

Chapter 4

Selected Examples of Interactions Between Natural Disturbances



**Jean-Claude Ruel, Beat Wermelinger, Sylvie Gauthier, Philip J. Burton,
Kaysandra Waldron, and Ekaterina Shorohova**

Abstract Understanding natural disturbance regimes and their impacts is crucial in designing ecosystem management strategies. However, disturbances do not always occur in isolation; the occurrence of one disturbance influences the likelihood or the effect of another. In this chapter, we illustrate the importance of disturbance interactions by focusing on a subset of interactions present in different parts of the boreal forest. The selected interactions include insects and wind, insects and fire, and wind and fire. The potential consequences of climate change on these interactions are also discussed.

J.-C. Ruel (✉)

Faculté de Foresterie, Géographie et Géomatique, Université Laval, Pavillon Abitibi-Price, 2405
rue de la terrasse, Québec, QC G1V 0A6, Canada
e-mail: Jean-Claude.Ruel@sbf.ulaval.ca

B. Wermelinger

Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Zürcherstrasse 111, 8903
Birmensdorf, Switzerland
e-mail: Beat.Wermelinger@wsl.ch

S. Gauthier · K. Waldron

Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, 1055 rue du
PEPS, P.O. Box 10380, Stn. Sainte-Foy, Québec, QC G1V 4C7, Canada
e-mail: Sylvie.gauthier@nrcan-rncan.gc.ca

K. Waldron

e-mail: Kaysandra.waldron@NRCan-RNCan.gc.ca

P. J. Burton

Ecosystem Science and Management, University of Northern British Columbia, 4837 Keith
Avenue, Terrace, BC V8G 1K7, Canada
e-mail: Phil.Burton@unbc.ca

4.1 Introduction

A forest ecosystem management approach that mimics natural forest dynamics requires a solid understanding of natural disturbance regimes. The previous chapters (Chaps. 2 and 3) have provided information on disturbance regimes and how climate change influences them. However, disturbances do not always act in isolation but often interact (Buma, 2015; De Grandpré et al., 2018). Some disturbances such as insect outbreaks and windstorms increase the raw material (food or fuel) upon which other disturbances can build and consequently augment their importance. Conversely, certain events such as fires and landslides remove or reduce the available biotic material on which subsequent disturbances can act, thus decreasing the occurrence of future disturbances. The marked heterogeneity of disturbances and general patterns generated by interacting disturbances can lead to complex disturbance regimes and landscapes (Cannon et al., 2019; Sturtevant & Fortin, 2021).

Interactions can take two major forms: (1) the occurrence of one disturbance influences the likelihood and impact of a second event, and (2) a disturbance influences the capacity of the ecosystem to recover from a previous event (Buma, 2015). Both forms may occur simultaneously. Infrequent, large disturbances would normally produce minimal long-term change, so long as they remain within the natural range of variability for disturbance frequency and severity (Kulha et al., 2020). Compound disturbances that occur within the period where the ecosystem is recovering from the initial disturbance may lead, however, to the long-term alteration of communities (Jasinski & Payette, 2005; Paine et al., 1998; Splawinski et al., 2019). Ecosystem recovery can also be compromised when a disturbance occurs in a community already affected by a chronic stress, e.g., drought, a situation that may become more common in the context of climate change (Jactel et al., 2012). However, there are also cases where a disturbance may reduce the probability, intensity, or severity of subsequent disturbances (Cannon et al., 2019). The amplifying or buffering nature of these interactions can even vary with the particular response variable (Cannon et al., 2019).

To assess disturbance interactions, we must discuss both the implicated mechanisms and their respective impacts on the ecosystem. Different forms of disturbance can affect various ecosystem components, and we require a means of describing these effects. Buma (2015) has suggested focusing on the legacies from each disturbance and the mechanisms involved. Traditionally, the amount of canopy removed has been used to describe disturbance severity in forests; however, Roberts (2007) suggested

E. Shorohova

Forest Research Institute of the Karelian Research Center, Russian Academy of Science,
Pushkinskaya str. 11, Petrozavodsk 185910, Russia

e-mail: shorohova@es13334.spb.edu; ekaterina.shorokhova@luke.fi

Saint Petersburg State Forest Technical University, Institutsky str. 5, Saint Petersburg 194021,
Russia

Natural Resources Institute Finland (Luke), Latokartanonkaari 9, 00790 Helsinki, Finland

that this measure is insufficient by itself to fully describe the impact of forest disturbances. This is particularly relevant when considering disturbance interactions. As an alternative, Roberts (2007) suggested describing disturbance severity along three axes: (1) percentage of canopy removed, (2) percentage of understory removed, and (3) percentage of forest floor and soil removed or disrupted.

