

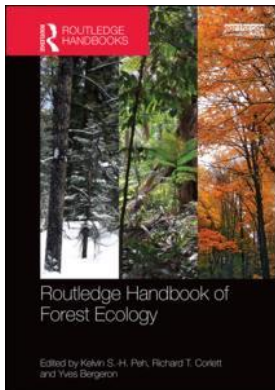
This article was downloaded by: 10.3.98.93

On: 26 May 2019

Access details: *subscription number*

Publisher: *Routledge*

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: 5 Howick Place, London SW1P 1WG, UK



Routledge Handbook of Forest Ecology

Kelvin S.-H. Peh, Richard T. Corlett, Yves Bergeron

Northern Temperate Forests

Publication details

<https://www.routledgehandbooks.com/doi/10.4324/9781315818290.ch3>

Lee E. Frelich, Rebecca A. Montgomery, Jacek Oleksyn

Published online on: 22 Oct 2015

How to cite :- Lee E. Frelich, Rebecca A. Montgomery, Jacek Oleksyn. 22 Oct 2015, *Northern Temperate Forests from: Routledge Handbook of Forest Ecology* Routledge

Accessed on: 26 May 2019

<https://www.routledgehandbooks.com/doi/10.4324/9781315818290.ch3>

PLEASE SCROLL DOWN FOR DOCUMENT

Full terms and conditions of use: <https://www.routledgehandbooks.com/legal-notices/terms>

This Document PDF may be used for research, teaching and private study purposes. Any substantial or systematic reproductions, re-distribution, re-selling, loan or sub-licensing, systematic supply or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The publisher shall not be liable for an loss, actions, claims, proceedings, demand or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

3

NORTHERN TEMPERATE FORESTS

Lee E. Frelich, Rebecca A. Montgomery and Jacek Oleksyn

Introduction

Biogeography

Three areas of northern temperate forest with large spatial extents occur in eastern North America, Europe, and eastern Asia; a conifer-dominated temperate rainforest also occurs in western North America (Figure 3.1, Whittaker 1975). These forests are found between boreal forest to the north, and subtropical forests, grasslands and savannas, or Mediterranean vegetation to the south. Many of the tree genera in temperate forests occur across North America, Europe and Asia: *Acer*, *Alnus*, *Betula*, *Carpinus*, *Carya*, *Castanea*, *Celtis*, *Fagus*, *Fraxinus*, *Larix*, *Pinus*, *Populus*, *Prunus*, *Quercus*, *Picea*, *Tilia*, and *Ulmus*. Other genera—*Liriodendron*, *Pseudotsuga* and *Tsuga*—occur in North America and Asia. Some tree genera are widespread across temperate and boreal biomes (e.g. some *Betula*, *Pinus*, *Picea*, and *Populus* species), others are almost totally restricted to the temperate zone (e.g. *Quercus*, *Tilia*, and some *Acer* species), while some occupy the transition zone plus limited portions of the southern boreal and northern temperate zones, and cannot be conveniently classified as temperate or boreal species (e.g. *Fraxinus nigra*, *Pinus resinosa*, and *Picea rubens* in North America). The species richness of trees and understory plants is highest in Asia, moderately high in North America, and lowest in European temperate forests, although within each continent species richness also varies from relatively high towards the southern edge of the temperate biome to relatively low at the northern edge.

Some tree communities have similar composition at the generic level across the three main occurrences of northern temperate forest. For example, *Fagus* (beechness), *Acer* (maple) and *Quercus* (oak) occur together on mesic sites: *A. mono*, *F. crenata* and *Q. mongolica* in Japan, *A. saccharum*, *F. grandifolia* and *Q. rubra* in eastern North America, and *A. platanooides*, *F. sylvatica* and *Q. robur* in northern Europe (Runkle 1982, Yamamoto *et al.* 1995, Svenning and Skov 2005).

Climate

Northern temperate forests have strong seasonality, with a cold-induced dormant season and a warm growing season that produces distinct annual rings in trees. Growing season lengths range



Figure 3.1 Location of the world's temperate forests

Source: Adapted from: Terpsichores (Own work) [CC BY-SA 3.0 (<http://creativecommons.org/licenses/by-sa/3.0/>)], via Wikimedia Commons

from about four months at the temperate–boreal ecotone in the north (long, cold winters and cool summers) to about eight months at the temperate–subtropical forest ecotone (short cool winters and long hot summers) in the south (Peel *et al.* 2007). Precipitation regimes vary from wet winter/dry summer in coniferous temperate rainforests such as the Pacific Northwest USA, to rainforests wet throughout the year (*Tsuga* forests in the Southeastern USA), to wet summer regimes with snow during the dormant season in most of the cold parts of the temperate forest, to droughty summers with erratic rainfall in places where temperate forest and savanna/grassland ecotones occur, such as in the continental interiors of North America and Eurasia (Whittaker 1975). In the colder temperate climates, snow plays an important role by limiting the depth to which the soil freezes, which would otherwise cause extensive root damage in mature trees and mortality to seedlings and herbaceous plants. Some colder regions, such as Upper Michigan, USA, and northern Japan, receive extreme amounts of snow due to lake-effect or ocean-effect snowfall generated by cold winds blowing over large water bodies before hitting land. These ‘snow forests’ have unique species composition—for example sugar maple (*Acer saccharum*) is the dominant tree species in such forests in the Midwestern USA, since its main competitor, hemlock (*Tsuga canadensis*)—is damaged by the load of snow landing on the branches, and restricted to areas with lower snowfall.

The transition from temperate to boreal forest depends on either low winter minimum temperatures or cool summers. The deep supercooling point of the cells in the cambium under the bark of most temperate tree species ranges from -40 to -45 degrees C, and if winter temperatures are commonly that cold then many of the dominant temperate tree species in genera such as *Quercus* and *Acer* cannot survive (George *et al.* 1974). In other areas near large bodies of water (e.g. Lake Superior in North America), winter temperatures are nowhere near cold enough to limit temperate tree species but short, cool summers throw the competitive balance to boreal species, creating shoreline belts of boreal forest that transition to temperate forest inland where summers are warmer. The ecotone between northern temperate and boreal forests is broad, with species from the two biomes commonly found growing together over a 500-km-wide region (Fisichelli *et al.* 2014). In North America, temperate *Betula alleghaniensis*, *Acer saccharum* and *Fagus grandifolia* are mixed with boreal *Abies balsamea* and *Picea glauca*, in Asia, temperate *Quercus mongolica* and *A. mono* mix with boreal *Pinus koraensis* and *P. sylvestris* var. *mongolica*, while in Europe temperate *A. platanoides*, *F. sylvatica* and *Q. robur* mix with boreal *B. pendula* and *Picea abies*.

