

Disturbances in deciduous temperate forest ecosystems of the northern hemisphere: their effects on both recent and future forest development

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Abstract Disturbances in forests can kill mature trees, but also create the conditions necessary for the establishment of new tree cohorts and create micro-habitats for new plant and animal species, thereby increasing the species diversity compared to undisturbed stands. We review the types and intensities of disturbances on forests in three regions of the temperate zone of the northern hemisphere: northeastern North America, Central Europe, and East Asia. We focus on (1) the ways in which disturbances affect forest stand development; (2) the differences among the three areas in this regard; (3) the consequences for future forest management. In both northeastern North America and East Asia, hurricanes and typhoons represent the major mode of natural disturbance, while in Central Europe winter windstorms occur after deciduous trees have lost their leaves. Tornadoes can have even greater destructive power (but affect relatively narrow strips of land), and the more severe of these mainly occur in North America. The general disturbance patch system therefore is relatively large in northeastern North America, small in Central Europe, and of intermediate size in temperate East Asia. In addition to wholly natural disturbance factors, human commerce and globalization have enabled new disturbance types by introducing pests and diseases from one region to another. In North America especially, several of the most important foundation species in temperate forests are strongly affected, so that not just the species composition but also the whole forest structure is changing fundamentally. In all three areas in the past the change in land use by growing human populations strongly affected the structure as well as the species composition of forests. Nearly all the recent forest stands of the temperate zone had been used in the past in a particular way, and many of today's forests had previously been converted into agricultural land. Finally climate change is superimposing itself on forest development worldwide. Nevertheless, climate

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change is not a new phenomenon, so forest ecosystems in all time periods have been exposed to changing climatic conditions and have had to adapt. Each forest stand therefore represents a unique recent expression of the interaction of environmental conditions and plant species, a “snapshot” of the relevant abiotic and biotic factors, including human impact.

Keywords Windstorms · Ice and snow · Bark beetles · Invasive pathogens and insects · Land use change · Climate change

Introduction

Ecosystems are dynamic entities, variable across both space and time, and these patterns of variability in ecosystem development are modulated by events or processes known as “disturbances”. According to the most recent definition (van Andel and Aronson 2012) “*a disturbance factor causes a change or “transformation” in an ecosystem’s steady state, in terms of the standing biomass, productivity or biodiversity, which may be followed by either recovery to the former state (through resilience or resistance) or a change to another state...*”. Without referring to a postulated “steady state” Pickett and White (1985) defined disturbance as “... *any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment*”. Most generally speaking, a disturbance is any discrete event that removes organisms (Townsend and Hildrew 1994; Begon et al. 1995), making both space and resources free to be used by new individuals. We will use the term in this broad sense and include wide spatial as well as time scales.

Disturbances are an intrinsic element of forest ecosystems (Foster et al. 1998). Dale et al. (2000) identified fire, drought, introduced species, insect and pathogen outbreaks, hurricanes, windstorms, and ice storms as “key forest disturbances”. Humans also exert a strong influence on the disturbance regimes of ecosystems, for example by introduction of alien invasive pests and diseases (fungi, insects) and by changing either frequency and/or intensity of natural disturbances, e.g. of fires and snow avalanches.

Types, frequencies and intensities of disturbances are different in different parts of the world. For example, fire is an important natural disturbance factor in many boreal forests, in savannah-type ecosystems, and also in high mountain dry-land ecosystems. It is associated with special adaptations like thick bark (e.g. *Pinus ponderosa*/southwestern North America), the ability to re-sprout after fire (e.g. *Pinus canariensis*/Canary Islands; *Pinus rigida*/eastern North America), or store seeds on the tree until a fire occurs (“pyrophytes”, e.g. *Banksia* spp./Australia; *Pinus contorta*/western North America). These kinds of adaptations are missing in the tree species found in many deciduous temperate forests, because they do not naturally experience frequent fire.

Forest disturbances can be classified into (i) physical and (ii) biological disturbances. Physical disturbances may include storms, snow breakage, snow avalanches, or fire, whereas biological disturbances may include animal activities such as insect outbreaks, water management (by beavers), soil digging (by wild boar), and browsing or other herbivory (by deer), but also the natural senescence or mortality of plant species (e.g. bamboo dieback). Landscape utilization by humans is a new category that includes both physical

(e.g. tree felling, clear-cutting) and biological components (e.g. biomass extraction, species selection, introducing of species new to the area).

Independent of whether a disturbance is more the product of physical or biological causes, it may affect areas of quite different sizes. A hurricane may affect thousands of square kilometers, a fire or a bark beetle outbreak several to hundreds of square kilometers, while a wild boar creates soil disturbances only on few square meters.

The effect of a disturbance may also depend on the species richness of the affected community. Temperate forests are relatively species-rich in eastern North America and northeastern Asia (China, Japan) as compared with those of Central Europe, where during the Ice Age(s) many species, especially woody species, disappeared.

We focus here on the temperate forests of the northern hemisphere with their three centers: (i) eastern North America (from the New England states throughout the Appalachian Mountains), (ii) Central Europe (from Denmark/Northern Germany to the Alps and from the coast of the Atlantic Ocean to Poland as well as a small strip up the Ural Mountains, and (iii) central East Asia from the Qinling Mountains (Shaanxi Province) to northeast of Beijing, including central Japan (Fig. 1).

We ask the following questions:

- What are the major disturbance types in each region?
- How do these disturbances affect forest stand development?
- What are the consequences for forest ecosystem development and for future forest management?

The main objective of this survey is to determine how the combination of different disturbance types including the human driven ones in each region might influence future forest development, especially in the context of global change.

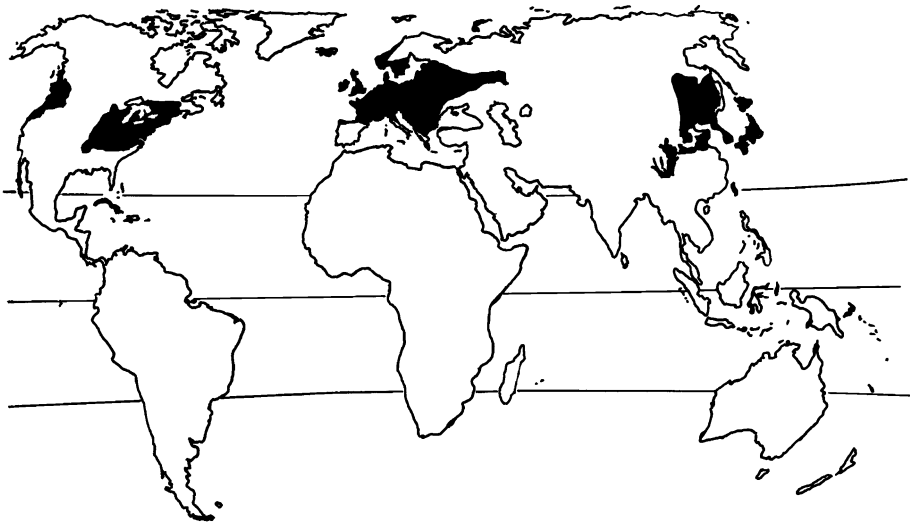


Fig. 1 Main areas of the temperate forests across the northern hemisphere

Natural physical forest disturbances

Windstorms

Wind occurs everywhere on the planet. It is no surprise therefore that windstorms are a major factor in the forest ecosystems of the temperate zone (Papaik and Canham 2006), influencing trees eco-physiologically (e.g. transpiration) as well as physically (e.g. uprooting, breaking; Zhu et al. 2004). Strong winds can throw down either single trees or small groups of trees (Table 1); this disturbance type is one of the main natural causes creating an uneven-aged forest structure (Lorimer 1980), and is also an important agent of gap expansion (Worrall et al. 2005). Larger forest areas may also be affected by wind-throw: (i) by strong winds connected with convective thunderstorms (Canham and Loucks 1984; Fischer et al. 1990), affecting areas of half an hectare up to several hectares, or (ii) by storms resulting from low pressure systems (Canham and Loucks 1984; Schönenberger et al. 2002) generally affecting areas of thousands of square kilometers, thus creating mosaics of disturbance across landscapes (Binkley 1999), but damaging forests strongly only on limited parts of this area: from stand scale to local scale (Table 1).