In this chapter, we illustrate specific regional interactions between the main natural disturbances of the boreal forest and discuss the potential effects of global change on these interactions. We recognize that we do not touch upon all possible interactions and regions; however, we believe that focusing on these selected cases can help design future ecosystem management strategies. Finally, we highlight some knowledge gaps and their associated research needs.

4.2 Windthrow and Insects

Interactions between windthrow and insects are common in the boreal forest biome. The implicated tree and insect species vary geographically, as does the nature of the interactions. Windthrow and insect disturbances can interact in two different manners. Insect damage can open the stand, exposing trees to higher wind speeds (Gardiner et al., 1997) and making them more susceptible to windthrow. Examples of this type of interaction include infestations of the spruce budworm (*Choristoneura fumiferana* Clemens) in northeastern North America and the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) in western North America. Nonetheless, windthrow and insects can also interact in a reverse manner. Windthrow can generate an ample supply of breeding material, supporting a population increase of some bark beetle species, which can then switch to attack living trees (e.g., Havašová et al., 2017).

4.2.1 Windthrow and Defoliators

In the absence of fire, windthrow and outbreaks of spruce budworm represent the main disturbances in the boreal forest of eastern Canada. Three major spruce budworm outbreaks occurred during the twentieth century (Navarro et al., 2018), mostly affecting forests dominated by balsam fir (*Abies balsamea* (L.) Mill.). Vulnerability to spruce budworm–related defoliation differs among tree species, balsam fir being the most vulnerable, followed by white spruce (*Picea glauca* (Moench) Voss), red spruce (*Picea rubens* Sarg.), and black spruce (*Picea mariana* (Mill.) BSP). Pines and hardwoods are unaffected.

Windthrow is a common feature of the Canadian boreal forest. Although the return period of total windthrow may exceed 4,000 years (Bouchard et al., 2009; Waldron et al., 2013), partial windthrow can be more frequent (Waldron et al., 2013).

Windthrow occurrence varies with wind exposure as well as soil and stand characteristics (Ruel, 1995, 2000). Vulnerability also depends on species, stem taper, and rooting depth. Balsam fir, which is the most vulnerable tree species to the spruce budworm, is also one of the species most vulnerable to windthrow in eastern Canada.

Defoliating insect outbreaks of intermediate severity or outbreaks occurring in mixed-species stands typically cause partial canopy mortality. Because of the increased tree spacing resulting from this partial mortality, wind load on residual trees is increased, potentially leading to windthrow (Girard et al., 2014; Morin, 1990). Spruce budworm-related defoliation can also lead to a reduction of the fine root biomass of surviving trees (Morin, 1990). This reduced size of the root system affects a tree's resistance to overturning. Taylor and MacLean (2009) documented an increase in wind-driven mortality 11 to 25 years after a spruce budworm-related defoliation. In mixedwood stands, hardwoods surviving a spruce budworm outbreak are also more wind resistant, thereby limiting the potential for disturbance interactions. In their study of Newfoundland forests that had previously been attacked by hemlock looper (*Lambdina fiscellaria* Guenée), Arsenault et al. (2016) reported a greater incidence of mappable windthrow patches. In both cases, the increased exposure of surviving trees after widespread insect-caused defoliation provoked elevated levels of windthrow.

Spruce budworm has a major but variable effect on the main forest canopy and generally a minor effect on the understory, although advance regeneration may be somewhat affected (Nie et al., 2018). The impact on the forest floor is, however, generally negligible. Because balsam fir is more vulnerable than other species, this perturbation can reduce the proportion of this species in the canopy over the short term; however, as a shade-tolerant species having relatively few seedbed requirements, balsam fir generally dominates the advance regeneration in mixed coniferous stands. Hence, the impact of the spruce budworm on the longer-term tree species composition tends to be minor (Girard et al., 2014).