Soil and site conditions

The northern portions of the temperate forest in North America and Europe were glaciated and have relatively young soils (about 9,000–14,000 years old) on top of glacial deposits or rocky surfaces sculpted by the glaciers, whereas older soils with a wide range of substrates, fertility, and topographical relief occur elsewhere. Mesic sites with loamy soils are most common, and usually dominated by *Acer*, *Fagus*, *Tilia*, and *Tsuga* species (Figure 3.2a). Dry-mesic to dry sites with soils that are sandy or shallow to bedrock are usually characterized by *Pinus* and *Quercus* species (Figure 3.2b). Swamps, peatlands and riparian areas are dominated by *Acer*, *Alnus*, *Betula*, *Fraxinus*, *Populus*, and *Salix* species. Gradients from wet to mesic and dry soils in complex topography are common. Temperate forest ecosystems cover an area of 10.4 million km² (about 6 percent of all Earth ecosystems) and store about 21 percent of carbon (139 PgC) in plants and 11.2 percent of carbon (262 PgC) in soils (Sabine *et al.* 2004).



(a)



(b)

Figure 3.2 (a) Temperate *Acer*-dominated forest on a mesic site, Michigan, USA. Photo: Jiri Schlaghamersky. (b) Prescribed fire in *Quercus* forest on a dry sandy site. Photo: Kalev Jogiste

Importance to society

High-density human settlement and land clearing, for timber and growing space for agriculture, have taken place in much of the northern temperate forest over the last several centuries in Asia, Europe, and eastern North America. This clearance was associated with the development of the Industrial Revolution in Europe during the late 1800s and its expansion to the rest of the world. For several centuries temperate forests were also essential wood sources for naval construction. Thus, the temperate forests have played a major role in shaping human society as it now exists. The need for ship wood also stimulated the development of the fields of forest science and forest management. The now recovering temperate forests constitute a large and growing source of carbon storage, wildlife habitat and watershed protection. Many important products come from the temperate forest, including sources of non-timber forest products (wild plants and fungi used as food, hunting animals for food, maple syrup [N. America] from *Acer saccharum*, and birch sap for traditional beverages and in folk medicine as an ingredient for different antiseptic and anti-inflammatory treatments [Central and NE Europe]), wood products (hardwood used for furniture and flooring, *Pinus* and *Quercus* used for construction lumber), and paper products (many species used for pulp). The forests also contribute greatly to the tourism industry through attractions such as remnant old-growth forests, large trees, spring wildflowers, brilliant fall colors, and habitat for migrant bird species, song birds, and other wildlife species commonly viewed by tourists.

Ecological processes

Nutrient cycling and decay processes

Soil structure in temperate forests usually has an organic horizon at the top of the soil profile composed of leaf litter in various stages of decay, from fresh leaves at the top to fragmented leaves in the middle and black humus at the bottom. Rate of decay is important for determining how fast nutrients are released from the organic horizon, and is determined by temperature and soil moisture, which in turn is determined by climate and soil texture. Organic horizon thickness is greater in colder climates and drier climates within the temperate zone, where decomposition of leaf litter is slower, in forests dominated by species with high C:N ratios and low nitrogen content of leaf litter (*Fagus*, *Picea*, *Pinus*, *Quercus*), in forests on sandy soils, and forests with low earthworm abundance. Cold temperatures in northern temperate and boreal forests depress organic matter decomposition, and may suppress nutrient movements in soil and their uptake by roots. Young, postglacial soils tend to be more N- than P-limited (Reich and Oleksyn 2004).

Changes in forestry practices that alter tree species composition, along with urbanization and other influences of human activity such as atmospheric deposition may alter cycles of ecologically important nutrients, including nitrogen, sulfur, hydrogen ions and base cations (Ca^{2+} , Mn^{2+} , Na^+ , and K^+ ; Hedin *et al.* 1995). Temperate old-growth forest ecosystems are particularly vulnerable to increases in atmospheric N deposition. In response to increased N supply (both from N deposition and faster litter mineralization enhanced by increasing temperatures), the pattern of N cycling may change and be accompanied by increased selection favoring nitrophilous plant species and a decrease in ground species richness (Tamm 1991). An example of large-scale changes in nutrient cycling and soil function caused by human activity has occurred in Europe during the late nineteenth and twentieth centuries. Coniferous trees including native (*Picea abies*, *Pinus sylvestris*), and North American (*Picea sitchensis*, *Pseudotsuga*

menziesii) species were widely planted to reverse eighteenth and nineteenth century deforestation and increase productivity, often replacing native deciduous species. Creation of large-scale coniferous monocultures contributed to further acidification of already acidic soils (65 percent of European topsoils have pH ≤ 4.5 , Augusto *et al.* 2002).

Disturbance and succession

Major disturbances that kill or level the forest canopy include logging, wind, fire, ice storm, landslides, and insect infestation. Note that all of these may also create partial disturbance with scattered tree mortality contributing to the gap dynamics of multi-aged stands described below. Whether stand-leveling disturbance initiates an episode of succession—defined as a directional change in species composition over time, usually establishment of a dominant cohort of early-successional pioneer tree species followed by its gradual replacement by a suite of later-successional species—is context dependent (Heinselman 1981, Finegan 1984). For example, canopy-leveling wind storms or logging of the large trees may leave a carpet of late-successional advanced regeneration intact on the forest floor, leading to initiation of an even-aged stand followed by a stand development sequence from even-aged to multi-aged, but not necessarily change in species composition. This has been shown to occur in North American *Acer saccharum* and *Tsuga canadensis* forests. On the other hand, high-severity disturbances such as windthrow followed by high-intensity fire, or landslide could easily wipe out the advanced regeneration, leading to establishment of shade-intolerant, early-successional species succeeding to shade-tolerant, late-successional species over the subsequent one to two centuries. Illustrative case studies include *Betula papyrifera* and *Populus tremuloides* succeeding to *Acer saccharum* and *Tsuga canadensis* in North America and *Betula grossa* succeeding to *Tsuga sieboldii* and *Fagus crenata* in Japan (Yoshida and Ohsawa 1996, Frelich 2002).

