

Chapter 3

Forest Arthropod Diversity



Christian Hébert

3.1 Introduction

Insects are the most diverse group of organisms on Earth with 952,794 described species (Roskov et al. 2021). They account for 85% of arthropod species, 67% of animal species and 47% of all species currently known on the planet (Roskov et al. 2021) (Fig. 3.1). However, this is an underestimate as the number of species of insects and other arthropods living on Earth is still unknown. More than 30 years ago, Robert May published a paper entitled “*How many species are there on Earth*” and concluded that the number of species living on Earth was not even known within an order of magnitude (May 1988). The most recent estimates of richness suggest that there are approximately 5.5 and 7 million species of terrestrial insects and arthropods, respectively (Stork 2018). This suggests that over 80% of species remain to be found and described. Although knowledge of the diversity of species present is fundamental information for managing natural ecosystems, determining the number of insect or arthropod species existing on Earth, in a biome or in any forest habitat is a great challenge for scientists. It is concerning to realize that forest ecosystems are managed without accurate knowledge of the diversity involved in the ecological processes critical to healthy forest ecosystems.

3.1.1 Plant–Insect Coevolution as a Driver for Diversification

Arthropods have existed on Earth for at least 400 million years and they are among the earliest animals known to have colonised terrestrial habitats, where they have co-evolved with plants (Grimaldi and Engel 2005). Insects arose before the Devonian,

C. Hébert (✉)

Canadian Forest Service, Laurentian Forestry Centre, Québec City, QC, Canada

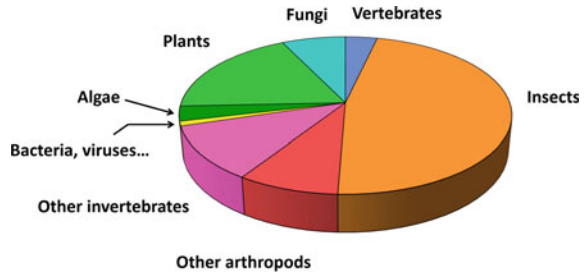
e-mail: christian.hebert@nrca-nrcan.gc.ca

© The Author(s) 2023

J. D. Allison et al. (eds.), *Forest Entomology and Pathology*,
https://doi.org/10.1007/978-3-031-11553-0_3

45

Fig. 3.1 Relative importance of major groups of organisms, based on a total of 2,026,387 described species, as of 10 June 2021. Data from the Catalog of Life website



from a Silurian aquatic arthropod (Gaunt and Miles 2002), after the first fossils of terrestrial plants were found from the Ordovician (Knoll and Nowak 2017) (Fig. 3.2). Fossil records showed that the first trees were recorded in the late Devonian and they diversified during the Carboniferous, which was followed by diversification of insects in the Late Carboniferous (Retallack 1997). Signs of attack by phytophagous arthropods have been recorded on fossil roots, leaves, wood and seeds, and the first wood boring Coleoptera were reported from the early Permian (Labandeira 2006). All phytophagous groups were present by the mid-Triassic; at this time, the dominant taxon was Coleoptera (Labandeira 2006). The type of leaf feeding revealed by fossils showed increasing complexity of interactions between arthropods and plants. For instance, the earliest leaves showed only marginal feeding while non-marginal leaf feeding, which requires specialized mouthparts, came later in the mid-Cretaceous after the arrival of angiosperms (Scott et al. 1992). Leaf-mining and gall production also coincided with plant diversification during the Cretaceous and Tertiary.

Today, plants (18.5%) and phytophagous insects (21.4%) represent about 40% of known terrestrial species. Also, it is estimated that at least one predacious or saprophagous insect species exists for every phytophagous insect species (Strong et al. 1984). Thus, globally, nearly 2 terrestrial species out of 3 depend on plants. This supports Ehrlich and Raven (1964) conclusion that “*the plant–herbivore interface may be the major zone of interaction responsible for generating terrestrial organic diversity*”. They suggested that the evolution of plant chemical defense in response to insect phytophagy resulted in a co-evolutionary arms race that generated high biodiversity in these two groups of organisms. However, it has been suggested that this coevolutionary arms race has been overemphasized and that deterrent effects of plant secondary chemicals for some phytophagous insects may have arisen from the need to avoid plants on which they were easily found by predators (Bernays and Graham 1988). In fact, coevolution is extremely difficult to demonstrate as it involves reciprocal adaptive changes in interacting species and this change must result from selection exerted by the other species (Thompson 1994). Nevertheless, the concept of coevolution between plants and phytophagous insects has been generally accepted as the basis of arthropod diversity (Janz 2011). Plant diversity was also shown to be a powerful predictor of the richness of other arthropod guilds (Basset et al. 2012).

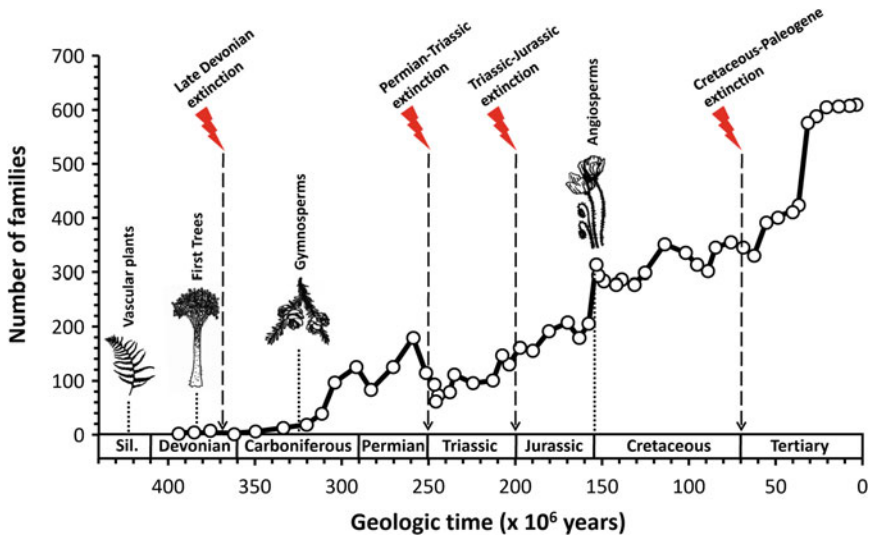


Fig. 3.2 Insect diversity, expressed as the number of insect families along Geological Time. Four major extinction events and the onsets of major groups of plants are highlighted. The geologic time events are from Figure 1 in Condamine et al. (2016) (reprinted with permission from Springer). The curve comes from Labandeira and Sepkoski (1993) (reprinted with permission from AAAS). Plant drawings were done by Jean-Michel Béland from the Canadian Forest Service (reprinted with permission from Jean-Michel Béland)

3.1.2 Wood as a Distinctive Forest Attribute and a Powerful Driver for Diversification

The most distinctive feature of trees comes from their vertical structure, which result from woody tissues that provide the mechanical support to permit their vertical growth. This allows trees to outcompete herbaceous plants and shrubs for light and produce the greatest amount of biomass among vascular plants. The resource abundance hypothesis suggests that plants offering greater amounts of resources should support more species and higher abundance of arthropod herbivores (De Alckmin Marques et al. 2000). The great aboveground biomass produced in forests may thus explain why these biotopes support so many species. Trees also tend to house more pest species than shrubs, which in turn have more than herbs (Strong and Levin 1979). Morphologically complex hosts provide diverse ecological niches and larger hosts are easier to find by arthropods. The greater size and morphological complexity of trees compared with shrubs and herbs likely explains the higher number of pest species on trees.

The structural heterogeneity of forests is both vertical, and horizontal, particularly in primary forests where closed areas alternate with clearings, which occur when trees die (Kuuluvainen 1994). Although forest ecosystems are often perceived as homogeneous at large scales, at smaller scales, forests show important horizontal

heterogeneity. Closed-canopy areas alternate with forest gaps resulting from tree death. In forest gaps, local abiotic conditions differ from those in closed canopy areas (Ritter et al. 2005). These gaps influence forest dynamics and provide a succession of microhabitats that promote biodiversity. Abiotic variables interact with biotic variables such as tree species, tree size and bark thickness to provide ecological niches to arthropods. For instance, vertical segregation of bark beetles has been reported in *Pinus taeda* (Paine et al. 1981) and *Pinus strobus* (Price 1984). The largest species (genus *Dendroctonus*) are found at the tree base while the smallest ones (genus *Ips*) are found higher on the bole and even in the canopy where species such as *Pityogenes hopkinsi* feed on small branches (Price 1984). Beetles compete for limited resources (phloem) and their interactions result in partitioning resources within trees (Paine et al. 1981). This might be driven by bark thickness, as this attribute is important for explaining community composition of early-arriving beetles in recently dead Scots pine (Foit 2010).

3.1.3 Latitudinal Gradient of Arthropod Diversity

There is no complete inventory of arthropods in any biome or in any type of forest ecosystem. However, the latitudinal gradient theory predicts decreasing species richness with increasing latitude (Pianka 1966; Hillebrand 2004). Latitude is a surrogate for environmental gradients (e.g. temperature, insolation and precipitation) (Willig et al. 2003), which also vary with elevation. Tropical regions receive more solar energy and precipitation, so they should be more productive than temperate regions (Pianka 1966; Willig et al. 2003). Habitats showing greater plant species richness usually exhibit greater arthropod richness (Speight et al. 2008). In addition, glaciation events have had negative impacts on biodiversity in temperate regions, but they have not had similar effects in tropical regions (Willig et al. 2003). Also, the warmer climate and higher moisture levels in tropical regions are not only more favorable for the growth and survival of most plant species, but also for groups such as fungi on which arthropods feed. Similarly, the importance of temperature for biodiversity diversification has been highlighted along a 3.7 km elevation gradient at Mt. Kilimanjaro, Tanzania (Peters et al. 2016). Species richness of single taxa vary in complex distribution patterns along elevation, according to their tolerance limits to environmental gradients (Peters et al. 2016). Similarly, the Ichneumonidae (Hymenoptera), a family of parasitoid wasps, do not follow the usual latitudinal gradient of biodiversity, their diversity peaking at mid-latitudes (Janzen 1981; Skillen et al. 2000).

3.2 Feeding Guilds of Arthropods Living in Forests

Traditionally, arthropods are described taxonomically but they can also be described on the basis of their diet and functional role. Those that feed on living plants are generally called phytophagous (Bernays 2009), while those that feed on living animals are called zoophagous. The term saprophagous is used for organisms that feed on decaying plants or animals, but can also include feeding on fungi since they are often interlinked with decaying organic matter (Natural Resources Canada 2015). Combining functional roles and niches allows grouping arthropods among guilds, which are groups of species that exploit the same type of resources in a similar way (Root 1967). Guilds help to structure ecological communities (Simberloff and Dayan 1991) and will be used to describe arthropods living in forests.

3.2.1 *Phytophagous Arthropods*

Phytophagous arthropods can be grouped into guilds according to their feeding mode, the plant part they exploit and whether they feed internally or externally on the plant (Novotny et al. 2010). To illustrate the concept and give an overview of the taxonomic composition of various guilds, the 116 most damaging phytophagous arthropods attacking trees in Quebec, Canada, were classified according to their feeding behavior on different parts of trees (Hébert et al. 2017) (Table 3.1). Arthropods that feed on tree foliage are called phyllophagous and they mainly belong to a few higher orders of insects, which have been able to overcome the defenses of higher plants (Strong et al. 1984). This is one of the largest group of arthropods found on trees and the largest single group damaging trees (Ciesla 2011). Overall, 65% of the most important arthropods attacking trees in Quebec are foliage feeders and 70% of them are larvae from the orders Lepidoptera and Hymenoptera (mainly sawflies). Among Lepidoptera, the Tortricidae and Geometridae are the most important phyllophagous families, with 13 and 7 species out of 40 pest species of trees in Quebec, while among the Hymenoptera, the Diprionidae and Tenthredinidae account for 8 and 7 species. Other phyllophagous taxa belong to several families of Lepidoptera as well as to several families of Coleoptera and Hemiptera, which include leaf-miners, leaf-suckers and gall-makers. Hemiptera often feed on tree sap by inserting their piercing-sucking mouthparts into most tree tissues. They are most often hidden (Table 3.1) under scales or galls caused by a mechanical disruption of vascular tissues or a physiological reaction from the tree to insect saliva (Barbosa and Wagner 1989). Phyllophagous arthropods will be discussed in detail in Chapter 9 and other groups briefly presented here are treated in Chapters 13–16.

Phytophagous arthropods also include those that feed on woody tissues, which are dominated by Coleoptera (Table 3.1). Those feeding on nutrient-rich subcortical tissues (phloem and cambium) are called phloeophagous and most belong to Curculionidae/Scolytinae (see Chapter 10), which are highly host-specific, at least

Table 3.1 Number of phytophagous arthropod taxa of various orders and feeding exposed or hidden on different parts of trees in Quebec, Canada

Order	Leaves or needles		Shoots or twigs		Woody tissues		Total
	Exposed feeder	Hidden feeder	Exposed feeder	Hidden feeder	Exposed feeder	Hidden feeder	
Coleoptera	5 ^a	2 ^a		3 ^e	2 ^e	16 ^{b, c, d}	28
Diptera		3 ^f					3
Hemiptera	1 ^c	5 ^{e, f}	2 ^c	5 ^{e, f}		6 ^{e, f}	19
Hymenoptera	13 ^a	3 ^a				1 ^d	17
Lepidoptera	17 ^a	23 ^a		4 ^{b, h}		1 ^d	45
Prostigmata	1 ^c	2 ^f					3
Thysanoptera	1 ^a						1
Total	38	38	2	12	2	21	116

^{a-h}See Chapters 9–16

Source of data: Hébert et al. (2017)

at the family level (Novotny et al. 2010). Buprestidae and Cerambycidae also bore galleries under bark or at the wood surface. Some Scolytinae and Platypodinae, another subfamily of Curculionidae, belong to a group called ambrosia beetles, which bore into the sapwood and feed on introduced symbiotic fungi (see Chapter 11). Insects that bore into the sapwood and even into the xylem are called xylophagous (see Chapter 12). They have strong mandibles and the most distinctive species belong to Cerambycidae and Siricidae (Hymenoptera), which are much larger than Scolytinae. Among wood boring insects, carpenterworms (Lepidoptera: Cossidae) are exceptions as they belong to an order of predominately phyllophagous insects.

3.2.2 Zoophagous Arthropods

Three types of zoophagous arthropods exist:

1. Predators, adults or larvae (but not necessarily both stages for a species) hunt, attack, kill and feed directly on prey. Predators are generally not host specific and they are larger than their prey or attack them in large numbers (e.g. ants).
2. Parasites, feed on a host without killing it. Parasites are generally smaller than their host and they can live at the expense of both, invertebrates or vertebrates. They can feed externally (often occasionally, such as mosquitoes) or internally on the host. Many parasites have claws or hooks to grasp their host, and often have piercing-sucking mouthparts.
3. Parasitoids, free-living adults locate a host, deposit their eggs on or in it, and larvae feed on and kill the host at the end of their development. Generally, parasitoids are smaller than their host and are selective, attacking specific life stages of one or closely related species.

Zoophagous arthropods from several orders and families feed on phytophagous and saprophagous arthropods that live in different microhabitats (e.g. canopy, trunks, litter, etc.). For instance, ladybird beetles, syrphid flies and lacewings prey on aphids

and other insects in tree canopies while many carabid beetles and spiders are voracious predators of invertebrates on the forest floor. Ants can prey on various arthropods in the tree canopy or at the ground level. Most predators use an active hunting strategy but web-spinning spiders use a sit and wait hunting strategy in various vegetation strata (Michalko et al. 2019). In dead and dying trees, predators of phloeophagous and xylophagous insects belong to several beetle families, Cleridae and Monotomidae being the most well-known.

Parasitoids are a diverse group of insects with most species belonging to the Diptera and Hymenoptera. The Hymenoptera have received more attention than the Diptera and they exhibit sophisticated host selection behaviors which involve olfactory responses by adult parasitoids to specific semiochemicals emitted by hosts or by damaged plants (Godfray 1994; Stireman 2002). Host selection is less-well known in Diptera, but some search visually, responding to host movement, while their response to plant odors is generally weak (Stireman 2002). Most families of Hymenoptera use a parasitic mode of life and parasitic Hymenoptera could represent up to 20% of all insect species (Gaston 1991). However, at least 75% of the parasitic Hymenoptera had not yet been described in the early 1990's (Lasalle 1993). Recent estimates suggest that Hymenoptera may have 2.5–3.2 times more species than Coleoptera, and thus, could be the most speciose animal order (Forbes et al. 2018). The Ichneumonidae and Braconidae are probably the most diversified families of parasitoids but many poorly known families of micro-Hymenoptera are also important in regulating arthropod populations. The full spectrum of host specificity can be found in the Ichneumonidae, with species that attack a single host known for species of *Megarhyssa* (Pook et al. 2016) to the highly polyphagous *Itopectis conquisitor*, which attacks hundreds of Lepidoptera species (Townes and Townes 1960). Natural enemies will be further discussed in Chapter 6.

3.2.3 *Saprophagous Arthropods*

Saprophagous arthropods which feed on rapidly decaying vegetation such as dead leaves are called detritivorous while those feeding on slowly decaying vegetation such as woody debris are called saproxylophagous. With the notable exception of the ambrosia beetles, arthropods that feed on fungi are traditionally included in the saprophagous group as they often feed on a mixture of mycelium and dead leaves or wood. More technically, species feeding on the aerial and visible parts of fungi are called fungivorous while those which feed on non-visible parts of fungi are either mycetophagous if they feed on fungal mycelium in the soil/litter or mycophagous if they feed on molds (Natural Resources Canada 2015). Arthropods feeding on dead animals are called necrophagous with those feeding more specifically on feces being called coprophagous or scatophagous.