In Central Europe windstorms of this type are the most common and widespread disturbance to forests with highest storm frequency in Germany, Austria, Switzerland and

Table 1 Intensity and severity of disturbances as well as size of affected area

Disturbance type	Intensity	Severity	Area affected					
			Point	Patch	Stand	Local	Regional	Landscape
Strong wind	l	l	X	X	→			
Thunderstorm	m	m	x	X	X			
Low pressure system storm	h	h	x	X	X	X		
Hurricane	vh	vh	x	x	x	x	X	X
Tornado	vh	vh	x	x	X	X		
Snow avalanche	vh	vh	X	X	x			
Fire	-	-						
Bark beetle	vl	vl	x	X	X	X		
Browsing game	vl	vl-vh	X	X	→			
Digging wild boar	vl	vl-h	X	X	→			
Beavers	l	m	x	X	X			
Invasive alien species	vl	h-vh	X	→				
Forest conversion	h	vh	X	X	X	X	X	X

1 m² 100 m² 1 ha 1 km² 100 km² 10,000 km² size →

Point Patch Stand Local Regional Landscape

Intensity and severity: from *very low* (vl) and *low* (l) to *moderate* (m), *heavy* (h) and *very heavy* (vh)

X means scale where it mainly works, x where it also works

arrows indicate size affected if this type of disturbance occurs frequently on larger scales

northern France (Gardiner et al. 2011, p. 4); according to these authors storms are responsible for more than 50 % of all primary abiotic and biotic damage by volume to European forests from catastrophic events. Examining the presettlement forests of Wisconsin, USA, Canham and Loucks (1984) calculated 51.8 patches larger than 1 ha of complete canopy wind throw covering a total of 4,828 ha annually, equivalent to the total replacement of forest cover across the entire region every 1,200 years. Meyer et al. (2003) found gap sizes smaller than the mean crown size of old trees in unmanaged *Fagus sylvatica* forests in Albania, and in a Slovakian virgin beech forest more than 50 % of the gaps were caused by the death of only one tree, and 80 % by the death of up to three trees (Dröbner and von Lüpke 2005). Similar results were found in *Pseudotsuga menziesii*, *Tsuga heterophylla*, and *Abies amabilis*-dominated forests in Oregon: 10 % of the forests of the study area have been affected by windthrow during the past century, concentrated on three main windstorm events: 1931, 1973, and 1983 (Sinton et al. 2000). These disturbance events result in a regular turnover of forest cover, with older trees and stands being replaced by new.

Windthrow causes a series of changes in the forest stand: (i) sudden change of forest structure by broken or uprooted trees, (ii) disturbance of the soil especially in the course of the uprooting event (pit-mound system, covering a wide range from 0 up to 90 % of the ground and remaining for up to 200–500 years, Šamonil et al. 2010), and (iii) change of microclimate (Lutz 1940; Schatzel et al. 1989).

Nonetheless, there is only very limited knowledge of natural forest development following this disturbance type (Cooper-Ellis et al. 1999), especially in Central Europe with its high human population density and resulting landscape utilization pressure. While a few studies have been carried out in Switzerland (Schönenberger et al. 2002), Denmark (Brunner 2002), and also in the boreal zone of Russia (Močalov and Lässig 2002; Ulanova 2000), the first and up to now longest permanent plot study of stand development after wind throw in temperate Europe was established in 1988, following a local, short but heavy summer storm in a near-natural spruce (*Picea abies*) forest area in the Bavarian Forest National Park in SE Germany (Fischer et al. 1990). Comparing uncleared windthrow areas with cleared stands where there was salvage of fallen timber but no replanting, it becomes clear that the successional pathways are different: on cleared (salvaged) areas a felled-area plant community emerges soon after clearing, with *Rubus idaeus* as a leading herb layer species followed by a *Betula pendula*/*B. pubescens*-dominated pioneer forest community (see also Kooijman et al. 2000 for Giant Mountains in Czech Republic). On totally unmanaged areas the former forest floor species remain and grow very well; felled-area herb species as well as birches are limited to the pit-and-mound structures around the former root plates of the fallen trees (Fischer and Fischer 2009). Reasons are the different survival pattern of the advance regeneration, different germination niches as well as different survival rates of the newly appearing tree species on cleared and not-cleared wind throw areas, respectively (Fischer and Fischer 2011; Schmidt and Heinrichs 2012). Without human impact (clearing or salvage) the ecosystems therefore remains rather close to the pre-disturbance situation, a phenomenon that also had been observed in temperate forests of central China (Xiang et al. 1999). The differences in tree layer structure and composition remain for decades or longer (Fischer et al. 2002). The reasons for these different pathways are (i) the activation of the soil seed bank (Fischer 1987), (ii) the availability of open space for species invading by anemochorous seeds from outside, and (iii) the new micro-sites offered for germination and seedling establishment on cleared areas. This pattern also determines the spatial distribution of trees of the future forest stand (Oliver and Stephens 1977; Ulanova 2000; Harrington and Bluhm 2001).

In certain cases, windstorms may also accelerate succession by preferential felling of early-successional tree species, e.g. *Populus tremuloides*, and favoring other deciduous species like *Quercus macrocarpa*, *Fraxinus pennsylvanica*, and *Ostrya virginiana* (Dyer and Baird 1997; along the prairie-forest ecotone in Minnesota).

Hurricane and typhoon

Cyclonic weather systems of tropical origin such as hurricanes (Atlantic Ocean, north-eastern Pacific Ocean) and typhoons (eastern and southeastern Asia and the northwestern Pacific Ocean) are very strong storms that create large-scale (regional- to landscape-scale; Table 1) disturbances and are known to be the major factor controlling forest ecosystem structure, function, and dynamics in the tropical regions they most commonly affect (Boose et al. 1994, 2001). In eastern Asia, typhoons will sometimes continue northward as far as the transition between temperate and boreal zones in northeastern China (more than 11,000 ha felled by the 1986 typhoon in Changbai Shan National Reserve, Xue and Wu 2009). Likewise, hurricanes also affect the temperate forests of northeastern North America, especially the New England states of the USA. Boose et al. (2001) listed eight Atlantic hurricanes of the highest damage class (F3 = most trees down; wood houses blown down; masonry buildings blown down or destroyed), that crossed New England since initial European settlement (1620–1997), and there were many more hurricanes with lower damage potential in the same period.

The most dramatic and significant hurricane event in the recorded history of New England was the 1938 hurricane (September 21, 1938) that featured wind speeds up to 200 km h⁻¹ (Foster and Boose 1992; Foster et al. 1998). Forest height (and therefore age), species composition, and site exposure were the most important factors controlling the patterns of forest damage that resulted (Foster 1988; Foster and Boose 1992), or more generally, the interaction of meteorological, physiographic, and biotic factors (Boose et al. 1994). Species like *Pinus strobus* and *Pinus resinosa* suffered great damage (especially from stem breakage), while slower growing species like *Acer rubrum*, *Quercus alba*, *Carya* spp., and *Tsuga canadensis* were much less affected (and these more from uprooting than stem breakage). As uprooting was actually more prevalent than stem breakage overall, soil structure was affected to a certain degree (Foster 1988).

To better understand the ecological implications of such extreme events, a “simulated hurricane blowdown” or “experimental hurricane” was carried out in the Harvard Forst/ Massachusetts (Cooper-Ellis et al. 1999): trees in a *Quercus rubra*–*Acer rubrum* forest were pulled over by a winch. The time of the experiment (peak hurricane season in late summer/early autumn), the tree species, the tree size, the direction as well as the percentage of damaged canopy were selected according to the 1938 hurricane event. Most important: a detailed forest stand record *before* the experimental blowdown was carried out, and a control site established. On the experimental hurricane plot early successional shrubs like *Rubus allegheniensis*, *R. idaeus*, and *Rhus typhina* increased from very low cover percent (close to zero) to around 0.5 %; one of the characteristic forest herb species, the fern *Dennstaedtia punctilobula*, from around 10 % cover before to around 20 % cover 3 years after the event. 92 % of the new species established on plots containing a pit and/or mound structure. *Betula alleghaniensis* and *Acer saccharum* had low rates of windfall and therefore may indirectly profit from storms. *Betula alleghaniensis* and *Fagus grandifolia* had lower probability of wind throw in old-growth stands than in second growth (Canham et al. 2001). Many of the uprooted, bent or broken individuals survived, re-leafed and/or re-sprouted, so that a new dense canopy established, at least in the first growing season. The

tree species responded differently to the experimental disturbance: while most of *Carya* spp. individuals were bent over, most of *Q. rubra* and *Betula papyrifera* individuals were uprooted. Species richness increased following the manipulation, then decreased soon thereafter. The authors conclude (p. 2693) “that the downed and damaged trees play an important role in forest recovery and ecosystem resilience. Logging kills the aboveground portions of the trees, eliminates leaf and woody biomass, decreases evapotranspiration, scarifies the soil surface, increases insolation, and damages many soil and organic structures created by disturbance... Thus, the potential exists to convert the damaged area from a relatively intact system to a strongly modified site in which ecosystem control is reduced”. Natural, not managed forests therefore would be richer in micro-topography and in forest stand structures.

A similar pattern of differential reaction of tree species to disturbance as well as differential regeneration has been reported in Korean *Pinus*-dominated forests, *Picea–Abies* forests, and *Betula ermanii* forests, respectively, as well as in the temperate-boreal transition zone in northeastern China (Changbai Shan, Guo et al. 2010).

Tornado

A tornado is a heavy atmospheric turbulence with wind speeds up to more than 300 km h⁻¹. The area affected by a tornado is relatively small (Table 1): the Massachusetts tornado of June 1st, 2011, for example, created a 63 km long damage track with a maximum width of 800 m only. While the effect of such a tornado on trees is strong—they become broken, twisted, and thrown, and the forest canopy is thereby totally destroyed—there is only little soil disturbance, because the trees are usually not uprooted. For forests in Wisconsin, Canham and Loucks (1984) calculated 5.0 patches (>1.0 ha) per year (out of 51.8 patches totally affected by wind throw), with a calculated return time of 2,832 years. That means: tornados are hard to predict, are restricted to small areas, but cause the strongest damages to trees in the affected forests. New micro-sites created by a tornado offering a variety of resources, support growth of existing seedlings as well as establishment of new seedlings, but the pre-tornado cohort of tree seedlings is favored over the post-tornado cohort (Harrington and Bluhm 2001).

