamics are explained by Vega and Hofstetter (2014). They note that epidemic populations, contrary to endemic, pass an equilibrium and may reach a critical eruptive threshold. A new regime persists in which positive density-dependent feedbacks prevail and allow populations to increase exponentially until resources are depleted. This is likely to be the case with seemingly unlimited substrate in the form of windthrown spruce trees, one or two years after a severe windthrow event in a spruce dominated stand, where beetles can proliferate without strong interspecific competition within widely distributed windthrown spruce.

According to an interview held on the 4th of January 2021 with Georg Lindner (Georg Lindner 2021), the forester of a spruce dominated mixed stand along the *Harz* in Germany, an important factor that has been observed during recent intense outbreaks has been a preceding drought, which strongly decreases the spruces capacity to defend itself against the wood boring attacks from the Eurasian spruce bark beetle. On his stand, an extreme heat wave during 2017 had interplayed with a storm of the previous year, with the subsequent massive beetle outbreak killing off all the Norwegian spruce over 100 hectares until the Summer of 2019. This portrays a well-studied sequence during heavy outbreaks (Wermelinger and Seifert 1999, Fahse and

Heurich 2011, Kärvemo, Van Boeckel et al. 2014, Potterf and Bone 2017), where the induced defenses and adaptive resistances cannot be upheld against ongoing infestations by a large number of beetles, because of very poor preformed resin and pre-existing physiological stresses for the living host trees. Hereby the infestation threshold required to overcome the trees defenses are lowered immensely, most often leading to colonization and subsequent death of the tree (Økland, Netherer et al. 2015).

Another important factor that drives the spatial dynamics of an outbreak is the dispersal of beetles. Presently, swarming can take place starting in April for Central and Southern Europe or be stalled until late into July for Northern Europe (Jönsson, Harding et al. 2007, Jönsson, Appelberg et al. 2009) and elevated sites (Jakoby, Lischke et al. 2019). Wichmann and Ravn (2001) amongst others (Wermelinger, Epper et al. 2012, Kärvemo, Van Boeckel et al. 2014, Potterf and Bone 2017) conclude that pioneer beetles are very crucial in determining how far the outbreak of one generation of beetles can reach within a year, with most beetles not venturing further than 500 metres (Kautz, Dworschak et al. 2011), but the majority (about 80%) of them attacking new hosts within the 250 metre range of their brood trees (Wichmann and Ravn 2001) and newly infested trees being less than 200 metres from old infestation patches in over 95% of the cases. A greater portion of emerging beetles have been observed to fly further than 500 metres (Wermelinger 2004), which raises further concern for the reemergence of females after first infestation of new host as sister broods (Davidková and Doležal 2017). These reemerged beetles replenish their energy sources for renewed oviposition or flight dispersal either in their first host or new host tree (Davidková and Doležal 2017). Nonetheless, this mostly creates a patchy pattern in coniferous forests dominated by Norwegian spruce, radiating outwards from individual host trees or infestation patches of the previous year (Heurich 2009, Kärvemo and Schroeder 2010, Kautz, Dworschak et al. 2011, Økland, Nikolov et al. 2016). By secreting aggregation pheromones the pioneer beetles then attract their conspecifics to attack a suitable host which is the main driver of the concentration of attacks in patches (Bakke, Frøyen et al. 1977, Wermelinger 2004, Økland, Netherer et al. 2015, Økland, Nikolov et al. 2016). This dispersal dynamic encompasses a distinct difference of a sporadic dispersal of spawn generations during endemic outbreaks versus the gradual concentrated spread during massive outbreaks. It should be noted that the dispersal is dependent on the local characteristics for topography, meso-climate and tree species distribution of forest stands (Kärvemo, Rogell et al. 2014).

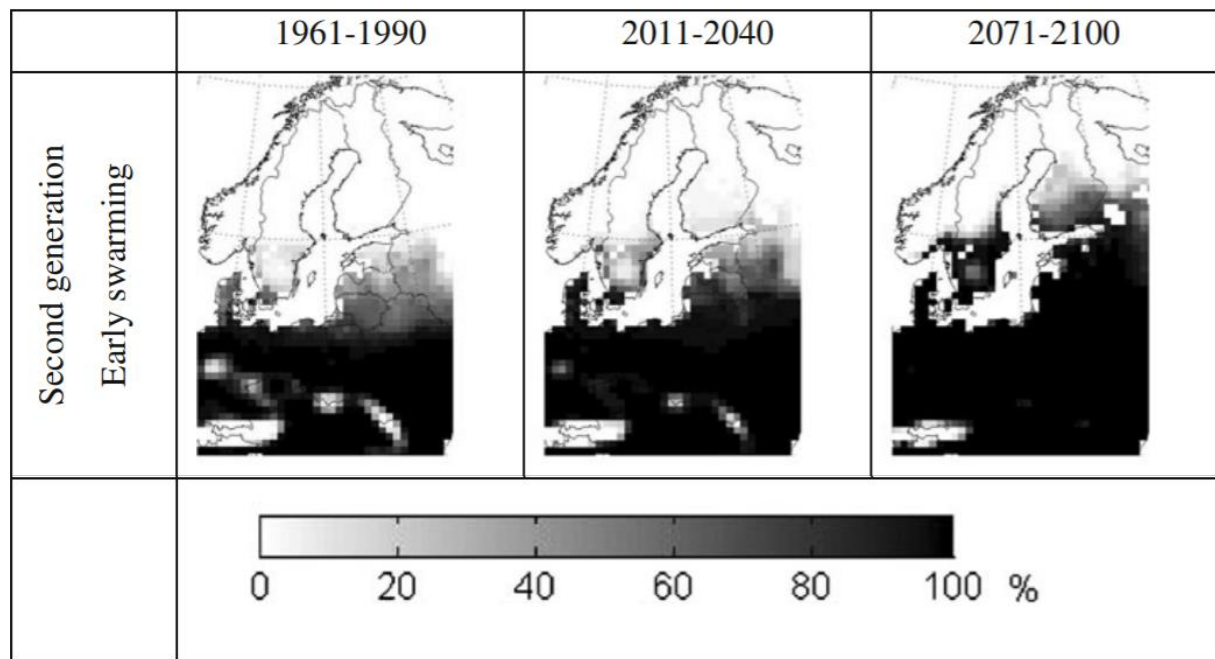


Figure 5: Simulation of percentage of years with a second and third generation based on an improved bark beetle phenology model, modified from Jönsson, Harding et al. (2011). Factoring in are frequencies of early swarming events with initiation of a second generation. This improved model factors in reproductive diapause initiated by photoperiodic and thermal cues and then run against climate data from reference period 1961-1990.

Lastly, voltinism, the amount of generations per year, plays a crucial role in the spatiotemporal dynamics of an *Ips typographus* outbreak with the ability of multivoltine populations to disperse after changing environmental conditions in spring to late summer. Depending on the region of the outbreak, Northern Europe has experienced mostly univoltine spruce bark beetle outbreaks with Denmark being the exception with a well-studied example within Scandinavia (Wichmann and Ravn 2001). During outbreaks from univoltine populations, adult beetles may reemerge from their host trees to infest new hosts as sister broods (Davidková and Doležal 2017). But winter in Northern Europe limits their phenology to undergo development under strict temperature thresholds in their adult stages. Once the vegetative period under early warm spring temperatures allow the beetles to emerge and undergo a second cycle until late summer can bivoltine populations cause havoc within spruce dominated stands, especially after extreme storm events. In Central Europe multivoltinism has reached several generations under favorable conditions (Müller, Bußler et al. 2008) and simulations (Figure 5) for Scandinavia show, that two generations may be frequent by mid- and achieve late summer swarming by late-21st century in Southern Norway (Figure 6) which is argued to be a strong determinant of spruce forest damage by *Ips typographus* (Jönsson, Harding et al. 2011).