3.2.3.1 Soil and Litter Feeders

The soil fauna is usually split among three groups according to their size: microfauna, which include invertebrates of less than 0.2 mm (mainly nematodes) that live in the water present between soil particles, mesofauna (0.2–2 mm) to which belong Enchytraeidae (not arthropods), Collembola and Acari (both arthropods), and macrofauna (>2 mm diameter), which include large oligochaetes (earthworms), most insects and large arthropods such as Diplopoda and Chilopoda (Brussaard et al. 1997; Lavelle 1997). A well-illustrated synthesis on soil organisms and associated food webs is provided by Zanella et al. (2018).

Generally, mesofauna dominates northern coniferous forests while macrofauna dominates temperate deciduous and tropical forests (Shaw et al. 1991; Lal 1988). Densities of 1 million arthropods/m² have been reported in black spruce forest soils (Behan et al. 1978), with 200,000 arthropods/m² being common in Canadian soils (Marshall et al. 1982). Most Acari living in the soil belong to the suborder Cryptostigmata (formerly called oribatid mites), and can account for up to 90% of estimated biomass in coniferous soils (Shaw et al. 1991). Collembola living in humus are called endogenous while those living in the litter are called epigeous. Endogenous species measure less than 1 mm, have an elongate form, very small appendices and non-pigmented eyes while epigeous species are larger, often of globular form and have well-developed appendices and eyes (Dajoz 1998). Collembola and Acari are wingless but mobility is not a major issue for species feeding on predictable and abundant resources. Dipterous larvae are also abundant and diverse in forest soils, the most prevalent families being Sciaridae, Cecidomyiidae, Phoridae and Mycetophilidae (Hibbert 2010). Earthworms (Oligochaetes) account for the highest biomass among groups forming the macrofauna and are dominant in Mull humus of temperate deciduous forests with 5,300 mg/m², their biomass falling to 200 mg/m² in Mor humus (Shaw et al. 1991). In the latter forests, Diplopoda and Chilopoda are prevalent (Shaw et al. 1991), while in tropical forests, termites and ants play important roles, where they are dominant in arid and semi-arid regions while earthworms are mainly important in humid and subhumid regions (Lal 1988).

3.2.3.2 Dead Wood Feeders

Dead wood is the habitat of numerous saproxylic species, which are defined as “*species that are dependent, during some part of their life cycle, upon the dead or dying wood of moribund or dead trees (standing or fallen), wood-inhabiting fungi, or the presence of other saproxylic organisms*” (Speight 1989). There is overlap between arthropods feeding on woody tissues (Sect. 3.2.1) and dead wood, particularly among phloeophagous species (Stokland 2012). Most bark beetles (Scolytinae) and many longhorn beetles (Cerambycidae) feed on phloem of moribund trees, which are technically still alive. These beetles are early colonizers of dead wood and the resource remains suitable for them until the phloem dries up and the bark gradually comes off the wood. Xylophagous species include insects of several orders: Coleoptera

(mainly Cerambycidae), Hymenoptera (Siricidae), Lepidoptera (Cossidae, Hepialidae, Sesiidae) and Diptera (Tipulidae and Chironomidae). Many of these species mainly feed on fungal mycelium involved in wood decay. Species of several families of Coleoptera (e.g. Ciidae, Anobiidae, Tenebrionidae, Tetratomidae) also feed and reproduce in bracket fungi, which develop on dead trees, and usually with much higher levels of host specificity than those feeding on mushrooms (Jonsell and Nordlander 2004). Numerous species of various orders also live in tree hollows (Ferro 2018), which highlights the diversity of microhabitats associated with dead wood.

3.2.3.3 Dung and Carrion Feeders

Animals return organic matter to the ecosystem throughout their lives by the dung or feces they produce and also when they die through their carcasses. Small detritivorous arthropods (e.g. collembola and acari) feed on dead organic matter, which is often mixed with soil, fungi and bacteria, particularly in advanced stages of decomposition. Woodlice (Crustacea: Isopods), feed preferentially on feces produced by *Operophtera fagata* caterpillars, a Geometrid that feeds on beech (*Fagus sylvatica*), rather than on the beech litter itself (Zimmer and Topp 2002).

A specialised fauna composed of larger arthropods develop in vertebrate dung and carrion, with Scarabaeinae, a subfamily of Scarabaeidae, being the most prevalent group of coprophagous beetles. They are commonly called dung beetles and are widely distributed, although they are most diverse in tropical forests where their burying behavior has been widely studied (Braack 1987). Dung beetle larvae feed on the microorganism-rich liquid component of dung, mainly of mammals but also from other vertebrates or from rotting fruits, fungus and carrion (Nichols et al. 2008).

Another type of organic matter provided by vertebrate animals is carrion. Blowflies (Diptera: Calliphoridae) are usually the first to colonize new carcasses (Paula et al. 2016) but over 20 families of flies feed in vertebrate carcasses (Payne 1965). Flies have good flight ability, and have developed efficient host selection behavior primarily based on olfactory and visual stimuli associated with carcasses. Conversely, ants and beetles are typically generalists that exploit carrion opportunistically, have a more limited dispersal capacity and often use habitat features for orientation (Barton and Evans 2017).

The most common beetles feeding on carrion belong to the family Silphidae. In addition to feeding on carrion they also prey on other species exploiting carrion. There are two subfamilies of Silphidae with different biologies. More is known about the Nicrophorinae, or burying beetles, than about the Silphinae because of their unusual behavior. One of the most striking behaviors of burying beetles is their reproductive cooperation and the extended adult biparental care of their progeny (Scott 1998), which is not observed in Silphinae. Nicrophorinae breed and feed in small carcasses such as mice and birds (<300 g), while Silphinae breed and feed in large carcasses where they compete with blow flies (Dekeirsschieter et al. 2011). Adult Nicrophorinae use olfactory stimuli to locate carrion (Scott 1998). Vertebrate carcasses are rare and unpredictable spatially and temporally. Progeny care in burying

beetles may be an adaptation to maximize fitness in these habitats (Scott and Gladstein 1993). When a carcass is located, males and females work together to move it to a suitable environment and dig beneath it to bury the carcass and prepare it as food for their progeny (Scott 1998). Because of the low number of available carcasses, several adult pairs may converge on fresh carcasses. If a carcass is large enough to support reproduction by several adult pairs, burying beetles work cooperatively to bury the carcass. If the carcass is too small, intraspecific fights occur and only the winners will reproduce. The burial chamber varies from a simple depression under leaf litter up to 60 cm underground (Scott 1998). Burying the carcass protects it from fly colonisation (Suzuki 2000) and reduces detection by other competitors (Shubeck 1985; Trumbo 1994). Beetles remove feathers or hair, shape the carcass as a ball and take care of it through regular cleaning and depositing anal and oral anti-microbial secretions, which suppress fungal and bacterial growth (Suzuki 2001) and reduce rates of decomposition (Hoback et al. 2004). Eggs are laid nearby and the newly hatched larvae require parental care for feeding (Scott 1998). About 75 species belong to the genus *Nicrophorus*, which is only present in the northern hemisphere (Scott 1998).

3.3 Functional Roles and Ecosystem Services

Arthropods are involved in nearly all ecological processes that drive ecosystem functioning (Jones et al. 1994). However, they represent less than 0.2% of the total biomass on the planet, dwarfed by plants, microbes and fungi (Bar-On et al. 2018). Uncertainty exists whether they are important drivers of ecological processes or whether they play only minor roles (Schmitz et al. 2014; Yang and Gratton 2014). The functional importance of arthropods in ecological processes has primarily been assumed and not based on experimental work quantifying the value of these functions. The few studies that do exist have primarily been conducted in agroecosystems (Noriega et al. 2018).

Arthropods are primary (herbivores) and secondary (carnivores) consumers in the food chain and thus, they depend on the production of primary producers, mainly trees in forest ecosystems. Thus, biomass transformation of living and dead plants and animals appears to be the most important functional role of arthropods in forest ecosystems (Yang and Gratton 2014) and as a result, they are involved in nutrient cycling and energy fluxes. These important ecosystem services are critical to ensure forest productivity but they are often overlooked. Apart from this central role in ecosystem functioning, arthropods are also involved in promoting plant reproduction through pollination and seed dispersal. Combined with insects that kill trees over wide areas, which strongly modify environmental conditions, these phytophagous insects influence forest succession. Secondary consumers (predators and parasitoids) account for a large part of forest arthropod diversity (Strong et al. 1984) and they are instrumental in regulating food webs.

Noriega et al. (2018) defined ecosystem services as “*the beneficial functions and goods that humans obtain from ecosystems, that support directly or indirectly their quality of life*”. Arthropods provide ecosystem services in all categories recognized by the Common International Classification of Ecosystem Services (CICES), i.e. regulation and maintenance (pollination, biological control, recycling organic matter), provisioning and cultural services (Ameixa et al. 2018). Pollination, biological control, recycling organic matter, and food provisioning have been the most studied ecosystem services but arthropods also provide cultural services, whether they be religious, artistic or recreational (Noriega et al. 2018). The latter includes hunting, fishing and wildlife observation, activities in which insects, as food sources, are estimated to account annually for \$2.7 billion in USA alone (Losey and Vaughan 2006). Insects are also used in arts and crafts, as cultural icons or religious symbols, and are often associated with tourist destinations (e.g. the Monarch Butterfly Reserves in Mexico) (Schowalter et al. 2018).

Although arthropods play key roles in the regulation and maintenance of several ecosystem services, these roles are usually assumed and their value has rarely been quantified experimentally (Noriega et al. 2018). Losey and Vaughan (2006) were the first to estimate the economic value of ecosystem services provided by insects to be at least \$57 billion annually in the United States and this only considers four ecosystem services provided by “wild” and native insects, for which data were available: pollination, pest control, wildlife nutrition and dung burial.

3.3.1 *Regulating Primary Production*

Phyllophagous arthropods feed on highly nutritious tissues, which are the basis of tree photosynthesis, namely leaves (Vergutz et al. 2012) and needles (Moreau et al. 2003). A low rate of herbivory stimulates primary production in natural forests while a high rate suppresses it (Mattson and Addy 1975). Defoliation of mature trees increases sunlight penetration to understory trees and saplings, which typically increase their growth as competition for light from overstorey trees decreases (Mattson and Addy 1975). Moderate defoliation ($\leq 50\%$) from *Orgyia pseudotsugata* stimulates Douglas-fir growth (Alfaro and Shepherd 1991), compensating for losses of severely defoliated trees. Herbivory appears to reduce variation in primary production and helps maintain it at intermediate levels (Schowalter 2012). Indeed, phytophagous insects have been presented as “regulators” of forest primary production (Mattson and Addy 1975; Belovsky and Slade 2000; Schowalter 2012), but this should be considered over long time intervals (see Sect. 3.4.2).

3.3.2 *Decomposition and Nutrient Cycling*

3.3.2.1 *Insect Feces and Cadavers*

Phyllophagous insects contribute to the cycling of rich organic matter produced by trees. Their feces provide high quality but ephemeral nitrogen pulses to soils, which are rapidly recycled by soil biota and assimilated into the foliage, often within the same season (Belovsky and Slade 2000; Frost and Hunter 2007). Zimmer and Topp (2002) recognized a “fast nutrient cycle” for feces of phytophagous animals (sensu McNaughton et al. (1988) who studied vertebrate herbivory in African grasslands) and a “slow cycle” for leaf litter and wood decomposition (plant material). Indeed, microbial degradation of *Operophtera fagata* feces took approximately half the time of beech leaf litter in microcosms (Zimmer and Topp 2002). Moreover, the addition of woodlice (isopods) tripled the rate of mass loss for both feces and litter. In fact, meso and macrofauna often reingest their faecal pellets a few days after deposition (Hassall and Rushton 1982). They then absorb organic compounds that have been released by microbial activity (Lavelle 1997). This is considered as a type of mutualism and referred to as external rumen digestion (Swift et al. 1979). Internal rumen digestion also exists in earthworms, termites and, to a lesser extent ants, as they interact internally with micro-organisms to produce various organo-mineral structures (Lavelle 1997).

Phyllophagous insects also return nutrients to the detritus pool when they die (Gessner et al. 2010). For instance, during outbreaks, insect cadavers are a major pulse of resources for detritivorous communities. However, models of ecological processes rarely consider this resource. Indeed, many predators are in fact omnivores and predation rates are often inflated in food-web research while scavenging is largely underestimated (Wilson and Wolkovitch 2011). For instance, ants are active scavengers of entomopathogenic nematode-killed insects (Baur et al. 1998) and it has been estimated that they account for 52% bait removal in tropical rain forests (Griffiths et al. 2018). This is particularly important as no other scavenger group compensated when ants were excluded, indicating a low functional redundancy of this important ecological role. Ants are estimated to make up 25% of animal biomass in tropical forests (Hölldobler and Wilson 1990) and are recognised as ecosystem engineers (Folgarait 1998). In North American temperate forests, the 17-year periodical emergence of cicadas (*Magicicada* spp.) provides a massive addition of insect cadavers and this increases bacterial and fungal abundance by 12 and 28% respectively (Yang 2004). The herbaceous plant *Campanulastrum americanum* then produce 9% larger seeds, highlighting the reciprocal links between above and belowground components of the ecosystem. Cicadas have patchy distributions and these resource pulses generate spatial and temporal heterogeneity in ecosystems (Yang 2004).

3.3.2.2 Leaf Litter

Less than 10% of the foliage produced by trees is consumed by phytophagous arthropods, over 90% entering the detritus pool as leaf litter (Gessner et al. 2010). Standardized litter types used in 336 sites across 9 biomes, showed that litter quality explained 65% of the variability in the early stages of decomposition, climate only having a significant effect when data were aggregated at the biome scale (Djukic et al. 2018). A meta-analysis also carried out at the biome scale showed that abiotic conditions controlled decomposition in cold and dry (harsh conditions) biomes while soil fauna had an important role in warm and wet (mild conditions) biomes (García Palacios et al. 2013). In tropical ecosystems, climate is likely less important than soil macrofauna (González and Seastedt 2001).

Soils are usually classified according to their physical and chemical properties, but they are regulated by complex interactions among the soil biota (Brussaard et al. 1997; Barrios 2007; Schmitz et al. 2014). Decomposition of dead organic matter involves the physical fragmentation of dead organic matter through feeding by arthropods and other invertebrates. This increases the surface/volume ratio of dead organic matter, which enhances fungal and microbial activity, releasing nutrients and making them readily available to plants (Barrios 2007). The decomposition of dead organic matter by living organisms and the progressive incorporation of released nutrients into the pool available in soils is at the basis of forest primary production and thus central to forest ecosystem functioning (Swift et al. 1979). Nevertheless, dead organic matter is rarely considered in ecological models and when included, it is usually treated as a single resource (detritus) that does not vary. However, nitrogen content varies widely among different types of dead organic matter (Fig. 3.3) and decay rates increase with nitrogen content. For instance, dead wood takes decades to decompose (Harmon et al. 1986) compared to months or years for leaf litter and days or weeks for animal dung and carrion (Wilson and Wolkovitch 2011).

3.3.2.3 Dead Wood

Severe and repeated defoliation by phyllophagous insects often results in tree death over wide areas. Before dying, trees progressively weaken and become vulnerable to wood feeding insects called secondary insects as they usually colonize trees physiologically stressed by another agent. This has been observed during and after spruce budworm (Belyea 1952a, b; Régnier 2020) and hemlock looper outbreaks (Béland et al. 2019). Stressed trees may emit volatiles that are attractive to secondary insects (Faiola and Taipale 2020) and thus, the functional role of secondary insects in forest ecosystems is to accelerate death of weakened trees and initiate the process of wood decomposition. Secondary insects generate openings in forest stands and thus increase ecosystem heterogeneity and promote plant succession. As herbaceous plants, shrubs and tree seedlings compete for light and nutrients, it results in complex successional dynamics that characterize different forest types. In natural

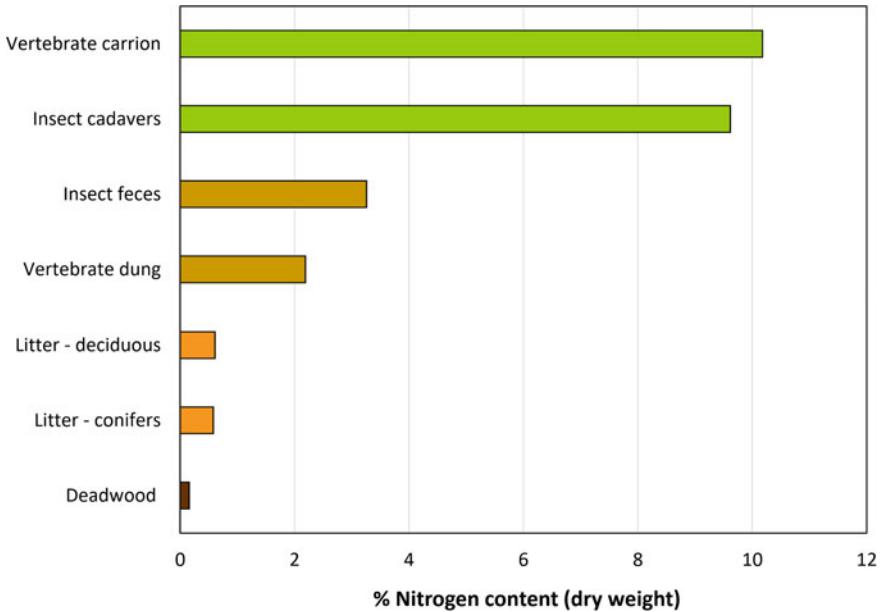


Fig. 3.3 Nitrogen content (% of dry weight) of various types of dead organic matter, both from animal and plant origin. Data from Parmenter and MacMahon (2009)—vertebrate carrion; Rafees (1971)—insect cadavers and insect feces; Holter and Scholtz (2007)—vertebrate dung; Taylor et al. (1989)—litter, deciduous and conifers; Piaszczyk et al. (2020)—deadwood

forest ecosystems, such dynamics also ensure continuity in dead wood stocks, which is important for maintaining diversity of saproxylic arthropods (Grove 2002).