Ice storm and snow breakage

Snow breakage is the consequence of specific weather conditions favoring high amounts of wet snow that accumulates on trees. It occurs in temperate forests across the northern hemisphere. In northeastern China (Liaoning Province) the 2003 wet snow event damaged mainly *Acer mono*, *Juglans mandshurica* and *Populus* spp.; tree damage was positively correlated with tree height but negatively with stem diameter (Li et al. 2004). So snow breakage may influence both species composition and forest stand structure. In southern China (zone of evergreen broad-leaved forest) a catastrophic ice, snow and snow break event took place from January, 10 to February 10, 2008. A number of ecological studies were carried out, and these show that site conditions are important for damage severity (Man et al. 2011), and that canopy density regulates tree species regeneration (Ou et al. 2011). In beech forests (*F. sylvatica*) in Central Europe the better light conditions as well as the improved nutrient availability (mineralization) following ice breakage helped some species (*Urtica dioica*, *Rubus idaeus*, *R. fruticosus* agg.) to strongly increase, while the typical forest species remained more or less constant; after nearly two decades the

differences between affected and not affected stands were only minor, giving a good example of resilience (Heinrichs et al. 2012).

Snow avalanche

Snow avalanches do not belong to the “key forest disturbances” according to Dale et al. (2000), and play only a minor role in terms of the area they affect. Avalanches are restricted to mountain areas with steep slopes, and mainly affect subalpine forest types (Bebi et al. 2009; Rixen et al. 2007; Veblen et al. 1994; Walsh et al. 2004). In a few cases, however, avalanches may run down into the deciduous forest belt, affecting an area of up to several hectares. These rare events were analyzed for Berchtesgaden National Park in southeastern Germany (Fischer et al. 2012), where an avalanche destroyed the tree canopy of a “mountain mixed forest” dominated by *F. sylvatica* in combination with *Acer pseudoplatanus* and *Fraxinus excelsior* as co-dominants. In forest stands with trees of the age of only around 50 years the trees were not uprooted but bent over. They survived, and those branches, now looking upwards, started to grow as stems (compare experimental hurricane at Harvard forest). Two decades later there was a dense “young” forest growing out of these former branches. These tree-like growing branches have the same ecological role as surviving young *Abies mariesii* individuals in a subalpine forest (>ca. 200 years old) in Japan (Kajimoto et al. 2004). Although the forest structure changed dramatically, after two decades the species composition (including ground flora and bryophytes) was not significantly different from the pre-avalanche situation because neither the micro-climatic parameters changed nor major soil disturbances took place. In a 200 year old forests stand closely related to the one mentioned above, another avalanche, however, the trees were uprooted and killed, soil strongly disturbed, and micro-climate drastically changed; here felled-area species increased in both frequency and coverage and changed the species composition, increased species diversity. The emerging mosaic of different structural units and different successional pathways may significantly increases biodiversity of such forests (Walsh et al. 2004; Fischer et al. 2012).

Fire

Fire is an intrinsic ecological component of many boreal forest ecosystems in North America (Veblen et al. 1994; McCullough et al. 1998), Northern Asia (Li et al. 2005) and Scandinavia (Bradshaw et al. 2010). It influences not only the plant species composition and the structure of forests but also the animal species composition (Hjältén et al. 2010; Hyvärinen et al. 2005), the latter mainly because of the loss of decaying wood. Both frequency and extent of fires may be either increased by human activities (Pausas and Vallejo 1999) or decreased because of intense fire prevention activities. In North America, fire suppression policies implemented in the early 1900s have resulted in profound changes in forest species composition and structure (McCullough et al. 1998; Norris 1990). These changes include accumulation of natural fuels, which in the absence of fire prevention would have been eliminated by frequent low-intensity wild fires (Norris 1990). Fire may also be important in subalpine ecosystems (ecologically equivalent to boreal ecosystems), as long as summers are usually dry, as in western US forests. For the subalpine zone of Yellowstone National Park a fire cycle of 300–400 years has been recorded, in which large areas burn during a short period (Romme 1982).

In China forest fires are common. Each year fires occur on 0.6 % of the total forest area, all together around 13,000 each year, with an average size of around 55 ha each (Lu 2011).

In the temperate forest zone of China, however, the fire frequency is much lower (Li et al. 2005; both on province and on county level) than in the boreal and subtropical/tropical regions, where most Chinese studies on forest fires have been performed (Luo 2002; Zhang 2008). In the deciduous temperate forest zone of north and northwest China the fires are concentrated in the arid winter time, while the monsoon climate prevents forests during summer time from burning (Lu 2011). It is most important to note that the majority of fires in China are man-made (Lin 2010), and not only in the temperate forests (Zhang et al. 2007); for Beijing district (deciduous forest zone) it could be shown that fire frequency decreases with increasing distance to the next road (Yang et al. 2009).

In certain regions of eastern North America, fire is the major determinant of forest structure and composition, for example in the *P. rigida*-dominated “pine barrens” of New Jersey and Long Island (Little 1979; Little and Garrett 1990), or the *Pinus palustris* savannah of the southern US coastal plain (Heyward 1939; Boyer 1990). The historical importance of fire as an ecosystem process in eastern North American forests outside of these regions is a controversial question, closely connected with the use of fire by Native American peoples as a landscape management tool (Day 1953; Russell 1983; Patterson and Sassaman 1988). While fire may be assumed to be only a minor factor in the temperate deciduous forests of eastern North America in the absence of human influence (Lorimer 1980), human influence has been significant and widespread on the North American landscape since the early Holocene, and the question of what ecological conditions and processes may be considered “natural” cannot be answered simply by removing humans from the system; these questions will be discussed in greater detail below (see “[Human driven direct disturbances: landscape utilization](#)” section). In particular, widespread suppression of fire in eastern North American forests in the last 100 years has been associated with the declining importance of *Quercus* spp. (because of regeneration failure) and increasing abundance of *Acer rubrum* (Abrams 1992, 1998), suggesting that the forests of the future may be very different in composition from those of the past.

Summarizing fire is a natural disturbance event in boreal, subalpine and to certain degree dry (coniferous) temperate forest ecosystems, but not in deciduous forests of the temperate zone (Table 1).

Natural biological forest disturbances

Bark beetles

In the temperate zone of Europe the most important bark beetle is *Ips typographus*, living on Norway spruce (*P. abies*), the latter occurring either as an admixed species in deciduous forests in the mountain belt (“mountain mixed forest”) or as the dominant species in the subalpine belt (in Central Europe most important in the Alps, the Bavarian/Bohemian Forest, and the Carpathians). While bark beetle populations are usually small and do not affect the structure of *P. abies* stands, the bark beetle population may rapidly increase as soon as breeding conditions are improved. This is true if (i) temperatures are higher than usual during summer, forcing more bark beetle generations per year, or (ii) if the breeding resource is high, e.g. when many *Picea* stems are felled by windstorms, but are still living. Since the mid 1990s in the Bavarian/Bohemian Forest (Germany/Czech Republic) it has been observed that *P. abies* forest regeneration after windstorm events is not occurring at the patch level, as in most deciduous temperate forests, but on the landscape level, as most of the *P. abies* trees in any given area have been killed by the bark beetle. Nevertheless it is

not the forest that is dying but a large number of trees, as has been shown by Bauer et al. (2008): there were many more *P. abies* saplings available than are needed for rebuilding the canopy: 7,000–8,000 saplings per ha larger than 10 cm in height, compared to fewer than 3,000 adult trees in unaffected close-to-natural *Picea* forest stands.

The situation is very similar in boreal forests worldwide (McCarthy 2001). Veblen et al. (1994) mentioned bark beetles (affecting *Pinus* spp. as well as *Picea*) as the second most important cause of forest ecosystem disturbance in the USA. Currently an outbreak of the mountain pine beetle (*Dendroctonus ponderosae*) is ongoing in western Canada (Nealis and peter 2008). The beetle has expanded its host-range (Cullingham et al. 2011) and breached the historical geographical barrier of the Canadian Rocky Mountains (Adams et al. 2013); it seems that beetle-associated bacterial symbionts contribute to the beetles ability to overcome tree defenses (Adams et al. 2013). In addition, in North American boreal forest ecosystems a strong relationship between fire and insect outbreaks had been observed: fire suppression has led to an increased vulnerability of forest stands to damage by defoliating insects (McCullough et al. 1998). Disturbance pulses are characteristic for such ecosystems, also in isolated conifer dominated high mountain areas within the temperate zone (Svoboda et al. 2012).

Not all bark beetles kill trees directly; they may also start an ecological cascade that finally leads to the death of the tree. This has been demonstrated for *Pinus armandi*, an element of the mountain mixed forest zone in the temperate forest area of Qinling Mountains in central China. The healthy tree is attacked by primary bark beetle species. They infect the tree with certain fungi that quickly weaken the tree's vigor. The weakened tree is then attacked by secondary bark beetles (*Ips acuminatus*, *I. sexdentatus*, and *Pityogenes japonicus*), which either kill the tree or are followed by new species which only live in senescent hosts and finally kill the tree (Chen et al. 1999). Biodiversity increases as a result.