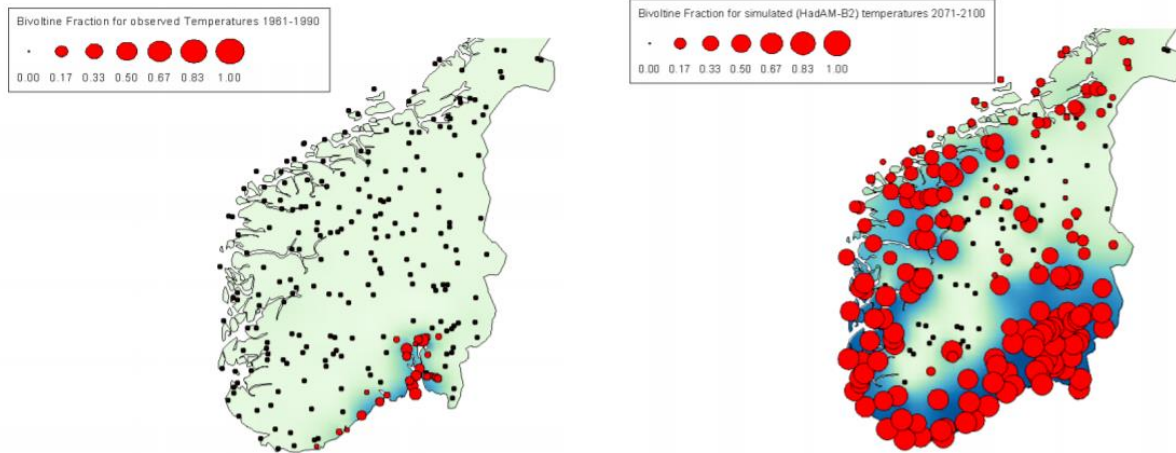


Figure 6: Modified from Lange, Økland et al. (2006) showing bivoltine potential (BP) as a value ranging from 0 to 1 for successful completion of a second generation, reaching adult stage. Based on their model and observed values of temperatures for 1961 to 1990, only areas around Oslofjord, Southern Vestfold and Agder show potential for bivoltinism. Simulations (using Hadley model B2) for 2071 to 2100 show ubiquitous bivoltine potential with some variability relating to orographical features.

6 Windthrow

Intermediate to strong winds do not only inflict physical damage to forests and are able to cause landscape-level destruction in forests, but are a constant force shaping forest dynamics (Mitchell 2013). Winds throughout their severity gradient are important in shaping microsite conditions, creating niche environments for specialist plant and animal species alike (Angelstam and Andersson 1997, Svensson and Jeglum 2001, Angelstam and Kuuluvainen 2004). Windthrow is known to cause different types of damage, depending on the spatial and temporal characteristics as well as its severity and intensity. These range from stand-replacing to partial windthrow with gap-producing events to tree-level damage (Angelstam and Kuuluvainen 2004). Severe stand-replacing windthrow is characterized by killing most canopy trees, some of the regeneration trees and causing major soil disturbances (Everham and Brokaw 1996, Ulanova 2000). Partial windthrow, affecting local clusters of trees, is more variable depending on site characteristics creating a diverse pattern of damage (Girard, De Grandpré et al. 2014). Hence, the disturbance regimes of these two phenomena differ characteristically in their spatial and temporal components, causing different biological legacies and successional dynamics. As soil is disturbed and roots uprooted, succession of individual tree stands, and soil mechanisms may be disrupted. This calls for a multi-component system that considers understory and soil disturbances in conjunction with tree stem damage (Roberts 2004). Furthermore, site specific micro-climatic factors and soil conditions may be affected by climate change, especially through drought stress, and altered freezing cycles of topsoil (Jönsson,

Linderson et al. 2004), whilst increasing the susceptibility of local stands to wind damage, particularly by uprooting (Bradshaw, Holmqvist et al. 2000).



Figure 7: An uprooted Norway spruce (*L. H.Karst.* from Gömörjová, Fleischer et al. (2017), providing microsite niches for early successional specialists (Lehnert, Bässler et al. 2013).

In Fennoscandia, changes in management and the long absence of forest fires have led to more mesic site types with increased amount of organic matter on poor sandy soils (Zackrisson 1977, Angelstam and Kuuluvainen 2004). Therefore, a climate driven shift in disturbance regimes may greatly alter the substrates nutrient cycles, communities and thus changing conditions for Norway spruce to proliferate. An increase in wet and unfrozen soil conditions, which is expected under climate change in Scandinavia (Jönsson, Linderson et al. 2004), could increase the susceptibility of Norway spruce forests to strong winds and concomitant uprooting (Mitchell 2013). Thus, seasonal cyclones, although hard to prognosticate in their frequency (Benestad 2005), should increasingly concern foresters during winter months as more windthrown spruce could be available for *Ips typographus* in spring and summer, which concurs with findings of Díaz-Yáñez, Mola-Yudego et al. (2016).

The extent of windthrow after extreme storm events in Norwegian forests edging towards maritime climate is variable, whereas inopportune freeze-thaw cycles may cause damages to spruce when hardening processes in autumn have not yet been fully initiated or due to frost damage during earlier onset of budburst during spring (Jönsson, Linderson et al. 2004). Maritime climate in Scandinavia could thus be a limiting factor for spruce vitality (Bradshaw, Holmqvist et al. 2000). On the contrary, Southern Sweden and Finland experience periodic storm systems that can have stand replacing magnitudes. Although not numerous in their return interval, they can have long-lasting effects on forest dynamics with only 5 storm events causing the vast majority of the damages sustained to Southern Scandinavia's forests during the late 20th century (Schlyter, Stjernquist et al. 2006) or one severe windstorm in Denmark and

Southern Sweden 1999, where vast *Picea* plantations were destroyed (Bradshaw, Holmqvist et al. 2000).

Studies from recent decades focusing on climate change point to a moderate increase in frequency of extreme weather events in Northern Europe (Overpeck, Rind et al. 1990, Kurz, Apps et al. 1995, Hanssen-Bauer, Achberger et al. 2005, Mitchell, Lowe et al. 2006, Bengtsson and Nilsson 2007, Bonan 2008, Larsen, Gregersen et al. 2009, Stott 2016), although the data does not necessarily point towards an alarming trend (Benestad and Chen 2006). Moreover, the increase in extreme windthrow events depends on changes in the cyclone intensity and frequency that reach the North Atlantic, which have only shown slight changes in recent decades (Benestad 2003, Hanssen-Bauer, Achberger et al. 2005, Benestad and Chen 2006). However, Norway may be a country that is affected by cyclonic windstorms associated with low atmospheric pressure, in the form of Atlantic landfall cyclones (Benestad 2005). Nonetheless, Schlyter, Stjernquist et al. (2006) predict that more significant factors such as land use changes, forestry practices, and changes in stand age and structure, and regional climate variability and environmental factors (soil conditions: horizon structure, type, nutrient availability; slope, southeastern exposure) will increase the susceptibility and decrease the vitality of forest stands (Anderegg, Hicke et al. 2015, Rehschuh, Mette et al. 2017, Blomqvist, Kosunen et al. 2018), thus making the consequential effects of climate driven increases in wind disturbances and drought more destructive.

6.1 Windthrow in *Picea abies* monocultures

Picea monocultures along its Southern ranges may only be grown and harvested with substantial losses to windthrow, markedly if the climate induced increase in susceptibility to windthrow intensifies (Bradshaw, Holmqvist et al. 2000, Rich, Frelich et al. 2007, Mitchell 2013). In spruce dominated stands homogenous soil in tree communities combined with high stem densities may lead to increased damages received from windthrow (Kuuluvainen 1994, Temperli, Veblen et al. 2015, Blomqvist, Kosunen et al. 2018, De Grandpré, Waldron et al. 2018). This could be due to spruce of the same age group competing, and growing thin stems, which in turn could lead to them being more prone to be damaged if wind penetrates cohort edges (Díaz-Yáñez, Mola-Yudego et al. 2017), even from partial windthrow. More frequent windthrow events that cause small-scale mortality may have significantly higher effect through unimodal stand age distribution, due to their return intervals being well within the average lifespan of Norway spruce (De Grandpré, Waldron et al. 2018).

6.2 Windthrow-induced outbreaks

The strong documented interaction between extreme windthrow events on massive outbreaks of European spruce bark beetle has shown its destructive potential after storms in 1977 in Norway (Bakke 1989) and 1987 (Økland and Berryman 2004), and others like *Lothar* in 1999 for Central Europe (Heurich 2009) and *Gudrun* in 2005 for Northern Europe (Wermelinger 2004, Kärverno, Rogell et al. 2014, Økland, Netherer et al. 2015).