The greatest amount of forest biomass is stored in woody tissues (Dajoz 1998) and thus wood decomposition after tree death is an important ecological process in forests (Harmon et al. 1986). Bark is a major physical barrier to the establishment of fungi, among which basidiomycetes are instrumental for decomposing the various structural components of wood (Strid et al. 2014). The first insects to colonize dying or recently dead trees are phloem feeders (Ulyshen 2016), and they bore holes through the bark to breed and feed on the nutritious phloem beneath the bark. Many woodboring insects transport fungi beneath the bark and their boring also provides access for fungi. Obligate insect-fungus mutualism increases the probability that fungi reach a suitable substrate (Birkemoe et al. 2018). Insects that have developed obligate-mutualisms with fungi, such as ambrosia beetles, are known to farm fungi within their galleries. These fungi possess wood-degrading enzymes which make essential nutrients from the wood available for insects. Similarly, the symbiotic fungi of wood wasps (Siricidae) serve as an “external rumen” for insects (Birkemoe et al. 2018). They produce enzymes that digest lignocellulosic compounds in the wood, which are then ingested by growing larvae (Thompson et al. 2014; Kukor and Martin 1983). According to Filipiak and Weiner (2014), wood-feeding insects are in fact fungivorous species or at least xylomycetophagous as their wood diet is supplemented with

fungi found in decaying wood. Without the essential nutritional elements provided by fungi, they estimated that the cerambycid *Stictoleptura rubra* would need between 40 (males) to 85 (females) years to develop into an adult.

Bark beetles also defecate under the bark, thus providing rich organic matter which contributes to fungal and microbial growth (Birkemoe et al. 2018). By feeding on the protein-rich subcortical tissues at the phloem/cambium interface and inoculating fungi, early colonizing bark beetles accelerate bark loss of dead trees (Ulyshen 2016), which is a type of insect-mediated ecosystem engineering (Birkemoe et al. 2018). Tunneling by wood-boring insects provides access into the xylem for fungi and improves aeration, which increases rates of decomposition (Dighton 2003). In temperate deciduous forests, bacterial and fungal densities increase with decay stages and reach their maximum during the “invertebrate channelization” stage. This stage occurs when logs are colonized by termites, carpenter ants and Passalid beetles which, as a community, can regulate the process of wood decomposition (Ausmus 1977).

A recent experimental study on the contribution of insects to forest deadwood decomposition, carried out in 55 sites on six continents, estimated that insects account for 29% of the carbon flux from deadwood, highlighting their functional importance in the process of wood decomposition (Seibold et al. 2021). Direct and indirect effects of insects accelerate decomposition in tropical forests but have weak positive or negative effects in temperate and boreal forests (Seibold et al. 2021). Termites and fungi are the most important determinant of wood decay in tropical regions while in temperate and boreal forests it appears to be moisture (González et al. 2008).

3.3.2.4 Vertebrate Dung and Carrion

By dispersing and incorporating vertebrate dung into the soil, dung beetles are involved in nutrient cycling, soil aeration, seed burial and parasite suppression. Several experimental studies have linked dung beetle effects on soil structure and nutrient content to increases in plant height and above-ground biomass (Nichols et al. 2008). Their activity increases soil porosity and soil water retention, which alleviates water stress on plants, even during a severe drought (Johnson et al. 2016). The effects of dung beetles on nutrient availability and ultimately plant growth may rival chemical fertilizers in agriculture. Further research is thus needed, particularly in tropical forests, where dung beetles can transfer mammal feces into the soil within a few hours (Slade et al. 2007).

Vertebrate carcasses do not provide major pulses but a rather low and steady supply of resources as it represents less than 1% of the overall nutrient budget of ecosystems (Hoback et al. 2020). However, locally, they significantly improve soil conditions. Carrion has a higher nutritional value than dung as the latter is composed of metabolic waste products and undigested remains of the original food (Frank et al. 2017). Vertebrate carrion decomposes faster than plant material as carrion N content (6–12%) is much higher than for plant litter (typically 1–2%) (Parmenter and MacMahon 2009). In tropical regions, blow flies can eat all soft-tissues of a carcass within four days during warm weather (Braack 1987). The decomposition of a carcass

produces an island of soil fertility, which increases stand heterogeneity. Soil nitrogen increases significantly under carcasses and large ones modify soil temperature, moisture and physical structure. Roots of neighboring plants that reach the modified soil area are influenced by these new micro-environmental conditions, which produce a “halo” effect (Parmenter and MacMahon 2009). Nutrients can be dispersed by insects, mainly ants and burying beetles, while bacteria and fungi may only increase nutrients in the soil under the carcass (Barton et al. 2013).

3.3.3 Seed Dispersal

Myrmecochory, or ant-mediated seed dispersal, is a widespread mutualistic interaction between ants and plants (Wenny 2001; Ness and Bressmer 2005). Seeds of myrmecochorous plants have lipid-rich appendages called elaiosomes, which are highly nutritious and attractive to ants (Ness and Bressmer 2005). Ant workers harvest seeds of these plants and bring them back to their nests. Unlike vertebrate frugivores which eat fruit pulp before dispersing seeds randomly, often far from the parent tree, ants typically disperse seeds over shorter distances but in more predictable and rich habitats, i.e. their nests (Wilson and Traverset 2000). The rich elaiosomes are then provided to the developing progeny and seeds are simply abandoned in the nest or discarded in middens outside the nest (Wenny 2001). This produces rich micro-environments where nutrient concentration is higher than in the surrounding soil, often resulting in higher rates of seed germination and seedling growth (Wenny 2001). It has also been suggested that ants could be responsible for seed arrival in rich and humid substrates favorable to seed germination and seedling growth, such as pits and rotting logs (Wenny 2001). By harvesting seeds, ants make them unavailable to vertebrates, lower the density of seeds beneath trees and, ultimately, increase seed germination rates and reduce competition among seedlings. Seed dispersal by ants is an important mechanism for increasing tree reproduction, particularly in tropical and temperate forests (Wilson and Traverset 2000).

3.3.4 Pollination

It has been estimated that 87.5% of angiosperms are pollinated by animals, ranging from 78% in temperate-zone communities to 94% in tropical ones (Ollerton et al. 2011). Most plants in tropical forests are pollinated by insects, with bees being the most important group of pollinators (Bawa 1990). Medium to large-sized bees are important in the forest canopy while small bees are prevalent in the subcanopy and understory (Bawa et al. 1985; Bawa 1990). Moths are the second most important pollinators in tropical forests, with sphinx moths being particularly active in the subcanopy (Bawa et al. 1985). Surprisingly, little is known about fly pollination in tropical forests (Bawa 1990). Bees dominate in tropical forests but flies outnumber

bees in both diversity and abundance as pollinators in cold regions (IPBES 2016). Although Diptera are known as the second most important order of insect pollinators, their role in pollination has been unappreciated (Larson et al. 2001; Orford et al. 2015). In recent years, concern has been expressed about the conservation of wild pollinators in North American forests and literature reviews have revealed significant knowledge gaps on forest pollinators (Hanula et al. 2016; Rivers et al. 2018).

3.3.5 *Top-Down Regulation of Phytophagous Arthropods*

Phytophagous arthropods experience strong selective pressures from the trees on which they feed (bottom-up pressure) and from organisms that feed on them (top-down pressure), including numerous invertebrate predators and insect parasitoids. A meta-analysis of the population ecology of phytophagous arthropods suggests that top-down forces have stronger effects than bottom-up forces, for chewing, sucking or gall-making arthropods (Vidal and Murphy 2018). Natural enemy communities can be complex and often overlap among arthropods. For example, the spruce budworm, *Choristoneura fumiferana* (Clemens) (Lepidoptera: Tortricidae) is an important pest of conifers in North America and part of a complex food web in which most parasitoids have at least two generations per year and need alternate hosts to complete their life cycle (Eveleigh et al. 2007). Requiring an alternate host limits the regulating potential of a parasitoid (Maltais et al. 1989), but parasitism by *M. trachynotus* was reported to increase up to 50% near the end of most outbreaks (McGugan and Blais 1959; Blais 1960). This may result from a slower development of the spruce budworm near the end of outbreak (Wilson 1973), which widens the window of availability of budworm larvae to parasitoids (Hébert 1989). Budworm larvae develop slower when they are affected by sublethal doses of a microsporidian (Bauer and Nordin 1989) or when they feed on needles with higher fiber content (Bauce and Hardy 1988), both of which become more common as outbreaks progress.

Egg parasitoids can be efficient natural enemies of phyllophagous insects but their importance for regulating pests has been overlooked in the past because of our poor knowledge of their biology and systematics (Anderson 1976). Some of the most efficient egg parasitoids of forest defoliating Lepidoptera belong to the genus *Telenomus* (Hymenoptera: Platygasteridae) (Anderson 1976; Bin and Johnson 1982; Hirose 1986; Orr 1988), which have contributed to the collapse of outbreaks of several lepidopteran pests (Hébert et al. 2001). These ecosystem services were overlooked for decades for the hemlock looper, *Lambdina fiscellaria* (Guenée) (Lepidoptera: Geometridae). A systematic study showed that previous identifications (*T. dalmani*) were incorrect and that three species were attacking the looper, one of these being new to science (Pelletier and Piché 2003). Moreover, most attacks were recorded in spring (50–100% parasitism), rather than fall ($\leq 3\%$) (Hébert et al. 2001). However, egg parasitism was estimated from fall eggs, when overwintering hemlock looper populations were sampled as part of control programs (Otvos and Bryant 1972; Otvos

1973; Hartling et al. 1991). Fall estimates only provided a partial estimate of egg parasitism.

Arthropod predators are also involved in the natural regulation of phytophagous arthropods, but they have been much less studied than parasitoids. However, Holling (1961) provided an excellent conceptual framework for the response of predators to prey species. The type II functional response, in which predators respond strongly to increasing prey density to a saturation level, is most common in predatory insects and parasitoids. The regulatory potential of predators then depends on the searching capacity and the attack rate but also involves handling and ingestion times. The behavior of a predator is thus important when evaluating its potential as a natural control agent. For instance, the carabid *Calosoma frigidum* Kirby kills more larvae of the spongy moth, *Lymantria dispar* L. (Lepidoptera: Erebidae) that it eats (Hébert 1983). Similarly, in Europe, an adult *Calosoma sycophanta* can annually kill up to 280 pine processionary moth larvae (Kanat and Mol 2008) or 336 larvae or pupae of the spongy moth (Dajoz 1998). This killing/feeding behavior is often observed in carabids when prey populations are abundant, and with their mobility, this makes them efficient predators of pest insects (Allen 1973).

Ants are omnivores but in some instances they were shown to be important primary predators of insect pests. They contributed up to 80% predation of prepupae of the spruce budmoth, *Zeiraphera canadensis* Mutuura and Freeman (Lepidoptera: Tortricidae), in young white spruce plantations in Quebec (Pilon 1965; Hébert 1990). They were opportunists as prepupae fall to the ground during about one hour each day in late afternoon for about one week. Once on the ground, prepupae rapidly wander through the litter to find a hidden location for pupation, 50% being no longer visible after 90s (Hébert 1990). Ants are social insects that use pheromone trails to rapidly locate food sources. This behavior explains their success in taking advantage of suddenly available resources.

Spiders are probably the most abundant and diverse group of generalist predators in terrestrial ecosystems and there is growing evidence that their communities play key roles in limiting arthropod populations (Riechert and Lockley 1984; Michalko et al. 2019). They consume up to 800 million metric tons of prey annually and they are also prey for other animals, attesting to their important functional role in food webs and ecological processes (Oxbrough and Ziesche 2013; Nyffeler and Birkhofer 2017). Spiders limit population growth of soil invertebrates and stabilize their populations (Clarke and Grant 1968) and through complex interactions with microarthropods, litter and fungi, they can slow down or speed up litter decomposition by preventing overgrazing of fungal populations (Lawrence and Wise 2004).

3.3.6 Food Provisioning and Medicines

Over 50% of bird food requirements are fulfilled by insects (Ollerton et al. 2011), but food provisioning to humans is another ecosystem service provided by forest insects for which interest is rapidly increasing. Historically, most insects consumed

by humans were harvested from trees or wood (Schabel 2010), attesting for the importance of forest conservation. Insects are 5 times more efficient than beef cattle at converting vegetation into tissues that can be consumed by others and as result, they could help reduce the human environmental footprint (Durst and Shono 2010). In addition to the nutritional value of insects, entomophagy could secure food supply for rural populations, reduce poverty and generate income (Schabel 2010). Entomophagy may need reduced pesticide use, reduced logging and thus favor biodiversity conservation of natural forests (DeFoliart 2005). For example, in the 1980's, the Native Paiute community succeeded in stopping US governmental agencies from spraying insecticides against Pandora moth caterpillars (*Coloradia pandora*), a Saturniid defoliator of pines, which is also a traditional food for this community (DeFoliart 1991). Edible Saturniid caterpillars are also of great value to indigenous cultures in Zambian forests, where the activity of harvesting caterpillars is ritually regulated (Mbata et al. 2002), attesting for the importance of this provisioning ecosystem service. In Thailand, forest insects are a preferred food source of local people, not just a cheap, nutritious and environmentally-responsible food source (Durst and Shono 2010).

Arthropods also have medicinal properties (Meyer-Rochow 2017). Recently, some novel antimicrobial anionic cecropins were found in the spruce budworm and could provide templates for the development of new anticancer drugs (Maaroufi et al. 2021). It has been suggested that systematic screening of forest insects would undoubtedly yield more species for entomophagy and medicine similar to bioprospecting in fungi and plants which has resulted in the identification of numerous new medicinal compounds.

3.4 Effects of Natural Disturbances on Forest Arthropods

Natural forests are dynamic ecosystems that always change as a result of tree growth and death and arthropods respond rapidly to these changes. Tree death is probably the most important mechanism for maintaining biodiversity in old forests as it produces gaps which increase light penetration to the forest floor and initiates succession (Watkins et al. 2017). Gap dynamics have been documented for both tropical and boreal forests and in both cases over 65% of the gaps were smaller than 100 m² (Brokaw 1982; Pham et al. 2004). Vegetation gradually recovers in these gaps and because gaps of varying sizes are added each year, they generate high levels of heterogeneity, especially in old-growth stands in which dead tree recruitment is continuous. In old-growth boreal forest, the richness of ground-dwelling beetles is best predicted by the composition component (i.e. number of tree species) of heterogeneity at the stand scale while richness of flying beetles is rather linked to the combined influence of structural (i.e. number of tree diameter classes) and compositional heterogeneity at both the stand and landscape scales (Janssen et al. 2009).

Forest ecosystems are also driven by stand-replacing natural disturbances which kill trees over large areas. They are caused by abiotic or biotic factors, which alter

Table 3.2 Comparison of conditions generated by abiotic and biotic disturbances for arthropods

	Abiotic disturbances	Biotic disturbances
Spatial and temporal predictability	<ul style="list-style-type: none"> • Can be forecasted few hours or days before the event 	<ul style="list-style-type: none"> • Can be forecasted several weeks or months before with efficient monitoring
Time duration	<ul style="list-style-type: none"> • Last few hours or days; kill most trees in a short period of time 	<ul style="list-style-type: none"> • Last months or years; kill trees progressively over a long period of time
Selectivity	<ul style="list-style-type: none"> • Affect all tree species to varying degrees 	<ul style="list-style-type: none"> • Affect only host tree species
	<ul style="list-style-type: none"> • Kill all types of trees, including healthy ones 	<ul style="list-style-type: none"> • Kill weak trees first, healthy ones dying only later
Soil disturbance	<ul style="list-style-type: none"> • Physically disturb soils 	<ul style="list-style-type: none"> • Do not physically disturb soils

environmental conditions and forest attributes in specific ways (Table 3.2) to which arthropod communities respond differently.

3.4.1 Abiotic Disturbances

Forest fires are probably the stand-replacing natural disturbance that has been most studied by forest ecologists and entomologists and contrary to popular belief, burned forests are not biodiversity deserts. For instance, the number of beetle species caught in recently burned boreal forests is more than twice that in unburned forests (Saint-Germain et al. 2004; Johansson et al. 2011). Certain insects have developed the ability to exploit recently burned trees, a resource that becomes available in large amounts after wildfire. Insects may be attracted to burned trees using cues coming from them (e.g. smoke). For example, the buprestid *Melanophila acuminata* uses paired pit sensory organs located on its mesothorax to detect infrared radiation (Evans 1964). This beetle may use these organs to locate burns from as far away as 5 km (Evans 1966). Moreover, this buprestid has antennal receptors that respond to methoxylated phenols released during the incomplete combustion of lignin (Schütz et al. 1999). Pyrophilic habits have been reported in several other insect orders: Hemiptera with *Aradus* (Aradidae) flat bugs (Wikars 1997a), Diptera with *Microsania* (Platypezida) smoke flies (Komarek 1969) and Lepidoptera with the Black Army Cutworm, *Actebia fennica* (Noctuidae) (Everaerts et al. 2000). Thus, several insects can take advantage of recently burned forests, making them unique habitats for specialised insect communities.

Not all beetles found in recently burned forest are “burned forest specialists” (Muona and Rutanen 1994) or “pyrophilic” species (Wikars 1997a, 2002; Saint-Germain et al. 2004). Some species found in recent burns are simply opportunists that take advantage of an abundant resource. For example, *Monochamus scutellatus*, which is abundant in burned trees, is also commonly found in trees stressed by insect

outbreaks (Régnier 2020), windthrows (Murillas Gómez 2013) and after logging (Bloin 2021). However, other species are closely associated with burned forests and are rarely found elsewhere. For instance, the small predator *Sphaeriestes virescens* LeConte (Coleoptera: Salpingidae) peaks one year postfire and then declines in abundance as time elapses (Jeffrey 2013). The Cerambycidae *Gnathacmaeops pratensis* (Laicharting), which is red-listed in Europe (as *Acmaeops pratensis*; Moretti et al. 2010) and rarely found in unburned boreal forests of eastern Canada, is also closely associated with wildfire. Unlike *S. virescens*, the strength of the relationship between *G. pratensis* and burned forests increases as time elapses (Boucher et al. 2012). Such species might become an interesting indicator of sustainable management in burned boreal forests (Boucher et al. 2016). The current hypothesis used to explain these pulses in insect populations is that forest fires generate optimal conditions for species associated with burns, and that these population increases could be important to maintain low insect populations in unburned forests until the next fire event. This suggests that species associated with burned forests have strong dispersal capacity as wildfires are stochastic unpredictable events (Wikars 1997b).