Multiple disturbance regimes occur in the northern temperate forest biome. The least severe regime occurs on good quality sites with moist climates, and is dominated by single to multiple treefalls, usually wind-dominated regimes with some insect, disease, and drought mortality, where gap dynamics are prominent (described in more detail below). Such forests are dominated by mid-to-late-successional species, and under natural conditions, episodes of succession depend on rare episodes of severe disturbance mentioned above. However, in the last one to two centuries, clear cutting followed by slash burning has mimicked the rare natural wind–fire combination and created much larger expanses of early-successional forests than would have occurred naturally, in regions undergoing human settlement. A second disturbance regime is that of frequent low-intensity fire, commonly occurring in *Quercus* and *Pinus* savannas/woodlands. These forests are also multi-aged and have little succession over time unless the natural disturbance regime is disrupted by humans, usually by fire exclusion. The tree species are adapted to frequent fire due to thick bark that insulates the base of the trees from being girdled (*Quercus* and *Pinus*), and/or the ability to sprout if top-killed by fire (*Betula*, *Populus* and *Quercus*), and ability to germinate in post-fire conditions with full sun and lack of leaf litter. Once established, these trees commonly live a century or more and survive many subsequent fires. These forests occupy relatively dry climates in the transition from temperate forests to grasslands or Mediterranean vegetation, as well as excessively well drained sites on sand plains and south-facing rocky hillsides within wetter climates. A third disturbance regime is that of mixed-intensity fire, whereby fires of variable intensity occur at irregular intervals. Fires may kill some, most or all trees in a given stand, and may come at short intervals so that there is no time for succession, maintaining the current successional status, or long intervals, allowing succession to take place between fires. Although successional pathways for these forests are

understood, i.e. they progress from shade-intolerant fire adapted species to shade-tolerant species, and these patterns are known for many regions, the irregular nature of the fire regime makes the actual successional trajectory in any one stand unpredictable over time (Frelich 2002). Forests with mixed-intensity fire regimes occupy sites with climates and/or soils between the first two regimes mentioned above. They include mixed *Betula*, *Pinus*, *Populus* and *Quercus* forests, sometimes succeeding to *Acer* and *Tsuga* in eastern North America, and *Pseudotsuga* potentially succeeding to *Abies*, *Picea* and *Tsuga* in western North America.

Canopy structure and gap dynamics

Large tracts of temperate forest occur on mesic sites where stand-leveling disturbances are rare, and gaps from single to several trees falling constitute the main type of disturbance (e.g. Payette *et al.* 1990). The dynamics of these treefall gaps, canopy turnover rates, canopy tree residence times, canopy structure, and recruitment of new trees into gaps have been studied at numerous sites. Such forests are usually multi-aged, and dominated by late-successional, shade-tolerant species, with some mid-tolerant species, and an occasional specimen of early-successional species. Fluctuations in relative abundance of the late-successional species occur over time due to influences on seedling success such as preferential deer grazing on seedlings, and neighborhood effects (structure and chemical properties of the leaf litter, sprouting; Brisson *et al.* 1994). The late-successional species generally exist as suppressed seedlings (or advanced regeneration) that will record a release from suppression if the tree above dies; this fact has been used to reconstruct the treefall history of forests going back as much as several centuries (Lorimer 1980, Payette *et al.* 1990). In contrast, the seedling bank of mid-tolerant tree species is rather small due to rapid turnover as seedlings die due to low light levels, but these species are adapted to enter new gaps by seed dispersal followed by rapid height growth that may surpass that of shade-tolerant species. Average tree residence times in the canopy vary from ≈ 100 –200 years in temperate forests, with a few trees living 2–3 times the average lifespan (Runkle 1982).

Gap formation creates microsites for seedling germination including relatively dry and wet mineral soil on mounds and in pits created by uprooted trees, above-ground light gaps and below ground ‘gaps’ in root occupancy of the soil created by fallen trees (Beatty and Stone 1986). These gaps can have not only more light, but higher soil and air temperatures, and more water (due to lack of use by the fallen tree), leading to more nutrient availability in the first few years as the fine roots of the fallen tree decay in the relatively warm, wet environment. Tree species mid-tolerant of shade (e.g. *Fraxinus* and *Tilia*, along with some species of *Acer*, *Betula*, *Carya*, *Pinus*, and *Quercus*) often take advantage of these gaps, which therefore help to maintain local species richness over time. In addition, treefalls create coarse woody debris, which, when it reaches an advanced state of decay, can also be a microsite for germination of some tree species that cannot tolerate thick leaf litter or the dense herbaceous vegetation that may cover the forest floor. These decaying logs often last 20–40 years for angiosperm species in genera such as *Acer*, *Quercus* and *Tilia*, but may last 1–2 centuries for gymnosperms such as *Picea*, *Pinus* and *Tsuga*. Decaying logs also are small-scale hot spots of biodiversity due to the large number of species of mosses, fungi, insects, and amphibians that use them as habitat due to their relatively high water content (Harmon *et al.* 1986).

Plant species interactions

Interactions of note in the northern temperate forest include the occurrence of mosaics formed by patches of evergreen conifer and broadleaf deciduous species, shade-tolerant and intolerant

species interactions, and the presence of numerous understory species that take advantage of a brief period of combined warmth and light in spring, and heterotrophic species that do not require sunlight to fuel carbon gain (e.g. saprophytic and parasitic plants).

Evergreen–deciduous mosaics of *Tsuga* or *Picea* with *Acer*, *Betula* and *Tilia* (mesic sites), or with *Pinus* and *Quercus* (drier sites) occur in the parts of the temperate forests with cooler climates, including the northern USA, northern Europe, and Asia. These mosaics (Figure 3.3) may be created by slight differences in the soil environment magnified by neighborhood effects of the trees themselves, through shading, leaf-litter chemistry, seed rain, interactions with disturbance and, in some cases, sprouting, so that the deciduous and evergreen species each favor their own reproduction and/or disfavor seedlings of the opposite group under their own canopies (Frelich *et al.* 1993).

