Chapter 4
Insect Ecology

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4.1 Introduction

Insect ecology is the study of how insects interact with the environment. The environment consists of both physical characteristics (abiotic) and other organisms (biotic). Insects are natural components of forests and perform a variety of essential functions that help maintain forests as ecosystems. As consumers of forest products, people sometimes compete with insects for forest resources. Most research and management efforts in forest entomology have focused on insects that damage or kill large numbers of ecologically or economically important trees. In this chapter, we consider the various environmental challenges that confront forest insects, and the adaptations they have evolved to be successful in forest ecosystems.

4.2 Insects Assume Many Roles in Forests

Insects are ubiquitous in forests because of many remarkable adaptations that allow them to survive and reproduce. They perform a wide variety of functions that influence and maintain ecosystem services. These functional roles fit into a hierarchy of trophic levels, characterized by who eats who (Price et al. 2011; Speight et al. 2008). Plants are primary producers because they convert electromagnetic energy (light) into chemical energy through photosynthesis. Herbivorous insects (and other animals) that eat seeds, flowers, leaves, stems, roots, or other plant parts are primary consumers. Insects (and other animals) that are predators and parasitoids that prey

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on herbivores are secondary consumers. A hyperparasitoid, a parasitoid that attacks another parasitoid, is an example of a tertiary consumer (Hajek 2004). Insects serve as prey for many other tertiary and quaternary consumers (mammals, reptiles, and birds). Some insects are detritivores (also called saprophages or decomposers) that consume and break apart organic matter (dead plants, animals, and fungi). The organic matter is subsequently recycled into its nutrient components by microbes (bacteria and fungi) and primary producers ultimately use the nutrient components. Feeding guilds are composed of consumers at the same trophic level, which in the case of forest insects, may be even further specialized. For example, seed and cone insects feed on reproductive tissue of trees, woodborers feed in woody tissue of trees, and sap feeders extract liquid from inside leaves or bark. Producers and consumers in a forest community form complex networks, or webs, rather than a simple food chain, because consumers often feed on more than one species of prey (and trophic level). Fundamentally, this web explains nutrient and energy flow, and cycles within forest ecosystems.

Forest insects can affect the balance in nutrient and energy flow from primary producers through all levels of consumers to decomposers. A natural component of forest ecosystems, insect populations (a group of individuals of the same species that inhabit an area) that increase to outbreak levels and cause landscape-scale tree mortality are agents of disturbance that can selectively kill certain tree species. Insect outbreaks can alter the structure, age class diversity, and composition of forest patches on the landscape, and in extreme cases this may re-set forest succession to an earlier stage (Coulson and Stephen 2006). Succession is the natural and predictable process of change in the forest community over time, from the earliest colonizers (e.g. fast-growing trees and other plants that are poor competitors and thrive in sunny conditions), to the latest (climax) colonizers (e.g. slow-growing trees and other plants that are good competitors and tolerant of shade).

The balance in nutrient and energy flow may be altered if a non-native species is introduced to a forest (Gandhi and Herms 2010), or if a native species expands its range into a forest it has not previously occupied. Some non-native species are more disruptive to nutrient and energy flow than others. For instance, the hemlock woolly adelgid, *Adelges tsugae* (Annand), threatens to kill nearly all eastern hemlock in North America (Ellison et al. 2005). In hemlock forests, wildlife and ecosystem processes (nutrient cycling, hydrology) depend heavily on eastern hemlock as a foundation species. Hemlock mediates soil moisture levels, stabilizes stream flow, and decreases daily variation in stream temperatures, which results in a community of freshwater invertebrates and other animals that cannot survive in a forest without hemlock (Ellison et al. 2005). In contrast, some invasive species seem to pose little threat to critical ecosystem functions and behave much like naturalized residents. For instance, the European woodwasp, *Sirex noctilio* F., mainly kills non-competitive and otherwise stressed pines in northeastern North America, and seems to coexist with a suite of other subcortical pine insects, essentially functioning as a forest thinning agent (Dodds et al. 2010; Foelker 2016; Haavik et al. 2018). When considering an insect a forest pest, it is important to keep in mind its natural functional role in the food web. If its presence or activity has altered the function/s of other members of

the web, such as with hemlock woolly adelgid, then the ecological balance of the system will be disrupted.