The bark provides efficient insulation against heat and phloem tissue often remains nutritious for many insects, particularly for trees with thick bark, or when burn severity is low to moderate (Cadorette-Breton et al. 2016). Indeed, burn severity is a determinant variable for predicting successful beetle colonization (Azeria et al. 2012; Boucher et al. 2012, 2016, 2020; Boulanger et al. 2010, 2013). Colonization by large numbers of phloeophagous and xylophagous insects is the first step in insect succession after a wildfire and it promotes secondary succession and wood decomposition (Boulanger et al. 2011). In the boreal forest, post-fire ant colonization of burned woody debris is positively related with woodborer boring activity and it influences decomposition as indicated by lower C:N ratios compared to uncolonized woody debris (Boucher et al. 2015).

Windthrow, another important abiotic disturbance, is less prevalent than fire in boreal forests but it is the most important driver of European temperate forest dynamics (Wermelinger et al. 2017). Climate change will likely favour more frequent and severe windstorms and as a result, windthrows will increase the amount of dead wood in forest landscapes. In addition to making dead wood available for arthropods, windthrows generate gaps which stimulate vegetation growth and promote the growth of flowering herbaceous plants that many saproxylic arthropods feed on to mature their eggs. Species assemblages differ between gaps and non-gap areas (Bouget and Duelli 2004), and twice as many species were found in windthrows than in undisturbed forests (Wermelinger et al. 2017). In Switzerland, during the first 10 years after a windthrow event, longhorn and buprestid beetles were 30–500 times more abundant and species richness was 2–4 times higher than in non-affected portions of the forest (Wermelinger et al. 2002). Overall arthropod richness increased by 17% and original species composition did not show any sign of recovery 10 years after the storm event (Duelli et al. 2002), indicating that windthrows initiate new successions that may have long lasting effects on biodiversity. Sun-exposed snags and large woody debris observed in windthrow gaps are rarely found in managed stands. In Sweden, where forests are managed intensively and dead wood has rarefied, 59%

of the 542 red-listed saproxylic invertebrates prefer sun-exposed sites (Jonsell et al. 1998). Windthrows also provide important habitat for wildlife including nesting sites for Megachilid bees (Warren and Key 1991) and shelter for many overwintering invertebrates (Alexander 1995). As windthrow provides abundant resources to saproxylics, it facilitates population growth and rare species can become more apparent (Wermelinger et al. 2002). Extensive windthrows have positive effects on the abundance of 20% of Swedish red-listed beetles and negative effects on only 4% (Berg et al. 1994).

Trees may be weakened by several agents among which drought is one of the most widely known. In many parts of the world, drought has become more frequent in recent decades, as a consequence of ongoing climate change (Moore and Allard 2011). By reducing root water uptake, drought induces stress for trees, mainly those which have shallow rooting systems. As a result, tree seedlings and saplings are much more vulnerable to drought than mature trees which have deeper rooting systems. Forest stands growing on shallow soils are also more susceptible to water deficits (Moore and Allard 2011). However, these general patterns may vary according to tree species. For example, after an extreme 4-yr drought in California, native bark beetles were instrumental in killing trees but important differences were noticed between tree species. Bark beetles killed mature pines regardless of their level of decline while the most affected firs were killed regardless of their age (Stephenson et al. 2018). Other extreme weather events linked with climate change will likely stress and weaken trees, making them more susceptible to secondary insects, including flooding and excessive rainfall that saturates poorly drained soils, leading roots to suffocate. Physical damage to roots or disturbances that interfere with water and nutrient uptake may result in tree dieback, thus increasing susceptibility and vulnerability to secondary insects.

3.4.2 *Biotic Disturbances*

Insect outbreaks are the most common biotic disturbance but their ecological impacts have received much less attention than their control. Like other types of disturbances, by killing trees, insect outbreaks influence forest structure and composition. Their impacts vary according to their severity, which in turn vary with forest composition (De Grandpré et al. 2018). These reciprocal interactions between forests and insect pests result, at the landscape scale, in forest mosaics with variable levels of heterogeneity. This is true in the boreal forest with the spruce budworm and the Mountain Pine Beetle, *Dendroctonus ponderosa* Hopkins (Coleoptera: Curculionidae) but also in temperate and Mediterranean forests where outbreaks from other species also occur but over smaller areas because of greater fragmentation of forest matrices. Tropical forests, previously thought to be free of outbreaks (Elton 1958), are also affected by insect outbreaks, but they are likely less frequent and extensive, as high tree diversity reduces risk (Dyer et al. 2012).

Few studies have documented the effects of biotic disturbances on insect communities. Those who did used flight interception traps 3 to 15 years after the outbreak.

Only weak responses have been reported from saproxylic beetles (Barnouin 2005; Vindstad et al. 2014). The impact of the two most damaging insect defoliators in Canada, the spruce budworm and the hemlock looper, differ. Both insects affect balsam fir but they produce different temporal patterns of tree mortality (Fig. 3.4). The spruce budworm feeds mainly on current-year foliage and tree mortality begins only after 4–5 years of heavy defoliation, following a progressive weakening of trees (MacLean 1980). Once tree mortality begins in a stand, it continues for up to a decade and even more (Taylor and MacLean 2009). On the other hand, hemlock looper larvae feed on needles of all age classes without eating them completely (Hébert and Jobin 2001; Iqbal and MacLean 2010). Affected needles then dry and fall in late summer-early fall. If trees are heavily defoliated, they may even die after a single year of defoliation (Fig. 3.5). As tree mortality is spread over a longer period during spruce budworm outbreak, the window of availability of suitable trees for secondary insects is much longer than during hemlock looper outbreaks. Greater diversity in arthropod communities is expected from disturbances that generate greater heterogeneity. For instance, the striped ambrosia beetle, *Trypodendron lineatum* (Olivier), was the only species to respond to balsam fir affected by the hemlock looper (Béland et al. 2019) while it was secondary to a melandryid, a sirex and another bark beetle in firs affected by the spruce budworm (Belyea 1952a, b; Régnier 2020).

The Cerambycid *Monochamus scutellatus* is also found in trees killed by the spruce budworm and the hemlock looper, but in much lower abundance than in trees killed by fire. The dominance of Cerambycidae, including *M. scutellatus*, in burned

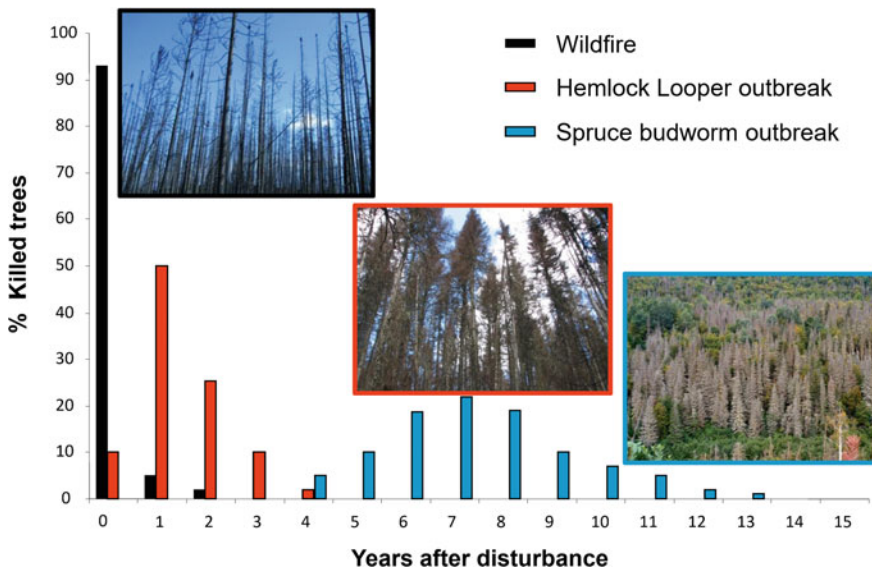


Fig. 3.4 Temporal patterns of tree mortality for three different natural disturbances in eastern Canada. Photos of insect outbreaks from C. Hébert and of wildfire from S. Bélanger (reprinted with permission of C. Hébert and S. Bélanger)



Fig. 3.5 Young stand of white spruce regenerating 20 years after a severe outbreak of the hemlock looper in an old-growth balsam fir stand on Anticosti Island. Photo from C. Hébert (reprinted with permission of *Le Naturaliste Canadien* and C Hébert)

trees, may be explained by the Jarman-Bell principle, a concept in herbivore nutritional ecology which states that the body size of herbivores is negatively correlated with diet quality (Steuer et al. 2014). After severe wildfire in boreal forests, large Cerambycidae dominate the habitat and small bark beetles are much less abundant. After insect outbreaks the reverse is true, suggesting that subcortical food quality might be poor after fire. Wood water content is a useful proxy for assessing food quality of subcortical tissues and it decreases with increasing fire severity (Cadorette-Breton et al. 2016). In trees recently killed by fire, water content is always below 30% (Jeffrey 2013; Cadorette-Breton et al. 2016) while it remains well-above 50% in trees defoliated by the spruce budworm (unpublished data). Even trees affected by non-lethal fires show phloem/cambium necrosis and misshapen xylem vessels, which lead to hydrolic dysfunction (Bar et al. 2019). On the other hand, defoliation induces a 20% reduction in the diameter of phloem channels, likely impacting sap transportation capability of trees and increasing the risk of vascular dysfunction (Hillbrand et al. 2019). Although defoliation reduces subcortical tissue quality, fire reduces it more extensively and more rapidly. Obviously, this influences the successional dynamics of saproxylic insect communities.

Bark beetles are also important pests of coniferous forests in many regions of the world (Morris et al. 2017). In western North America, the Mountain Pine Beetle has affected >27 M ha of mature forest stands and has had major impacts on forest ecosystem dynamics, biodiversity (Bunnell et al. 2011; Saab et al. 2014)

and ecosystem services (Dhar et al. 2016; Audley et al. 2020). The outbreak has increased diversity of understory plants and this certainly has affected arthropod communities, but this has not been documented. However, higher diversity of alpine bees was linked with the increased availability of floral resources in post-outbreak stands affected by the spruce beetle, *Dendroctonus rufipennis* Kirby (Davis et al. 2020), a similar species.

3.5 Effects of Forest Logging on Arthropods

Remote-sensing assessments showed that only 22% of the world's forest landscape was classified as intact in 2000 and had decreased to 20.4% between 2000 and 2013 (Potapov et al. 2017). Expansion of agriculture and pasture in tropical regions were responsible for 60% of this reduction. Old-growth forests have virtually disappeared from Europe (Wirth et al. 2009) and they have become rare in many parts of North America, mainly due to timber harvesting (Potapov et al. 2017; Schowalter 2017). Where they still exist, old-growth forests are often limited to small remnant areas which might not be representative of the original forest matrix.

3.5.1 Clear-Cuts

The first reported impacts of logging on biodiversity were associated with the widespread use of clearcutting which resulted in the loss and fragmentation of old-growth forests. From the perspective of biodiversity conservation, clear-cuts are inappropriate for maintaining some forest species (Spence 2001), particularly those which are closely associated with old-growth forests (Spence et al. 1996; Niemelä 1997; Siitonen and Saaristo 2000; Buddle et al. 2006; Pohl et al. 2007). Clear-cuts initiate forest succession and homogenize stand structure and composition for several decades, often over large areas, and thus rarify old-growth forest attributes, which are important drivers of arthropod diversity (Janssen et al. 2009). Moreover, intensive forestry has used short rotations in order to optimize wood production and avoid reaching the senescent forest stage in which a certain amount of trees die, i.e. when forests recover certain attributes characterizing old-growth forests.

In Scandinavia, where boreal forests have been managed intensively, the amount of dead wood has decreased to extremely low levels, severely impacting numerous saproxylic species (Kaila et al. 1997; Grove 2002; Stenbacka et al. 2010). In the late 1990s, nearly 70% of red-listed forest invertebrates were saproxylics (Jonsell et al. 1998). In Canada, mature balsam fir stands are usually harvested at 50 years of age as they are then highly vulnerable to the spruce budworm and also because they are considered to have reached their silvicultural maturity. Dead trees are rare in 50 year old balsam fir stands and short rotations could thus lead to a rarefaction of dead wood (Norvez et al. 2013). This is a first step towards breakage of forest

continuity, a concept which refers to the continuous availability of a certain amount of micro-habitats (e.g. dead wood) or appropriate conditions (e.g. close-canopy cover) to ensure survival of living organisms (Jonsell and Nordlander 2002). Populations of several saproxylic beetles are still less abundant in 50-yr post-harvest balsam fir stands than in older stands regulated by spruce budworm outbreaks (Bouchard 2000), suggesting that forest continuity in dead wood may be broken by short rotations. This may result in a subtle erosion of saproxylic insect diversity characterizing naturally disturbed forests (Norvez et al. 2013).

Arthropods with poor dispersal ability are particularly vulnerable to the loss of old-growth forests, to habitat fragmentation and to a breakage in forest continuity (Koivula 2002). Several carabid beetles, common in old-growth forests, persist temporarily in recent clear-cuts but they were scarce or had disappeared from stands by 27 years post-harvest in Alberta, Canada (Spence et al. 1996). In addition to drastically modified environmental conditions, old-growth specialists face competition from open-habitat species that heavily colonize clear-cut patches. The surrounding landscape is important as the impact of clear-cuts is lower in a matrix of old-growth boreal forest stands, highlighting the importance of source habitats for recolonizing harvested stands (Le Borgne et al. 2018). In heterogeneous landscapes, beetle community assembly is mainly driven by interspecific interactions rather than by habitat attributes (Le Borgne et al. 2018).

3.5.2 *Salvage Logging*

For economic and phytosanitary reasons, salvage logging after natural disturbances has become increasingly prevalent all over the world (Lindenmayer et al. 2008). A meta-analysis revealed that salvage logging significantly decreases species richness of saproxylic beetles, which is not surprising as habitat is removed (Thorn et al. 2018). It has been estimated that to maintain 90% of saproxylic beetle richness, 85% of these disturbed forests would need to be retained (Thorn et al. 2018). Richness of springtails also decreases after salvage logging, these micro-arthropods being very sensitive to the drying out of the soil following canopy and tree removal. However, richness of ground-dwelling spiders and carabids increase, many species of these groups being typically associated with open habitats (Thorn et al. 2018). Indeed carabid recovery is typically rapid with the retention of almost any disturbed patches in postfire forests (Koivula and Spence 2006).

As in clear-cutting, the impact of salvage logging lasts decades. For instance, habitat attributes still differ between unsalvaged and salvaged balsam fir stands, 20 years after the end of a spruce budworm outbreak (Norvez et al. 2013). As in most natural disturbances, insect outbreaks rarely kill all trees, survivors being important legacies in forest dynamics as they contribute to the maintenance of ecological continuity in dead wood recruitment. This legacy is illustrated through the larger amount and greater diversity of coarse woody debris in unsalvaged stands compared with salvaged ones (Norvez et al. 2013) (Fig. 3.6).

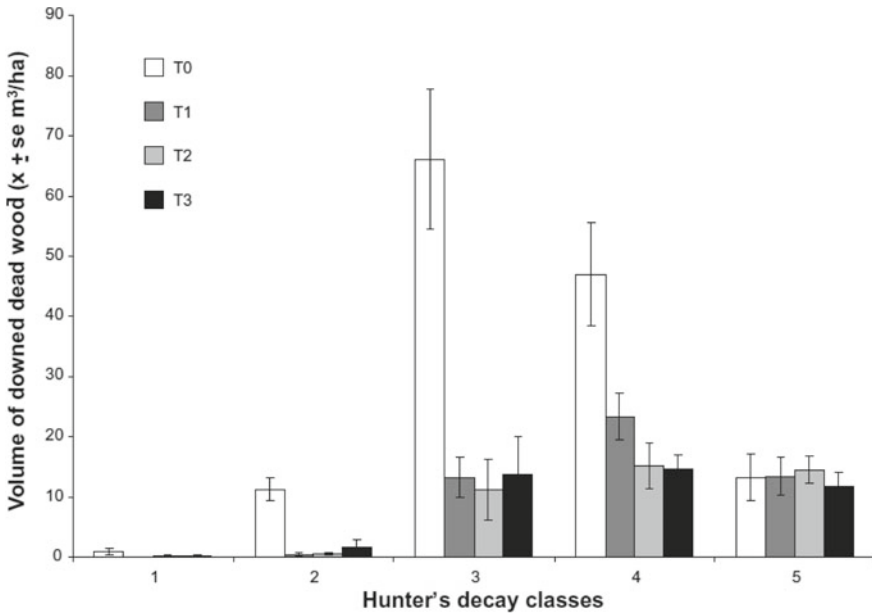


Fig. 3.6 Distribution of downed dead wood volumes according to Hunter's decay classes in four types of stands, 20 years after the end of a spruce budworm outbreak in balsam fir forest. T₀: unsalvaged stands, T₁: salvage logging only, T₂: salvage logging followed by a pre-commercial thinning, T₃: salvage logging followed by scarification and black spruce plantation and mechanical release. From Norvez et al. (2013) (reprinted with permission of Elsevier)

3.5.3 Partial Cuts

In recent years, partial cutting has been used as a more socially and environmentally acceptable silvicultural treatment than clear-cuts (Franklin et al. 1997; Harvey et al. 2002). Partial cutting removes only a portion of the trees (usually up to 45%) and thus, it maintains a forest cover useful for biodiversity. It also ensures a continuous recruitment of dead trees necessary to maintain unique elements of forest biodiversity, namely saproxylic organisms that only live in this habitat. These dead trees are also important components for generating heterogeneity in forest ecosystems and providing habitats for non-saproxylic organisms. By maintaining structural and compositional attributes of mature forests (Harvey et al. 2002), partial cuts limit landscape fragmentation (Warkentin and Bradshaw 2012) and maintain ecological functions of forest ecosystems. Partial cuts generate new niches that are absent in closed canopy forests, maintain similar amounts of snags and coarse woody debris as in closed canopy forests and as a result, beetle communities in partial cuts remain similar to those found in old-growth boreal forest (Légaré et al. 2011). Similarly, in Finland, the carabid assemblages of thinned (10–30% tree removal) and mature stands were similar (Koivula 2002). Partial cuts help to reduce the impact of logging on forest

ecosystems and have become a useful tool for implementing ecosystem-based forest management (see Sect. 3.6.2).