Shade tolerance or avoiding shade is necessary for any plant species to reproduce in these forests given dense canopies and forest floor light levels ranging from 1–10 percent of full sunlight. Plant species have evolved a variety of strategies. Spring ephemerals are species that grow rapidly as soon as winter ends, taking advantage of the sunlight available on the forest floor prior to canopy leaf out. Included are species in the genera *Allium* (wild leek), *Cardamine* (toothwort), *Corydalis*, *Dicentra* (Dutchman’s breeches), *Erythronium* (trout lily), and *Mertensia* (bluebell), which complete their above-ground life cycle of growth, flowering, seed set and die back to a dormant phase within 4–6 weeks (Figure 3.4). Some of these genera have vicarious species (related species that live in similar environments with similar ecological niche) among the major occurrences of temperate forest, for example, *Erythronium americanum* in the eastern USA, *E. dens-canis* in central and southern Europe, and *E. japonicum* in eastern Asia.

Other early blooming species are commonly misclassified as spring ephemerals, but they keep their leaves for much of the summer—these include geophytes such as *Trillium*, and herbs



Figure 3.3 Old-growth forest mosaic of deciduous (*Acer*, *Tilia*, *Betula*), and coniferous (*Tsuga*, *Thuja*, *Picea*) trees. Porcupine Mountains, Michigan, USA. Photo: Jiri Schlaghamersky



Figure 3.4 Spring ephemeral yellow trout lily (*Erythronium americanum*) in an *Acer* and *Betula* forest
Source: Jiri Schläghamersky

such as *Arisaema* (jack-in-the-pulpit), *Sanguinaria* (bloodroot), and *Viola* (violets), which can use energy stored in a bulb or rhizomes to produce leaves early on in full sun, but continue to photosynthesize in deep shade after canopy leaf out. Saprophytic plants such as *Corallorhiza* (coral root orchids), *Monotropa uniflora* (Indian pipe) and parasitic plants such as *Epifagus virginiana* (beech drops) and *Conopholis americana* (squaw root) get their energy from decomposing organic matter or attachments to tree roots, and do not require sunlight.

A number of plant species take advantage of treefall gaps, where higher than average light levels last a few decades, to grow up into the canopy (e.g. *Betula*, *Quercus*) or to complete their life cycle and create long-lived buried seeds that await the next gap a century or more later—e.g. *Prunus pensylvanica* (pin cherry), *Rubus* (raspberry), and *Geranium bicknellii*. Another group of species has short life cycles within gaps but produce plumed seeds that float long distances through the air to ‘find’ new gaps (e.g. *Epilobium angustifolium*, fireweed). Shade-tolerant shrubs in forest understories can create complex spatial dynamics for tree regeneration. Understory dwarf bamboo (*Sasa* spp.) in Asian forests can exclude seedling establishment, even for shade-tolerant tree species. For example, beech (*Fagus crenata*) and maple (*Acer mono*) seedlings in Japanese forests are restricted to small patches where bamboo is absent (Yamamoto *et al.* 1995).

Plant–animal interactions

Many symbiotic and antagonistic plant–animal interactions occur in northern temperate forests, involving seed dispersal, pollination, defoliation, insect herbivory, and preferential grazing by large mammals (deer, moose) that can alter successional trajectories. Although many species of temperate trees have wind dispersed seeds, animal dispersal (zoochory) also occurs. One well-known case is for acorns of northern red oak (*Quercus rubra*) that are cached by various animal

species in the fall for later use during winter. Gray squirrels (*Sciurus carolinensis*) bury acorns in the soil and are known to remember the locations of several thousand acorns, but during mast years, they often bury more than they retrieve, leaving many to germinate, and at the same time hiding those acorns from consumption by deer (*Odocoileus virginianus*), black bear (*Ursus americanus*), and turkey (*Meleagris gallopavo*). Blue jays (*Cyanocitta cristata*) can carry acorns, and commonly fly several hundred meters to two kilometers from the parent tree, scatter hoarding thousands of acorns across the landscape (Johnson and Webb 1989). In Europe, acorns of *Quercus coccifera*, *Q. robur*, *Q. petraea*, *Q. ilex*, *Q. suber*, and *Q. faginea* and *Fagus* nuts are dispersed by the Eurasian jay (*Garrulus glandarius*). Analysis of the seed dispersal service performed by the Eurasian jay in the Stockholm National Urban Park, Sweden has shown that depending upon seeding or planting technique chosen, the cost of replacement per pair of jays through human means in the park is 2,100 US\$ (seeding) to 9,400 US\$ (planting) per hectare, respectively (Hougnier *et al.* 2006). Such estimates provide a good example of the value of management strategies securing critical breeding and foraging habitats of seed dispersal animals.

Despite the fact that the Eurasian jay prefers acorns of native *Quercus robur* it is also efficient in dispersing invasive North American *Q. rubra* (Myczko *et al.* 2014). Increase of red oak leads to significant reduction of native species abundance and diversity (Woziwoda *et al.* 2014).

Seed dispersal by ants is known as myrmecochory, and is common among temperate forest understory plant species (Gomez and Espadaler 1998). The spring wildflower genera *Trillium* (North America and Asia) and *Viola* (North America, Europe and Asia) are examples, with a number of species dispersed by ants, although other vectors also exist. The seeds of these species have a fat-rich elaiosome attached to each seed, which the ant can detach for consumption, commonly after moving the seed one or two meters.