4.3 Species Interact in Many Ways

Forest insects have a variety of different relationships with other species. These symbiotic relationships often facilitate acquisition of resources for one or more members of the association. They are best considered on a continuum, in which the relationship between two species ranges from positive, to neutral, to negative (Price et al. 2011) (Fig. 4.1). These relationships are fluid, and sometimes difficult to delineate. They can change throughout insect life cycles, in different environments, and throughout evolutionary time in response to varying selection pressures.

Interactions between herbivorous insects and trees are of particular concern to forest scientists and managers. These interactions might have negative outcomes for the tree and the forest products it provides. Insects gain nutrition from feeding on a tree organ (e.g. cones or acorns, leaves, bark, phloem, wood, or roots); as a result, the tree can lose essential reproductive, photosynthetic, vascular, structural, or nutrient-acquiring tissue. Alternatively, the interaction could be positive. Pollination is a classic example of mutualism: pollinating insects (e.g. beetles, butterflies, moths, bees, ants) gain nutrition from the plant by feeding on nectar or pollen, and the plant gains a method of dispersal for its genes, as the insect carries pollen grains from one plant to fertilize another. In mutualistic partnerships, insects often serve as dispersal

Fig. 4.1 Possible relationships between two species, A and B. Adapted from and see Price et al. (2011) page 234 for details
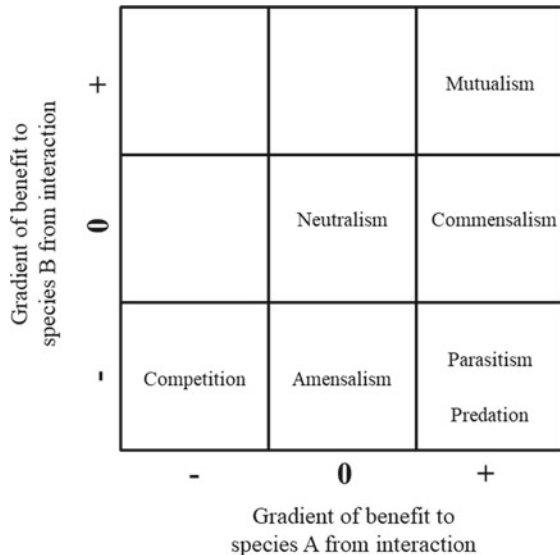
agents for organisms that lack or have limited mobility, such as fungi, mites, plants, or nematodes.

More complex, multi-species symbiotic relationships among forest insects and other organisms involve bark beetles, several other insects, mites, and fungi (Hofstetter et al. 2015). A well-known example is the southern pine beetle, *Dendroctonus frontalis* Zimmerman, system. Southern pine beetles often carry three different species of fungi on their bodies or in specialized structures termed mycangia. All three fungi gain dispersal from the beetles and grow in phloem or xylem tissues. Two fungi compete with one another for phloem and are clear mutualists for the beetle, creating a more nutritious substrate than pine phloem for beetle larvae to eat. The role of the third fungal species is under debate, and seems to be important for initial colonization of the tree (Klepzig and Hofstetter 2011). Southern pine beetles also carry mites, in a potentially commensal manner, because the mites benefit from transportation by the beetles, though a strong positive or negative effect on the beetles has not yet been observed (Klepzig and Hofstetter 2011). In addition, by colonizing and killing pines, southern pine beetles facilitate a suitable food resource (dying trees) for over 100 other insects, including *Ips* bark beetles and wood borers (primarily *Monochamus* species), some of which will ultimately compete with one another for phloem (Dixon and Payne 1979).