An important aspect when comparing these two disturbance agents is that for each, specificity plays an important role. Specificity, according to Gauthier (2009) and De Grandpré, Waldron et al. (2018) relates to the “selective nature of a disturbance towards particular species, forest type, seral stage or stand characteristics”. The European spruce bark beetle is specialized to attack its host tree species, and although windthrow does not select a specific tree species per se, Norway spruce may be more prone to suffer damage from windthrow through its physiological traits. Norway spruce stem to root system ratio, its growth rate and the stands age along with specific site characteristics may all contribute to an increased damage sustained at all spatial scales (Eriksson, Pouttu et al. 2005, Eriksson, Neuvonen et al. 2007).

How do the dynamics of windthrow induced massive outbreaks differ from normal conditions in their disturbance regimes? By supplying a high quantity of substrate for the beetle to complete their development in, intense windthrow events play a major role in magnifying beetle population sizes. With the densities of maternal galleries in windthrown spruces kept within thresholds of interspecific competition (Anderbrant, Schlyter et al. 1985, Anderbrant 1990, Økland and Berryman 2004), the offspring surviving winter may reach exceptionally high numbers. By being able to overpower individual host trees defenses with high population densities the following year, beetles are exempt from having to disperse very far, which may result in strong local infestation patches. Thus, endemic populations transition from windfall dynamics to epidemic gap dynamics through the interaction of windthrow over the course of two or more years (Økland, Nikolov et al. 2016).

7 Drought

To assess the severity of the most destructive windthrow-induced *Ips typographus* outbreaks, drought has increasingly been found to be a key factor in determining a stands preconditioned ability to withstand massive outbreaks. Particularly, Central and Eastern European spruce stands have been found to sustain vast mortality from spruce bark beetle outbreaks under

drought stress from prolonged heat waves and multi-year droughts (Führer, Lindenthal et al. 1997, Jactel, Petit et al. 2012, Netherer, Matthews et al. 2015, Netherer, Pennerstorfer et al. 2018). Whereas windthrow has been found to undeniably aid spruce bark beetle populations to reach epidemic population dynamics, drought stress remains uncertain in its effect on massive outbreaks of spruce bark beetles (Netherer, Matthews et al. 2015, Netherer, Panassiti et al. 2019, Pettit, Voelker et al. 2020), although acute drought stress does combine with the affinity of spruce bark beetles to Norway spruce and is likely to increase damages to spruce stands in following years after acute drought stress (Faccoli 2009, Netherer, Matthews et al. 2015, Netherer, Pennerstorfer et al. 2018, Netherer, Panassiti et al. 2019). In the case of chronic and extreme drought, and in the absence of windthrow events, the aforementioned Austrian study by Netherer, Matthews et al. (2015) also found forest stands to be less prone to spruce bark beetle attacks, when grown on “shallow, xeric, and low moisture soil conditions”, which is in conjunction with the findings of Netherer, Panassiti et al. (2019). They argue that soil conditions might hereby possess protective properties making certain sites inherently less susceptible to bark beetle attacks. Rehschuh, Mette et al. (2017) follow up on this argument, by stating that “the risk of drought induced tree mortality appears to be affected by soil conditions”, where shallow, well-drained soils decreased associated spruce growth and increased drought susceptibility.

Temperature represents a direct effect on *Ips typographus* development, dispersal through flight activity and its voltinism (Wermelinger and Seifert 1999, Wermelinger 2004, Økland and Berryman 2004). Drought stress, on the other hand, is the result of a prolonged heat waves that weakens spruce trees defensive abilities and overall physiological health, thus indirectly increasing spruce bark beetles success in overcoming these defenses and infesting mature and healthy spruce under epidemic conditions (Führer, Lindenthal et al. 1997, Netherer, Pennerstorfer et al. 2018). The covariance of temperature and drought make the differentiation of each significance for the proliferation of beetles difficult (Pettit, Voelker et al. 2020). The cross-regional effect of drought extends to boreal and montane forests, where frozen soil further limits spruce abilities to transport water and preform resin (Bowling, Logan et al. 2018), but the variation on local scales alone cannot explain larger beetle outbreaks according to Pettit, Voelker et al. (2020). The phenology model *PHENIPS* along with the *ROSALIA ROOF* Project, focusing on physiological experiments on Norway spruce sheds light on why differentiation between acute and chronic drought stress was overlooked as underlying factor in massive

outbreaks in previous studies, next to salvage logging, stand age and temperature (Netherer, Matthews et al. 2015, Netherer, Pennerstorfer et al. 2018, Netherer, Panassiti et al. 2019).

Larsen, Gregersen et al. (2009) simulate that within 50 years, extreme precipitation events will occur more frequently, and Scandinavia is to experience the highest increase out of European countries. These increases in extreme precipitation events coupled with modelled increases in heat wave frequencies in coming decades will likely exacerbate physical damages and acute physiological stress on forest stands in Northern Europe (Mitchell, Lowe et al. 2006, Jactel, Petit et al. 2012, Pachauri, Allen et al. 2014, Change 2018, Venäläinen, Lehtonen et al. 2020).

8 Climate driven changes

Bark beetles such as *Ips typographus* play a vital role in coniferous forest ecosystems, but with an increasingly warming climate extreme events are likely to exacerbate their impact on spruce stands (Venäläinen, Lehtonen et al. 2020). The effect of environmental factors on *Ips typographus* phenology and propagation are well documented (Wermelinger and Seifert 1999, Wermelinger 2004) as are model simulations on potential future scenarios (Bradshaw, Holmqvist et al. 2000, Fahse and Heurich 2011, Seidl, Fernandes et al. 2011, Jönsson, Schroeder et al. 2012, Kärvelo, Van Boeckel et al. 2014, Potterf and Bone 2017). These point to the projected risk of prolonged activity of the spruce bark beetle across Central and Northern Europe and an intermediate risk of increasing number of massive outbreaks, primarily following trends in human-induced management and the concurrence of a changing climate with the temperature thresholds of *Ips typographus*. Secondly, and harder to estimate, the risk of massive outbreaks due to the increase in extreme weather events in Northern Europe leading to higher quantities of windthrown spruce and concurrent heat waves with episodes of timely inopportune low precipitation (Benestad 2003, Benestad 2005, Mitchell, Lowe et al. 2006, Larsen, Gregersen et al. 2009, Seidl, Schelhaas et al. 2014).

Through a strong temperature dependence of *Ips typographus* spring flight activity, timing of swarming, duration of development, parasitoid and predator activity, disturbance tolerance by spruce and frost damage to spruce trees, the absence of thermal limitations poses a significant risk for extreme outbreaks of the Eurasian spruce bark beetle, and raises questions for climate driven changes in its mortality due to warmer winters, natural enemy populations and changing forest dynamics (Wermelinger 2004, Schlyter, Stjernquist et al. 2006, Díaz-Yáñez, Mola-Yudego et al. 2016).

A high risk for Scandinavian spruces forests are the proliferation of sister broods and even more so, multivoltinism whose emergence has been studied in detail (Wermelinger and Seifert 1999, Wermelinger 2004, Lange, Økland et al. 2010, Davidková and Doležal 2017). It is argued that these two have increased and will increase as a result of increased degree-days and prolonged vegetative period due to rising temperature averages and earlier onset of spring warming (Overpeck, Rind et al. 1990, Økland, Netherer et al. 2015, Marini, Økland et al. 2017). The voltinism in Southern Sweden (around 56° 05'' in latitude) is modelled and projected until 2099 to increase to a faster development, and bivoltinism although the increase in average temperature may not fulfil the temperature requirements every year for a second generation (Jönsson, Harding et al. 2007, Jönsson, Appelberg et al. 2009). It stands to note that the photoperiod in Northern Europe acts as a limit to enhanced voltinism, since beetles are forced to cease their development (Wermelinger and Seifert 1999, Wermelinger 2004, Økland, Netherer et al. 2015). The facultative adult diapause of spruce bark beetles is controlled by photoperiodicity, which is initiated below 15 hours of light conditions (Wermelinger 2004, Økland, Netherer et al. 2015). This presents a latitudinal limitation for a boundless proliferation of *Ips typographus*. Nonetheless, bivoltine populations of spruce bark beetles are expected to expand their northern ranges (Økland, Netherer et al. 2015).