A large number of bee species occur in temperate forests (often 50 or more species in one stand), which pollinate most of the forest understory species with brightly colored flowers and limited pollen production, and a few of the tree genera such as *Acer* (in part, wind dispersal also occurs), *Prunus*, and *Tilia*. Folivorous insects are common, with many species that cause ongoing low-to-moderate levels of defoliation, that interact with plant defense compounds in leaves such as phenols and terpenoids. Other insect species have periodic outbreaks every decade or longer, during which the forest may be almost totally defoliated. For example, deciduous forests in eastern North America can be defoliated by saddled prominent moth (*Heterocampa guttivitta*) caterpillars during droughts that prevent trees from defending themselves against insects, and on a more regular 10–12 year cycle by the forest tent caterpillar (*Malacosoma americanum*) (Horsley *et al.* 2002). These defoliation events usually cause scattered tree mortality, especially to older trees with other health problems, but seldom cause extensive tree death at the landscape scale. Much more serious are growth losses and tree mortality after outbreaks of the common pine sawfly (*Diprion pini*). Defoliation by this late season feeder causes higher losses than herbivory by early season feeders, e.g. the European pine sawfly (*Neodiprion sertifer*). During severe outbreaks in Finland, approximately 500,000 ha were defoliated by *D. pini* resulting in high tree mortality and growth losses in the following year and later. Mortality rates in Europe after an outbreak are typically 4–24 percent and it can take 10 to 15 years for radial growth to recover (Lyytikäinen-Saarenmaa *et al.* 2003).

Grazing animals, especially ungulates like deer, elk and moose can regulate plant community composition and direct succession through their plant species preferences. Many ungulates in the temperate zone consume woody plants during winter and herbaceous plants during summer. If the deer to plant ratio is high, they can regulate the balance between relatively palatable and unpalatable plant species. The strength of these influences on composition is in turn embedded in a trophic cascade. For example, wolves in Wisconsin, USA create a patchy

distribution in deer density across the landscape, due to predation and deer avoidance of wolf pack territories. This in turn influences lushness, composition, and species richness of herbaceous plants (Callan *et al.* 2013).

Soil animals such as earthworms, beetles, and many other taxonomic groups (whether native or invasive), also influence plant community composition by altering the structure of the organic horizon, moving seeds to different layers within the soils, consuming seeds, and regulating water and nutrient cycles within the soils. There are considerable ecological cascades within the soil (Eisenhauer *et al.* 2009); for example, earthworms can change leaf-litter structure to favor or disfavor certain fungal species that in turn may be involved in symbiotic relationships with tree roots as mycorrhizas that help trees absorb nutrients, or with symbiotic relationships with seed germination, for example orchid seeds.

Conservation issues

Land use conversion, fragmentation, and harvesting

The temperate zone has historically had high human populations, especially in Europe and Asia, and for the last century in North America as well. Therefore, much of the forest has been converted to croplands and cities, and almost all that remains forested has been logged at least once. In Europe and Asia most forests have been logged multiple times and planted regeneration is used on a widespread basis to supplement natural regeneration after harvesting, while in North America most forests have been logged once or twice, and natural regeneration is much more common. In recent decades, the wildland–urban interface, an area with widely scattered isolated houses, has encroached on large tracts of forested land, creating numerous foci for introduction of invasive species, and fragmenting the landscape, favoring certain species that do well along forest edges. A very small amount of primary temperate forest remains as compared to tropical and boreal forest biomes, commonly less than 1 percent of the original forest (Frelich 2002). Most of these primary remnants have been identified by conservationists and set aside in well-known preserves. Some examples include Great Smoky Mountains National Park (Tennessee and North Carolina), Adirondack State Park (New York), Porcupine Mountains Wilderness State Park (Michigan), and Olympic National Park (Washington) in the USA, and Bialowieza Forest in Poland and Belarus. These primary forest remnants serve as templates for restoration of secondary forests, and as a baseline for the occurrence of ecosystem processes as compared to forests that are harvested. However, in many regions with thousands of years of human influence, no natural templates for restoration exist. In such cases a multi-disciplinary synthesis of historic records, silvicultural and paleoecological evidence may be needed to develop management techniques that mimic disturbances and other conditions needed to maintain the diversity of native tree species and smaller species dependent on them, and maintenance of certain cultural features of the landscape may also become a priority (Lindbladh *et al.* 2007).

Fragmentation manifested as small woodlands of a few to a hundred hectares surrounded by agricultural lands or cities, is common in the temperate forest biome throughout the eastern USA, Europe and Asia (Wilcove *et al.* 1986). This has led to conservation problems including: (1) facilitation of invasive plant species; (2) over populations of edge-loving native wildlife species such as deer and certain birds like the cowbirds (*Molothrus* spp.), which then parasitize nests of songbirds; and (3) potential inbreeding over time and loss of populations of many species. Island biogeography theory predicts that it is not possible to maintain as many species on a small fraction of the extent of forest that existed prior to deforestation and fragmentation. The term ‘extinction debt’ has been used to describe the situation where many species with

long lifespans still exist within fragmented landscapes, but are predicted to eventually go extinct (Tilman *et al.* 1994).

Overgrazing by ungulates and domestic livestock

Overgrazing is a common problem for maintenance of biodiversity and regeneration of trees (Côté *et al.* 2004). For example, in North America, white-tailed deer (*Odocoileus virginianus*) prefer seedlings of northern white cedar (*Thuja occidentalis*), yellow birch (*Betula alleghaniensis*), red oak (*Quercus rubra*), and hemlock (*Tsuga canadensis*) during winter, leading to widespread difficulties in regeneration of those species (Figure 3.5). This limits the ability of forest managers to direct succession towards desired tree species and to maintain species richness. During the growing season, deer prefer many herbaceous species in the families *Liliaceae* and *Orchidaceae*. Deer can drive succession to unpalatable trees such as beech (*Fagus grandifolia*) and understory species including ferns and sedges (*Carex* spp.) that are not favored or that can tolerate heavy grazing. Effects of deer overabundance in different parts of the temperate forest can be idiosyncratic. Sika deer (*Cervus nippon*) in Japan can prevent *Fagus* recruitment (rather than favoring it as in North America), but can also have similar effects on herbaceous vegetation as in North America, by favoring graminoids and ferns in the herbaceous vegetation layer (Takatsuki 2009). Lowering deer densities through hunting has been controversial since members of the public often equate more deer with a healthy ecosystem, and the effectiveness of hunting may become limiting in an increasingly urbanized world where relatively few people learn to hunt. Livestock such as cows can also cause similar problems if allowed to graze freely within woodlands without sufficient rotation to different areas throughout the growing season. Overgrazing may be a problem for national parks where plants as well as grazer populations are protected from human exploitation. For example, in the Bialowieza Forest National Park in Poland where the European bison (*Bison bonasus*) has been successfully restored after extinction in the wild at the beginning of the twentieth century, recent study has shown that consumption of trees and shrubs by bison increased with decreasing access to supplementary fodder, ranging from 16 percent in intensively fed bison to 65 percent in non-fed bison using forest habitats. Bison browsed mainly on *Carpinus*, *Corylus* and *Betula*, tree species of relatively low economic importance in the region, so that impacts on forestry may be relatively small. However, more investigation of bison impacts is needed to develop management plans to meet other objectives, such as maintaining plant diversity within the park and reducing damage to agriculture surrounding the park (Kowalczyk *et al.* 2011).