When spruce budworm damage does lead to windthrow, the additional consequences on the understory layer tend to be limited (Girard et al., 2014); however, substantial changes occur on the forest floor. The creation of a pit and mound microtopography by windthrow disrupts the herbaceous layer and exposes mineral soil or mixtures of mineral soil and organic material. This microtopography contributes to an increased post-disturbance seedbed heterogeneity, which can improve seedling establishment and increase plant species richness (Ulanova, 2000). Given the aggressiveness of balsam fir regeneration, however, balsam fir typically remains the main tree species and may even increase its relative abundance (Fig. 4.1; Girard et al., 2014; Morin, 1990). The effect may differ within stands that have yet to reach the understory reinitiation stage (*sensu* Oliver, 1980). In these latter stands, the seedling bank is not yet developed, and the insect can reduce the production of seeds, thereby compromising new seedling establishment (Côté & Bélanger, 1991).

Climate change may modify the phenology of both the tree host and the insect. This modification could lead to the expansion of the insect's range and increase damage severity (Pureswaran et al., 2015). Climate warming is expected to reduce the period when soils are frozen in most regions of eastern Canada. Although there



Fig. 4.1 Stand originating from the combined action of spruce budworm and windthrow in eastern Québec, Canada. *Photo credit* François Girard

is as of yet no clear evidence of an increased occurrence of strong wind events in the boreal forest, budworm-impacted stands may become more exposed to the strong winds that typically occur in late fall, without benefiting from the increased resistance to overturning provided by a frozen soil and snowpack (Saad et al., 2017). This interaction could become more important in the future because of the possible extension of the area vulnerable to outbreaks. This frozen soil–windthrow–insect interaction could therefore become a significant issue in the parts of eastern Canada, where a low occurrence of fires and an associated abundance of uneven-aged stands would see an increased use of partial cuttings, further heightening the vulnerability of these stands to windthrow (Anyomi & Ruel, 2015).

4.2.2 Windthrow and Bark Beetles

Mass outbreaks of bark beetles are natural events, particularly in the long-term dynamics of coniferous forests. Bentz et al. (2010) identified 14 species of bark beetles that have the potential to cause landscape-level mortality of trees making up western North American forests. In European forests, 8% of all forest damage is caused by bark beetles (Schelhaas et al., 2003). The most destructive species in Europe is the spruce bark beetle (*Ips typographus* (L.)) (Wermelinger, 2004). This beetle almost exclusively colonizes Norway spruce trees (*Picea abies* (L.) Karst.). In central Europe, generally two generations of spruce bark beetle develop per year,

whereas in Fennoscandia and at elevations above approximately 1,500 m asl, only one generation per year develops.

During its latency phase at normal population levels, the spruce bark beetle develops at low densities under the bark of dead trunks or stumps. Because of poor phloem quality, interspecific competition with other bark dwellers, and mortality imposed by natural enemies, bark beetle populations remain low (Raffa et al., 2008). Under these conditions, healthy conifers are generally not colonized because the trees can physically and chemically defend themselves against these attacking insects by releasing resins containing toxic terpenoid compounds (Krokene, 2015).

However, windthrow in a spruce-dominated forest changes the situation for the spruce bark beetle. The fallen trees offer an ample supply of fresh, poorly defended bark, easily colonized by adult beetles (Eriksson et al., 2005). The still-soft and nutrient-rich phloem of the windthrown trees provides a high-quality substrate for the development of the bark beetle offspring. The beetles quickly propagate in the windthrown timber, and their population levels increase. However, at higher latitudes and under endemic conditions, small windthrow patches may produce too few bark beetles to allow the subsequent attack of adjacent living trees (Eriksson et al., 2007). Depending on local conditions, the phloem of windthrown trees becomes desiccated after one to three years and thereafter unsuitable for further colonization (Dodds et al., 2019; Wermelinger, 2004).