Competitive interactions beneath the bark of southern pines have been difficult to specify, partly because the habitat is cryptic and partly because the resource is ephemeral. The southern pine sawyer, *Monochamus titillator* (F.), is attracted to and develops in stressed, damaged and weakened pine trees. Adult *Monochamus* are attracted to host trees by a combination of host volatiles, including α-pinene and ethanol. Ipsenol, the aggregation pheromone of *Ips* bark beetles, is also a powerful attractant to many *Monochamus* species (Allison et al. 2001; Miller et al. 2013). *Monochamus* beetles are much larger than bark beetles, and consequently consume much more phloem. Laboratory and field studies found that *Monochamus* larvae will feed on bark beetle larvae in the phloem, termed facultative intraguild predation (Dodds et al. 2001; Schoeller et al. 2012). *Monochamus* larvae can thus outcompete bark beetle larvae for phloem indirectly and feed on them directly. *Monochamus titillator* may be an important facultative natural enemy of bark beetles, potentially contributing to the collapse of southern pine beetle infestations (Stephen 2011). In addition, there are numerous parasitoids, as well as predators, that comprise the natural enemy complex that preys upon southern pine beetle and its phloem-consuming associates (Stephen et al. 1993). Many other complex relationships among species in forest ecosystems remain undescribed.

4.4 Life Histories Vary

In order to survive from egg to adult, and to reproduce successfully, insects must escape or endure environmental extremes, avoid predation, avoid or endure parasitism, acquire the nutrients necessary to grow, and find mates. Forest insects have

evolved a myriad of adaptations to cope with these environmental challenges. Many theoretical categories have been developed to group species with similar adaptations, life history traits, and the trade-offs that accompany them. Below, we consider some of these important ideas as they relate to forest insects.

4.4.1 K- and r-Selection: Forces in the Environment Dictate Reproductive Adaptations

MacArthur and Wilson (1967) introduced the idea of natural selection operating to favor high reproductive ability (r) for individuals occurring in uncrowded populations, and to favor competitive ability (K) in crowded populations (see Fig. 4). This idea has been modified, adapted and criticized by numerous authors since its inception. Interpreted as a general framework, it can be a useful tool to evaluate the relative importance of challenges posed to insects by biotic versus abiotic components of the environment (Table 4.1).

Species that reside in harsh habitats, where climatic conditions may be extreme or unpredictable, may share some common life history characteristics (Table 4.1). Species that are small in size, short lived, have high dispersal abilities, and a high population growth rate are said to be r-selected. They are likely to have high fecundity, reproduce early in their life, and reproduce only once. They often exist in early stage successional environments, at population levels well below the carrying capacity of the environment, and the mortality they incur is often from density-independent factors (see Chapter 5).

r-Selected species can be contrasted with species living in habitats that are environmentally stable. For these K-selected species, body size tends to be larger, and individuals live longer, disperse less, and have a lower population growth rate. They may reproduce later in life, and more than once. They produce fewer eggs but invest more energy in each one. They are effective competitors, and their population densities are often nearer to the carrying capacity of the environment (see Sect. 4.6.1). The mortality factors that affect their populations are normally from biotic, density-dependent agents (see Chapter 5).

Some bark beetles could be considered r-selected species, because they are extremely small (only a few mm in length), reproduce in great numbers (100 or so eggs per female) and develop in a nutrient-poor, ephemeral environment (phloem of dying trees). In comparison, their parasitoid natural enemies could be considered K-selected, because they reproduce in fewer numbers (10s of eggs per female), often have lower population growth rates, and develop in a nutrient-rich, relatively stable environment (often feeding within the bodies of developing bark beetles). It is important to remember that the concepts of r and K strategies in relation to life history traits are meaningful only in a relative sense. A given organism is more or less an r strategist only in comparison with another organism, for example.

Table 4.1 Generalized characteristics of insects, populations, processes and environments in relation to r- and K-selection

Characteristic	r-selected	K-selected
Body size	Small	Large
Colonization ability	Opportunistic	Non opportunistic
Dispersal ability	High	Low
Development rate	Fast	Slow
Egg size	Small	Large
Fecundity	High	Low
Parental investment in offspring	Small	Large
Longevity	Short	Long
Age of reproduction	Early	Late
Frequency of reproduction	Once (few)	Repeated (many)
Intrinsic rate of increase	High	Low
Population density level	Fluctuating	Stable
Intraspecific competition	Scramble	Contest
Sex ratio	Female biased	Neutral
Ecological succession	Early seres	Late (climax)
Density in relation to carrying capacity	Well below	At or near
Importance of density-dependent processes	Less important	Very important

Adapted from MacArthur and Wilson (1967), Price et al. (2011), and Speight et al. (2008)