3.6 Conservation and Management

The concept of sustainable development defined by Brundtland (1987) has led to changes in forest management. Henceforth, development must meet the needs of the present without compromising the ability of future generations to meet their own needs. Applying this concept requires a better balance between economic, environmental and social issues. The importance of biodiversity conservation to achieve the environmental goal of sustainable development was recognized with the agreement of the Convention on Biodiversity signed after the Earth Summit in 1992 (United Nations 1992). The implementation of sustainable forest management then required different approaches to integrate the objective of maintaining biodiversity while continuing logging (Thorpe and Thomas 2007). Although in some rare cases single species are protected by regulations, conservation of arthropod diversity is usually approached globally. Protecting single species through regulation forbids their capture and trade, and sometimes protects their habitat. This approach has rarely been successful (Samways 2018). Conservation strategies now look at larger spatial scales. Developing resilient forest landscapes is an emerging field of interest in conservation biology, but preserving forest arthropods remains a challenge for scientists and policy-makers.

3.6.1 Protected Areas

The establishment of protected areas is the first measure proposed by conservation biologists to protect biodiversity as it maintains habitats (Jenkins and Joppa 2009; Samways 2007). It requires protecting large areas of primary forests, which are rapidly declining in tropical areas, and which are already small or strongly modified in most north-temperate areas (Samways et al. 2020). Also, as biodiversity is never fully inventoried, delimiting protected areas is usually based on surrogates (plant endemism, vegetation classification), which assume that this approach is efficient for protecting non-sampled and poorly known biodiversity, which include arthropods (Rodrigues and Brooks 2007). The use of vascular plant endemism to delineate hotspots of biodiversity is controversial (Marchese 2015), but it was shown to be efficient in protecting bush crickets (Orthoptera: Tettigoniidea) in South Africa (Bazelet et al. 2016). Also, an analysis of the efficacy of protected areas in Italy showed that 91% of the 150 red-listed saproxylic beetles were present (D'Amen et al. 2013). Foresters could consider it as a success while it could be viewed as a failure for conservationists as 9% of red-listed species are still absent. However, as the full extent of a species geographic range was captured for only 7% of these red-listed

species, the reserve network was considered inadequate to protect Italian saproxylic insect diversity (D'Amen et al. 2013). It is possible that protected areas designed to be representative of large-scale vegetation regions are less effective than a small-scale inventory of endemic plants. In addition, protected areas are often established on the basis of aesthetic criteria (e.g. spectacular landscapes), or for political reasons, which rarely meet biodiversity conservation objectives. Protected areas may also complicate political decisions related with land use planning, particularly when, without appropriate pest management, insect outbreaks may kill trees. Decisions regarding whether and how to manage protected areas to preserve biodiversity and sustain ecosystem services, usually involve public debate. In Germany, numerous trees died during a large-scale outbreak of *Ips typographus* but red-listed species populations increased as well as the overall biodiversity, providing support for the policy of allowing the natural course of natural disturbances in protected areas and promoting recovery processes that characterize post-natural disturbance successional stages (Beudert et al. 2015).

The ability of current networks of protected areas to protect biodiversity and ecological processes will undoubtedly be affected by changing climate. These areas are spatially fixed and may not host the same species in the future as climate change will cause range shifts or reductions for many species (Hannah et al. 2007). The functional connectivity between protected areas should be improved to enable species range expansion in response to climate change (Samways et al. 2020).

3.6.2 *Ecosystem-Based Forest Management*

The concept of ecosystem-based forest management aims to maintain forest ecosystems within their natural range of variability, using natural disturbance regimes as references, with the underlying idea that species should not experience conditions they never faced before (Hunter 1990). Natural processes that regulate forest ecosystem dynamics should be preserved, thus ensuring progress toward sustainable forest management (Attiwill 1994; Angelstam 1998; Bergeron et al. 1999; Gauthier et al. 2008).

Unlike natural disturbances, forest logging typically (in particular clear-cuts) reduces heterogeneity and the amount of dead wood for decades. Thus, adapting silvicultural practices so that managed forests more closely replicate natural forests has been, and continues to be, a major challenge for forest managers. Ecosystem-based forest management is primarily implemented by mimicking the spatial arrangement produced by natural disturbances in terms of size and distribution of logging patches. At the stand level, it attempts to maintain key structural elements produced by natural disturbances such as snags and coarse woody debris (Niemelä 1997; Harvey et al. 2002; Bauhus et al. 2009). It is difficult to mimic the conditions generated by natural disturbances with logging as tree harvesting reduces the future amount of dead wood in the forest while natural disturbances do the opposite. Dead wood still present after logging is almost entirely under the form of woody debris on the ground, where

it decays rapidly (Grove 2002). Thus, saproxylic organisms using snags lose their habitat and those that use dead wood on the ground will lose it soon after logging as decomposition progresses. It is possible to increase dead wood stocks by girdling trees (Dufour-Pelletier et al. 2020) or by leaving a certain amount of high stumps when stands are harvested (Jonsell et al. 2004). Supplementing them with logs of various tree species on the ground is recommended (Andersson et al. 2015). However, in western North America and in other dry regions of the world where wildfire is already a major issue, and likely to worsen with climate change, this approach should not be used as it would increase fuel loading. In these regions, silvicultural practices aimed to reduce fire risk by managing fuel loads is a critical forest management objective.

In areas where dead wood has rarefied, short-term measures aimed to increase the amount of dead wood must be accompanied by medium and long-term measures to avoid critical gaps in the continuity of deadwood (Grove 2002). Therefore, it is crucial to determine the minimum amount of dead wood, under various forms, necessary to maintain biodiversity along all post-harvest successional stages. This requires leaving enough live trees to ensure continuous recruitment of dead wood to avoid breakage of forest continuity. The retention of patches of varying sizes is now used in the context of ecosystem-based boreal forest management. In the short-term, 2.5 ha patches are efficient to maintain beetle communities in boreal forest but negative effects could increase with time (Bouchard and Hébert 2016), highlighting the importance of long-term studies.

3.6.3 *Restoration*

Adapting forestry practices to maintain biodiversity associated with old-growth forests or at least with natural mature forests is a major challenge of contemporary forestry (Niemelä 1997). In regions where old-growth forests no longer exist, the challenge is two-fold: first, it is recommended to lengthen rotations to reach the senescent stage in which certain old-growth forest attributes are recovered and second implementation of restoration programs.

Tree planting after clear-cutting or salvage logging is the most widely used restoration method. It is usually applied when natural regeneration will result in seedling density too low to maintain stand productivity. Although tree planting provides habitat to maintain certain forest arthropods, planted forests have been reported to have lower abundance and species richness of beetles, compared to old-growth forests, and up to a 40% difference in species composition (Albert et al. 2021). Tree planting appears particularly unsuited to tropical forests where it does not reproduce the complex and diverse microhabitats and biotic interactions of old-growth tropical forests (Gibson et al. 2011). Monospecific plantations of exotic trees have strong negative effects on beetle communities and they should be restricted to areas where old-growth forests are scarce and highly fragmented, and where planting native trees is not an option (Albert et al. 2021). Negative effects of forest plantations are less

significant in other biomes, particularly when native tree species are planted (Albert et al. 2021). Thus, when used in combination with ecosystem-based forest management and protected areas, native tree plantations could be helpful to help restoring a portion of arthropod diversity in temperate and boreal forests. However, stand conversion toward another native tree species can also have detrimental effects. For example, converting mature balsam fir stands severely affected by the spruce budworm to black spruce plantations after salvage logging moves beetle communities farther away from the original stands than salvage logging alone or salvage logging followed by pre-commercial thinning (Norvez et al. 2013).

Another approach that can be used in forest restoration and which is consistent with ecosystem-based forest management is the reintroduction of natural processes through direct intervention. For example, prescribed burning is used to manage forest fuel and reduce fire risks (Fernandes and Botelho 2003), but it is also used to regenerate certain pine species, such as the eastern white pine, *Pinus strobus* L. in Canadian National Parks (Hébert et al. 2019). Eastern white pine was much more prevalent in pre-settlement forests of eastern North America than it is today (Doyon and Bouffard 2009). It is well adapted to low-severity surface fires as it has thick bark that efficiently insulates subcortical tissues (Hengst and Dawson 1994), but also because this tall tree has deep roots and a branch-free lower trunk (Farrar 1995). By reducing competition from saplings of other shade-tolerant tree species, and increasing light penetration, prescribed burning improves seedbed quality and helps white pine seedlings to sprout and grow (Hébert et al. 2019). Prescribed burning was shown to be efficient to increase the richness of both saproxylic and non-saproxylic beetles, suggesting that burning treatments do not only increase the amount of dead wood but also favour other attributes found in post-fire environments (Domaine 2009). Moreover, prescribed burning significantly increased the number of rare beetles, attesting for the usefulness of this restoration practice for biodiversity conservation.

3.7 New Challenges

The efficacy of management and conservation measures presented in the previous sections are challenged by arthropod declines highlighted in recent reports (Hallmann et al. 2017; Kunin 2019; Seibold et al. 2019; Wagner 2020). In 2017, the publication of a paper reporting a 76% drop in insect biomass in protected areas of Germany (Hallmann et al. 2017), received attention in the media and raised awareness of the general population. Reports of insect decline have existed for decades, perhaps best documented with light traps within the Rothamsted Insect Survey network which has sampled moths in Great Britain since 1968 (Conrad et al. 2006). The magnitude and geographic extent of arthropod decline remains largely unknown and vigorously debated (Wagner 2020).

Most data showing arthropod decline mainly come from open habitats, but arthropod decline has been also reported in forest habitats, although the effects do not appear as strong (Kunin 2019; Seibold et al. 2019). Drivers of arthropod

decline in forests is unclear but in grasslands, it is associated with the importance of agriculture in the landscape (Seibold et al. 2019). Apart from agricultural intensification (including pesticide use), factors suggested as possible causes of arthropod decline include habitat destruction (including deforestation), climate change, invasive species, atmospheric nitrification from burning fossil fuels and drought (Wagner 2020). Arthropod decline raises important ecological and economic issues as it will generate unpredictable cascading effects on ecosystems linked with the expected losses of ecological services provided by arthropods (Hallmann et al. 2017). Monitoring biodiversity and climate appear more important than ever as the impacts of these ecological crises intensify (O'Connor et al. 2020). This highlights the importance of long-term data using standardized methods and appropriate tools to manage and analyse these data, and ensure their long-term storage (Kunin 2019).

Climate change and biodiversity issues are closely linked and both the Intergovernmental Panel on Climate Change (IPCC) and the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) have called for urgent action to reduce the human ecological footprint (IPBES 2019; IPCC 2018). Without a doubt, the crises of climate change and biodiversity will be at the heart of the ecological agenda for the next decade.

References

- Albert G, Gallegos SC, Greig KE, Hanisch M, de la Fuente DL, Fost S, Maier SD, Sarathchandra C, Phillips HRP, Kambach S (2021) The conservation value of forests and tree plantations for beetle (Coleoptera) communities: a global meta-analysis. *For Ecol Manage* 491:119201
- Alexander K (1995) The use of freshly downed timber by insects following the 1987 storm. In: Buckley G (ed) *Ecological responses to the 1987 great storm in the woods of Southeast England*. *English Nature Science* 23:134–150
- Alfaro RI, Shepherd RF (1991) Tree-ring growth of interior Douglas-fir after one year's defoliation by Douglas-fir tussock moth. *For Sci* 37:959–964
- Allen DC (1973) Review of some parasite/predator-prey interactions in the forest soil microcommunity. *Proceedings of the first soil microcommunities conference*. Syracuse, New York, 18–20 Oct 1971. State University, New York, pp 218–226
- Ameixa OMCC, Soares AO, Soares AMVM, Lillebø AI (2018). Ecosystem services provided by the little things that run the World. In: Şen B, Grillo O (eds) *Selected studies in biodiversity*. IntechOpen, Chapter 13, pp 267–302. <https://doi.org/10.5772/intechopen.74847>
- Anderson JF (1976) Egg parasitoids of forest defoliating Lepidoptera. In: Anderson JF, Kaya HK (eds) *Perspectives in forest entomology*. Academic, New York, pp 233–249
- Andersson J, Hjäältén J, Dynesius M (2015) Wood-inhabiting beetles in low stumps, high stumps and logs on boreal clear-cuts: implications for dead wood management. *PLoS ONE* 10(3):e0118896. <https://doi.org/10.1371/journal.pone.0118896>
- Angelstam PK (1998) Maintaining and restoring biodiversity in European boreal forests by developing natural disturbance regimes. *J Veg Sci* 9:593–602
- Attwill PM (1994) The disturbance of forest ecosystems: the ecological basis for conservative management. *For Ecol Manage* 63:247–300
- Audley JP, Fettig CJ, Munson AS, Runyon JB, Mortenson LA, Steed BE, Gibson KE, Jorgensen CL, McKelvey SR, McMillin JD, Negron JF (2020) Impacts of mountain pine beetle outbreaks on lodgepole pine forests in the Intermountain West, U.S., 2004–2019. *For Ecol Manage* 475:118403

- Ausmus BS (1977) Regulation of wood decomposition rates by arthropod and annelid populations. *Ecological Bulletins No 25, Soil Organisms as Components of Ecosystems*, pp 180–192
- Azeria ET, Ibarzabal J, Hébert C (2012) Effects of habitat characteristics and interspecific interactions on co-occurrence patterns of saproxylic beetles breeding in tree boles after forest fire: null model analyses. *Oecologia* 168:1123–1135
- Bar A, Michaletz ST, Mayr S (2019) Fire effects on tree physiology. *New Phytol* 223:1728–1741
- Bar-On YM, Phillips R, Milošević R (2018) The biomass distribution on Earth. *PNAS* 115:6506–6511
- Barbosa P, Wagner MR (1989) *Introduction to forest and shade tree insects*. Academic Press, Inc., San Diego, CA
- Barnouin T (2005) Évaluation de l'importance des forêts affectées par la tordeuse des bourgeons de l'épinette. *Choristoneura fumiferana* (Clem.), dans le maintien de la diversité des coléoptères saproxyliques. MSc Thesis, Université Laval, 59 p
- Barrios E (2007) Soil biota, ecosystem services and land productivity. *Ecol Econ* 64:269–285
- Barton PS, Cunningham SA, Lindenmayer DB, Manning AD (2013) The role of carrion in maintaining biodiversity and ecological processes in terrestrial ecosystems. *Oecologia* 171:761–772
- Barton PS, Evans JM (2017) Insect biodiversity meets ecosystem function: differential effects of habitat and insects on carrion decomposition. *Ecol Entomol* 42:364–374
- Basset Y, Cizek L, Cuénoud P, Didham RK, Guilhaumon F, Missa O, Novotny V, Ødegaard F, Roslin T, Schmid J, Tishechkin AK, Winchester NN, Roubik DW, Aberlenc H-P, Bail J, Barrios H, Bridle JR, Castaño-Meneses G, Corbara B, Curlletti G, Duarte da Rocha W, De Bakker D, Delabie JHC, Dejean A, Fagan LL, Floren A, Kitching RL, Medianero E, Miller SE, de Oliveira EG, Orivel J, Pollet M, Rapp M, Ribeiro SP, Roisin Y, Schmidt JB, Sørensen L, Leponce M (2012) Arthropod diversity in a tropical forest. *Science* 338:1481–1484
- Bauce E, Hardy Y (1988) Effects of drainage and severe defoliation on the raw fiber content of balsam fir needles and growth of the spruce budworm (Lepidoptera: Tortricidae). *Environ Entomol* 17:671–674
- Bauer LS, Nordin GL (1989) Effect of *Nosema fumifennae* (Microsporida) on fecundity, fertility, and progeny performance of *Choristoneura fumiferana* (Lepidoptera: Tortricidae). *Environ Entomol* 18:261–265
- Bauhus J, Puettmann K, Messier C (2009) Silviculture for old-growth attributes. *For Ecol Manage* 258:525–537
- Baur ME, Kaya HK, Strong D (1998) Foraging ants as scavengers on entomopathogenic nematode-killed insects. *Biol Control* 12:231–236
- Bawa KS (1990) Plant-pollinator interactions in tropical rain forests. *Annu Rev Ecol Syst* 21:399–422
- Bawa KS, Bullock SH, Perry DR, Coville RE, Grayum MH (1985) Reproductive biology of tropical lowland rain forest trees. II. Pollination systems. *Am J Bot* 72:346–356
- Bazelet CS, Thompson AC, Naskrecki P (2016) Testing the efficacy of global biodiversity hotspots for insect conservation: the case of South African Katydid. *PLoS ONE* 11(9):e0160630
- Behan VM, Hill SB, Kevan DKMcE (1978) Effects of nitrogen fertilizers, as urea, on Acarina and other arthropods in Quebec black spruce humus. *Pedobiologia* 18:249–263
- Béland J-M, Bauce É, Cloutier C, Berthiaume R, Hébert C (2019) Early responses of bark and wood boring beetles during an outbreak of the hemlock looper *Lambdina fuscicollis* (Guenée) (Lepidoptera: Geometridae) in a boreal balsam fir forest of North America. *Agric For Entomol* 21:407–416. <https://doi.org/10.1111/afe.12347>
- Belovsky GE, Slade JB (2000) Insect herbivory accelerates nutrient cycling and increases plant production. *PNAS* 97:14412–14417
- Belyea RM (1952a) Death and deterioration of balsam fir weakened by spruce budworm defoliation in Ontario. *Can Entomol* 89:325–335
- Belyea RM (1952b) Death and deterioration of balsam fir weakened by spruce budworm defoliation in Ontario. Part II. An assessment of the role of associated insect species in the death of severely weakened trees. *J Forest* 50:729–738