When the spruce bark beetle attains very high population levels, it attacks living trees. The beetles initially target nearby trees, particularly those within 250 m of the windthrown stems (Fig. 4.2; Havašová et al., 2017; Seidl & Blennow, 2012). These trees may have root damage caused by the storm, and the previously shaded stems become exposed to detrimental irradiation from the sun, i.e., sunburn. During this time, further infestation spots caused by single overthrown trees emerge in the stand interior. The bark beetles increase their population levels further and become sufficiently abundant to overcome the defenses of even healthy trees through the mass attack throughout the stand. Only at this point—extremely high populations of adult beetles—can bark beetles successfully colonize vigorous trees. The insects profit from an almost infinite supply of living trees, containing high-quality phloem and without competing phloem feeders except for their conspecifics. With the positive feedback of a high-reproductive output and successful colonization through mass attack, the populations reach a self-sustaining dynamic that may last for several years. A compilation of the most significant outbreaks of the last few decades in central Europe and Scandinavia revealed that the propagations last between 5 and 12 years (Wermelinger & Jakoby, 2019). Often, these outbreak dynamics are sustained by dry and hot summers, recurring smaller disturbances (e.g., heavy snowfall events), and heavy seed masts, all of which deplete the energy reserves of the trees (Nüsslein et al., 2000). Post-windthrow spruce bark beetle outbreaks lasting two to six years have been reported for different boreal forest regions in Russia (Maslov, 2010). In Sweden, peak infestations were attained in the third summer after the windthrow event (Kärvemo et al., 2014; Schroeder & Lindelöw, 2002), a timing that also holds for higher elevations in the Alps (Wermelinger, 2004).



Fig. 4.2 Damage from the bark beetle (*Ips typographus*) in a subalpine spruce forest in Switzerland. A windthrow event gave rise to a subsequent infestation of the adjacent spruce trees. *Photo credit* Beat Wermelinger

Outbreaks cease for various reasons. These include consistently high host-tree resistance stemming from sufficient precipitation and relatively cooler weather, increased bark beetle mortality because of intraspecific competition, natural enemies, human control measures (Stadelmann et al., 2013), a decreasing supply of host trees, or a combination of these factors (Marini et al., 2017). Bark beetle populations eventually fall below the critical threshold required for successfully attacking live trees, and the mass infestation thus ends.

The transition from colonizing low-defense substrates in latency to infesting high-defense trees in the eruptive phase is most commonly triggered by an abiotic disturbance. In Europe, windthrow is the main trigger of bark beetle outbreaks (cf. Table 1 in Wermelinger & Jakoby, 2019). More recently, pronounced dry spells have also led to large-scale infestations by temporarily compromising the defense capacities of living spruce trees. Moreover, higher temperatures have allowed the production of a third generation of bark beetles in central Europe (Jakoby et al., 2019) and a second in Scandinavia (Jönsson et al., 2009; Neuvonen & Viiri, 2017). The interactions between tree resistance and bark beetle population size are crucial for the dynamics of an infestation (Fig. 4.3). The number of simultaneously attacking beetles required to successfully colonize a tree is positively related to the health and vigor of the tree (Mulock & Christiansen, 1986; Nelson & Lewis, 2008). With climate change, the projected increased frequency of hot and dry summers (and possibly more storm events) will favor an increased spruce tree mortality and a distinct decline of this tree species in central Europe (Jakoby et al., 2019; Jönsson et al., 2007).

In North American forests, the mountain pine beetle is the most devastating bark beetle. This coleopteran has a similar biology to that of the European spruce bark

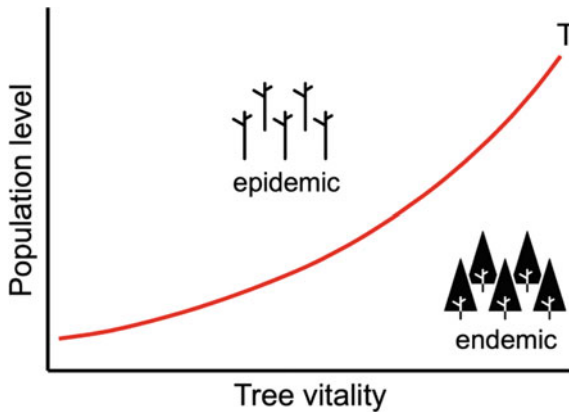


Fig. 4.3 Relationship between tree vitality and population levels of bark beetles required to cross the threshold (T) separating endemic and epidemic stages. Modified from Wermelinger and Jakoby (2019) with permission from Haupt Verlag

beetle; however, it is restricted to living pine tree hosts, and outbreaks are often provoked by drought or a series of mild winters. During an unprecedented mass propagation in the decades at the turn of the twenty-first century, the mountain pine beetle expanded its natural outbreak range toward the northeast and to higher elevations. During this process, the beetle also colonized—in addition to its preferred host of lodgepole pine (*Pinus contorta* var. *latifolia* Dougl. ex. Loud.)—whitebark pine (*P. albicaulis* Engelm.) and jack pine (*P. banksiana* Lamb.) (Raffa et al., 2013). Several years of higher temperatures, which reduced levels of winter mortality for this beetle, and the large-scale availability of old, even-aged, and drought-stressed pine forests (Logan & Powell, 2001; Taylor & Carroll, 2004) allowed the growth and spread of these extensive and long-lasting outbreaks (Stahl et al., 2006).