Because in deciduous temperate forests needle trees are only admixed, bark beetles usually affect only single trees or small groups of such trees (Table 1). In subalpine and boreal forests, however, extended areas may be affected by insect outbreaks.

Browsing game

Ungulates are an inherent component of forest ecosystems, using the plant biomass as a food resource: browsing (mainly on dicots: leaves and twigs of woody plants as well as herbs and forbs) and grazing (mainly on monocots: grasses and sedges; Gordon and Prins 2008). The disturbance may influence single individuals or groups of individuals, thus working on a very small scale (Table 1). In eastern North America the white-tailed deer (*Odocoileus virginianus*) is the most important browsing ungulate, whereas roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), and in mountainous areas the chamois (*Rupicapra rupicapra*) are the major species in Central Europe. The last aurochs (*Bos primigenius*) died in 1627 in Poland, and the last wild living European bison (*Bison bonasus*) was killed in 1927 in the Caucasus. Hunting pressure on these species was high for centuries, driving several of them to extinction. On the other hand, hunting in Europe became a privilege of royalty in the 18th and 19th centuries, and as a consequence populations strongly increased, especially populations of the majestic red deer.

The effects of browsing can be analyzed either by direct observation of the browsing animal (Klötzli 1965), by exclosure experiments (Schmidt 1978) or by rapid reduction of browsing deer population (de la Cretaz and Kelty 2002). As a result it has become clear that browsing is selective, i.e. not just the uptake of biomass but the expression of a preference for

certain plant species, and therefore has an influence on species composition. In Europe, herbs and shrubs like *Epilobium angustifolium*, *Geranium robertianum*, *Rubus idaeus* and *R. fruticosus* agg. and trees like *Abies alba* are preferably browsed by red and roe deer, causing a change in species composition. In eastern North America, the fern *Dennstaedtia punctilobula* has been observed to increase with browsing, behaving as a “native aggressive species” and showing differential interference among seedlings of different tree species, thereby acting as an “ecological filter” on regeneration (de la Cretaz and Kelty 2002).

To a certain degree, the intensity of browsing seems to vary according to micro-site. A set of different micro-sites is offered by uprooted trees (pit-mound microtopography); in North America browsing by white-tailed deer is reported to be less frequent on tree-fall mounds, and *T. canadensis* has a greater seedling density there (Krueger and Peterson 2006). Such refugia from browsing therefore create different species assemblages across closely related micro-sites.

Herbivory not only influences plant species composition (in terms of both quantity and quality) but also the composition of other ecosystem members such as invertebrates (Myseru et al. 2010); because different species may react totally differently to a given browsing impact, the new species composition of such groups is hard to predict.

Browsing of ungulates also interferes with different kinds of land use in the same area (e.g. forestry, hunting, tourism, conservation), and therefore has a political dimension (Graham et al. 2010). For forest management, for example, the basic management unit is the forest stand, while ungulate browsing because of the moving animals usually works on larger (regional) scales. Emerging conflicts therefore can be solved only at larger scales, requiring the cooperation of all relevant stakeholders.

Wild boar and soil seed banks

Every soil represents a pool of viable seeds of species that were living at the same location years, decades, or even centuries ago: the “soil seed bank”. Fischer (1987) summarized soil seed bank analyses from forests all over the world. Forest soil seed banks reach from a minimum of 3 to around 2,500 viable seeds per square meter under boreal and subalpine forests, up to a maximum of around 15,000 seeds per square meter in dry sclerophyll Australian forests. Just one out of 21 studies did not record any viable seed: a subarctic forest in Canada. In a 200 year old *Quercus–Carya* forest in North Carolina, approximately 1,800 viable seeds were present per square meter, while under 85 and 112 year old *Pinus* forests 4,200 and 1,450 viable seeds, respectively (analyzed soil depth 13 cm; Oosting and Humphreys 1940). The highest numbers of viable seeds in temperate Europe were found in a typical *Fagus sylvatica* forest (Melico-Fagetum) with around 8,800 seeds in the upper 6.2 cm, and 27,300 in the upper 20.2 cm (Fischer 1987). Only very few of buried seeds, however, belong to tree species.

Buried viable seeds are able to germinate after mechanical disturbance of the soil surface, when they are exposed to light. Uprooting of wind thrown trees (pit-mound microtopography) is one important disturbance that allows these buried viable seeds to germinate; digging of large animals like wild boar (*Sus scrofa*), originally distributed across large parts of Eurasia including its temperate zone, is another one. While the area where buried viable seeds may become exposed to light, either because of tree uprooting or of wild boar digging, is few square meters or less, a group of wild boars will affect a much larger area. As a consequence, wild boar are creating small-scale disturbances (Table 1), that may be essential for the emergence of plant individuals and plant species, respectively, that had not been present on that site for a long time. Wild boars also are vectors for

dispersal of plant species. Because they prefer certain trees as rubbing trees, the transported seeds are preferentially deposited there, thereby increasing viable seed densities (Heinken et al. 2006).

Animals as landscape designers

Beavers (*Castor fiber* in Eurasia, *C. canadensis* in North America) exert an important influence on the development of plant communities through their management of local hydrology. The effects of beavers may be regarded as a subcategory of flooding disturbance (Foster et al. 1998), modifying only small areas in the valleys of streams and rivers but having a more widespread effect when the activities of multiple beaver colonies are summed across a landscape (Table 1). By impounding water behind their dams, beavers alter not just stream morphology but also stream carbon and nitrogen budgets (Naiman et al. 1986). Beavers act as “ecosystem engineers”, affecting vegetation dynamics and even patterns of species richness on a landscape scale (Wright 2009). The *Carex*-dominated “beaver meadows” that formed on sites formerly flooded after the breaching of dams may have been historically important as seedbeds for the establishment of new stands of tree species such as *Acer rubrum* and even *Pinus strobus* in North America (Marshall 2011).

Bamboo dieback

The cyclic mortality of bamboo (Poaceae, subfamily Bambusoideae) populations is well known. In the northern hemisphere, bamboos are present only in Asia. As Taylor and Qin (1992) have pointed out, the growing bamboo layer in temperate Asian forests may regulate the tree establishment after formation of gaps, favoring the establishment of various tree species over others. Following bamboo dieback, yet another set of tree species may be favored, thereby enforcing a certain diversity in the species composition of the developing forest stand.

Forest disturbances caused by humans

Humans influence or create disturbances in different ways:

- (1) Change in either frequency and/or intensity of naturally occurring disturbances. For example: fire (see chapter “fire”), snow avalanche (because of deforestation).
- (2) Micro-organisms, fungi and insects may be transported to areas where they did not occur in the past, but where they now find adequate living conditions. They may occupy the new area either with no change in species composition, vegetation structure and ecosystem processes (“alien species”), or they may suppress, replace or even totally kill native species (“invasive alien species”).
- (3) Conversion of former forest stands for use in agriculture, horticulture, or other novel purposes such as urbanization, infrastructure, or recreation is a major disturbance, totally destroying the former forest ecosystem. These changes are not always permanent, however, as such utilization practices may change with time, and intensively used areas may eventually return to forest cover.

We will focus here on invasive alien species and land use.

Human driven indirect disturbances: invasive alien pathogens and species

Since medieval times there is an increasing stream of trade from Asia to Europe, also carrying propagules of plants, animals, and micro-organisms to Europe. In the early 17th century European settlers not only brought crops and livestock to northeastern North America but again also organisms (plants, animals, and microbes), some of which have become invasive. These are aspects of the emerging global phenomenon of “invasion biology” (Davis 2009). In contrast to a single disturbance event that may affect just a single tree or stand of trees, outbreaks of insects or pathogens may reach the landscape scale and alter patterns of diversity and ecosystem function throughout the whole distribution of a tree species or forest type (Table 1).

Dutch elm disease

Dutch elm disease is caused by a fungus (*Ophiostoma* = *Ceratocystis ulmi*, ascomycete), that lives in the vessels of the youngest annual ring (the only one that is able to transport water) of elm (*Ulmus*) species. It hinders water transportation and therefore kills the tree within few weeks. The fungus originates in East Asia. It came to Europe with imported timber, and then spread rapidly in the 1920s and 1930s, killing the European elm species (mainly *Ulmus campestris* and *U. glabra*), which are now rare as old trees. The vector in Europe is the European elm bark beetle (*Scolytus multistriatus*).

From Europe both the vector and the fungus were introduced with logs imported to the USA, where it was first recorded there in 1930 (French et al. 1980). In North America the American elm bark beetle (*Hylurgopinus rufipes*) is able to transfer the fungus, enabling its movement from tree to tree even in the absence of the original vector, and in many parts of temperate North America the disease has now killed most of the old elm trees (*Ulmus americana* especially). The fungus in North America changed into a more aggressive form (*Ophiostoma novo-ulmi*), and was then (re-)imported to Europe, strongly intensifying the elm dieback there.

In the last few decades, an insect of East Asian origin that feeds on elm leaves has been invading eastern Europe (Blank et al. 2010) and it has recently arrived in Central Europe (Germany; Zeitler 2012): the Hymenopteran *Aproceros leucopoda*. Because it feeds on all European elm species, elms are facing another obstacle.