4.4.2 Some Insects Specialize by Feeding on Trees in a Particular Condition

Some herbivorous forest insects have been categorized by the condition of the host tree that they typically colonize. This helps forest managers predict which trees and whether a large number of them are likely to be damaged or killed. Bark and woodboring beetles have been grouped as follows: (1) primary bark beetles and wood borers are capable of colonizing healthy trees; (2) secondary bark beetles and wood borers colonize trees that have been stressed or weakened by some other biotic agent or abiotic factor; and (3) saprophytic bark beetles and wood borers colonize dead, or extremely moribund, trees (Hanks 1999; Lindgren and Raffa 2013; Raffa et al. 2015). These groupings can be further subdivided or even considered fluid for

some species, especially those that typically attack stressed trees, though are able to colonize healthy trees during outbreaks.

There are far fewer species of primary bark beetles than secondary bark beetles. It has been hypothesized that this may be because primary species have highly specific adaptations to overcome tree resistance mechanisms and to establish associations with symbionts (Lindgren and Raffa 2013). These adaptations likely evolved from intense competition with other species for ephemeral host resources, i.e. dying trees (Lindgren and Raffa 2013). Primary bark beetles such as the southern and mountain pine beetles, *D. frontalis* and *D. ponderosae* (Hopkins), are of significant concern to forest managers because when their densities reach outbreak levels, they have the capacity to kill large numbers of trees very quickly, and outbreaks continue until all suitable trees have been killed. Secondary bark beetles, such as engravers, e.g. *Ips pini* (Say), *Ips grandicollis* (Eichhoff), and *Ips confusus* (LeConte), can also be a threat, especially following environmental disturbance, such as wildfire or drought, although their populations return to low levels once environmental stress has abated.

Much less is known regarding the primary vs. secondary nature of wood borers. Most economically important wood borers are secondary mortality agents that can become aggressive during periods of environmental stress, especially in their native habitats on their co-evolved hosts. Although some, such as the emerald ash borer, *Agrilus planipennis* Fairmaire, Asian longhorned beetle, *Anoplophora glabripennis* (Motschulsky), and the European woodwasp, *Sirex noctilio* F., have aggressively killed apparently healthy trees outside of their native geographical and host ranges. Wood borers that colonize healthy trees usually inhabit branches or twigs and rarely outbreak or kill trees (Solomon 1995). When outbreaks of wood borers do occur, the impact is usually far less severe than an outbreak of primary bark beetles.

Foliage feeders have been termed primary insects (Jactel et al. 2012; Manion 1991), because they also feed on healthy trees and can have landscape-scale impacts. It is not clear whether defoliators consistently prefer trees of a particular condition (Jactel et al. 2012), though outbreaks are often linked to weather (Haynes et al. 2014; Myers 1998), and weakened trees are usually the first and most likely individuals to die from defoliation (Davidson et al. 1999). Major defoliators in North America, such as eastern and western spruce budworms, *Choristoneura fumiferana* (Clemens) and *C. freemani* (syn *occidentalis*) (Freeman), respectively; the non-native European spongy moth, *Lymantria dispar dispar* (L.); Douglas-fir tussock moth, *Orgyia pseudotsugata* (McDunnough); and forest tent caterpillar, *Malacocoma disstria* Hübner, can consume entire forest canopies during outbreaks. Many of these species repeatedly defoliate the same trees for several successive years, which leads to branch dieback and top kill, and sometimes mortality. Most importantly, though, repeated defoliation weakens trees and makes them more susceptible to secondary insects and diseases (Manion 1991). For instance, even though the polyphagous European spongy moth will consume foliage from trees of all susceptible species in a stand, stressed or suppressed trees, especially oaks, will die first (Davidson et al. 1999). Stressed oaks are then usually killed by the secondary mortality agents, twolined chestnut borer, *Agrilus bilineatus* (Weber), and *Armillaria* spp. root disease (Wargo 1977). Healthy oaks that are completely defoliated in spring can draw on stored carbon reserves to

re-foliate by summer (Davidson et al. 1999). However, repeated severe defoliation weakens healthy oaks enough that they can also be killed by twolined chestnut borer or *Armillaria* spp. or both (Wargo 1977).