Contrary to the previous situations in which windthrow or climate anomalies triggered bark beetle outbreaks, surprisingly little attention has been given to the reverse interaction, namely the effect of bark beetle attack on subsequent windthrow events. As in other cases of insect attack in mixed-species stands, the death of pine trees exposes nonhost trees to higher wind loads, making them more vulnerable to wind. In addition, trees killed by the mountain pine beetle will gradually lose functional integrity in their stem and roots, resulting in the eventual deterioration and collapse of dead trees over time. Furthermore, the rate of bole collapse may be accelerated by windsway, and high winds are often directly responsible for the collapse of beetle-killed trees.

The annual monitoring of tree health and condition during and after an outbreak of mountain pine beetle in a forest stand dominated by lodgepole pine in central British Columbia provides an example of windthrow following a bark beetle outbreak. An eddy flux tower documented a remarkable recovery of the stand's function as a net carbon sink within three years of the outbreak despite 90% of the tree layer having died (Brown et al., 2012). The status of these dead trees over 15 years (Fig. 4.4)

showed a clear uptick in the rate of bole collapse between 2013 and 2014. This collapse—31% of the total number of fallen trees—was related to a wind event in December 2013 that had sustained average wind speeds of 36 km/h. Unfortunately, there were no nearby lodgepole pine stands unaffected by the mountain pine beetle for comparison purposes. Nonetheless, the observed treefall rates were much higher than background rates in stands dominated by living trees. It is interesting to note that stronger winds had been recorded several times in 2009 but without a noticeable increase in windthrow. Wind drag is reduced soon after a tree dies as needles gradually fall off; however, the stem and root resistance remain unaffected during the initial three years after a beetle attack. This example illustrates the importance of case-specific and dynamic lag effects in detecting and understanding disturbance interactions (Burton et al., 2020). Furthermore, in accelerating post-beetle tree collapse, wind contributes to the accumulation of boles resting on the ground and having contact with the forest floor. This accumulation further accelerates fungal attack and decomposition and elevates the rate of CO₂ release due to tree decay (Kaytor, 2016). Although inadequately documented, greater concentrations of fallen beetle-killed trees could plausibly result in more intense wildfires (Jenkins et al., 2012), especially if fallen trees are *jack-strawed*, i.e., collapsed at multiple intersecting angles with many boles elevated above the ground and staying well dried, leading to a three-way interaction between insects, wind, and fire.

Bark beetle attacks in living stands markedly reduce canopy cover, especially in pure stands of host species; however, the understory and the forest floor are normally minimally affected. When dead trees are subsequently damaged by wind, the level

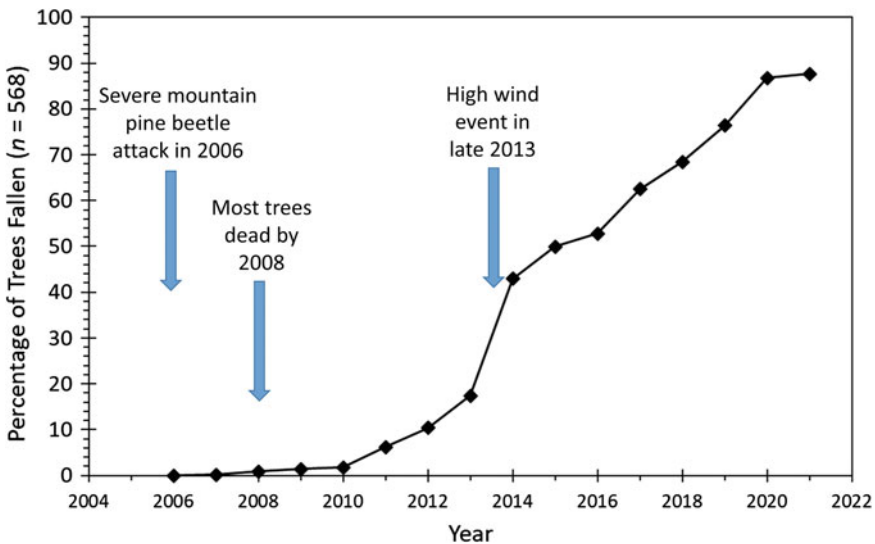


Fig. 4.4 Progression of treefall after a mountain pine beetle attack of a lodgepole pine stand in central British Columbia, Canada, accelerated by extreme winds in late 2013. Unpublished data from Dale Seip and Vanessa Foord, Government of British Columbia

of soil disturbance is typically less than the soil disturbance experienced with the windthrow of living trees, as the root systems of the dead trees will have degraded to some extent. The amount of advance regeneration then likely influences stand regeneration.