Already in the last decade, outbreaks in Finland and Sweden have shown first signs of multivoltinism (Jönsson, Harding et al. 2007, Jönsson, Harding et al. 2011, Jönsson, Schroeder et al. 2012, Kärvelo, Van Boeckel et al. 2014, Blomqvist, Kosunen et al. 2018, Venäläinen, Lehtonen et al. 2020). In 2010, Southern Finland experienced an alarming bivoltine outbreak of *Ips typographus* along with preceding drought and storms, and the conditions lasted until a population peak in 2013 (Venäläinen, Lehtonen et al. 2020). These represent some of the natural range of Norway spruce and are thus highly indicating of climate driven changes in population dynamics of *Ips typographus*, in part also because these habitats are naturally dominated by the duo of Norway spruce and Scots pine *Pinus sylvestris*.

Spruce grown outside its natural habitat faces a dilemma with climates allowing for spruce bark beetles to have more than one generation in a year (Schlyter, Stjernquist et al. 2006). Again, location specific characteristics remain important for Norwegian spruce to equip itself with defensive chemicals, which is heavily undermined when climate driven heatwaves could cause reoccurring drought over the course of this century (Rehsehuh, Mette et al. 2017). In addition, monocultures where tree patches are in the mature state of 60 years and older are favored by

the spruce bark beetle and may be susceptible for massive outbreaks aided on by climate change.

Another factor is the uncertainty whether Norwegian spruce might be more susceptible to damage from spruce bark beetle outbreaks during a potential second flight period in July or August than to the current one during April or May in Southern Scandinavia (Lange, Økland et al. 2006, Lange, Økland et al. 2010, Økland, Netherer et al. 2015). Although there are limitations to the response of bark beetle propagation to climate change, it generates changes that could increase the destructive potential of massive outbreaks. The changes in climate-driven forest structure of natural stands and function due to extreme events that shift entire stand age distributions leading to higher susceptibility to further natural disturbances may call for ecosystem-based management of boreal forests, enabling natural stands to mitigate changes in climate.

9 Management implications

9.1 Spruce forest management

The spruce and pine dominated forests of Northern Europe and Eurasia have long been of great socio-economic value. Consequently, the investment of ubiquitous spruce for industrial purposes limits forest managers to seek solutions in other boreal tree species. Adapting spruce towards sustaining epidemic spruce bark beetle outbreaks after windthrow could mean decreasing Norway spruce proportions in Southeast Norwegian stands where voltinism is set to increase to two generations for the end of the century, to ensure beetles cannot proliferate into epidemic populations by spring boarding infestations of windthrown logs. Thus, natural succession of more climatically acclimatized species could be allowed in these stands whilst ensuring natural enemy diversity of the spruce bark beetle through niche diversity.

Another potential management tool to decrease the susceptibility of the forest to bark beetle outbreaks is argued to be the density of host species of the spruce bark beetle in forest stands, which clearly is high in monocultures. A high density of spruce likely favors the massive outbreaks (Økland and Berryman 2004, Kausrud, Grégoire et al. 2011), since infestation patches are not dependent on long distance dispersal of beetles. On top of this, the higher susceptibility to wind damage in spruce dominated than in mixed stands may further favor windthrow-associated outbreaks (Kärvemo, Van Boeckel et al. 2014). A proposed decrease in

the portion of spruce within managed forest areas could lower the risk of overall disturbances (Brang 2001, Brang, Schönenberger et al. 2001, Stadelmann, Bugmann et al. 2013).

A further option would be to invest resources into salvaging operations, proper storage of windthrown spruce and sanitation felling technology that undermines the development of *Ips typographus*. To mitigate wind damages by naturally fortifying forest structure in exposed areas would mean decreasing the potential of massive spruce bark beetle outbreaks to occur. Considering monocultures, the risk of bark beetle outbreaks in local stands could be kept small, where the management work force is sufficient, and silviculture can be done thoroughly including monitoring and control of beetle populations.

Stands consisting mainly of only a few tree species or monocultures, have often been managed for centuries, in effect changing the ecosystem properties (Gauthier 2009). As Verkerk, Costanza et al. (2020) argue, this long-term management makes managed stands less impactful to combat climate change for increasing species richness, or saturating their carbon stocks. Moreover, Verkerk, Costanza et al. (2020) add that other ecosystem services can emerge from utilizing sustainable forest management approaches to achieve a higher share of broadleaved species, hence being more effective to assist in decarbonizing the world markets by using more carbon-moderate woody materials as a sustainable resource, as well as not being reliant on a few productive timber species alone. Shifting resources to harvesting a wider range of wood products derived from various tree species may counteract the losses to salvage operations of spruce after natural disturbances. However, spruce dominated stands that are not as susceptible to climate-driven natural disturbances, or could be cost-effectively managed through changes in silviculture, are to remain to mainly produce spruce timber.

With the age distribution of spruce monocultures representing a rotation period of about 60 years or more, aligning with *Ips typographus* target spruce age, which is not synchronized with the needs of foresters. (Wermelinger 2004, Økland, Netherer et al. 2015). Spruce dominated forest stands in Central Europe have shown high mortality of mature spruce after more than two consecutive years of epidemic populations after heavy windthrow and concurring drought, where no actions have been initiated or as in some cases, neighboring unmanaged forest stands have allowed the continuous dispersal of *Ips typographus* (Heurich 2009, Sommerfeld, Rammer et al. 2021).

While the sustained yield paradigm is being promoted by most forest management plans in European boreal forests up until the 21st century, it results in the absence of old-growth forest (Angelstam and Kuuluvainen 2004), factoring in rotation periods of Norway spruce around 60 to 100 years. There remains a varying degree of intact old growth boreal forest in Scandinavia: Old growth forest constitutes 0.2% of Finland's forests (Hanski 2000) and in Sweden about 5% can be counted as natural forest (Angelstam and Andersson 1997, Hultgren 2001). Angelstam and Kuuluvainen (2004) argue that the boreal forest has changed dramatically in the past 150 years and is undergoing a final shift from natural stands to solely managed stands of varying degrees. Old-growth forest of ages from one to several centuries, depending on the species and location, is desirable for conservation management due to its diverse set of niches for specialized species benefiting from functional and structural heterogeneity (Angelstam and Kuuluvainen 2004). A collapse of regional and local boreal forests may be expected due to biome shifts brought on by climate induced increases in natural disturbances of wind and bark beetle outbreaks that not only shift forests to younger age classes, but cause ranges of more temperate species to establish themselves further north and out-compete boreal species such as *Norway spruce* and *Scots pine* during forest succession regimes (Angelstam and Kuuluvainen 2004, Bonan 2008). As Norway spruce has historically lagged in its range expansion with an estimated century after potential living conditions set in, albeit following climate change more closely in recent centuries, disturbances may gain an upper hand when it comes to decimating monoculture stands through extreme disturbance events. Subsequently, species compositional changes may be mitigated in mixed stands under climate change (Bradshaw, Holmqvist et al. 2000).

9.2 Management under climate change

Due to the proposed climate-driven effect on natural disturbances in boreal forests, a reinvestigation of forest management may be required. Previous forest management has been based on the sustained yield paradigm (Schelhaas, Nabuurs et al. 2003, Angelstam and Kuuluvainen 2004, Díaz-Yáñez, Mola-Yudego et al. 2016), but has progressed in the last decades towards the sustainable management of forests, even though many issues associated with biodiversity and ecosystem services are not yet prioritized in many cases (Burton, Messier et al. 2003).

Control efforts on spruce bark beetle outbreaks have focused on two main measures. Firstly, preventing outbreaks by salvage logging of storm-damaged timber and secondly, sanitation

felling to lower population sizes in infestation spots, especially after storm events, thus either removing potential and susceptible host trees before infestation or bark beetle infested spruce trees before the generation of beetles emerges in early summer (Stadelmann, Bugmann et al. 2013). As Kautz, Dworschak et al. (2011) and Wichmann and Ravn (2001) argue, the distance between old and new infestation patches are, depending on local topography, most likely within 100 to 200 metres from each other with some beetles travelling between 100 and 500 metres from old infestation patches. These findings have encouraged forest managers to concentrate efforts of sanitation felling to patches of forests close to infestation spots and thanks to findings of ecologists (Grodzki, Jakuš et al. 2003, Müller, Bußler et al. 2008, Kausrud, Grégoire et al. 2011, Kärvemo, Rogell et al. 2014) close to favored spots by the spruce bark beetle such as forest edges, clearings and sun-exposed patches. The challenge for sanitation felling remains with being able to detect infested trees early enough before mass swarming of beetles, because infestation cues like tree browning and death may only set in during later stages of infestation (Økland, Netherer et al. 2015). Additionally, depending on the severity of storm events the damage in forests can be extremely heterogenous (De Grandpré, Waldron et al. 2018), with windthrown spruce patches being hard to detect and remove. This calls for early warning mechanisms, or evaluation of general risk areas of local spruce stands.