All herbivorous insects face many environmental challenges that affect their ability to colonize and gain sufficient nutrition from their hosts including weather, natural enemies, and plant resistance (defense) (Cornell and Hawkins 1995; Herms and Mattson 1992); which of those is most influential depends on the insect species, environmental conditions, and how environmental conditions impact the host plant. There is strong selection for various adaptations to avoid, tolerate, overcome, or detoxify physical and chemical mechanisms of plant resistance (see Chapter 7). It is useful to think of primary, secondary, and saprophytic forest insects on a continuum, where a species may tend towards one or the other extreme depending on environmental factors and how those factors affect the insects and the condition of their host trees.

4.5   Abiotic Conditions Alter Insect Growth and Survival

In addition to biotic elements, insects are challenged by the physical or environmental characteristics of forest habitats. Important abiotic factors that affect insects are temperature and moisture (precipitation), which we will consider directly in relation to forest insects and indirectly through the trees that they eat. Environmental conditions that influence insects as individuals or at the population level include extreme weather and regional climate or weather patterns. If abiotic conditions trigger an increase or decrease in the size of a forest insect population, the amount of damage to trees is also likely to change.

4.5.1   Temperature Affects Behavior and Development

Insects are poikilothermic animals, meaning they do not regulate their own body temperature. Consequently, ambient temperatures dictate aspects of insect behavior and development. Many insects in temperate climates possess behavioral and physiological adaptations to tolerate or avoid extreme cold (Danks 1978). Insects may undergo a dormant period during winter. This escape of harsh environmental conditions in time is categorized as a diapause that is genetically programmed and is either obligate, occurring at a specific time during development, or facultative, dictated by adverse environmental conditions. Alternatively, some insects only undergo a quiescence, initiated by unfavorable conditions, after which development resumes. During the dormant period, a series of energetically expensive biochemical changes occur that involve synthesis of glycerol and other cryoprotectants that act through several mechanisms as solutes to slow the formation of ice within cells (Danks 1978). The supercooling point, the temperature at which insect body fluids begin to freeze, and

the lower lethal temperature, the point at which mortality occurs, both vary seasonally within and among insect species and populations. For instance, cold tolerance of larch casebearer, *Coleophora laricella* Hübner, was greatest in mid-winter and reduced in spring and autumn (Ward et al. 2019). Investigating insect cold tolerance can be especially useful for predicting suitable geographic range of introduced insects or even for native species undergoing range expansion.

Migration represents the most extreme behavioral adaptation to avoid cold in space. Monarch butterflies, *Danaus plexippus* (L.), are an excellent example of insects that overwinter in forest canopies in southern California, Florida, or Mexico, and travel northward throughout the growing season, with some populations reaching Canada (Solensky and Oberhauser 2004). On a more local scale, the microhabitat in which forest insects overwinter can provide some protection from the cold. Many bark- or wood-boring insects overwinter as adults or larvae under the bark, which can be several degrees warmer than the surrounding air temperature (Vermunt et al. 2012). Some foliage feeding insects overwinter at the base of trees in the soil or leaf litter, which also offers insulation from the cold. Others overwinter in the egg stage in bark crevices or other protected places.

Adult insects are often more active during warm, favorable weather. Females may seek warm, bright locations to lay eggs. For instance, emerald ash borer and bronze birch borer, *Agrilus anxius* Gory, females prefer to oviposit on the sunny, southern exposures of tree trunks (Akers and Nielsen 1990; Timms et al. 2006).

Temperature also regulates the rate at which insects develop. Typically, there is a lower temperature threshold below which development does not occur, an optimum temperature at which development is most rapid, and above the optimum, development rate slows until the upper temperature threshold is reached and mortality occurs (Fig. 4.2). For instance, larvae of the Pales weevil, *Hylobius pales* (Herbst), require about 220 days to complete development at 9 °C, 27 days at 30 °C, and 37 days at 32 °C (Salom et al. 1987). Small changes in weather and climate can therefore translate to large changes in generation time. For example, larval development in the six-spined engraver, *Ips calligraphus* (Germar), can range from 18 to 224 days, depending on temperature (Wagner et al. 1987). Generation time is somewhat plastic for many subcortical forest insects, and variations are usually related to regional weather or climate, which are predictable by latitude and elevation. The southern pine beetle is an extreme example, and completes between one and nine generation(s) per year, developing from egg to adult in 26–54 days, dependent upon geographic location in its range (Hain et al. 2011; Thatcher 1960, 1967), which is directly related to growing season length and ultimately temperature.