When a bark beetle outbreak develops from wind-killed trees, the on-site effects will mostly reflect the wind's impact: a reduced canopy cover, a minor effect on the understory, and the local perturbation of the forest floor. However, the consequences of the beetle outbreak will extend to neighboring stands, where it will mostly affect canopy cover. After the collapse of the infestation, the development of a new stand in managed forests depends largely on silvicultural measures such as planting and fostering preferred tree species. In unmanaged or extensively managed forests, natural regeneration and future stand development depend on multiple factors, including elevation, climate conditions, the spatial magnitude of the infestation, the density of advance regeneration, and the proximity of seed trees. In high-elevation natural spruce forests, even-aged spruce stands are likely to develop.

4.3 Fire Interaction with Other Disturbances

Large fires are frequent in the boreal forest of North America. In Canada, for instance, almost 2 million ha of forests burn every year on average, with some years experiencing more than 8 million ha burned (Hanes et al., 2019). Broad-scale fires have also been increasing in size since 1959 (Hanes et al., 2019). These disturbances are one of the main factors controlling the age structure, and thus composition, of boreal forest stands (Gauthier et al., 2009). Fire can eliminate or greatly reduce the abundance of the hosts of several insect species at the landscape level, thereby reducing the chance of these insect populations exploding to an epidemic level in the region. This scenario is the case for balsam fir, one of the major hosts of the eastern spruce budworm, and a species not adapted to regenerate quickly after a fire. On the other hand, fire can also favor species such as trembling aspen (*Populus tremuloides* Michx.), which can become dominant over large areas and be possibly affected by the forest tent caterpillar (*Malacosoma disstria* Hübner). The large areas of lodgepole pine originating from the 1880–1920 fires in British Columbia provided a large continuous food source for the growth of the mountain pine beetle population in the late 1990s (Burton, 2010). With the forecasted increase in fire activity (Boulanger et al., 2014), the abundance of the preferred hosts for different insect species will change. Shorter fire-return intervals will likely increase the proportion of early successional species, favoring certain insect species. It should be noted, however, that negative feedbacks emerge when fire-return intervals are short. Successive fires within a short period do not allow forest fuels to accumulate, resulting in a de facto decrease in fire risk (Erni et al., 2018; Heon et al., 2014).

Short intervals between successive fires can be responsible for a change in ecosystem state in which closed forests are replaced by open woodlands owing to a lack of seeds for forest regeneration (Jasinski & Payette, 2005; Splawinski et al.,

2019). Short intervals between insect disturbances and fire can also produce such a state change (Simard & Payette, 2001).

Surface fires are frequent in the European boreal forest (Shorohova et al., 2011), and surviving trees are subjected to subsequent windthrow and bark beetle attacks (Fig. 4.5; Ananyev et al., 2016). A similar situation has been described for surface fires and insect outbreaks in Siberian *light coniferous* forests dominated by Siberian larch (*Larix sibirica* Ledeb.); within two years of a fire, 18–30% of surviving trees were attacked by insects (Isaev, 1962). In *dark coniferous* forests, dominated by Siberian pine and fir (*Pinus sibirica* Du Tour and *Abies sibirica* Ledeb., respectively), forest fires typically induce fungal diseases (Pavlov, 2015) and insect outbreaks (Kharuk et al., 2016, 2017).