- Berg A, Ehnstrom B, Gustafsson L, Hallingback T, Jonsell M, Weslien J (1994) Threatened plant, animal, and fungus species in Swedish forests: distribution and habitat associations. *Conserv Biol* 8:718–731
- Bergeron Y, Harvey B, Leduc A, Gauthier S (1999) Stratégies d'aménagement forestier qui s'inspirent de la dynamique des perturbations naturelles: considérations à l'échelle du peuplement et de la forêt. *For Chron* 75:55–61
- Bernays E (2009) Phytophagous insects. In: Resh VH, Cardé RT (eds) *Encyclopedia of insects*. Academic Press, Burlington, MA, Chapter 201, pp 798–800
- Bernays E, Graham M (1988) On the evolution of host specificity in phytophagous arthropods. *Ecology* 69:886–892
- Beudert B, Baussler C, Thorn S, Noss R, Schroder B, Dieffenbach-Fries H, Foullois N, Muller J (2015) Bark beetles increase biodiversity while maintaining drinking water quality. *Conserv Lett* 8:272–281
- Bin F, Johnson NF (1982) Potential of Telenominae in biocontrol with egg parasitoids (Hym., Scelionidae). In: INRA Public (ed) *Les Trichogrammes*, Antibes (France), 20–23 Avril 1982. Coll. INRA 9, pp 275–287
- Birkmoe T, Jacobsen RM, Sverdrup-Thygesen A, Biedermann PHW (2018) Insect-fungus interactions in dead wood systems. In: Ulyshen MD (ed) *Saproxylic insects—diversity, ecology and conservation*. Springer, Chapter 12
- Blais JR (1960) Spruce budworm parasite investigations in the Lower St. Lawrence and Gaspé region of Quebec. *Can Entomol* 92:384–396
- Bloin P (2021) Réponse à court terme des insectes saproxyliques à la disponibilité du bois mort. MSc Thesis, Université Laval, 79 p
- Bouchard M (2000) Effets de la coupe à blanc et de la structure de la forêt sur les communautés de léiodides (Coleoptera: Leiodidae) dans des sapinières boréales. MSc Thesis, Université Laval, Québec, Canada, 33 p
- Bouchard M, Hébert C (2016) Beetle community response to residual forest patch size in managed boreal forest landscapes: feeding habits matter. *For Ecol Manage* 368:63–70. <https://doi.org/10.1016/j.foreco.2016.02.029>
- Boucher J, Azeria ET, Ibarzabal J, Hébert C (2012) Saproxylic beetles in disturbed boreal forest: temporal dynamics, habitat associations and community structure. *Ecoscience* 19:328–343
- Boucher J, Hébert C, Ibarzabal J, Bauce E (2016) High conservation value forests for burn-associated saproxylic beetles: an approach for developing sustainable post-fire salvage logging in boreal forest. *Insect Conserv Divers* 9:402–415
- Boucher J, Bauce E, Hébert C (2020) A flexible approach for predicting and mapping postfire wood borer attacks in black spruce and jack pine forests using the differenced normalized burn ratio (dNBR). *Can J For Res* 50:880–889
- Boucher P, Hébert C, Francoeur A, Sirois L (2015) Postfire succession of ants (Hymenoptera: Formicidae) nesting in dead wood of northern boreal forest. *Environ Entomol* 44:1316–1327
- Bouget C, Duelli P (2004) The effects of windthrow on forest insect communities: a literature review. *Biol Cons* 118:281–299
- Boulanger Y, Sirois L, Hébert C (2010) Distribution of saproxylic beetles in a recently burnt landscape of the northern boreal forest of Québec. *For Ecol Manage* 260:1114–1123
- Boulanger Y, Sirois L, Hébert C (2011) Fire severity as a determinant factor of the decomposition rate of fire-killed black spruce in the northern boreal forest. *Can J For Res* 41:370–379
- Boulanger Y, Sirois L, Hébert C (2013) Distribution patterns of three long-horned beetles (Coleoptera: Cerambycidae) shortly after fire in boreal forest: adults colonizing stands versus progeny emerging from trees. *Environ Entomol* 42:17–28
- Braack LEO (1987) Community dynamics of carrion-attendant arthropods in tropical african woodland. *Oecologia* 72:402–409
- Brokaw NVL (1982) The definition of treefall gap and its effect on measures of forest dynamics. *Biotropica* 14:158–160

- Brundtland GH (1987) Our common future. The world commission on environment and development. Oxford University Press, New York
- Brussaard L, Behan-Pelletier VM, Bignell DE, Brown VK, Didden W, Folgarait P, Fragoso C, Wall Freckman D, Gupta VVSR, Hattori T, Hawksworth DL, Klopatek C, Lavelle P, Malloch DW, Rusek J, Soderstrom B, Tiedje JM, Virginia RA (1997) Biodiversity and ecosystem functioning in soil. *Ambio* 26:563–570
- Buddle CM, Langor DW, Pohl GR, Spence JR (2006) Arthropod responses to harvesting and wildfire: implications for emulation of natural disturbance in forest management. *Biol Cons* 128:346–357
- Bunnell FL, Kremsater LL, Houde I (2011) Mountain pine beetle: a synthesis of the ecological consequences of large-scale disturbances on sustainable forest management, with emphasis on biodiversity. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC. Information Report BC-X-426, 99 p
- Cadorette-Breton Y, Hébert C, Ibarzabal J, Berthiaume R, Baucé E (2016) Vertical distribution of three longhorned beetle species (Coleoptera: Cerambycidae) in burned trees of the boreal forest. *Can J For Res* 46:564–571
- Ciesla WM (2011) Forest entomology: a global perspective. Wiley-Blackwell, Hoboken NJ
- Clarke RD, Grant PR (1968) An experimental study of the role of spiders as predators in a forest litter community. Part 1. *Ecology* 49:1152–1154
- Condamine FL, Clapham ME, Kergoat GK (2016) Global patterns of insect diversification: towards a reconciliation of fossil and molecular evidence? *Scientific Reports* 6:19208
- Conrad KF, Warren MS, Fox R, Parsons MS, Woiwod IP (2006) Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. *Biol Cons* 132:279–291. <https://doi.org/10.1016/j.biocon.2006.04.020>
- D’Amen M, Bombi P, Campanaro A, Zapponi L, Bologna MA, Mason F (2013) Protected areas and insect conservation: questioning the effectiveness of Natura 2000 network for saproxylic beetles in Italy. *Anim Conserv* 16:370–378
- Dajoz R (1998) Les insectes et la forêt : rôle et diversité des insectes dans le milieu forestier. Editions Tec & Doc Lavoisier Londres, Paris, New York, 594 p
- Davis TS, Rhoades PR, Mann AJ, Griswold T (2020) Bark beetle outbreak enhances biodiversity and foraging habitat of native bees in alpine landscapes of the southern Rocky Mountains. *Sci Rep* 10:16400
- De Alckmin Marques ES, Price PW, Cobb NS (2000) Resource abundance and insect herbivore diversity on woody Fabaceous desert plants. *Environ Entomol* 29:696–703
- De Grandpré L, Waldron K, Bouchard M, Gauthier S, Beaudet M, Ruel J-C, Hébert C, Kneeshaw D (2018) Incorporating insect and wind disturbances in a natural disturbance-based management framework for the boreal forest. *Forests* 9(8):471. <https://doi.org/10.3390/f9080471>
- DeFoliart G (1991) Forest management for the protection of edible caterpillars in Africa. *The Food Insects Newsletter* 4(2):1–2
- DeFoliart G (2005) Overview of role of edible insects in preserving biodiversity. In: Paoletti MG (ed) Ecological implications of mini livestock. Science Publisher, Enfield, NH, pp 123–140
- Dekeirsschieter J, Verheggen F, Lognay G, Haubruge E (2011) Large carrion beetles (Coleoptera, Silphidae) in Western Europe: a review. *Biotechnol Agron Soc Environ* 15:435–447
- Dhar A, Parrott L, Heckbert S (2016) Consequences of mountain pine beetle outbreak on forest ecosystem services in western Canada. *Can J For Res* 46:987–999
- Dighton J (2003) Fungi in ecosystem processes, 2nd edn. CRC Press, New York
- Djukic I, Kepfer-Rojas S, Kappel Schmidt I, Steenberg Larsen K, Beier C, Berg B, Verheyen K, Composition T (2018) Early stage litter decomposition across biomes. *Sci Total Environ* 628–629:1369–1394
- Domaine E (2009) Effets des brûlages dirigés sur la régénération du pin blanc et la diversité des coléoptères du Parc national du Canada de la Mauricie. MSc Thesis, Université Laval, 116 p
- Doyon F, Bouffard D (2009). Enjeux écologiques de la forêt feuillue tempérée québécoise, Québec. Pour le ministère des Ressources naturelles et de la Faune, Direction de l’environnement et de

- la protection des forêts. 63 p. Available from: <http://www.mrnf.gouv.qc.ca/forets/amenagement/amenagement-ecosystemique.jsp>
- Duelli P, Obrist MK, Wermelinger B (2002) Windthrow-induced changes in faunistic biodiversity in alpine spruce forests. *For Snow Landsc Res* 77:117–131
- Dufour-Pelletier S, Tremblay JA, Hébert C, Lachat T, Ibarzabal J (2020) Testing the effect of snag and cavity supply on deadwood-associated species in a managed boreal forest. *Forests* 11:424. <https://doi.org/10.3390/f11040424>
- Durst PB, Shono K (2010) Edible forest insects: exploring new horizons and traditional practices. In: Durst PB, Johnson DV, Leslie RN, Shono K (eds) *Forest insects as food: humans bite back*. Proceedings of a workshop on Asia-Pacific resources and their potential for development. 19–21 Feb 2008, Chiang Mai, Thailand, pp 1–4
- Dyer LA, Carson WP, Leigh Jr EG (2012) Insect outbreaks in tropical forests: patterns, mechanisms, and consequences. In: Barbosa P, Letourneau DK, Agrawal AA (eds) *Insect outbreaks revisited*. Wiley-Blackwell, Hoboken, NJ, Chapter 11
- Ehrlich PR, Raven PH (1964) Butterflies and plants: a study in coevolution. *Evolution* 18:586–608
- Elton CS (1958) *The ecology of invasions by animals and plants*. Chapman & Hall, London
- Everaerts C, Cusson M, McNeil JN (2000) The influence of smoke volatiles on sexual maturation and juvenile hormone biosynthesis in the black army cutworm, *Actebia fennica* (Lepidoptera: Noctuidae). *Insect Biochem Mol Biol* 30:855–862
- Evans WG (1964) Infrared receptors in *Melanophila acuminata* De Geer. *Nature* 202:211
- Evans WG (1966) Perception of infrared radiation from forest fires by *Melanophila acuminata* De Geer (Buprestidae, Coleoptera). *Ecology* 47:1061–1065
- Eveleigh ES, McCann KS, McCarthy PC, Pollock SJ, Lucarotti CJ, Morin B, McDougall GA, Strongman DB, Huber JT, Umbanhowar J, Faria LDB (2007) Fluctuations in density of an outbreak species drive diversity cascades in food webs. *PNAS* 104:16976–16981
- Faiola C, Taipale D (2020) Impact of insect herbivory on plant stress volatile emissions from trees: a synthesis of quantitative measurements and recommendations for future research. *Atmos Environ* 5:100060
- Farrar JL (1995) *Les Arbres du Canada*. Service canadien des forêts, Ressources Naturelles Canada et Fides, Saint-Laurent, Canada
- Fernandes PM, Botelho HS (2003) A review of prescribed burning effectiveness in fire hazard reduction. *Int J Wildland Fire* 12:117–128
- Ferro ML (2018) It's the end of the wood as we know it: insects in veteris (highly decomposed) wood. In: Ulyshen MD (ed) *Saproxylic insects, diversity, ecology and conservation*. Zoological Monographs 1, Springer
- Filipiak M, Weiner J (2014) How to make a beetle out of wood: multi-elemental stoichiometry of wood decay, xylophagy and fungivory. *PLoS ONE* 9(12):e115104
- Foit J (2010) Distribution of early-arriving saproxylic beetles on standing dead Scots pine trees. *Agric For Entomol* 12:133–141
- Folgarait PJ (1998) Ant biodiversity and its relationship to ecosystem functioning: a review. *Biodivers Conserv* 7:1221–1244
- Forbes AA, Bagley RK, Beer MA, Hippee AC, Widmayer HA (2018) Quantifying the unquantifiable: why Hymenoptera, not Coleoptera, is the most speciose animal order. *BMC Ecol* 18:21. <https://doi.org/10.1186/s12898-018-0176-x>
- Frank K, Brückner A, Hilpert A, Heethoff M, Blüthgen N (2017) Nutrient quality of vertebrate dung as a diet for dung beetles. *Sci Rep* 7:12141
- Franklin JF, Berg DR, Thornburgh DA, Tappeiner JC (1997) Alternative silvicultural approaches to timber harvesting: variable retention harvest systems. In: Kohm KA, Franklin JF (eds) *Creating a forestry for the 21st century: the science of ecosystem management*. Island Press, Washington, DC, pp 111–139
- Frost CJ, Hunter MD (2007) Recycling of nitrogen in herbivore feces: plant recovery, herbivore assimilation, soil retention, and leaching losses. *Oecologia* 151:42–53

- García Palacios P, Maestre FT, Kattge J, Wall DH (2013) Climate and litter quality differently modulate the effects of soil fauna on litter decomposition across biomes. *Ecol Lett* 16:1045–1053
- Gaston KJ (1991) The magnitude of global insect species richness. *Conserv Biol* 5:283–296
- Gaunt MW, Miles MA (2002) An insect molecular clock dates the origin of the insects and accords with palaeontological and biogeographic landmarks. *Mol Biol Evol* 19:748–761
- Gauthier S, Vaillancourt M-A, Leduc A, De Granpré L, Kneeshaw D, Morin H, Drapeau P, Bergeron Y (2008) Aménagement écosystémique en forêt boréale. Presses de l'Université du Québec, Québec, 568 p
- Gessner MO, Swan CM, Dang CK, McKie BG, Bardgett RD, Wall DH, Hattenschwiler S (2010) Diversity meets decomposition. *Trends Ecol Evol* 25:372–380
- Gibson L, Lee TM, Koh LP, Brook BW, Gardner TA, Barlow J, Peres CA, Bradshaw CJA, Laurance WF, Lovejoy TE, Sodhi NS (2011) Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature* 478(7369):378–381
- Godfray HCJ (1994) Parasitoids: behavioral and evolutionary ecology. Princeton University Press, Princeton, NJ
- González G, Seastedt TR (2001) Soil fauna and plant litter decomposition in tropical and subalpine forests. *Ecology* 82:955–964
- González G, Gould WA, Hudak AT, Hollingsworth TN (2008) Decay of Aspen (*Populus tremuloides* Michx.) wood in moist and dry boreal, temperate, and tropical forest fragments. *Ambio* 37:588–597
- Griffiths HM, Ashton LA, Walker AE, Hasan F, Evans TA, Eggleton P, Parr CL (2018) Ants are the major agents of resource removal from tropical rainforests. *J Anim Ecol* 87:293–300
- Grimaldi D, Engel M (2005) Evolution of the insects. Cambridge University Press, New York and Cambridge
- Grove SJ (2002) Saproxylic insect ecology and the sustainable management of forests. *Annu Rev Ecol Syst* 33:1–23
- Hallmann CA, Sorg M, Jongejans E, Siepel H, Hofland N, Schwan H, Stenmans W, Müller A, Sumser H, Hörrn T, Goulson D, de Kroon H (2017) More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS ONE* 12:e0185809
- Hannah L, Midgley G, Anelman S, Araújo M, Hughes G, Martinez-Meyer E, Pearson R, Williams P (2007) Protected area needs in a changing climate. *Front Ecol Environ* 5:131–138
- Hanula JL, Ulyshen MD, Horn S (2016) Conserving pollinators in North American forests: a review. *Nat Areas J* 36:427–439
- Harmon ME, Franklin JF, Swanson FJ, Sollins P, Gregory SV, Lattin JD, Anderson NH, Cline SP, Aumen NG, Sedell JR, Lienkaemper GW, Cromack K Jr, Cummins KW (1986) Ecology of coarse woody debris in temperate ecosystems. *Adv Ecol Res* 15:133–302
- Hartling L, MacNutt P, Carter N (1991) Hemlock looper in New Brunswick: notes on biology and survey methods. Department of Natural Resources and Energy. Timber Manage. Branch For. Pest Manage. Sec. Rep. 1991
- Harvey BD, Leduc A, Gauthier S, Bergeron Y (2002) Stand-landscape integration in natural disturbance-based management of the southern boreal forest. *For Ecol Manage* 155:369–385
- Hassall M, Rushton SP (1982) The role of coprophagy in the feeding strategies of terrestrial Isopods. *Oecologia* 53:374–381
- Hébert C (1983) Bio-écologie et contrôle naturel d'une population de *Lymantria dispar* L. (Lepidoptera: Lymantriidae) de la Mauricie, Québec. Mémoire de Maîtrise, Université du Québec à Trois-Rivières, 231 p
- Hébert C (1989) Bio-écologie de la mouche *Winthemia fumiferanae* et comparaison de sa relation parasitique avec la tordeuse des bourgeons de l'épinette à celle de l'hyménoptère braconide *Meteorus trachynotus*. Thèse de Doctorat, Université Laval, 138 p
- Hébert C (1990) Biologie et contrôle naturel de *Zeiraphera canadensis* Mut. & Free. (Lepidoptera: Tortricidae) dans la région de Matapédia, Québec. Rapport présenté au Ministère de l'énergie et des ressources du Québec, Service de la protection contre les insectes et les maladies, 61 p