The tight link between temperature and insect development rate can facilitate accurate predictions of seasonal timing of different insect life stages, particularly adult flight. Degree-day models rely on this premise. The number of heat units (°F or °C) that accumulate above a certain minimum threshold temperature at which insect development proceeds—or conversely, is halted below that threshold (Higley et al. 1986)—is typically calculated during a growing season and can be used to predict when certain insect life stages are present in the forest.
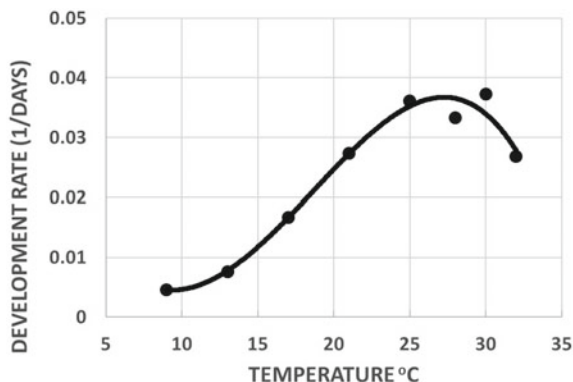
Fig. 4.2 Development rate curve for pales weevil, *Hylobius pales*, larvae at constant temperatures. Dots represent the observed median development rates and the solid line the predicted values over the range of observed development. Lower development threshold (or base temperature) is ca. 9 °C, optimum is ca. 27 °C and upper threshold is ca. 32 °C. Data and adapted figure from Salom et al. (1987)

4.5.2 Precipitation Indirectly Affects Insects by Its Impacts on Trees

Some forest insect outbreaks are linked to drought (Jactel et al. 2012; Mattson and Haack 1987a). Outbreaks of several *Dendroctonus*, *Ips*, *Scolytus*, and *Agrilus* species are often preceded by warm and dry environmental conditions (Mattson and Haack 1987a). It is thought that changes in tree physiology induced by periods of insufficient soil moisture improve suitability of trees for insect growth and development, which in turn results in greater insect survival and reproduction, and increased population growth (see Sect. 4.6). These physiological changes are either related to compromised resistance (defense) or enhanced nutritional value of drought-stressed trees (Mattson and Haack 1987b; Rhoades 1979, 1985; White 1984).

Trees have various mechanisms to tolerate or minimize the effects of drought (Bréda et al. 2006; Pallardy 2008). One mechanism is to adjust solute content in cells, which prevents water loss, by break-down and mobilization of sugars and proteins (i.e. osmotic adjustment). This process presumably makes these essential nutrients more readily available for insect consumption (White 1984). There has been indirect, observational evidence in several feeding guilds that supports this claim and the general theory that plant stress results in improved insect performance (White 2015), but experimental support is lacking. Relationships among environmental stress, insects, and their host trees that result in altered nutrition for insects are likely complex and variable in time.

Trees can invest vast amounts of energy into resisting or tolerating insect attack. For instance, the outcome of bark beetle attack and subsequent colonization of conifers is completely dependent on tree resistance, usually through two systems, constitutive and induced, related to resin production (Berryman 1972; Raffa and

Berryman 1983) (see Chapter 7). If one or both of those systems is compromised as soil moisture becomes limiting for trees, then bark beetles may be more likely to successfully colonize trees or produce more progeny or both. For example, experimental drought predisposed piñon pine, *Pinus edulis*, to bark beetle attack and subsequent mortality (Gaylord et al. 2013), although reduced resin flow was only partially responsible (Gaylord et al. 2015). Resistance in hardwoods has been less studied, but appears to be related to overall tree health and vigor. For instance, landscape-scale oak mortality may result from repeated drought that eventually causes imbalance in carbon storage and use, which reduces tolerance to colonization by secondary wood borers (Haavik et al. 2015).