Regarding the removal of windthrown spruce from forests, debarking trees before they are left or stored away has been proven to be less time-consuming management tool than moving vast quantities of windthrown timber (Eriksson, Neuvonen et al. 2007, Kausrud, Grégoire et al. 2011, Stadelmann, Bugmann et al. 2013, Kärvemo, Rogell et al. 2014). The removal of bark may be a useful tool against the development of the Eurasian spruce bark beetle, as the insulation effect of the bark is crucial for keeping temperature thresholds for larvae and hibernating beetles (Wermelinger and Seifert 1999, Wermelinger 2004). A new method in debarking measures in ‘scratching’ windthrown spruce has been outlined by Hlásny, Krokene et al. (2019), which presents foresters with a time- and cost-effective alternative along with comparable efficacy to complete debarking, albeit the handling of scratching tools requires training (Figure 8). Since trees can remain hostable for up to three years after windthrow if the conditions are suitable, it could be of interest to continue salvaging and debarking windthrown spruces in consecutive years. The importance of timing for sanitation felling is highlighted in the literature (Wermelinger 2004, Seidl, Rammer et al. 2008, Stadelmann, Bugmann et al. 2013, Hlásny, Krokene et al. 2019), which state that the felling needs to happen before the first

generation of beetles emerge from their host trees in summer, albeit as discussed above, timely detection of infestation is an impediment to sanitation felling.



Figure 8: From Hlásny, Krokene et al. (2019) - Bark scratching in the Bavarian Forest National Park, Germany. Photos: Jörg Müller.

Since semiochemicals, which the beetles utilize as attraction hormones, have been successfully identified and synthesized, and used in Europe for the past 40 years (Regnander and Solbreck 1981, Niemeyer, Schröder et al. 1983) hormone traps have been used to trap beetles with varying success. The local representativeness is debated, as a combination of the phenology of re-emerging beetles, the tree species distribution, topography and trap density seem to determine the catch rate (Wermelinger 2004). These findings imply that the attraction radius of traps ranks their success in monitoring uses over their application as control measures. Where mixed forest stands come into the equation, a “push-pull” effect was proposed by Wichmann and Ravn (2001) and Zhang and Schlyter (2003), by which deciduous trees emit phytohormones which in turn drive beetles further towards specific host trees, posing further questions for choice of species distribution throughout mixed forest stands at risk from massive outbreaks. Buffer stands that do not consist of Norway spruce or other potential hosts or deadwood could have the potential to prevent the unimpeded dispersal of beetles to new patches of forest (Hlásny, Krokene et al. 2019), but questions remain on the required depth to hinder pioneer

beetles from locating new hosts and attracting other beetles. Also, at montane and sub-alpine elevations, buffer stands may be hard to realize since conditions might not be suited for other species than a few conifers, that may, nonetheless, springboard the beetle's dispersal. By guiding beetles to isolated stands of spruce trees, buffer stands and the 'push-pull effect' should be included in management considerations. As Wermelinger (2004) summarizes, trap trees have been used effectively to protect vulnerable stands by leaving decaying or recently dead trees lined with pheromones at vulnerable edges of spruce patches, although this application is proving to demand a significant amount of effort from forest managers.

To simulate different forest management strategies in outbreak risk areas, Seidl, Rammer et al. (2008) simulated four different strategies for a forest management unit in Austria for 2000-2100. By disregarding bark beetle management strategies in one of the simulations, such as salvage logging, their findings point towards a considerable effect for stand dynamics and spruce stocks for epidemic outbreaks under climate change. In their study, simulated management scenarios that promoted mixed species forest stands, both under idle and climate induced changes, resulted in reduced damages sustained by bark beetle outbreaks as well as losses to salvaged timber (Seidl, Rammer et al. 2008). The scenario presented a beech-spruce mix by introducing beech in already existing patches of naturally regenerating spruce stands. If this strategy could prove to avoid damages caused by *Ips typographus* in Central European sub-alpine and montane environments, a proposition of naturally occurring *Betula pubescens* along with fire-resilient *Pinus sylvestris* could be of interest for forest managers in highly susceptible spruce stands in Northern Europe.

An accompanied advantage of increasing species richness in managed stands could be the mitigation of wind damage, with subsequent reductions in host material for the spruce bark beetle. As increased old-growth spruce forests are prone to be windthrown, other species possessing characteristics that resist windthrow, such as higher root-stem ratios and radial growth (Angelstam and Kuuluvainen 2004), may increase the protection of the spruce standing stock by filling out gaps that would otherwise be exposed to wind. Mixing tree species may also aid in optimizing the vertical structure in spruce stands to reduce its windthrow susceptibility (Hlásny, Krokene et al. 2019). On the other hand, managed spruce stands require optimal densities for desired growth characteristics and age distributions designed for harvesting actions (Burton, Messier et al. 2003), and this should thus be incorporated in management decisions, to maximize resource allocation (i.e. light) to spruce trees within high

output stands. The heterogeneity of disturbance regimes must be included in model simulations of management outcomes for representative Northern European studies.

A management strategy for silviculture and management resource allocation is to be based on the local prioritization of needs and abilities to produce ecosystem services under climate change (Verkerk, Costanza et al. 2020). Hereby, stands that are deemed for high output, where soil conditions and ecosystem stability allow it, may continue to be harvested at rotation periods fitted to mature Norway spruce, given ample site conditions. On the other hand, managed and unmanaged stands that are increasingly susceptible to uni- or even multivoltine *Ips typographus* outbreaks due to worsening climatic factors such as higher fluctuations in precipitation and extreme weather events, could be allocated to provide other ecosystem services by increasing mixed forest species distributions with small patches of old-age forest characteristics.

With CSF and or ecosystem-based approaches in management the susceptibility of spruce stands to natural disturbances is hypothesized to be attenuated, thus mitigating climate driven changes in the dynamics of boreal forests, securing ecosystem services of spruce dominated stands and enabling a sustainable output of timber (Schoene and Bernier 2012, Nabuurs, Delacote et al. 2017). The general goals of foresters, scientists and government institutions alike for Scandinavia's forests could be stated as improving timber and soil quality, increasing the growing stock and carbon sequestration, opening and widening wildlife corridors and increasing γ -diversity and resolving long standing issue of combining values of stakeholders to compromise between maximizing natural state of forest stands without losing value of economic tree species. Limiting the extent of damages to Southern boreal forests by climate-driven biotic disturbances may prove to be in large part covering losses of spruce stands, which may not be sustainable with environmental changes within the century, and covering economic losses especially when timber markets are flooded with salvaged timber. Including the aforementioned goals of foresters by applying CSF theory to local forest stand management with site specific requirements may improve timber harvest quality and minimize harvest losses.

10 Climate Smart Forestry

Climate Smart forestry is a forestry strategy aimed at increasing carbon sequestration, whilst increasing the efficiency of economically important forests, thus mitigating climate change

impacts and securing the provision of ecosystem services (Brang, Schönenberger et al. 2001, Seidl, Rammer et al. 2007, Thom and Seidl 2016, Nabuurs, Verkerk et al. 2018, Yousefpour, Augustynczyk et al. 2018, Bowditch, Santopuoli et al. 2020, Temperli, Blattert et al. 2020, Verkerk, Costanza et al. 2020). Although a multifaceted change in forestry seems difficult to achieve, forestry has undergone a strong paradigm shift throughout the past century, leading to a slow shift towards sustainable forest management of many European forests (Burton, Messier et al. 2003, Angelstam and Kuuluvainen 2004). However, as foresters have mostly clung on to economically viable management, rotation periods of valuable timber species such as Norway spruce are increasingly showing their vulnerability under changing climatic conditions (Bradshaw, Holmqvist et al. 2000, Jönsson, Linderson et al. 2004). To optimize harvesting and securing standing stock volume and timber quality, Northern European forest managers have the opportunity to jump ahead of the eminent dangers that climate induced natural disturbances impose on its forests by adopting new strategies proposed by CSF. The adaptation to the risk of extreme events should constitute one of the primary incentives for forest managers to adopt CSF, juxtaposing government insurances for damages caused by the most prominent natural disturbances in Northern Europe, windthrow and massive bark beetle outbreaks next to forest fires (Schoene and Bernier 2012).