Hemlock woolly adelgid (HWA)

Eastern hemlock (*Tsuga canadensis*) is one of the most-long-lived tree species of eastern North America and, together with several deciduous species, is one of the principal components of temperate forests in this region. *T. canadensis* is affected by *Adelges tsugae*, an aphid-like insect native to eastern Asia that was first recorded in North America (in Oregon) in the 1920s. A recent dispersal simulation experiment (Turner et al. 2011) showed that 90 % of the individuals may be expected to stay within 25 m of their origin, but that dispersal distances of up to 400 m are possible for single dispersal events, thus providing a basis for the rapid infestation of new *T. canadensis* stands. Throughout the range of *T. canadensis* this insect kills trees of all sizes, and as a result the tree is expected to disappear functionally from temperate forests in eastern North America in the coming decades (Ellison et al. 2005). According to these authors, pre-emptive salvage logging is not a method to fight against HWA: the logging procedure initiates more rapid changes of the ecosystem than the dieback of the trees as a result of HWA alone, e.g. nitrogen cycling

is more affected by cutting than by the pest itself. At risk is not just the loss of a formerly dominant and economically valuable tree species, but also the loss of a key species with respect to ecosystem regulation: as one of the main evergreen trees in the temperate forests of eastern North America it has, in contrast to deciduous species, relatively stable water fluxes throughout the year, and this ecohydrological role cannot be filled by any other native species (Ford and Vose 2007). Should this come to pass, it would represent as dramatic a change in North American forests as the loss of the American chestnut to chestnut blight in the early 20th century, described below.

Chestnut blight

The American chestnut (*Castanea dentata*) was a major co-dominant forest tree in the Appalachian Mountains in eastern North America for nearly four millennia. It was the last major tree species to migrate northward into New England after the end of the last ice age, arriving as recently as 2,500–1,500 years ago (Davis 1969; Ellison et al. 2005), possibly by intentional introduction by Native Americans as a food crop (Russell 1987). Chestnut blight, caused by the canker pathogen *Cryphonectria* = *Endothecia parasitica*, was introduced to North America from Asia in the late 19th century. First noted in 1904 in New York, it rapidly (~ 37 km year⁻¹) spread across the range of the American chestnut, killing the aboveground portion of the tree by girdling the stem (Ellison et al. 2005). Instead of being still a co-dominant of temperate forests in North America, chestnut now is an understory shrub that only rarely flowers but persists by sprouting from stumps and surviving root systems.

Beech bark disease (BBD)

Beech bark disease (BBD) is a complex of (i) the “beech scale” insect (*Cryptococcus fagisuga*; Hemiptera) and (ii) a bark killing Ascomycete fungus of the genus *Nectria* (Houston 2005). The beech scale is of European origin, living on the bark of *Fagus sylvatica* and sucking sap from the bark parenchyma tissue. It was accidentally introduced to North America (where it adopted *F. grandifolia* as a new host) before 1890 in Halifax/ Nova Scotia. From there it expanded to the south and west, reaching New England in the 1950s, New York in the 1960s, and Pennsylvania in the 1970s (Houston et al. 2005). It is, however, not the insect itself that kills *Fagus* trees but the *Nectria* fungus: *Nectria ditissima* and *N. coccinea* in Europe, *N. ditissima* and *N. faginata* in North America. Although *N. faginata* has only been recorded in North America, genetic analyses suggest that it originates from Europe (therefore also named *N. coccinea* var. *faginata*; Houston 2005, Global Invasive Species Database). The fungus needs the initial damage to the tree bark by the sucking insect to enter the tree; it then kills host tissue and may girdle the stem, causing it to die (Global Invasive Species Databases).

Most of the temperate forests of New England are now affected by BBD. The American beech (*F. grandifolia*), once one of the main tree species of North American temperate forests, is expected to disappear as a foundation species. According to Global Invasive Species Databases only about 1 % of *F. grandifolia* is estimated to be resistant to the disease complex.

This resistance, however, may also cause a problem. In contrast to European and Asian *Fagus* species, *F. grandifolia* is able to regenerate by sprouting. Although dying trees produce fewer sprouts than vigorous trees, the sprouts are taller and have a larger basal

diameter than those of not dying (resistant) trees; the dying (susceptible!) trees therefore yield their growing space to their root suckers (MacKenzie 2005) and increase in number.

Gypsy moth

Gypsy moth (*Lymantria dispar*) was introduced to North America (Massachusetts) from Europe around 1869 to evaluate its suitability as the basis of a silk-spinning industry (Lovett et al. 2006). The larvae feed on foliage and prefer leaves of oak (*Quercus* spp.), but, in contrast to the two examples above, also make use of other deciduous trees. During outbreak phases especially they “will consume almost anything green” (Lovett et al. 2006, p. 397), completely defoliating whole stands of trees. *Gypsy moth* is still expanding its North American range, and only about 1/4 to 1/3 of susceptible forests are currently infested (map in Lovett et al. 2006). The effect on ecological processes is strong, e.g. for the nitrogen cycle: the sudden loss of nitrogen by insect feeding, leaf loss, and accumulation of insect biomass together with allocation of stored nitrogen to reflushed foliage will deplete the tree’s nitrogen reserves (Lovett et al. 2002).

White pine blister rust (WPBR)

White pine blister rust (WPBR) is caused by the fungus *Cronartium ribicola*, which is native to Europe and Asia and lives on 5-needled pines (*Pinus* subgenus *Strobus*) as well as *Ribes* species, but is naturally not aggressive (Kirisitis 2007; Ellis and Horst 2010). However, the North American white pines (*P. strobus*) introduced to Europe in the 18th century were not resistant to WPBR; the disease was first recorded in 1865 in the Baltics and spread across European *P. strobus* populations. *Pinus strobus* was once expected to be an important future tree species in Europe, but because of the disease it is now of no importance to European forestry. At the beginning of the 20th century, when large quantities of *P. strobus* seedlings were needed for reforestation efforts in eastern North America (see section on “landscape history”), the disease was introduced to that continent with nursery stock that had been brought from Europe, and spread throughout large areas of the temperate zone there (map in Lombard and Bofinger 1999); its severity, however, has declined strongly in recent years, largely as a result of the intentional elimination of *Ribes*, its alternate host.

Ash dieback

In the mid-1990s a new disease of European ash (*Fraxinus excelsior*) was found in the field, first in the Baltic States, later in Poland, since around 2002 in Germany, and since around 2007 in Switzerland, causing a rapid ash mortality. The *Fraxinus* individuals affected (all age classes are susceptible) show necrotic lesions in the bark and xylem; as a consequence they lose their leaves in early summer. The pathogen first had been identified as a common fungus that had not previously been reported as pathogenic (*Hymenoscyphus albidus*, ascomycete, with its secondary form *Chalarea fraxinea*, the latter not known before 2006). Recent studies, however, indicate that the relevant pathogen is actually a closely related species that can only be separated from *H. albidus* by means of molecular analyses: *H. pseudoalbidus* (Queloz et al. 2010). At present it is not clear if the new, pathogenic fungus developed in Europe or was introduced from elsewhere. Nevertheless, in many parts of Europe during the second half of the 2000s, many *Fraxinus* individuals

showed signs of infection and damage, and many were killed; therefore it seems that this formerly co-dominant tree species in forests on soils with good water supply will decrease or in some areas go completely extinct, at least as large and old trees.

Exotic earthworms in North America

Earthworms (Lumbricidae) were absent from most soils in the glaciated portions of North America prior to the arrival of European settlers in the 1600s. The introduction of Eurasian earthworms to the forests of eastern North America has resulted in dramatic changes in forest soils, including the mixing of organic and mineral soil horizons and decreased soil carbon storage, in addition to possible effects on nitrogen and phosphorus cycling. The loss of soil organic matter has altered the soil microbial foodweb, resulting in changes in the diversity of soil fungi as well as soil-dwelling arthropods and other invertebrates at affected sites. Similarly, the abundance and diversity of herbaceous understory vegetation has been observed to decline steeply following earthworm invasion (Bohlen et al. 2004).

One herbaceous plant species that is observed to be positively associated with earthworm invasions in North America is the European forest herb *Alliaria petiolata*, known as “garlic mustard” (Bohlen et al. 2004). This invasive species (also introduced from Europe by early settlers) has an allelopathic effect on soil fungi, inhibiting the formation of mycorrhizal mutualisms between the fungi and tree seedlings, a “novel weapons” strategy that has not been observed in the plant’s native range in Europe (Callaway et al. 2008).

Human driven direct disturbances: landscape utilization

Second to global climate change, landscape utilization is the most striking, the most incisive, and the most large-scale disturbance affecting forest ecosystems of the temperate zone (Sala et al. 2000). For a long time, “landscape utilization” meant cutting trees, felling forests, burning the remaining biological material, and preparing the area mainly for agriculture. However, conversion of land for infrastructural purposes (e.g. for housing, industrial complexes, roads and highways, railways) has increased strongly in the last 100 years. The ecological effects of land use change are manifold, but we will concentrate here on the conversion of forest ecosystems to other purposes, and the subsequent capacity of trees and forests to re-colonize the same areas when that landscape utilization ceases.