- Hébert C, Jobin L (2001) The Hemlock looper. Ressour. nat. Can., Serv. can. for., Cent. for. Laurentides, Sainte-Foy, Qc. Inf. Leaf. LFC 4E
- Hébert C, Berthiaume R, Dupont A, Auger M (2001) Population collapses in a forecasted outbreak of *Lambdina fiscellaria* (Lepidoptera: Geometridae) caused by spring egg parasitism by *Telenomus* spp. (Hymenoptera: Scelionidae). *Environ Entomol* 30:37–43
- Hébert C, Comtois B, Morneau L (2017) *Insectes des arbres du Québec*. Les Publications du Québec, Québec, 299 p
- Hébert C, Domaine É, Bélanger L (2019) Prescribed burning used to restore white pine forests in La Mauricie National Park of Canada. Book Chapter In: National Parks, IntechOpen. <https://doi.org/10.5772/intechopen.86224>
- Hengst GE, Dawson JO (1994) Bark properties and fire resistance of selected tree species from the central hardwood region of North America. *Can J For Res* 24:688–696
- Hibbert A (2010) Importance of fallen coarse woody debris to the diversity of saproxylic Diptera in the boreal mixedwood forests of Eastern North America. MSc Thesis, Université du Québec à Montréal, 87 p
- Hillabrand RM, Hacke UG, Lieffers VJ (2019) Defoliation constrains xylem and phloem functionality. *Tree Physiol* 39:1099–1108
- Hillebrand H (2004) On the generality of the latitudinal diversity gradient. *Am Nat* 163:192–211
- Hirose Y (1986) Biological and ecological comparison of *Trichogramma* and *Telenomus* as control agents of lepidopterous pests. *J Appl Entomol* 101:39–47
- Hoback WW, Bishop AA, Kroemer J, Scalzitti J, Shaffer JJ (2004) Differences among antimicrobial properties of carrion beetle secretions reflect phylogeny and ecology. *J Chem Ecol* 30:719–729
- Hoback WW, Freeman L, Payton M, Peterson BC (2020) Burying beetle (Coleoptera: Silphidae: *Nicrophorus* Fabricius) brooding improves soil fertility. *Coleopt Bull* 74:427–433
- Hölldobler B, Wilson EO (1990) *The ants*. Belknap Press of Harvard University Press, Cambridge, MA
- Holling CS (1961) Principles of insect predation. *Annu Rev Entomol* 6:163–182
- Holter P, Scholtz CH (2007) What do dung beetles eat? *Ecol Entomol* 32:690–697
- Hunter ML (1990) *Wildlife, forests and forestry. Principles of managing forests for biological diversity*. Prentice-Hall, Englewood Cliffs, NJ, 370 p
- IPBES (2016) The assessment report of the intergovernmental science-policy platform on biodiversity and ecosystem services on pollinators, pollination and food production. In: Potts SG, Imperatriz-Fonseca VL, Ngo HT, (eds) Secretariat of the intergovernmental science-policy platform on biodiversity and ecosystem services. Bonn, Germany, 552 p
- IPBES (2019) Global assessment report on biodiversity and ecosystem services of the intergovernmental science-policy platform on biodiversity and ecosystem services. In: Brondizio ES, Settele J, Díaz S, Ngo HT (eds) IPBES secretariat, Bonn, Germany, 1148 p. <https://doi.org/10.5281/zenodo.3831673>
- IPCC (2018) Summary for policymakers. In: Masson-Delmotte V, Zhai P, Pörtner H-O, Roberts D, Skea J, Shukla PR, Pirani A, Moufouma-Okia W, Péan C, Pidcock R, Connors S, Matthews JBR, Chen Y, Zhou X, Gomis MI, Lonnoy E, Maycock T, Tignor M, Waterfield T (eds) Global warming of 1.5°C. An IPCC special report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty. World Meteorological Organization, Geneva, Switzerland, 32 pp
- Iqbal J, MacLean DA (2010) Estimating cumulative defoliation of balsam fir from hemlock looper and balsam fir sawfly using aerial defoliation survey in western Newfoundland, Canada. *For Ecol Manage* 259:591–597
- Janssen P, Fortin D, Hébert C (2009) Beetle diversity in a matrix of old-growth boreal forest: influence of habitat heterogeneity at multiple scales. *Ecography* 32:423–432
- Janz N (2011) Ehrlich and Raven revisited: mechanisms underlying codiversification of plants and enemies. *Annu Rev Ecol Evol Syst* 42:71–89

- Janzen DH (1981) The peak in North American Ichneumonid species richness lies between 38° and 42° North. *Ecology* 62:532–537
- Jeffrey O (2013) Effets des coupes de récupération sur les successions naturelles de coléoptères saproxyliques le long d'une chronoséquence de 15 ans après feu en forêt boréale commerciale. MSc Thesis, UQAC, 96 p
- Jenkins CN, Joppa L (2009) Expansion of the global terrestrial protected area system. *Biol Cons* 142:2166–2174
- Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. *Oikos* 69:373–386
- Jonsell M, Nordlander G (2002) Insects in polypore fungi as indicator species: a comparison between forest sites differing in amounts and continuity of dead wood. *For Ecol Manage* 157:101–118
- Jonsell M, Nordlander G (2004) Host selection patterns in insects breeding in bracket fungi. *Ecol Entomol* 29:697–705
- Jonsell M, Weslien J, Ehnstrom B (1998) Substrate requirements of red-listed saproxylic invertebrates in Sweden. *Biodivers Conserv* 7:749–764
- Jonsell M, Nittérus K, Stighäll K (2004) Saproxylic beetles in natural and man-made deciduous high stumps retained for conservation. *Biol Cons* 118:163–173
- Johansson T, Andersson J, Hjalten J, Dynesis M, Ecke F (2011) Short-term responses of beetle assemblages to wildfire in a region with more than 100 years of fire suppression. *Insect Conserv Diver* 4:142–151
- Johnson SN, Lopaticki G, Barnett K, Facey SL, Powell JR, Hartley SE (2016) An insect ecosystem engineer alleviates drought stress in plants without increasing plant susceptibility to an above-ground herbivore. *Funct Ecol* 30:894–902
- Kaila L, Martikainen P, Punttila P (1997) Dead trees left in clear-cuts benefit saproxylic Coleoptera adapted to natural disturbances in boreal forest. *Biodivers Conserv* 6:1–18
- Kanat M, Mol T (2008) The effect of *Calosoma sycophanta* L. (Coleoptera: Carabidae) feeding on the pine processionary moth, *Thaumetopoea pityocampa* (Denis & Schiffermüller) (Lepidoptera: Thaumetopoeidae), in the laboratory. *Turk J Zool* 32:367–372
- Knoll AH, Nowak MA (2017) The timetable of evolution. *Science. Advances* 3:e1603076
- Koivula M (2002) Boreal carabid-beetle (Coleoptera, Carabidae) assemblages in thinned uneven-aged and clear-cut spruce stands. *Annales Zoology Fennici* 39:131–149
- Koivula M, Spence JR (2006) Effects of post-fire salvage logging on boreal mixed-wood ground beetle assemblages (Coleoptera, Carabidae). *For Ecol Manage* 236:102–112
- Komarek EV (1969) Fire and animal behavior. In: Komarek EV (conference chairman). *Proceedings tall timbers fire ecology conference: No 9. Tall Timbers Research Station, Tallahassee, FL*, pp 160–207
- Kukor JJ, Martin MM (1983) Acquisition of digestive enzymes by siricid woodwasps from their fungal symbiont. *Science* 220(4602):1161–1163
- Kunin WE (2019) Robust evidence of insect declines. *Nature* 574:641–642
- Kuuluvainen T (1994) Gap disturbance, ground microtopography, and the regeneration dynamics of boreal coniferous forests in Finland: a review. *Ann Zool Fennici* 31:35–51
- Labandeira CC (2006) The four phases of plant-arthropod associations in deep time. *Geol Acta* 4:409–438
- Labandeira CC, Sepkoski JJ Jr (1993) Insect diversity in the fossil record. *Science* 261(5119):310–315
- Lal R (1988) Effects of macrofauna on soil properties in tropical ecosystems. *Agr Ecosyst Environ* 24:101–116
- Larson BMH, Kevan PG, Inouye DW (2001) Flies and flowers: taxonomic diversity of anthophiles and pollinators. *Can Entomol* 133:439–465
- Lasalle J (1993) Parasitic hymenoptera, biological control and biodiversity. In: Lasalle J, Gauld ID (eds) *Hymenoptera and biodiversity*. CAB international, pp 197–215
- Lavelle P (1997) Faunal activities and soil processes: adaptive strategies that determine ecosystem function. *Adv Ecol Res* 27:93–132

- Lawrence KL, Wise DH (2004) Unexpected indirect effect of spiders on the rate of litter disappearance in a deciduous forest. *Pedobiologia* 48:149–157
- Le Borgne H, Hébert C, Dupuch A, Bichet O, Pinaud D, Fortin D (2018) Temporal dynamics in animal community assembly during post-logging succession in boreal forest. *PLoS ONE* 13(9):e0204445. <https://doi.org/10.1371/journal.pone.0204445>
- Légaré J-P, Hébert C, Ruel J-C (2011) Alternative silvicultural practices in irregular boreal forests: response of beetle assemblages. *Silva Fenn* 45:937–956
- Lindenmayer DB, Burton PJ, Franklin J (2008) *Salvage logging and its ecological consequences*. Island Press, Washington, DC
- Losey JE, Vaughan M (2006) The economic value of ecological services provided by insects. *Bioscience* 56:311–323
- Maaroufi H, Potvin M, Cusson M, Levesque RC (2021) Novel antimicrobial anionic cecropins from the spruce budworm feature a poly-L-aspartic acid C-terminus. *Proteins* 89:1205–1215
- MacLean DA (1980) Vulnerability of fir-spruce stands during uncontrolled spruce budworm outbreaks: a review and discussion. *For Chron* 56:213–221
- Maltais J, Régnière J, Cloutier C, Hébert C, Perry DF (1989) Seasonal biology of *Meteorus trachynotus* Vier. (Hymenoptera: Braconidae) and of its overwintering host *Choristoneura rosaceana* (Harr.) (Lepidoptera: Tortricidae). *Can Entomol* 121:745–756
- Marchese C (2015) Biodiversity hotspots: a shortcut for a more complicated concept. *Glob Ecol Conserv* 3:297–309
- Marshall VG, Kevan DKM, Matthews JV, Tomlin AD (1982) Status and research needs of Canadian soil arthropods. *Bulletin of the Entomological Society of Canada, Supplement* 14: 5 p
- Mattson WJ, Addy ND (1975) Phytophagous insects as regulators of forest primary production. *Science* 190:515–522
- May RM (1988) How many species are there on Earth? *Science* 241:1441–1449
- Mbata KJ, Chidumayo EN, Lwatula CM (2002) Traditional regulation of edible caterpillar exploitation in the Kopa area of Mpika district in northern Zambia. *J Insect Conserv* 6:115–130
- McGugan BM, Blais JR (1959) Spruce budworm parasite studies in Northwestern Ontario. *Can Entomol* 91:758–783
- McNaughton SJ, Ruess RW, Seagle SW (1988) Large mammals and process dynamics in African ecosystems. *Bioscience* 38:794–800
- Meyer-Rochow VB (2017) Therapeutic arthropods and other, largely terrestrial, folk-medicinally important invertebrates: a comparative survey and review. *J Ethnobiol Ethnomed* 13:31 p. <https://doi.org/10.1186/s13002-017-0136-0>
- Michalko R, Pekár S, Entling MH (2019) An updated perspective on spiders as generalist predators in biological control. *Oecologia* 189:21–36
- Moore BA, Allard G (2011) Abiotic disturbances and their influence on forest health. A review. *Forests Health & Biosecurity Working Paper FBS/35E*, Rome, Italy
- Moreau G, Quiring DT, Eveleigh ES, Bauce E (2003) Advantages of a mixed diet: feeding on several foliar age classes increases the performance of a specialist insect herbivore. *Oecologia* 135:391–399
- Moretti M, De Caceres M, Pradella C, Obrist MK, Wermelinger B, Legendre P, Duelli P (2010) Fire-induced taxonomic and functional changes in saproxylic beetle communities in fire sensitive regions. *Ecography* 33:760–777
- Morris JL, Cottrell S, Fettig CJ, Hansen WD, Sherriff RL, Carter VA, Clear JL, Clement J, DeRose RJ, Hicke JA, Higuera PE, Mattor KM, Seddon AWR, Seppa HT, Stednick JD, Seybold SJ (2017) Managing bark beetle impacts on ecosystems and society: priority questions to motivate future research. *J Appl Ecol* 54:750–760
- Muona J, Rutanen I (1994) The short-term impact of fire on the beetle fauna in boreal coniferous forest. *Ann Zool Fenn* 31:109–121
- Murillas Gómez M (2013) Impact du longicorne noir, *Monochamus scutellatus scutellatus*, sur l'épinette noire et le sapin baumier à la suite de chablis en forêt boréale irrégulière. MSc Thesis, Université Laval, 46 p

- Natural Resources Canada (2015) Trees, insects and diseases of Canada's forests. <https://tidcf.nrcan.gc.ca/en/insects/diet>
- Ness JH, Bressmer K (2005) Abiotic influences on the behaviour of rodents, ants, and plants affect an ant-seed mutualism. *Ecoscience* 12:76–81
- Nichols E, Spector S, Louzada J, Larsen T, Amezcuita S, Favila ME, The Scarabaeinae Research Network (2008) Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. *Biol Cons* 141:1461–1474
- Niemelä J (1997) Invertebrates and boreal forest management. *Conserv Biol* 11:601–610
- Noriega JA, Hortala J, Azcárate FM, Berg MP, Bonada N, Briones MJI, Del Toro I, Goulson D, Ibanez S, Landis DA, Moretti M, Potts SG, Slade EM, Stout JC, Ulyshen MD, Wackers FL, Woodcock BA, Santos AMC (2018) Research trends in ecosystem services provided by insects. *Basic Appl Ecol* 26:8–23
- Norvez O, Bélanger L, Hébert C (2013) Impact of salvage logging on stand structure and beetle diversity in boreal balsam fir forest, 20 years after a spruce budworm outbreak. *For Ecol Manage* 302:122–132
- Novotny V, Miller SE, Baje L, Balagawi S, Basset Y, Cizek L, Craft KJ, Dem F, Drew RAI, Hulcr J, Leps J, Lewis OT, Pokon R, Stewart AJA, Samuelson GA, Weiblen GD (2010) Guild-specific patterns of species richness and host specialization in plant–herbivore food webs from a tropical forest. *J Anim Ecol* 79:1193–1203
- Nyffeler M, Birkhofer K (2017) An estimated 400–800 million tons of prey are annually killed by the global spider community. *Sci Nat* 104:30
- O'Connor B, Bojinski S, Roosli C, Schaeppman ME (2020) Monitoring global changes in biodiversity and climate essential as ecological crisis intensifies. *Eco Inform* 55:101033
- Ollerton J, Winfree R, Tarrant S (2011) How many flowering plants are pollinated by animals? *Oikos* 120:321–326
- Orford KA, Vaughan IP, Memmott J (2015) The forgotten flies: the importance of non-syrphid Diptera as pollinators. *Proc R Soc B* 282:20142934
- Orr DB (1988) Scelionid wasps as biological control agents: a review. *Fla Entomol* 71:506–528
- Otvos IS (1973) Biological control agents and their role in the population fluctuation of the eastern hemlock looper in Newfoundland. *Environ. Can. Can. For. Serv. Newfoundland For. Res. Cent. St. John's, NF. N-X-102*
- Otvos IS, Bryant DG (1972) An extraction method for rapid sampling of eastern hemlock looper eggs, *Lambdina fiscellaria fiscellaria* (Lepidoptera: Geometridae). *Can Entomol* 104:1511–1514
- Oxbrough A, Ziesche TM (2013) Spiders in forest ecosystems. In: Kraus D, Krumm F (eds) Integrative approaches as an opportunity for the conservation of forest biodiversity. European Forest Institute, Chapter 3.6, pp 186–193
- Paine TD, Birch MC, Svihra P (1981) Niche breadth and resource partitioning by four sympatric species of bark beetles (Coleoptera: Scolytidae). *Oecologia* 48:1–6
- Parmenter RR, MacMahon JA (2009) Carrion decomposition and nutrient cycling in a semiarid shrub-steppe ecosystem. *Ecol Monogr* 79:637–661
- Paula MC, Morishita GM, Cavarson CH, Gonçalves CR, Tavares PRA, Mendonça A, Suarez YR, Antonialli WF Jr (2016) Action of ants on vertebrate carcasses and blow flies (Calliphoridae). *J Med Entomol* 53:1283–1291
- Payne JA (1965) A summer carrion study of the baby pig *Sus scrofa* Linnaeus. *Ecology* 46:592–602
- Pelletier G, Piché C (2003) Species of *Telenomus* (Hymenoptera: Scelionidae) associated with the hemlock looper (Lepidoptera: Geometridae) in Canada. *Can Entomol* 135:23–39
- Peters MK, Hemp A, Appelhans T, Behler C, Classen A, Detsch F, Ensslin A, Ferger SW, Frederiksen SB, Gebert F, Haas M, Helbig-Bonitz M, Hemp C, Kindeketa WJ, Mwangomo E, Ngereza C, Otte I, Röder J, Rutten G, Schellenberger Costa D, Tardanico J, Zancolli G, Deckert J, Eardley CD, Peters RS, Rödel M-O, Schleuning M, Ssymank A, Kakengi V, Zhang J, Böhning-Gaese K, Brandl R, Kalko EKV, Kleyer M, Nauss T, Tschapka M, Fischer M, Steffan-Dewenter I (2016) Predictors of elevational biodiversity gradients change from single taxa to the multi-taxa community level. *Nat Commun* 7:13736. <https://doi.org/10.1038/ncomms13736>