Considering the wide range of site-specific characteristics, CSF can vary in its application to meet local requirements. To be able to successfully accomplish the viability of European spruce forests, local demands need to be considered. Due to the large influence of the type or level of damage (tree, gap and stand level damage) derived from extreme storm events, windthrow may lead to complex pattern of infestation by the spruce bark beetle (Wichmann and Ravn 2001, Jönsson, Appelberg et al. 2009, Marini, Lindelöw et al. 2013, Kärvelo, Rogell et al. 2014, Sommerfeld, Rammer et al. 2021). Hence, understanding this dynamic, will be important for initial risk assessments and management solutions under CSF.

The selection of stands managed to increase the functional diversity of local stands as well as on a regional scale along with the selection of highly productive stands least susceptible to environmental stressors such as storms and drought could counteract the impact of windthrow induced massive spruce bark beetle outbreaks. The increase in proportion of other species into spruce dominated stands, whilst deviating the age distribution to make spruce stands less attractive to bark beetles may be accompanied by the inherent capability of selected stands soil conditions to mitigate massive outbreaks by rendering spruce stands even more unattractive to

spruce bark beetles (Seidl, Rammer et al. 2007, Seidl, Rammer et al. 2008, Nabuurs, Verkerk et al. 2018, Temperli, Blattert et al. 2020).

If the future climate allows spruce to dominate in the northernmost regions of mainland Scandinavia, spruce bark beetle voltinism is thereby limited primarily by photoperiod, given that nighttime temperatures remain below flight activity thresholds (Økland, Netherer et al. 2015). However, Southern spruce stands are dependent on management decisions to mitigate changes in spruce bark beetle dynamics. Thus, even though CSF aims to incorporate new management guidelines such as mixed stand management, it needs to be complemented by focusing on improved *Ips typographus* monitoring methods, potential buffer stands of non-host tree species, revised silviculture and site-specific management (Seidl, Rammer et al. 2007, Seidl, Rammer et al. 2008, Hlásny, Krokene et al. 2019) to allow for ecosystem provision under climate change.

11 Discussion

Successional dynamics of boreal forests in relation to site conditions are well understood, but according to Angelstam and Kuuluvainen (2004) the interaction of natural disturbances in boreal forests require more attention to climate-induced changes due to the increasing rate of change. Although windthrow and Eurasian spruce bark beetles continue to serve a vital ecological role in boreal forests, climate change induced changes are likely to exacerbate managers losses in standing stock, harvesting timber volumes and timber quality. The management of boreal forest does not seem to be in tune with the biome shift in Southern Scandinavia, especially within the spruce-dominated forest stands, where bark beetle outbreaks transition between endemic to epidemic and multivoltine outbreaks. According to Burton, Messier et al. (2003), traditional forest management attempting to manage biodiversity, leaning on the sustained yield paradigm, has met challenges with interpreting the relationships between climate, site factors, natural disturbance regimes [...] and forest dynamics and mosaic patterns, as well as to integrate natural stand dynamics into silviculture for regional and local site specific conditions. With an ecosystem-based approach, regional stands could be singled out and managed according to their specific disturbance regimes to mitigate the effect of climate change on the ecosystem services they provide.

Whether extreme events in Northern Europe increase in frequency and severity or not, remains more uncertain than their underlying potential to exacerbate windthrow-induced epidemic

outbreaks of *Ips typographus*. This means that long-term aims to keep harvesting spruce in Northern Europe will demand a renewed forest management framework, encompassing the increasing impact of windthrow and drought on bark beetle outbreaks, ensuring that spruce forests within their natural range do not suffer the same fate as monocultures grown outside of it.

Converging information on the effect of landscape and local site types on bark beetle proliferation, signifies the inclusion of the high variability in forest features and local natural disturbance regimes into the management framework. Instead of utilizing management frameworks as “one tool fits all” strategies in boreal forests, management should instead be modified depending on local bark beetle and windthrow dynamics. Management guidelines have to include risk assessments of natural disturbances, as well as policies for maintaining post harvesting and salvage logging biological legacies (De Grandpré, Waldron et al. 2018) which assist in producing more old-growth characteristics in forests stands that are deemed vulnerable by these criteria. While shorter rotation periods may counteract the susceptibility of aging forests to windthrow and consequent massive outbreaks of the spruce bark beetle, trade-offs between ecosystem service provision and shortening the rotation period of Norway spruce need to be considered, as Temperli, Blatter et al. (2020) argue, that increased frequencies could alter a stands condition by increasing the frequency of human disturbances.

The spruce bark beetle is a keystone species to many early successional species. Thereby applying natural forest management in carefully selected stands, especially ensuring natural early succession, could mitigate climate induced changes and benefit forest managers and other stake holders (Lehnert, Bässler et al. 2013). But for economically important species such as Norway spruce, the solution to climate induced natural disturbances will have to extend over prioritization of old-growth forests to include high output spruce stands, and ensure other ecosystem service provision through careful selection of functional units of forest stands.

With renewed management methods at the disposal of foresters, such as mixed stand management and scratching (Hlásny, Krokene et al. 2019), more options need to be investigated, including buffer stands of non-host regenerative tree species of younger age which are placed around high output spruce stands (Pettit, Voelker et al. 2020). These buffer stands will have to take the dispersal abilities of *Ips typographus* into account with a minimum of one to five hundred meters from target trees, which needs to be field-tested.

Dilemmas for mixed stand management strategy remains with hard-to-manage high altitude stands that enable corridors for bark beetles to disperse and pin-point harvesting that will have to strategize on whether the whole spruce cohort is harvested and the regeneration of the complete stand is initiated anew, or the forest patches are left to shift the age-distribution and renew the vertical structure of the forest stand. Out of European countries, Switzerland is one aiming for natural state management of high altitude stands, which creates ample opportunity to monitor dispersal dynamics of spruce bark beetles and the role of natural stands to springboard spruce bark beetle populations to new infestation patches. Scratching, however, shows much promise as it represents a more cost-effective method than debarking and provides living space for niche insects and other forest species.

The political question for managers remains on how much freedom they should be allowed to have when managing local stands where the high risk of natural disturbances is known. The boreal forest management should include a combination where strategies are fitted to specific local requirements (soil, natural state, diversity, socio-economic interests) and regional climatic suitability. In addition, the effect of slope (exposure, soil drainage and fertility) marks the importance of site-specific characteristics on bark beetle proliferation (Blomqvist, Kosunen et al. 2018). The selection of salvageable host trees along forest edges, margins of clear-cuts, small clearings or along forest roads require an attention to detail with managing local spruce stands by identifying susceptible spruce trees with these characteristics (Grodzki, Jakuš et al. 2003). As a large proportion of Scandinavian forest stands are manipulated in their structure, dead wood, and species distribution, successional patterns are hard to discern in their effect on the assessment of risk of bark beetle attack. The structural features of forest stands are crucial, also after recent management actions that may have altered these features (Netherer, Panassiti et al. 2019). Climate change could thus influence how succession and patch dynamics are able to maintain functional connectivity and stable conditions for specialized species to remain in local managed and unmanaged stands.

Climate induced changes

With climate change comes a potential change in scale of disturbances. The borealization of subarctic environments is slowly underway, but temperate conditions in hemiboreal forests could arise sooner than expected with successional character changes through novel succession patterns that are followed by the northward spread of epidemic spruce bark beetle disturbances (Angelstam and Kuuluvainen 2004). The current age structure of managed boreal forest is prone

to climate driven increases in disturbance intensity as well as severity. Historically, mesic sites in Europe with long fire rotation meant mostly old-growth type forest structures and dynamics, especially considering stand-replacing disturbance regimes (Kuuluvainen, Syrjänen et al. 1998). Thus prominent in landscapes of old-growth forests are partial disturbances (Angelstam and Kuuluvainen 2004). Is there a possibility of this changing due to increased frequency of stand-replacing storms?