A dramatic example of the effects of historical changes in landscape utilization on forest ecosystems may be seen in North America. Native Americans arrived in temperate eastern North America at least 15,000 years ago (Delcourt and Delcourt 2004). They were limited in number and had limited techniques available, so their impact on forests is assumed to have been small, although they did introduce agriculture and may have employed fire as a landscape management tool. Notwithstanding certain areas of native grassland and heathland that are known to have existed in coastal areas (Bromley 1935; Vickery and Dunwiddie 1997), forest cover in New England in the period prior to European settlement may be assumed to have been at least 90 % of the total area of the region.

With the arrival of settlers from Europe at the beginning of the 17th century the area covered by forests quickly began to decrease in North America. In the interior of New England (for example, at the Harvard Forest/Massachusetts; Raup 1966; Donahue 2007) the first settlers started to clear the area for agricultural purposes in the first half of the 18th century. By 1830 most of the forests of the region had been cut and converted to agricultural use, including both pasture and arable cropland. Around 1850 a severe period of farmland abandonment started as new lands in the US Midwest became available for

settlement and agricultural development. Neglected farmland was quickly colonized by *Pinus strobus*, with the help of its numerous highly mobile seeds, forming pure even-aged stands (Marshall 2011). These *Pinus* stands occupied sites that in most cases were previously settled by hardwood forest (both *Quercus–Carya* and *Acer–Fagus–Betula* associations). As the *P. strobus* reached commercial maturity at the age of 60–80 years it was harvested for timber, especially for the manufacture of wooden boxes and other shipping containers. Removal of the *P. strobus* canopy released seedlings of hardwoods that had become established in the understory, leading to the formation of the vigorous and species-rich secondary forest that is now dominant in the region.

In summary, after a more or less total forest cover up to around 1,600, forest area was reduced to around 55 % for the New England states overall, and as little as 30 % in Connecticut, Rhode Island and Massachusetts in the 1820s and 1830s (Harper 1918; Foster and Aber 2004; Donahue 2007). By the 20th century it had increased again to around 80 % (for New England overall) and 60–65 % (Connecticut, Rhode Island, Massachusetts), respectively, because of farmland abandonment. In recent decades forest cover has begun decreasing once more as a result of population pressure and urbanization, but it remains far above the minimal levels of the early 19th century. Nevertheless there are only few primary forest remnants left: for the Lake states in northern USA Frelich (2002) has calculated 1.1 % for all forests, and 0.02 % for the *Quercus–Carya* forest type in particular. Tree felling and forest removal as a direct human-caused disturbance has been done nearly everywhere in these regions and influences both species composition and forest structure up to date.

In Central Europe forest area change is showing similar trends, but on a quite different time scale. Here in the Neolithic Age people started to settle and introduce agriculture, long before today's potentially dominant tree species, *Fagus sylvatica*, arrived (Küster 1992; Fischer and Fischer 2012). Celtic as well as German tribes spread agriculture largely by reducing the forest area. A minimum was reached around 1250–1300 AD, when at most 20 % of the previous forest cover remained. As a consequence of pestilence (the Black Death) in the 14th century, the human population decreased significantly, allowing trees to re-occupy former agricultural land, now abandoned (Bork et al. 1998). Since then the forest coverage remained constant (around 30 %). Stands of temperate forest that have never been used by humans (“virgin forest”) are therefore extremely rare in Central Europe: very small patches of *Fagus*-dominated and mixed-species forests remained in few mountain areas (Alps: Zukrigl et al. 1963; Carpathians: Korpěl 1995; Bohemia: Průša 1985; Croatia: Mayer et al. 1980) as well as a complex of *Quercus–Carpinus*-forests in northeastern Poland (Falinski 1986). Primeval *F. sylvatica* forests of significant extent today exist only in the Ukraine (Brändli and Dowhanytsch 2003).

The southern part of the Loess Plateau of central China represents a major part of the potential temperate forest zone in southeastern Asia. Here the cradle of the Chinese population and culture is situated. The area has been densely populated for more than three thousand years, leading to a nearly total loss of forests, and resulting in enormous loess soil erosion (Fischer and Fischer 2012). It was not until the early 1950s that the first restoration activities started, now leading to a real recovery of forests. Nearly all of today's forest area in the Loess Plateau has been used in the past (secondary forests), and nearly all young forests had been afforested in just the past few decades.

South of the Loess Plateau, at the southern site of the Qinling Mountains, temperate mixed forests remained virgin until the middle of the 20th century. It can be shown that within the last five decades, in parallel to increasing utilization (and forest cutting), both landscape diversity and species richness increased (Wang et al. 2010); this reflects the

occurrence of man-made ecosystems in an area where more or less natural forest ecosystems are still present (but on reduced area).

In conclusion, most (or nearly all) recent stands of temperate forests, in eastern North America, in Central Europe, as well as in eastern Asia had been cut in the past and were non-forest systems for decades or centuries. Most of them represent (natural or man-made) reforestation steps following the disturbance of conversion of the former forest to arable land. Opportunistic tree species have been able to increase drastically, as did white pine (*P. strobus*) in the 19th century and red maple (*A. rubrum*) in the 20th century in the temperate forests of eastern North America following a variety of disturbances, such as logging, land clearing, agricultural abandonment, wind throw, insect and disease outbreaks, changing fire regimes, and increased deer (*O. virginianus*) population (Abrams 1998, 2001).

Differences and similarities between the three distribution areas

The three temperate areas of the northern hemisphere are quite different in terms of the “composite” of natural disturbances:

- (1) In eastern North America, hurricanes represent the most important natural forest disturbance factor, acting on a large-scale and with frequent heavy affects. With a mean hurricane-return interval of 10–200 years, a typical forest stand can be expected to experience at least one such event within any single-tree life cycle (Boose et al. 2001). Snow, ice, and beavers work on a moderate to small special scales. Tornados are most destructive, but affect only limited areas.
- (2) In Southeast Asia, very heavy storms (typhoons) are most important for forest stand development, but in the temperate zone of Asia they seem to occur less frequently than in North America. On islands such as the Japanese archipelago or Taiwan, however, they occur regularly. Snow and ice breakage plays a moderate role as well as bark beetles at higher altitudes in the mountains.
- (3) In Central Europe, strong winds are the most common natural disturbance type; compared to hurricanes, typhoons and tornados, the destructive power of these windstorms is limited. Low pressure systems, sometimes the remains of former North American hurricanes, arrive mostly in autumn and winter, when the deciduous trees do not have leaves, so that their effect is reduced (see Bayer. LWF 1995: during the winter storm 1990 in Bavaria 3,3 % of the total growing stock of *P. abies* was windthrown as well as 1.4 % of *Pinus sylvestris*, but only 0.7 % of *Fagus* and 0.4 % of *Quercus*). It is only since needle-leaved trees (mainly *P. abies*) became the most important commercial tree species in Central Europe about two centuries ago that such storms create significant damages here. Snow and ice breakage usually occurs only in mountain areas, and snow avalanches are very rare in temperate forests. In the high mountain belt with boreal-like forest ecosystems, both wind throw and bark beetle are naturally relevant.

The several kinds of windstorms are relevant on all spatial scales (Table 1). Snow avalanches are restricted to mountain areas and steep slopes, working mainly on a patch scale, while fires are mostly restricted to dry sites. Natural biological disturbances like browsing and soil digging work on the point to patch scales, but because both browsing and soil digging may occur everywhere in forest ecosystems, nearly all forests are or may be affected by this type of disturbance. Bark beetles as a disturbance factor are mostly limited in the temperate zone to unfavorable conditions such as the subalpine belt. Beaver

activities are restricted to valleys. Beavers had been extirpated from large areas of the northern hemisphere, but following their re-introduction beavers are again common in many regions.

Beyond the conversion of forests into agricultural land, or into settlements and infrastructure, there are new, human-caused disturbances that affect forests strongly: most important of these is the introduction of new diseases and pests (pathogens and insects). This process in North America has been ongoing for the last 100 years or more, and it is changing the forest species composition there fundamentally. Although working on the point scale (the mortality of individual trees), the whole landscape is affected by a general change in tree species composition.

A general change in site conditions much stronger than all recent disturbances, however, was the Ice Age. Low temperature and continental glaciation caused extensive extinction of forests in the today's temperate zone. The general sequence of re-invading tree genera after the end of the Pleistocene epoch, around 12,000 years ago, was similar in both North America and Europe, although with different species. In the early Holocene in Europe as well as in North America, pines increased in pollen profiles (maximum in southern New England around 9,000 BP; Davis 1969): *Pinus strobus* in New England versus (mainly) *P. sylvestris* in Europe (Lang 1994). The pines were replaced by hardwoods, especially *Quercus* spp. In North America, *Acer saccharum* and *Acer rubrum* arrived together with *Quercus* spp. (Davis 1969) as well as *Tsuga canadensis*. Here *Fagus grandifolia* survived the Pleistocene glaciation by finding refugia in the southeastern United States, spreading from there to the north and northeast (Bennett 1985; Cogbil 2005), and reaching its maximum in New England 5,000–6,000 years BP, followed by *Carya* spp. and finally *Castanea dentata*. The pre-settlement forest species composition therefore was established around 2,000 years ago in eastern North America (Davis 1969). Two thousand years earlier in Europe, *Fagus sylvatica*, arriving from Southern Italy and from Greece, was at its maximum and had occupied nearly its whole recent distribution area (Lang 1994, Fig. 4.3.3.-24).