Invasive species

Intercontinental movements of temperate plant and animal species have occurred over the last few centuries, with accelerating rates of new introductions in recent decades corresponding to the larger human population and commercial trade in plants and animals (Kalusova *et al.* 2013). Some examples for plants invading mesic forests include: common buckthorn (*Rhamnus cathartica*), tatarian honeysuckle (*Lonicera tatarica*) and garlic mustard (*Alliaria petiolata*) have moved from Eurasia to North America, and black cherry (*Prunus serotina*), honey locust (*Gleditsia triacanthos*), black locust (*Robinia pseudoacacia*), and red oak (*Quercus rubra*) have moved from North America to Europe. Freed from competing species adapted to their presence, from leaf and seed-eating insects, from large herbivores that prefer them over other species, and from diseases in their native habitat, these invasive plants often become much more abundant on their new continent than their home continent, filling forest understories, reducing the



(a)



(b)

Figure 3.5 Forests dominated by *Tsuga* and *Acer* with low (a) and high (b) levels of deer browsing; note the large difference in abundance of *Tsuga* saplings. Photos: Jiri Schlaghamersky

abundance of native tree seedlings, and necessitating expensive management actions to remove them and/or to restore native species.

Invasive animals include the North American gray squirrel (*Sciurus carolinensis*) invading European forests where they displace the native red squirrel (*Sciurus vulgaris*), and the raccoon dog (*Nyctereutes procyonoides*) from Asia invading European forests (Genovesi *et al.* 2012). Earthworms as invasive species can have profound impacts on ecosystems around the world (Hendrix *et al.* 2008). A recent body of research shows that European earthworms in North America change soil structure, eliminating the organic horizon and increasing bulk density, making soils drier, depleting nutrients, and changing seedbed conditions (Hale *et al.* 2005, Resner *et al.* 2015). Ecological cascade effects include reduced tree growth, reduced native plant species richness, favoring a different suite of plant species, and facilitating invasive plant species that coevolved with the worms on their home continent (Nuzzo *et al.* 2009, Frelich *et al.* 2006, Larson *et al.* 2010).

Diseases and insect pests of trees moving from one continent to another have caused huge aesthetic, economic and habitat losses, wiping out tree species that are foundational to ecosystem function (Parry and Teale 2011). North America has been the recipient of many devastating tree pandemics including chestnut blight (*Cryphonectria parasitica*), Dutch elm disease (*Ophiostoma ulmi*), emerald ash borer (*Agrilus planipennis*), gypsy moth (*Lymantria dispar dispar*), balsam woolly adelgid (*Adelges piceae*), and hemlock woolly adelgid (*Adelges tsugae*). In combination, these pests and diseases have the capacity to greatly reduce the species richness of the tree canopy in eastern North American forests, with cascading ecological impacts on nutrient and light regimes, as well as physical structure of the forest habitat.

Climate change

The temperate forest is projected to shift to the north 200–700 km by the end of the twenty-first century, depending on local and global magnitude of warming (Galatowitsch *et al.* 2009). Two types of progression are likely to occur: warm–dry scenarios, and warm–wet scenarios. Warm–dry scenarios will likely lead to increases of oak, pine, and grass species at the expense of mesic species as the environmental niche of mesic species shrinks. This is likely to occur in mid-continental temperate forests adjacent to grassland biomes. Significant drought stress and mortality of temperate trees are expected. The second, warm–wet scenarios, would be much less stressful for most tree species, and would allow for gradual replacement of existing species with species from further south. Invasions of savanna and grasslands into mesic forest, and subtropical forest into temperate forest, are likely within several hundred kilometers of the southern margin of the northern temperate forest biome. At the same time, at the northern margin, temperate forest is likely to invade the southern boreal forest, at first forming a wider mixed temperate–boreal ecotone, as temperate species are freed from limitation of extreme winter cold and/or short summers, and later on decline of boreal tree species as warm temperature thresholds for those species are crossed.

A number of factors are likely to interact with climate change, including invasive species, deer grazing, insects, wind storms, fires, and fragmentation (Frelich and Reich 2010). Invasive species, which as a group are generally tolerant of a wide variety of climates and disturbances, have abundant seed production and long-distance dispersal, therefore giving them an advantage in a rapidly changing forest community. Deer preference for grazing on certain species of tree seedlings could either oppose climate-induced change (e.g. by consuming temperate maple and oak seedlings, but not spruce and fir seedlings at the temperate–boreal ecotone, retarding temperate invasion into boreal stands), or exacerbate climate-induced change (e.g. consuming

oak seedlings along the prairie–forest border, reinforcing the movement of grasslands into temperate forest). In the first decade of the twenty-first century, several consecutive years of severe drought and heat stress that occurred in most European countries caused deterioration of *P. abies* stands, predisposing them to catastrophic bark beetle infestation (Przybył *et al.* 2008). Reconstructions of surface temperature for Europe in the last 1,500 years has shown that the late twentieth and early twenty-first century European climate is very likely warmer than that of any time during the past 500 years (Luterbacher *et al.* 2004). Therefore, this episode of drought and insect damage is a harbinger of future impacts of a warming climate. A warmer climate with higher evaporation and more erratic precipitation is likely to lead to more fires over much of the temperate forest, which will potentially increase the proportion of early-successional (e.g. *Betula*, *Populus*, *Quercus*, *Pinus*) forests on the landscape, and alter the dynamics of tree species migration. In large swaths of the northern temperate forest that are highly fragmented, movement of species to the north to respond to climate change will be hindered; there are a large number of species with very limited dispersal distances and long establishment times, for example the previously mentioned myrmecochorus plant species. Forest managers and the public will have to decide whether to employ the controversial practice of assisted migration for such cases (Buma and Wessman 2013).