Anthropogenic drivers through land use has forced changes in current age structure of boreal forests (Castagneri, Storaunet et al. 2013), which almost lack old Norway spruce forests. To counter the deficit in diverse age distribution and structural diversity, the size-selective mortality (larger spruce trees are more likely to be windthrown) could be reduced with a wider age distribution. Climate could however counteract the acclimatization of spruce of varying ages and stem diameters, through increased productivity. Hereby, faster growing trees would be more susceptible to ‘sudden’ severe disturbance events, not having allocated their resources in hardiness or chemical defenses (Rich, Frelich et al. 2007). The changes in boreal forest productivity may be however over-estimated due to frost damage with potential future increase in repair costs with freeze-thaw cycles (Jönsson, Linderson et al. 2004). Disturbance regimes that increase in importance for the Norwegian spruce under climate change, such as freeze-thaw cycles (Jönsson, Linderson et al. 2004) must be included when trying to understand site specific pressures on spruce stands and their risks for massive beetle outbreaks.

Since climate change is likely to offset acclimatization capabilities of spruce to extreme windthrow and drought, competition through a mixed stand with early successional stages of other species may ameliorate its weakened defenses. Mixed stands or spruce grown on unfavorable microsites may push slow-growing spruce that allocate more resources to chemical tree defense and reach windthrow-susceptible sizes later in life (Castagneri, Storaunet et al. 2013). Wood densities of individual spruce trees may thus also be improved, to gain economic value of the spruce within the mixed stand. As senescence may be more related to size than age (Castagneri, Storaunet et al. 2013), pushing for diversified vertical structure including old age forest characteristics, as to not produce slender and tall spruce trees from highly dense forest stands, may call for different silvicultural approaches.

Given *Picea abies* life-strategy being more susceptible to wind damage, specificity to spruce applies to windthrow. As Givnish (1995) asserts, shade-tolerant species are generally thought to allocate more resources to rapid growth, instead of overall structural strength, leading them

to be less windfirm. In the case of Norway spruce, exogenous small-scale disturbances are likely to drive stand development in spruce stands owning old-growth characteristics, where climate change enhanced windthrow has the potential to break down mature spruce even earlier (Castagneri, Storaunet et al. 2013).

Beetle dynamics

Damages sustained to spruce stands by massive bark beetle outbreaks in the past 50 years that have been preceded by extensive windthrow and heatwaves already show signs of increasing magnitude in Europe. With the direction of damage being transposed under massive outbreak dynamics, the coordinated mass attacks on individual mature and healthy spruces brought on by the attraction pheromones of pioneer males, environmental cues may lead to larger infestation patches which increase the within-stand replacement rate, which in turn enables exponential growth (Vega and Hofstetter 2014). The expansion of changing bark beetle dynamics are manifested in transient states in respect to the bivoltinism of *Ips typographus*, which presently can be said for Norway (Økland, Nikolov et al. 2016). Transition states extend beyond the northward reach of voltinism and dispersal, but also to elevated stands. Although multivoltine populations will likely not yet be a frequent site in Norway, sister broods may contribute to the propagation of univoltine outbreaks by maximizing population growth within one generation (Wermelinger and Seifert 1999).

When massive spruce bark beetle outbreaks are initiated, they have been experienced to be exacerbated by nearby unmanaged stands, which beetles may favor for the amount of deadwood that is not salvaged (Müller, Bußler et al. 2008). The dilemma of protected reserves bordering on managed forest stands is debated since the dispersal is not necessarily linked to these stands as topography, elevation and other factors may limit exchange between populations. This management dilemma may call for salvage operations within protected reserves under special circumstances, if vulnerable patches of forest can be reached by logging operatives. Lastly, a management implication for mixed stand management is the non-specificity or ability for non-host species transition of *Ips typographus*, whether spruce bark beetles can infest adjacent conifer species or are able to overwinter in non-host trees.

Uncertainties of climate driven *Ips typographus* outbreaks

With a changing climate, challenges for the Eurasian spruce bark beetle may arise as well. Inconvenient extreme weather periods may hinder them from swarming in spring, which are

strongly dependent on local site conditions. Thus, even when a storm hits a vulnerable region one year, can subsequent years be favorable for trees in the precipitation regime, strengthen their defenses and otherwise limiting thermal sums for the beetles prevent them to propagate in massive outbreaks. Furthermore, brood trees that have been windthrown, uprooted or otherwise damaged may not be as suitable for the coming generations when left uncolonized for a year, thus limiting the bark beetles to endemic population levels in close to normal quantities of brood trees. Negative density feedbacks have also been studied to be natural regulating mechanisms impeding long-term propagation of outbreaks (Marini, Lindelöw et al. 2013). More research is needed to establish risks for local sites of spruce stands to effectively allocate resources for management, silvicultural and control measures.

Although model simulations are simplified approximations of multiplex processes, concerning the interaction of windthrow and epidemic beetle outbreaks, they may be able to deliver solid reasoning for adjusting management decisions on the heterogenous boreal landscape. If site conditions were more homogenous, difficulties would arise from leaning on scenarios that could alter greatly from projections if only one (i.e. mean annual spring temperature increase or increase in heat wave severity) would change (Overpeck, Rind et al. 1990). Økland, Netherer et al. (2015) also hint towards that models and simulations remain conservative considering the outbreak potential and environmental constraints on the Eurasian spruce bark beetle, with most models assuming total mortality of beetles that haven't completed their development during winter, as well as a strict diapause for reproduction.

It is important to bear in mind, that site-specific conditions are key to these models and simulations (Blomqvist, Kosunen et al. 2018), firstly because the disturbance regimes of each forest stand at different scales may determine the impact of a changing climatic conditions. The topography of a forest stand creates a significant gradient for the bark beetle where two subpopulations inhabiting the same region may strongly vary in their voltinism and activity (Davidková and Doležal 2017). The spruce bark beetles preference for sun-exposed forest edges may for example be undermined by unfavorable soil and undergrowth conditions, especially where no human-made corridors and open patches have been created (Kuuluvainen 1994, Angelstam and Kuuluvainen 2004).

Implications of environmental conditions

Intensely managed spruce stands in their native range do not face immediate biome shifts due to climate change, since Norway spruce can be successfully grown outside its native range at Central and Southern European latitudes, albeit under (evapotranspirational) stresses. Drought stress in Northern Europe has only been observed to be detrimental (driver of bark beetle population dynamics) in warmest locations (Marini, Lindelöw et al. 2013), but these could indicate of what is to come for drought susceptible localities and extreme years in other parts of Scandinavia. Severe acute and chronic drought is detrimental to the vitality of spruce and makes it more susceptible to damage from natural disturbances (Schlyter, Stjernquist et al. 2006). Climate change is likely to be accompanied with increases in infrequent heavy precipitation in Scandinavia (Larsen, Gregersen et al. 2009), but also increases in evaporation as well as concomitant increases in drought (Benestad 2005, Venäläinen, Lehtonen et al. 2020). Scandinavian spruce and fir forests are well accustomed to wind disturbances, but drought could lead to extreme conditions, where the disturbance regime proves too severe and frequent, factoring in massive bark beetle outbreaks, especially in Southern parts of Scandinavia and forest fires. Future increases in fire disturbances due to prolonged heat waves, would likely enable fire tolerant tree species such as Scots pine to establish itself on heavily disturbed spruce stands. Lastly, extreme weather events are not limited to windthrow, but also stand-level damages from heavy snowfall (snow loading), where tree damage is exacerbated with less topsoil being frozen (Venäläinen, Lehtonen et al. 2020).

Monocultures of spruce, on the other hand, with only a few age classes may lead to scenarios where during massive outbreaks entire stands can be eradicated if temperature thresholds allow for populations to reach several generations within one growing season. As seen with Engelmann spruces in Northern America under massive bark beetle outbreak conditions, mature spruces are attacked first, but through high beetle numbers and densities, younger spruce may also be targeted at later stages into the outbreak, (Pettit, Voelker et al. 2020). This phenomenon should be studied further for *Ips typographus* and *Picea abies*, to ensure that management decisions are not only focusing on older age classes of spruce.

Severe disturbance regimes of windthrow induced beetle outbreaks mean very different things for natural or mixed stands, as “Disturbance intensity is strongly driven by drought stress and species composition” (Seidl, Rammer et al. 2008). Reduced growth rates resulting from competition or unfavorable microsites (Castagneri, Storaunet et al. 2013) in mixed stands juxtapose uniform growth rates in managed monocultures with equidistant horizontal forest structure, where wind can attack unabatedly. Mixed stands are likely to diversify soil

conditions, influencing runoff, water retention, soil nitrogen and rootage. In addition to aboveground attributes such as stem density and vertical structure, they may dampen evapotranspirative losses or ameliorate gap and stand level damages.