Fire ignition, spread, behavior, and burned area can also be affected by the fuel inputs from tree and shrub mortality stemming from other disturbances, such as drought, insect outbreaks, and windthrow. The pulse created by this influx of dead and dry fuel can vary in duration depending on the tree species, the rate of the mortality process, and the regional weather/climate conditions. Recent drought has caused significant episodes of mortality, increasing the fuel load available to burn when the weather becomes conducive for fire, thereby increasing fire intensity (Ruthrof et al., 2016). Windthrow can increase the probability, intensity, and/or severity of subsequent fires by increasing the fuel load (Fig. 4.6). In Siberia, outbreaks of the Siberian silkmoth (*Dendrolimus sibiricus* Tschetv.) increase the risk of fires. Forest stands affected by an outbreak burn seven times more frequently than unaffected



Fig. 4.5 Bark beetle–induced decline and wind breakage six years after a surface fire in a mixed primeval boreal forest, Vodlozersky National Park, Russia. *Photo credit* Ilkka Vanha-Majamaa

stands, and the burned area in a silkmoth-affected forest is 20 times larger than in unaffected stands (Kharuk & Antamoshkina, 2017). On the other hand, fire kills the natural enemies of silkmoth and thus can trigger an outbreak (Baksheeva et al., 2019).

Interactions between fire and other disturbances can also affect the postfire recovery potential by removing propagule sources (Cannon et al., 2019). However, these interactions are complex and influenced by disturbance intensity and severity, which are often highly heterogeneous, and the interval between disturbances. The degree to which plant community recovery reflects the compound effects of a bark beetle outbreak and fire disturbance depends strongly on fire severity (Edwards et al., 2015). In some situations, such as low-intensity fire conditions, buffering effects can also be observed, i.e., by reducing fuels that otherwise might support more severe



Fig. 4.6 Fuel load in a black spruce stand after severe windthrow in eastern Québec, Canada. *Photo credit* Kaysandra Waldron

fires, thereby conferring a degree of forest resistance to subsequent disturbances for some time (Cannon et al., 2017, 2019).

The action of fire strongly influences the legacies of interactions between fire and other disturbances. Windthrow involves a reduction of forest cover, an increase in soil disturbance, and some modification of the understory layer (Waldron et al., 2013). Insect defoliation has a similar effect on the forest cover but with less effect on the understory layer and forest floor. However, when one of these disturbances precedes a fire event, its effects will become relatively minor relative to that of fire, which has a dominant impact on all constituents. When surface fires lead to windthrow or bark beetle attacks, the second disturbance will add to the canopy reduction, although the understory and the forest floor will remain dominated by the impact of fire.

4.4 Interactions Between Natural Disturbances and Forest Management Practices

In addition to interactions between natural disturbances, forest management practices can also interact with disturbances. For instance, partial cutting is a central element of many forest ecosystem management strategies (Bergeron & Harvey, 1997). By opening the forest canopy, standing trees become exposed to higher wind speeds, and damage due to increased wind has often been observed (Coates et al., 2018; Hanell & Ottoson-Lofvenius, 1994; Hautala & Vanha-Majamaa, 2006; Montoro Girona et al., 2019; Ruel & Gardiner, 2019). Salvage logging often follows high-severity disturbances and greatly modifies the legacies from natural disturbances, including the removal of residual living trees, the reduction of snags and downed woody debris, and the added disturbance to the understory and forest floor. These added effects can damage advance regeneration, increase fire risk (Donato et al., 2006), and decrease biodiversity (Thorn et al., 2018). Salvage logging in black spruce-dominated stands defoliated by the spruce budworm could increase the defoliation of black spruce regeneration. In turn, this loss of regeneration would influence stand development trajectories and eventually increase future stand vulnerability to the insect (Cotton-Gagnon et al., 2018). Partial cutting in defoliated stands would also lead to increases in regeneration defoliation although to a lesser extent than in clear-cut stands (Lavoie et al., 2021).

4.5 Conclusion

This chapter has focused on disturbance interactions where the occurrence of one disturbance influences the likelihood of another. We have shown that the interactions may significantly impact ecosystem processes and attributes. There are knowledge gaps in our understanding of these effects, and further research is required. For

example, other instances of compound disturbances can occur when two consecutive disturbances occur in sequence, without a causal relationship between them. These can also lead to significant effects on ecosystems, but their occurrence and impacts are less predictable without a direct relationship. The lack of suitable controls typically constrains evaluations of the interactive or compound effects of natural disturbances; that is, the effects of disturbance A without disturbance B and those of disturbance B without disturbance A are difficult to study under similar conditions as experienced for the interacting disturbances. As climate and weather influence many of these interactions, further research should target the possible effects of climate change on these interactions. Research should also expand the temporal scale being analyzed because studies of disturbance interactions are often conducted opportunistically and over the short term, covering only the initial years post-disturbance. The age structure of forest landscapes further influences the vulnerability of certain stands to disturbances and their possible interactions, an effect that must be better documented and understood.

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