- Pham AT, De Grandpré L, Gauthier S, Bergeron Y (2004) Gap dynamics and replacement patterns in gaps of the northeastern boreal forest of Quebec. *Can J For Res* 34:353–364
- Pianka ER (1966) Latitudinal gradients in species diversity: a review of concepts. *Am Nat* 100:33–46
- Piaszczyk W, Lasota J, Blonska E (2020) Effect of organic matter released from deadwood at different decomposition stages on physical properties of forest soils. *Forests* 11:24
- Pilon J-G (1965) Bionomics of the spruce budmoth, *Zeiraphera ratzeburgiana* (Ratz.) (Lepidoptera: Olethreutidae). *Phytoprotection* 46:5–13
- Pohl GR, Langor DW, Spence JR (2007) Rove beetles and ground beetles (Coleoptera: Staphylinidae, Carabidae) as indicators of harvest and regeneration practices in western Canadian foothills forests. *Biol Cons* 137:294–307
- Pook VG, Sharkey MJ, Wahl DB (2016) Key to the Species of *Megarhyssa* (Hymenoptera, Ichneumonidae, Rhysinae) in America, North of Mexico. *Deutsche Entomologische Zeitschrift* 63:137–148
- Potapov P, Hansen MC, Laestadius L, Turubanova S, Yaroshenko A, Thies C, Smith W, Zhuravleva I, Komarova A, Minnemeyer S, Esipova E (2017) The last frontiers of wilderness: tracking loss of intact forest landscapes from 2000 to 2013. *Sci Adv* 3:e1600821
- Price PW (1984) *Insect ecology*, 2nd edn. Wiley, New York, NY
- Rafes P-M (1971) Pests and the damage which they cause to forests. In: Duvigneaud P (ed) *Productivité des écosystèmes forestiers*. Unesco, Paris, pp 357–367
- Régnier M (2020) Colonisation, par les insectes xylophages, du sapin baumier défolié par la tordeuse des bourgeons de l'épinette. MSc Thesis, Université Laval, 72 p
- Retallack GJ (1997) Early forest soils and their role in Devonian global change. *Science* 276:583–585
- Riechert SE, Lockley T (1984) Spiders as biological control agents. *Annu Rev Entomol* 29:299–320
- Ritter E, Dalsgaard L, Einhorn KS (2005) Light, temperature and soil moisture regimes following gap formation in a semi-natural beech-dominated forest in Denmark. *For Ecol Manage* 206:15–33
- Rivers JW, Galbraith SM, Cane JH, Schultz CB, Ulyshen MD, Kormann UG (2018) A review of research needs for pollinators in managed conifer forests. *J Forest* 116:563–572
- Rodrigues ASL, Brooks TM (2007) Shortcuts for biodiversity conservation planning: the effectiveness of surrogates. *Annu Rev Ecol Evol Syst* 38:713–737
- Root RB (1967) The niche exploitation pattern of the Blue-Gray Gnatcatcher. *Ecol Monogr* 37:317–350
- Roskov Y, Ower G, Orrell T, Nicolson D, Bailly N, Kirk PM, Bourgoin T, DeWalt RE, Decock W, van Nieukerken E, Zarucchi J, Penev L (eds) (2021) *Species 2000 & ITIS catalogue of life, 2021-06-10*. Digital resource at www.catalogueoflife.org. Species 2000: Naturalis, Leiden, the Netherlands. ISSN 2405-8858
- Saab VA, Latif QS, Rowland MM, Johnson TN, Chalfoun AD, Buskirk SW, Heyward JE, Dresser MA (2014) Ecological consequences of Mountain Pine Beetle outbreaks for wildlife in Western North American forests. *For Sci* 60:539–559
- Saint-Germain M, Drapeau P, Hébert C (2004) Comparison of Coleoptera assemblages from a recently burned and unburned black spruce forests of northeastern North America. *Biol Cons* 118:583–592
- Samways MJ (2007) Insect conservation: a synthetic management approach. *Annu Rev Entomol* 52:465–487
- Samways MJ (2018) Insect conservation for the twenty-first century. In: *Insect science—diversity, conservation and nutrition*. Intech Open, Chapter 2
- Samways MJ, Barton PS, Birkhofer K, Chichorro F, Deacon C, Fartmann T, Fukushima CS, Gaigher R, Habel JC, Hallmann CA, Hill MJ, Hochkirch A, Kaila L, Kwak ML, Maes D, Mammola S, Noriega JA, Orfinger AB, Pedraza F, Pryke JS, Roque FO, Settele J, Simaika JP, Stork NE, Suhling F, Vorster C, Cardoso P (2020) Solutions for humanity on how to conserve insects. *Biol Cons* 242:108427

- Schabel H (2010) Forest insects as food: a global review. In: Durst PB, Johnson DV, Leslie RN, Shono K (eds) *Forest insects as food: humans bite back*. Proceedings of a workshop on Asia-Pacific resources and their potential for development. 19–21 Feb 2008, Chiang Mai, Thailand, pp 37–64
- Schmitz OJ, Raymond PA, Estes JA, Kurz WA, Holtgrieve GW, Ritchie ME, Schindler DE, Spivak AC, Wilson RW, Bradford MA, Christensen V, Deegan L, Smetacek V, Vanni MJ, Wilmer CC (2014) Animating the Carbon cycle. *Ecosystems* 17:344–359
- Schwalter TD (2012) Insect herbivore effects on forest ecosystem services. *J Sustain For* 31:518–536
- Schwalter TD (2017) Arthropod diversity and functional importance in old-growth forests of North America. *Forests* 8:97. <https://doi.org/10.3390/f8040097>
- Schwalter TD, Noriega JA, Tschardt T (2018) Insect effects on ecosystem services – Introduction. *Basic Appl Ecol* 26:1–7
- Schütz S, Weissbecker B, Hummel HE, Apel K-H, Schmitz H, Bleckmann H (1999) Insect antenna as a smoke detector. *Nature* 398:298
- Scott MP (1998) The ecology and behavior of burying beetles. *Annu Rev Entomol* 43:595–618
- Scott MP, Gladstein D (1993) Calculating males? An empirical and theoretical examination of the duration of paternal care in burying beetles. *Evol Ecol* 7:362–378
- Scott AC, Stephenson J, Chaloner WG (1992) Interaction and coevolution of plants and arthropods during the Palaeozoic and Mesozoic. *Philos Trans R Soc Lond B* 335:129–165
- Seibold S, Gossner MM, Simons NK, Blüthgen N, Müller J, Ambar D, Ammer C, Bauhus J, Fischer M, Habel JC, Linsenmair KE, Nauss T, Penone C, Prati D, Schall P, Schulze E-D, Vogt J, Wöllauer S, Weisser WW (2019) Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature* 574:671–674
- Seibold S, Rammer W, Hothorn T, Seidl R, Ulyshen MD, Lorz J, Cadotte MW, Lindenmayer DB, Adhikari YP, Aragón R, Bae S, Baldrian P, Barimani Varandi H, Barlow J, Bässler C, Beauchêne J, Berenguer E, Bergamin RS, Birkemoe T, Boros G, Brandl R, Brustel H, Burton PJ, Cakpo-Tossou YT, Castro J, Cateau E, Cobb TP, Farwig N, Fernández RD, Firn J, Gan KS, González G, Gossner MM, Habel JC, Hébert C, Heibl C, Heikkala O, Hemp A, Hemp C, Hjältén J, Hotes S, Kouki J, Lachat T, Yu Liu JL, Luo Y-H, Macandog DM, Martina PE, Mukul SA, Nachin B, Nisbet K, O'Halloran J, Oxbrough A, Pandey JN, Pavlíček T, Pawson SM, Rakotondranary JS, Ramanamanjato J-B, Rossi L, Schmidl J, Schulze M, Seaton S, Stone MJ, Stork NE, Suran B, Sverdrup-Thygeson A, Thorn S, Thyagarajan G, Wardlaw TJ, Weisser WW, Yoon S, Zhang N, Müller J (2021) The contribution of insects to global forest deadwood decomposition. *Nature* 597:77–81. <https://doi.org/10.1038/s41586-021-03740-8>
- Shaw CH, Lundkvist H, Moldenke A, Boyle JR (1991) The relationships of soil fauna to long-term forest productivity in temperate and boreal ecosystems: processes and research strategies. In Dyck WJ, Mess CA (eds) *Long-term field trials to assess environmental impacts of harvesting*. Proceedings, IEA/BE T6/A6 Workshop, Florida, February 1990. IEA/BE T6/A6 Report No 5. Forest Research Institute, Rotorua, New Zealand, FRI Bulletin No 161, pp 39–77
- Shubeck PP (1985) Orientation of carrion beetles to carrion buried under shallow layers of sand (Coleoptera: Silphidae). *Entomol News* 96:163–166

- Siitonen J, Saaristo L (2000) Habitat requirements and conservation of *Pytho kolwensis*, a beetle species of old-growth boreal forest. *Biol Cons* 94:211–220
- Simberloff D, Dayan T (1991) The guild concept and the structure of ecological communities. *Annu Rev Ecol Syst* 22:115–143
- Skillen EL, Pickering J, Sharkey MJ (2000) Species richness of the Campopleginae and Ichneumoninae (Hymenoptera: Ichneumonidae) along a latitudinal gradient in eastern North America old-growth forests. *Environ Entomol* 29:460–466
- Slade EM, Mann DJ, Villanueva JF, Lewis OT (2007) Experimental evidence for the effects of dung beetle functional group richness and composition on ecosystem function in a tropical forest. *J Anim Ecol* 76:1094–1104
- Speight MC (1989) Saproxyllic invertebrates and their conservation. *Nature and Environment Series*, No 42. Council of Europe, Strasbourg. 79 p
- Speight MR, Hunter MD, Watt AD (2008) *Ecology of insects: concepts and applications*, 2nd edn. Wiley-Blackwell, Oxford, UK
- Spence JR (2001) The new boreal forestry: adjusting timber management to accommodate biodiversity. *Trends Ecol Evol* 16:591–593
- Spence JR, Langor DW, Niemelä JK, Cárcamo HA, Currie CR (1996) Northern forestry and carabids: the case for concern about old-growth species. *Ann Zool Fenn* 33:173–184
- Stenbacka F, Hjalten J, Hilszczanski J, Ball JP, Gibb H, Johansson T, Pettersson RB, Danell K (2010) Saproxyllic parasitoid (Hymenoptera, Ichneumonidea) communities in managed boreal forest landscapes. *Insect Conserv Divers* 3:114–123
- Stephenson NL, Das AJ, Ampersee NJ, Bulaon BM, Yee JL (2018) Which trees die during drought? The key role of insect host tree selection. *J Ecol* 107:2383–2401
- Steuer P, Sudekum K-H, Tutken T, Muller DWF, Kaandorp J, Bucher M, Clauss M, Hummel J (2014) Does body mass convey a digestive advantage for large herbivores? *Funct Ecol* 28:1127–1134
- Stireman JO III (2002) Host location and selection cues in a generalist tachinid parasitoid. *Entomol Exp Appl* 103:23–34
- Stokland JN (2012) The saproxyllic food web. In: Stokland JN, Siitonen J, Jonsson BG (eds) *Biodiversity in dead wood*. Cambridge University Press, Cambridge.
- Stork NE (2018) How many species of insects and other terrestrial arthropods are there on Earth? *Annu Rev Entomol* 63:31–45
- Strid Y, Schroeder M, Lindahl B, Ihrmark K, Stenlid J (2014) Bark beetles have a decisive impact on fungal communities in Norway spruce stem sections. *Fungal Ecol* 7:47–58
- Strong DR, Levin DA (1979) Species richness of plant parasites and growth form of their hosts. *Am Nat* 114:1–22
- Strong DR, Lawton JH, Southwood R (1984) *Insects on plants: community patterns and mechanisms*. Blackwell Scientific Publications, Harvard University Press, Cambridge, MA
- Suzuki S (2000) Carrion burial by *Nicrophorus vespilloides* (Coleoptera: Silphidae) prevents fly infestation. *Entomol Sci* 3:269–272
- Suzuki S (2001) Suppression of fungal development on carcasses by the burying beetle *Nicrophorus quadripunctatus* (Coleoptera: Silphidae). *Entomol Sci* 4:403–405
- Swift MJ, Heal OW, Anderson JM (1979) *Decomposition in terrestrial ecosystems*. University of California Press, Berkeley and Los Angeles
- Taylor BR, Parkinson D, Parsons WFJ (1989) Nitrogen and lignin content as predictors of litter decay rates: a microcosm test. *Ecology* 70:97–104
- Taylor SL, MacLean DA (2009) Legacy of insect defoliators: increased wind-related mortality two decades after a spruce budworm outbreak. *For Sci* 55:256–267
- Thompson BM, Bodart J, McEwen C, Gruner DS (2014) Adaptations for symbiont-mediated external digestion in *Sirex noctilio* (Hymenoptera: Siricidae). *Ann Entomol Soc Am* 107:453–460
- Thompson JN (1994) *The coevolutionary process*. University of Chicago Press, Chicago, IL
- Thorn S, Bässler C, Brandl R, Burton PJ, Cahall R, Campbell JL, Castro J, Choi C-Y, Cobb T, Donato DC, Durska E, Fontaine JB, Gauthier S, Hébert C, Hothorn T, Hutto RL, Lee E-J, Leverkus AB, Lindenmayer DB, Obrist MK, Rost J, Seibold S, Seidl R, Thorn D, Waldron K, Wermelinger

- B, Winter MB, Zmihorski M, Müller J (2018) Impacts of salvage logging on biodiversity: a meta-analysis. *J Appl Ecol* 55:279–289. <https://doi.org/10.1111/1365-2664.12945>
- Thorpe HC, Thomas SC (2007) Partial harvesting in the Canadian boreal: success will depend on stand dynamic responses. *For Chron* 83:319–325
- Townes H, Townes, M (1960) Ichneumon-flies of America North of Mexico: subfamilies Ephialtinae, Xoridinae, Acaenitinae. United States National Museum Bulletin 216, Part 2. Smithsonian Institution Press, Washington, 676 p
- Trumbo ST (1994) Interspecific competition, brood parasitism, and the evolution of biparental cooperation in burying beetles. *Oikos* 69:241–249
- Ulyshen MD (2016) Wood decomposition as influenced by invertebrates. *Biol Rev* 91:70–85
- United Nations (1992) Convention on biological diversity. 28 p. <https://www.cbd.int/convention/text/>
- Vergutz L, Manzoni S, Porporato A, Ferreira Novas R, Jackson RB (2012) Global resorption efficiencies and concentrations of carbon and nutrients in leaves of terrestrial plants. *Ecol Monogr* 82:205–220
- Vidal MC, Murphy SM (2018) Bottom-up vs. top-down effects on terrestrial insect herbivores: a meta-analysis. *Ecol Lett* 21:138–150
- Vindstad OPL, Schultze S, Jepsen JU, Biuw M, Kapari L, Sverdrup-Thygeson A, Ims RA (2014) Numerical responses of saproxylic beetles to rapid increases in dead wood availability following Geometrid moth outbreaks in sub-arctic mountain birch forest. *PLoS ONE* 9:e99624
- Wagner DL (2020) Insect declines in the Anthropocene. *Annu Rev Entomol* 65:457–480
- Warkentin IG, Bradshaw CJA (2012) A tropical perspective on conserving the boreal ‘lung of the planet.’ *Biol Cons* 151:50–52
- Warren MS, Key RS (1991) Woodlands: past, present and potential for insects. In: Collins NM, Thomas JA (eds) *The conservation of insects and their habitats*. Academic Press, London, pp 155–212
- Watkins E, Kitching RL, Nakamura A, Stork NE (2017) Beetle assemblages in rainforest gaps along a subtropical to tropical latitudinal gradient. *Biodivers Conserv* 26:1689–1703
- Wenny DG (2001) Advantages of seed dispersal: a re-evaluation of directed dispersal. *Evol Ecol Res* 3:51–74
- Wermelinger B, Duelli P, Obrist MK (2002) Dynamics of saproxylic beetles (Coleoptera) in windthrow areas in alpine spruce forests. *For Snow Landsc Res* 77:133–148
- Wermelinger B, Moretti M, Duelli P, Lachat T, Pezzatti GB, Obrist MK (2017) Impact of windthrow and salvage-logging on taxonomic and functional diversity of forest arthropods. *For Ecol Manage* 391:9–18
- Wikars L-O (1997a) Pyrophilous insects in orsa Finnark, central Sweden: biology, distribution and conservation. *Entomol Tidskr* 118:155–169
- Wikars L-O (1997b) Effects of forest fire and the ecology of fire-adapted insects. *Acta Univ. Ups. Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science and Technology* 272.35 pp. Uppsala. ISBN 91 -554-3954-3
- Wikars L-O (2002) Dependence on fire in wood-living insects: an experiment with burned and unburned spruce and birch logs. *J Insect Conserv* 6:1–12
- Willig MR, Kaufman DM, Stevens RD (2003) Latitudinal gradients of biodiversity: pattern, process, scale and synthesis. *Annu Rev Ecol Evol Syst* 34:273–309
- Wilson GG (1973) Incidence of microsporidia in a field population of spruce budworm. *Environ. Can. For. Serv. Bi-Monthly Research Notes* 29:35–36
- Wilson EE, Wolkovitch EM (2011) Scavenging: how carnivores and carrion structure communities. *Trends Ecol Evol* 26:129–135
- Wilson MF, Traverset A (2000) The ecology of seed dispersal. In: Fenner M (ed) *Seeds: the ecology of regeneration in plant communities*, 2nd edn, Chapter 4, pp 85–110
- Wirth C, Gleixner G, Heimann M (2009) Old-growth forests: function, fate and value—an overview. In: Wirth C, et al (eds) *Old-growth forests*. Ecological Studies 207. Springer-Verlag, Berlin Heidelberg, Chapter 1

- Yang LH (2004) Periodical Cicadas as resource pulses in North American forests. *Science* 306:1565–1567
- Yang LH, Gratton C (2014) Insects as drivers of ecosystem processes. *Curr Opin Insect Sci* 2:26–32
- Zanella A, Ponge J-F, Briones MJI (2018) Humusica 1, article 8: terrestrial humus systems and forms – Biological activity and soil aggregates, space-time dynamics. *Appl Soil Ecol* 122:103–137
- Zimmer M, Topp W (2002) The role of coprophagy in nutrient release from feces of phytophagous insects. *Soil Biol Biochem* 34:1093–1099

Open Access This chapter is licensed under the terms of the Creative Commons Attribution 4.0 International License (<http://creativecommons.org/licenses/by/4.0/>), which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license and indicate if changes were made.

The images or other third party material in this chapter are included in the chapter's Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the chapter's Creative Commons license and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder.