Forest scientists and managers of forests in commercial and natural area settings face many challenges in the temperate forest biome. In a biome where climate change, overgrazing, invasive species, and fragmentation are pervasive, creative research, comparison of remnant natural forests with commercial forests, and development of adaptive management techniques, will be paramount in order to allow continued existence of productive forests capable of maintaining ecological function and native species diversity.

References

- Augusto, L., Ranger, J., Binkley, D., and Rothe, A. (2002) 'Impact of several common tree species of European temperate forests on soil fertility' *Annals of Forest Science*, vol. 59, pp. 233–253
- Beatty, S.W., and Stone, E.L. (1986) 'The variety of soil microsites created by tree falls' *Canadian Journal of Forest Research*, vol. 16, pp. 539–548
- Brisson, J., Bergeron, Y., Bouchard, A. and Leduc, A. (1994) 'Beech-maple dynamics in an old-growth forest in southern Quebec, Canada' *Ecoscience*, vol. 1, pp. 40–46
- Buma, B., and Wessman, C.A. (2013) 'Forest resilience, climate change, and opportunities for adaptation: A specific case of a general problem' *Forest Ecology and Management*, vol. 306, pp. 216–225
- Callan, R., Nebbelink, N.P., Rooney, T.P., Wiedenhoef, J.E., and Wydeven, A.P. (2013) 'Recolonizing wolves trigger a trophic cascade in Wisconsin (USA)' *Journal of Ecology*, vol. 101, pp. 837–845
- Côté, S.D., Rooney, T.P., Tremblay, J-P, Dussault, C.D., and Waller, D.M. (2004) 'Ecological impacts of deer overabundance' *Annual Review of Ecology and Systematics*, vol. 35, pp. 113–147
- Eisenhauer, N., Schuy, M., Butenschoen, O., and Scheu, S. (2009) 'Direct and indirect effects of endogeic earthworms on plant seeds' *Pedobiologia*, vol. 52, pp. 151–162
- Finegan, B. (1984) 'Forest succession' *Nature*, vol. 312, pp. 109–114
- Fisichelli, N.A., Frelich, L.E. and Reich, P.B. (2014) 'Temperate tree expansion into adjacent boreal forest patches facilitated by warmer temperatures' *Ecography*, vol. 37, pp. 152–161
- Frelich, L.E. (2002) *Forest dynamics and disturbance regimes*, Cambridge University Press, Cambridge, England
- Frelich, L.E. and Reich, P.B. (2010) 'Will environmental changes reinforce the impact of global warming on the prairie–forest border of central North America?' *Frontiers in Ecology and Environment*, vol. 8, pp. 371–378
- Frelich, L.E., Calcote, R.R., Davis, M.B. and Pastor, J. (1993) 'Patch formation and maintenance in an old growth hemlock–hardwood forest' *Ecology*, vol. 74, pp. 513–527

- Frelich, L.E., Hale, C.M., Scheu, S., Holdsworth, A., Heneghan, L. and others (2006) 'Earthworm invasion into previously earthworm-free temperate and boreal forests' *Biological Invasions*, vol. 8, pp. 1235–1245
- Galatowitsch, S., Frelich, L.E. and Phillips-Mao, L. (2009) 'Regional climate change adaptation strategies for biodiversity conservation in a midcontinental region of North America' *Biological Conservation*, vol. 142, pp. 2012–2022
- Genovesi, P., Carnevali, L., Alonzi, A., and Scalera, R. (2012) 'Alien animals in Europe: updated numbers and trends, and assessment of the effects on biodiversity' *Integrative Zoology*, vol. 7, pp. 247–253
- George, M.F., Burke, M.J., Pellett, H.M. and Johnson, A.G. (1974) 'Low temperature exotherms and woody plant distribution' *Hortscience*, vol. 9, pp. 519–522
- Gomez, C. and Espadaler, X. (1998) 'Myrmecochorous dispersal distances: a world survey' *Journal of Biogeography*, vol. 25, pp. 573–580
- Hale, C.M., Frelich, L.E., Reich, P.B., and Pastor, J. (2005) 'Effects of European earthworm invasion on soil characteristics in northern hardwood forests of Minnesota, USA' *Ecosystems*, vol. 8, pp. 911–927
- Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V. and others (1986) 'Ecology of coarse woody debris in temperate ecosystems' *Advances in Ecological Research*, vol. 15, pp. 133–302
- Hedin, L.O., Armesto, J.J. and Johnson, A.H. (1995) 'Patterns of nutrient loss from unpolluted, old-growth temperate forests: Evaluation of biogeochemical theory' *Ecology*, vol. 76, pp. 493–509
- Heinselman, M.L. (1981) 'Fire and succession in the conifer forests of northern North America', in D.C. West, H.H. Shugart, and D.B. Botkin (eds), *Forest Succession, Concepts and Application*, Springer-Verlag, New York
- Hendrix, P.F., Callahan, M.A., Jr., Drake, J.M., Huang, C-Y., James, S.W. and others (2008) 'Pandora's box contained bait: the global problem of introduced earthworms' *Annual Reviews of Ecology and Systematics*, vol. 39, pp. 593–613
- Horsley, S.B., Long, R.P., Bailey, S.W., Hallett, R.A. and Wargo, P.M. (2002) 'Health of eastern North American sugar maple forests and factors affecting decline' *Northern Journal of Applied Forestry*, vol. 19, pp. 34–44
- Hougnér, C., Colding, J. and Söderqvist, T. (2006) 'Economic valuation of a seed dispersal service in the Stockholm National Urban Park, Sweden' *Ecological Economics*, vol. 59, pp. 364–374
- Johnson, W.C. and Webb III, T. (1989) 'The role of blue jays (*Cyanocitta cristata* L.) in the post-glacial dispersal of fagaceous trees in eastern North America' *Journal of Biogeography*, vol. 16, pp. 561–571
- Kalusova, V., Chytrý, M., Kartesz, J.T., Nishino, M. and Pyšek, P. (2013) 'Where do they come from and where do they go? European natural habitats as donors of invasive alien plants globally' *Diversity and Distributions*, vol. 19, pp. 199–214
- Kowalczyk, R., Taberlet, P., Coissac, E., Valentini, A., Miquel, C. and others (2011) 'Influence of management practices on large herbivore diet—Case of European bison in Białowieża Primeval Forest (Poland)' *Forest Ecology and Management*, vol. 261, pp. 821–828
- Larson, E.R., Kipfmüller, K.F., Hale, C.M., Frelich, L.E., and Reich, P.B. (2010) 'Tree rings detect earthworm invasions and their effects in northern hardwood forests' *Biological Invasions*, vol. 12, pp. 1053–1066
- Lindbladh, M., Brunet, J., Hannon, G., Niklasson, M., Eliasson, P. and others (2007) 'Forest history as a basis for ecosystem restoration. A multidisciplinary case study in a south Swedish temperate landscape' *Restoration Ecology*, vol. 15, pp. 284–295
- Lorimer, C.G. (1980) 'Age structure and disturbance history of a southern Appalachian virgin forest' *Ecology*, vol. 61, pp. 1169–1184
- Luterbacher, J., Dietrich, D., Xoplaki, E., Grosjean, M. and Wanner, H. (2004) 'European seasonal and annual temperature variability, trends, and extremes since 1500' *Science*, vol. 303, pp. 1499–1503
- Lyytikäinen-Saarenmaa, P., Niemelä, P., and Annila, E. (2003) 'Growth responses and mortality of Scots Pine (*Pinus sylvestris* L.) after a Pine Sawfly outbreak' *Proceedings: IUFRO Kanazawa 2003—Forest Insect Population Dynamics and Host Influences*, pp. 81–85
- Myczko, Ł., Dylewski, Ł., Zduniak, P., Sparks, T.H., Tryjanowski, P. (2014) 'Predation and dispersal of acorns by European Jay (*Garrulus glandarius*) differs between a native pedunculate oak (*Quercus robur*) and an introduced northern red oak (*Quercus rubra*) in Europe' *Forest Ecology and Management*, vol. 331, pp. 35–39
- Nuzzo, V.A., Maerz, J.C., and Blossey, B. (2009) 'Earthworm invasion as the driving force behind plant invasion and community change in northeastern North American forests' *Conservation Biology*, vol. 23, pp. 966–974