Dramatic changes in species composition of forests, originating from outbreaks of pests and insects, are not just a modern phenomenon. Today's *Tsuga canadensis* decline (due to Hemlock Woolly Adelgid) is not the first decline of this species since the end of the Pleistocene: about 5,400–4,200 years B.P., *T. canadensis* declined in a short period of time throughout its range because of massive insect outbreaks (*Lambdina fiscellaria*) that caused mass mortality because of defoliation and lasted for about one millenium (Bhiry and Filion 1996; Calcote 2003). It is assumed that the insect outbreak was caused by changes in climatic conditions: decreased January temperature combined with lower precipitation in the mid-Holocene as compared with today.

However, today's ongoing human-driven "globalization" of species, meaning the introduction of species into new areas (mixing formerly separated floras and faunas), is of a new dimension. Corresponding to the developing intercontinental trade during the past millennium, the most important "movement" of pests and diseases is from East Asia via Central Europe to eastern North America, although the way back is possible (see new form of Elm Disease).

Disturbances and pathogens affect forests of different species richness in the three areas. In temperate North America, tree species richness is high (e.g. 1 *Fagus*, >10 *Quercus*, 3 *Fraxinus*, >5 *Acer*, several *Ulmus*, 1 *Liriodendron*, 1 *Tsuga*, 1 *Sassafras* species), as it is in southeast Asia (several *Fagus*, > 5 *Quercus*, > 10 *Acer*, several *Ulmus*, 1 *Ginkgo* species), while in Central Europe species richness is low (1 *Fagus*, few *Acer*, 1–2 *Quercus*, few *Ulmus* species). One reason for this pattern is that during the Ice Age the east–west

stretching Alps as well as the east–west stretching Mediterranean Sea precluded southward movement of tree species, while in North America as well as in eastern Asia species were able to move to warmer areas farther south. Nevertheless, a disturbance regime lacking severe damage in Central Europe may be (one of) the reason(s) that here just one of these few species (*Fagus sylvatica*) is by far the most competitive one, forming nearly single-species stands in close-to-natural forests, while in both North America and southeast Asia mixed deciduous forests occur.

To conclude, there really are differences in disturbance regimes, especially with regard to the destructive potential of wind storms, among the three temperate forest areas of the northern hemisphere. There are also differences in vegetation history resulting in differing tree species diversity in the three areas. Indeed the structure of the European temperate forests (mono-dominance) is quite different from the structure of the temperate forests in Asia and North America (mixed forests).

Disturbances and forest stand development

Natural forest disturbances tend to increase structural diversity. Sometimes soil is mechanically disturbed, offering safe sites for the germination and establishment of anemochorous species as well as for seeds deposited in the soil seed bank; sometimes trees die while standing, sometimes they become broken or thrown, sometimes only bent over. Each of the disturbances therefore contributes to maintaining high biodiversity (in terms of species, structure, and successional pathways).

Disturbances originating indirectly from human activities are relatively new to forest ecosystems. The introduction of alien pests and/or insects are expected to change the composition and structure of the temperate forests in eastern North America fundamentally: several of the main species of these forests (e.g. *T. canadensis*, *C. dentata*, *F. grandifolia*) forming large parts of the canopy and influencing the ecological processes in the ecosystem, have been lost or are in the process of being lost. Because of their importance for forest structure and ecosystem functioning they are called “*foundation species*” (Ellison et al. 2005; kind of “keystone species”, but with a focus on structure). Loss of several foundation species will lead to a completely new quantitative and qualitative species composition, a new structure, and a re-arrangement of ecological processes in the forest ecosystems affected, not only locally but on a landscape scale. The North-American temperate forest is going to become a completely new forest type. This has consequences for both future forest management (which species should be promoted in the future?) and for forest protection (which vegetation types should be protected?).

In European forest ecosystems up to now, only co-dominant trees, mainly growing under more extreme site conditions, are influenced by such invasive alien (or recently modified) species (e.g. *Ulmus* spp. by Dutch Elm Disease, *Fraxinus excelsior* by Ash Dieback). For several years the *Phytophthora* Beech Disease, caused by several native *Phytophthora* species (*P. plurivora* = *citricola*, *P. cambivora*, *P. cactorum*; www.bfw.ac.at) has been expected to become a problem for European beech (*F. sylvatica*). In Bavaria in the early 2000s, the disease was found in 54 out of 57 analyzed forest stands (Jung 2004). Although many trees may be infected by *Phytophthora*, and although some of them actually succumb to the infection, especially those on soils which tend to be wet during summer, a large beech dieback up to now can not be seen. Especially on the well-drained soils that are preferred by *F. sylvatica*, there seems to be an equilibrium between destruction of tree roots by *Phytophthora* and root regeneration (Jung 2004). Thus in

Europe the main canopy tree species, *F. sylvatica*, is not thought to be facing total collapse in the decades to come.

For interpreting the ecological relevance of disturbance, it is essential to differentiate between disturbance *intensity* and disturbance *severity* (Frelich 2002): while intensity refers to the amount of energy released by the physical process of disturbance, severity refers to the amount of (tree) mortality that occurs in a disturbed area. For wind disturbance both intensity and severity increase parallel to each other. Browsing animals, in contrast, have a very low intensity, but—if population of browsing deer is high—tree regeneration may be totally impossible. Estimated values of intensity and severity, respectively, for the mentioned disturbance types, are given in Table 1.

After disturbance intensity and severity, the size of the area (Table 1) that is affected by the disturbance is also important, both for forest development and forest management. Disturbances may be extremely intense and extremely severe, but because of limited occurrence (e.g. tornado or snow avalanche) may play a minor role on the landscape scale. On the other hand, as in the Central European deciduous forests dominated by *F. sylvatica*, windstorms occur, and mainly during wintertime when deciduous trees are leafless, so their destructive power is minimized.

Frelich (2002) also introduced a simple conceptual model explaining the dominance of either early-successional or late-successional species, or the coexistence of both, as a function of the cumulative disturbance severity (Fig. 2a). The lack of large-scale frequent severe disturbances may be one reason that one species—*F. sylvatica*—became the absolute dominant tree species in temperate European forests around 5,000 years ago. Primary *Fagus*-dominated forests in the Carpathian Mountains of Ukraine show that practically the whole area is occupied by *Fagus* stands, with only small gaps caused by local and low-severity windstorms.

The model of Frelich should, however, be extended by a third (ordinal) axis (Fig. 2b): the disturbance type (quality). Stand replacing fire, hurricane wind-throw, and large-scale bark beetle attack, respectively, lead to quite different starting conditions for forest stand regeneration with regard to soil surface structure, degree of open soil, seed bank activation, seedling population (in both quantitative and qualitative terms), and the regeneration niches of the different species.

A kind of “mega-disturbance” is what is called “global climate change”. Change in climatic conditions has taken place since the earth has been in existence, and five mass extinctions of species within the past 540 million years are documented (“big five”; Barnosky et al. 2011). Nevertheless such mega-disturbances had also led to the development of completely new groups of organisms. The recent, human-driven climate change (IPCC 2007), however, is happening with a speed that has never occurred before, at least not within the last 10,000 years. The more cold-adapted species may decline, the more warm-adapted species increase, a process called “*thermophilization*” (Gottfried et al. 2012). Species are starting to extend their distribution areas either farther north (*Ilex aquifolium*, Berger and Walther 2007) or to higher elevations (*Quercus* spp., Peñuelas and Boada 2003), not just in forests but also in alpine ecosystems (Grabherr et al. 1994; Gottfried et al. 2012). Also in European beech forests a thermophilization effect can be seen, but up to now explaining only 6 % of the variance, and it is still hard to resolve these changes at the species level (Jantsch et al. 2013). Modeling studies show that the forest belt will move northwards if the expected climate change continues as outlined for both China (Cheng and Yan 2007) and eastern North America (Box et al. 1999; Louis et al. 2008). Not all species will be able to find new home ranges: a lot of them will disappear (Pompe et al. 2008). The temperature increase is expected not to influence species and ecosystems