The ‘push-pull-effect’ of deciduous tree volatiles (Wichmann and Ravn 2001), certainly depends on local characteristics. Nonetheless, caution should be used with management decision involving mixed stands or buffer stands, where only a few other tree species are grown alongside Norway spruce. More studies need to be invested in the guidance principle of beetles dispersal and attraction processes.

CSF and ecosystem services

Norway and the rest of mainland Scandinavia remain important suppliers of spruce from boreal forest. Natural disturbances force forestry to not only consider the security of natural stands, ensuring biodiversity provision, but also the security of high output stands which deliver a sustainable flow of woody raw material which eventually mitigates climate change as well by steering economies towards renewable biological resources (Verkerk, Costanza et al. 2020).

It seems economically and ecologically unlikely that other boreal tree species than Norway spruce be of similar importance for timber and paper pulp industry in Northern Europe. CSF should thus be considered as an alternative future forest management tool to ensure ecosystem provision by assigning ‘roles’ to local and regional boreal forest stands. Firstly, the most susceptible ones to climate-induced massive spruce bark beetle outbreaks brought on by drought and windthrow need to be identified. Secondly, local site conditions need to be assessed to confirm their vulnerability and determine whether soil and landscape characteristics are most suitable for economically productive spruce dominated forests, mixed stands or require natural states with old growth characteristics for niche construction of specialized species and successional legacies that fill up adjacent regenerative abilities of managed stands. Byproducts of utilizing CSF could mean an increase in efficiency of harvesting while decreasing losses to natural disturbances, improving quality of timber by mitigation and changes in forest structure and improve forest management policy creating more independence for foresters by allowing them to tailor individual strategies for small-scale stands.

Monitoring & risk assessment

According to Temperli, Hart et al. (2014) the most suited predictor variable for timing of death of Engelmann spruce in the Rocky mountains, North America, due to woodboring insects might be tree size rather than age. This constitutes an interesting aspect for risk assessment purposes and should be explored in Europe for the case of *Ips typographus*. The mediation of stands with largest trees could serve as a management suggestion, when prioritization is difficult for expansive forest stands (Anderegg, Hicke et al. 2015). Lobinger (1996) argues that at the beginning of bark beetle outbreaks (progradation phase) the sex ratio of beetles leaned towards females when caught in pheromone traps and reapproached a balance towards the end (retrogradation phase). This could constitute an early danger detection and possible monitoring index. However, caution needs to be exercised with pheromone traps as they have not been showing sufficient efficacy of capturing beetles, even when caught at short distances from infested tree or patches.

Even though infested trees are hard to spot and pheromone traps give off insufficient results, renewed early detection tools are being developed and field-tested (Hlásny, Krokene et al. 2019) and many ecologists are hoping to see changes in management decisions such as Hlásny, Mátyás et al. (2014) put it, should “focus on risk management rather than on indicators of productivity in silviculture and forest planning”.

Knowledge gaps and future efforts

The link between changing seasonal mean temperatures, changes in precipitation regimes and extreme weather events to *Ips typographus* outbreaks is fairly well understood (Jönsson, Harding et al. 2007, Faccoli 2009, Kausrud, Økland et al. 2012, Økland, Krokene et al. 2012, Temperli, Veblen et al. 2015, Økland, Netherer et al. 2015, Marini, Økland et al. 2017, Venäläinen, Lehtonen et al. 2020). What has also increased are small-scale studies concerning site specific conditions, how these interact with the proliferation of the spruce bark beetle and other wind disturbances (Grodzki, Jakuš et al. 2003, Økland and Berryman 2004, Eriksson, Pouttu et al. 2005, Heurich 2009, Fahse and Heurich 2011, Kausrud, Grégoire et al. 2011, Kärvemo, Rogell et al. 2014, Blomqvist, Kosunen et al. 2018, Venäläinen, Lehtonen et al. 2020).

Current knowledge on the climate driven effect on natural disturbances communicates no steep increase in frequency of severe weather events over Northern Europe, but other factors have changed across Europe such as land use, forest management, ecosystem interactions, soil

conditions in Norway, and borealization of Northernmost Scandinavia as a result of both climate and invasive species. Seidl, Thom et al. (2017) add that a publication bias remains with direct effects of climate change on disturbances and call for more indirect effects, such as natural disturbance interactions and on climate driven successional patterns. The question posed by De Grandpré, Waldron et al. (2018) of whether tree mortality is a strong enough proxy for disturbance event severity could be relevant when studying disturbance events. Hereby, other damage criteria factoring in damages to roots, exposed soil and amount of woody debris could deliver a more accurate picture of state of forest stand after disturbance, successional character and susceptibility to local bark beetle infestation patches, which could be used by managers to identify these patches during salvage operations.

Successional dynamics of boreal forests are well understood and utilized in rotation periods of spruce dominated stands, but losses by salvage operations and changes to geochemical site conditions will only show their eminent effects in decades after large-scale disturbances. Hereby, early successional stages after stand-scale damages derived from bark beetle outbreaks need to be studied further to determine how early succession may interact with adjacent natural stands and increase regeneration of desired forest characteristics, using information on biological legacies such as the study of De Grandpré, Waldron et al. (2018). What are the remaining questions about consequential effects of natural disturbances to forest structure? The data derived from forest inventories could be applicable to disturbance regimes under climate change in heavily managed forests, to assess large scale structural changes and create vegetation models to track biome shifts through successional patterns in heavily disturbed transition zones. Securing ecoregions within boreal forest that contain certain features which are highly adaptable to climate change efforts or are extremely vulnerable to change should be utilized through differential management regimes.

12 Conclusion

The synthesis of studies on the consequential effects of forest damages by massive spruce bark beetles present forest management with the knowledge of creating adaptation plans for spruce dominated boreal forest stands.

Disturbance agents such as frost, drought, windthrow and snow can have immediate, direct effects on forests, whilst others such as insect outbreaks and fungal pathogens may have a delayed impact on the vitality of individual trees and susceptibility of tree stands to other

disturbances, thus making an interactive disturbance regime an increasing risk for spruce forest stability under climate change (De Grandpré, Waldron et al. 2018). Climate driven disturbances have the largest effect in Norway spruce stand structure and age dynamics (Angelstam and Kuuluvainen 2004, Díaz-Yáñez, Mola-Yudego et al. 2016). While some disturbances in the boreal forest may induce mortality throughout all age classes, the highly specialized Eurasian spruce bark beetle *Ips typographus* favors mature spruce trees, but can kill off spruce trees in all age classes during massive breakouts due to increased infestation success, even more so by multivoltinism (Wermelinger and Seifert 1999, Wermelinger 2004, Müller, Bußler et al. 2008, Lange, Økland et al. 2010, Davidková and Doležal 2017). The dynamics of windthrow-induced *Ips typographus* outbreaks should not be singled out in light of the significance of the effect of drought on creating conditions for epidemic populations, since they can be attributed to the most destructive spruce bark beetle outbreaks in recent decades.

The goal of forest managers could concretely mean a tradeoff between spruce dominated stands entailing old-growth characteristics for niche and soil diversity, and mixed forest management to mitigate windthrow-induced bark beetle outbreaks which provides ecosystem services and ensures economically productive forests guided by climate smart forestry. Regarding the Eurasian spruce bark beetles, outbreak control efforts have focused on phytosanitary measures that combine salvage logging, debarking and sanitation felling, whereas pheromone trapping has proven to deliver some success on monitoring *Ips typographus* populations to establish recent risk assessment endeavors (Vité 1989, Hlásny, Krokene et al. 2019).

For future methods of adapting the boreal forest to climate-driven disturbances, monitoring within the least susceptible stands may be conducted with traps focusing on increasing the accuracy for representation of current population levels. However, fast reaction plans in susceptible stands are required as well as improved infestation detection tools that identify infested trees through cost-effective methods. An adapted management framework through changes in forest structure planning, for instance management plans of including more diversity of climatically suitable species into spruce dominated stands as well as changes in vertical structure to prevent severe windthrow, thus undermining development of epidemic *Ips typographus* populations. Additionally, forest owners need to be increasingly made aware of the use of said methods in Southern parts of Norway, so that outbreaks are limited to small parts and cannot replenish other patches of infestation. Lastly, the renewed silvicultural methods should be appropriated to the needs and susceptibility of local stands, thus allocating resources efficiently.

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