- Parry, D. and Teale, S.A. (2011) 'Alien invasions: the effects of introduced species on forest structure and function', in J.D. Castello and S.A. Teale (eds), *Forest Health, an integrated perspective*, Cambridge University Press, Cambridge, England
- Payette, S., Filion, L. and Delawaide, A. (1990) 'Disturbance regime of a cold temperate forest as deduced from tree-ring patterns: the Tantaré Ecological Reserve, Quebec' *Canadian Journal of Forest Research*, vol. 20, pp. 1228–1241
- Peel, M.C., Finlayson, B.L., and McMahon, T.A. (2007) 'Updated world map of the Köppen-Geiger climate classification' *Hydrology and Earth System Sciences*, vol. 11, pp. 1633–1644
- Przybył, K., Karolewski, P., Oleksyn, J., Łabędzki, A. and Reich, P.B. (2008) 'Fungal diversity of Norway spruce litter: effects of site conditions and premature leaf fall caused by bark beetle outbreak' *Microbial Ecology*, vol. 56, pp. 332–340
- Reich, P.B. and Oleksyn, J. (2004) 'Global patterns of plant leaf N and P in relation to temperature and latitude' *Proceedings of the National Academy of Sciences of the United States of America*, vol. 101, pp. 11001–11006
- Resner, K., Yoo, K., Sebestyen, S.D., Aufdenkampe, A., Hale, C. and others (2015) 'Invasive earthworms deplete key soil inorganic nutrients (Ca, Mg, K, and P) in a northern hardwood forest' *Ecosystems*, vol. 18, pp. 89–102
- Runkle, J.R. (1982) 'Patterns of disturbance on some old-growth mesic forests of eastern North America' *Ecology*, vol. 63, pp. 1533–1546
- Sabine, C.L., Heimann, M., Artaxo, P., Bakker, D.C.E., Chen, C.T.A., Field, C.B., Gruber, N. and LeQuéré, C. (2004) 'Current status and past trends of the global carbon cycle', in C.B. Field and M.R. Raupach (eds), *The Global Carbon Cycle: Integrating Humans, Climate, and the Natural World*, SCOPE 62, Island Press, Washington DC
- Svenning, J.-C. and Skov, F. (2005) 'The relative roles of environment and history as controls of tree species composition and richness in Europe' *Journal of Biogeography*, vol. 32, pp. 1019–1033
- Takatsuki, S. (2009) 'Effects of sika deer on vegetation in Japan: A review' *Biological Conservation*, vol. 142, pp. 1922–1929
- Tamm, C.O. (1991) *Nitrogen in Terrestrial Ecosystems, Questions of Productivity, Vegetational Changes, and Ecosystem Stability*, Springer-Verlag, Berlin
- Tilman, D., May, R.M., Lehman, C.L. and Nowak, M.A. (1994) 'Habitat destruction and the extinction debt' *Nature*, vol. 371, pp. 65–66
- Whittaker, R.H. (1975) *Communities and Ecosystems. 2nd Edition*, MacMillan, New York
- Wilcove, D.S., McLellan, C.H. and Dobson, A.P. (1986) 'Habitat fragmentation in the temperate zone', in M. Soulé (ed.) *Conservation Biology, the Science of Scarcity and Diversity*. Sinauer Associates, Sutherland, Massachusetts, USA
- Wozniwoda, B., Kopeć, D., Witkowski, J. (2014) 'The negative impact of intentionally introduced *Quercus rubra* L. on a forest community' *Acta Societatis Botanicorum Poloniae*, vol. 83, pp. 39–49
- Yamamoto, S., Nishimura, N., and Matsui, K. (1995) 'Natural disturbance and tree species coexistence in an old-growth beech – Dwarf bamboo forest, southwestern Japan' *Journal of Vegetation Science*, vol. 6, pp. 875–886
- Yoshida, N., and Ohsawa, M. (1996) 'Differentiation and maintenance of topo-community patterns with reference to regeneration dynamics in mixed cool temperate forests in the Chichibu Mountains, central Japan' *Ecological Research*, vol. 11, pp. 351–362