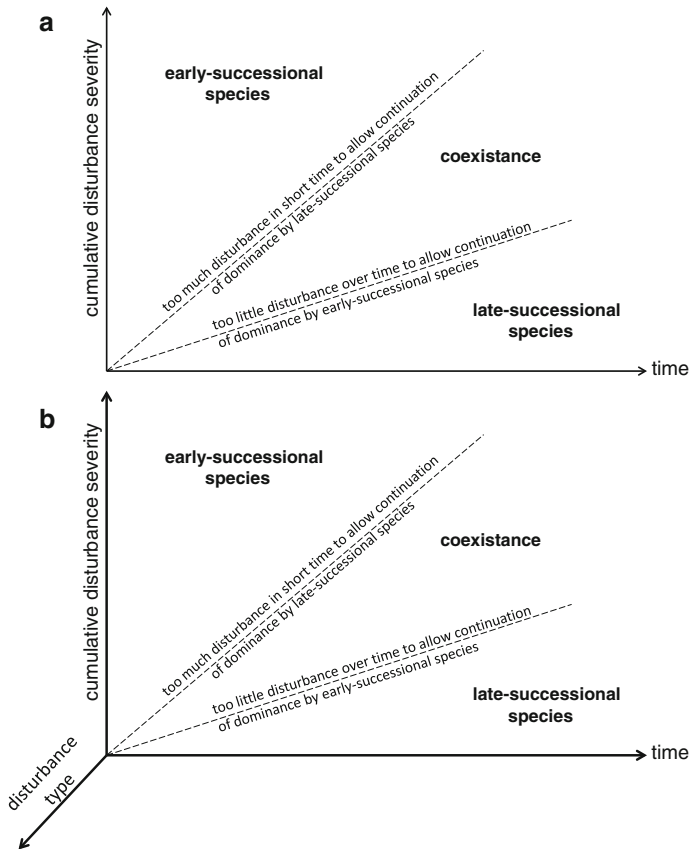


Fig. 2 **a** Cumulative disturbance severity determining species composition of forest stands. After Frelich (2002), modified. **b** Same model, completed by a third dimension: the disturbance type

directly (by “worming up”) but indirectly by favoring pathogens and insects, which may disturb forest ecosystems more frequently and more intensively in the future. Indeed the total area affected by forest pests is increasing in China (Ye 2000), and forest pests and diseases are going to move northwards (Zhao et al. 2003). Management options cover a broad range: from selecting of species that are better adapted to warmer and drier climates to helping species to move into new habitats: “assisted migration” (McLachlan et al. 2007) or “assisted colonization” (Hunter 2007).

As a result, we must realize that disturbances prevent forest stands from reaching a “final equilibrium”. Disturbances may kill trees, but they also offer space and habitat to new species: pioneer trees (see above), species with a permanent soil seed bank (Fischer 1987; Apffelstaedt and Bernhardt 1996), and animals, e.g. bats preferring gaps of different sizes (Fukui et al. 2011).

Forest insects and pathogens are much more “mobile” than forest plants. According to Logan et al. (2003), forest insects are the major agent of natural disturbance in North American forests overall, approximately 45 times that of fire. Global warming will result in intensification in all aspects of outbreak behavior. To indicate the importance of insect pests in the frame of global climate change the authors summarize: “We will probably

experience ecological catastrophes such as the loss of high-elevation five-needle pines long before we are paddling sea kayaks in Central Park [New York City]". As a consequence, it is not the direct influences of global climate changes on single herb or tree species and their population development that may change temperate forests fundamentally, but the new and powerful combination of pests and pathogens.

Conclusions for future forest structure and management

One of the first concepts in forest ecology dealing with the "nature" of forest ecosystems was introduced by Clements (1936, p. 261): the climax concept. According to this concept the vegetation of a certain landscape is determined mainly by climate, and its "*development regularly terminates in the community capable of maintaining itself under a particular climate*". Disturbances are part of the system, "*constantly and universally at work*", but "*in the absence of civilized man this is within the fabric of the climax and not destructive of it*" (p. 256).

Our recent survey shows that forest ecosystems are influenced by numerous of external factors to an extreme degree, not only external *abiotic* factors but also by *biotic* factors: species that arrive in a new area and change species interactions fundamentally (e.g. leading to a decline of former foundation species). Many different types of disturbances permanently push back vegetation to an earlier stage, and the regeneration pathways following disturbance may be different depending on the very special set of site conditions that occurs at each single place. As a result, and in contrast to Clements' climax concept, each forest stand, both regarding species composition and structure, should be interpreted as a unique recent expression of the interaction of environmental conditions and plant species, depending on (1) quality and quantity of abiotic factors (physical/chemical site conditions) and (2) of biotic factors (plant species, animal species, and pathogens), which may enter or exit the system, changing the network of interactions within the ecosystem permanently. Each forest stand therefore represents a "snapshot" of the actually relevant abiotic and biotic factors including human impacts, which may/will change in the course of time.

All these factors may change either continuously (e.g. soil development) or abruptly, the latter being called "disturbances". These disturbances act on different special scales: from single point (e.g. a tree sapling eaten by deer) to the landscape level (e.g. hurricane, or invasion of a pathogen). And they act on different time scales: from a moment (e.g. a storm uprooting a tree) to decades (e.g. spread of invasive alien species) to centuries or millennia (as a consequence of a fundamental climate change: e.g. the end of the Ice Age). Each forest stand therefore represents a unique combination of abiotic and biotic factors including their more or less sudden changes to a different extent in both space and time. Forests are under permanent reorganization. In addition, there are important and large-scale human impacts on forest stands today, influencing both stand structure and species diversity; in a meta-analysis of European forests. Paillet et al. (2009, p. 101) found that species richness was slightly higher in unmanaged than in managed forests.

This has important consequences for all kinds of forest management in the temperate forests of the northern hemisphere. Methods of timber production and harvesting that avoid large-scale clear-cuts by extraction of individual trees (single-tree selection methods) or groups of trees (gap cutting or group selection), give preference to patchy harvesting units, and which mainly use natural regeneration of (native) tree species come closer to the natural functioning of temperate deciduous forests than uniform methods (e.g.

shelterwood). For European temperate forests Fischer (2011) showed that such selective cutting practices may mimic natural forest disturbances such that the resulting species diversity (vascular plants, soil fungi, soil Carabidae beetles) is very similar to a close-to-primeval forest. Certain tree species such as pines (*Pinus* spp.) and oaks (*Quercus* spp.) whose seedlings have a high light requirement may need larger gap sizes to ensure adequate natural regeneration, but even in these cases patchiness is preferable to uniformity. Forest management concepts that include this kind of spatial variation in disturbance are therefore seen as being beneficial for forest regeneration (Wang et al. 1999), and it is important if the maintenance of total biodiversity in forests is a concern (Qin et al. 2011). In Germany for example, regulated selective cutting systems have been using as standard silvicultural method since the 19th century (Heske 1938). The size of such patches may vary depending on the dominant disturbance type (e.g. larger if hurricanes regularly occur, smaller if “only” windstorms occur).

Disturbances emerge not only in pristine forests, but also in managed forests. It is a general question of forest management how to deal with forests that have been affected by disturbances. As shown in this review, natural regeneration after such disturbances comes much closer to the former species composition than after management impact; nutrient cycles are much less disturbed than after preemptive or salvage harvesting. Sometimes natural disturbances cause no significant change in species composition (Fraver and White 2005). Foster and Orwig (2006) summarize that management impacts on forest ecosystems after such disturbances often impose greater ecosystem impacts than the disturbances themselves, and that many ecological benefits are derived from leaving forests alone when affected by disturbance; the authors conclude that “*doing nothing is a viable alternative*”. “Alternative” does not mean using this option generally and everywhere, but it is an option that may be the best in certain situations, best not only from an ecological but also economical point of view (Lässig and Močalo 2000; Kompa and Schmidt 2006; Fischer et al. 2012).

The *absence* of formerly occurring disturbances may also influence ecosystems strongly, as noted for fire management above. Recently Fox et al. (2012) discussed the option to re-introduce bison to sandhill landscapes in northern Canada; the bison had been identified as a key factor in maintaining active erosion in the areas it inhabits, an important precondition for long-term survival of many plant and animal species as well as for the whole sandhill ecosystem.

Such a re-introduction of a formerly common natural disturbance agent may represent a step towards increased naturalness (after man-made reduction). It is, however, difficult or impossible to find “natural equivalents” to new emerging site conditions (e.g. climate change) or to new types of disturbances (e.g. introduced alien species, or new pathogens and insects). Also, the topic of game browsing, important in many managed temperate forests, is hard to clarify in terms of naturalness: What is the “natural” level of browsing intensity in a landscape where the natural predators of browsing game have been extirpated centuries ago, and a large part of the landscape has been converted to totally new (e.g. agricultural) ecosystems?

Human-caused changes of site conditions like global climate change and the worldwide transportation of species (most important: pathogens and insects) cannot be stopped or compensated for in an individual forest stand or protected area (e.g. a national park). The new climate, the new species, the new disturbances (qualitatively and quantitatively) will form “novel” ecosystems (Hobbs et al. 2009). If we want to slow down this process we can try to reduce the increase of CO₂-output, to avoid further transportation of species across biogeographic barriers, and to reduce human pressure on existing ecosystems.

Global biodiversity is strongly decreasing and could exceed recent rates of extinction in the 21st century by two orders of magnitude (Pereira et al. 2010) and reach the extend of a sixth mass extinction within just a few centuries (Barnosky et al. 2011). Around 50 % of all terrestrial plant species are living on only 2.3 % of the land area, highlighted as “hotspots of biodiversity”—and most of these hotspots host or are dominated by forest ecosystems (Seligmann et al. 2007). That means that forestry is not only responsible for sustainable production of a renewable resource that can be used for many purposes (e.g. building construction, biomass energy, CO₂-mitigation) but also to protect natural biodiversity with a long-term perspective.

Temperate forests are manifold, because they developed in different parts of the world separated from one other. As in all forest ecosystems, disturbances are a major driver for species and structural diversity. This diversity cannot be maintained as it is frozen in time. Therefore in strongly protected areas it should be “the process of development” that should be protected and allowed, respectively, but no special constellation of either species or structures set as a goal. Also in managed forests disturbances should not only be seen as a production obstacle but as a chance to incorporate natural ecosystem processes into production systems.

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