The degree to which enhanced nutritional value or reduced resistance capacity, or both, contribute to improved conditions for insects when trees are stressed by drought is not completely understood, and is likely variable spatially and temporally. Ultimately, trees must balance energy investment among growth, maintenance, defense, and reproduction (Herms and Mattson 1992). Inadequate precipitation can cause the re-distribution or depletion of energy supplies and stores or both, and some insects may take advantage of this situation. Not all forest insects benefit from drought. The relationship between drought and insect damage to trees is complex and seemingly related to whether the insect species is primary or secondary in nature, its feeding guild, and the severity of drought (Huberty and Denno 2004; Jactel et al. 2012).

4.5.3 *Extreme Weather Can Have Indirect Effects Through Trees*

Weather events of shorter duration than prolonged stressors like drought can also weaken trees and render them more suitable hosts for insects. For example, frosts that occur late in spring, once hardwoods have already leafed out, temporarily alter normal physiological functions, and may deplete energy reserves needed to defend against insects and diseases. Late-spring frosts have contributed to outbreaks or greater abundance of several forest insects, including twolined chestnut borer (Nichols 1968; Staley 1965), oak splendor beetle, *A. biguttatus* (Fabricius) (Hartmann and Blank 1992; Thomas et al. 2002), and sugar maple borer, *Glycobius speciosus* (Say) (Horsley et al. 2002). Ice storms, tornadoes, or other blowdowns that cause breakage of tree limbs and branches also facilitate increased survival and population growth of insects by providing abundant, yet ephemeral host material for reproduction and development. Some forest insects specialize on broken branches and stems. Pine engravers, *Ips* spp.; Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins; the European spruce bark beetle, *Ips typographus* (L.); and the European pine shoot beetle, *Tomicus piniperda* (L.) readily colonize windthrown and freshly cut trees (Gothlin et al. 2000; Rudinsky 1966; Schlyter and Lofqvist 1990).

4.5.4 Climate and Weather Patterns Affect Population Density of Insects Regionally

Fluctuations in insect population density often occur at the same time over large geographic areas, in regions of forest not immediately adjacent to one another. This synchronous timing of landscape-scale insect outbreaks may be driven by large-scale weather and climate patterns. This phenomenon is termed the Moran effect (Moran 1953) and emphasizes the influence of factors acting at larger scales than within a single stand or forest on outbreaks of forest insects. The Moran effect seems to be important in the population dynamics of several different defoliator species, and weather plays at least a partial role. For example, spatially synchronous outbreaks of European spongy moth were determined to be most likely driven by patterns of rainfall (Haynes et al. 2013). Jack pine budworm, *Choristoneura pinus pinus* Freeman, outbreaks are often synchronous across the landscape as well, which could signify Moran processes, but other factors such as budworm dispersal have not been ruled out (McCullough 2000). Similarly, climatic variation was correlated with regional outbreaks of eastern spruce budworm, though spatial variation in outbreaks was more closely linked to forest landscape structure and management history (Robert et al. 2018). Cool springs, which were also associated with a certain point in the sunspot cycle, coincided with outbreaks of several different forest caterpillars on three continents (Myers 1998).

Weather patterns could influence insect development directly or indirectly through the effects on hosts or natural enemies. Spring temperatures are especially important, as insects exit diapause or quiescence, and resume development (see Sect. 4.5.1). Cool springs could directly cause insects to become active later in the season, whereas warm springs may initiate insect activity earlier. Indirectly, timing of budburst is important for foliage feeders that eat new buds or flowers. To avoid reduced fitness (survival or fecundity), these insects, such as western and eastern spruce budworms and winter moth, *Operophtera brumata* (L.), need to be phenologically synchronized with their hosts (van Asch and Visser 2007). A departure from normal spring temperatures can cause a phenological mismatch with budburst for some of these defoliators, which could affect outbreak frequency or intensity (Pureswaran et al. 2015; Visser and Holleman 2018). Prevalence or spread of natural enemies can also be affected by regional or local weather patterns. Cool, wet springs are favorable for spread of *Entomophaga miamaiga*, a fungal pathogen of European spongy moth (Hajek and Tobin 2011), which may influence the collapse of spongy moth outbreaks (Hajek et al. 2015). Thus, in a variety of ways, regional weather patterns can have landscape-scale influence over forest insect activity.

4.6 Insect Population Growth Is a Function of Births, Deaths, and Movement

Abundance of herbivorous insects in a forest usually indicates whether they are likely to be a problem. In other words, are numbers high enough that they will damage or kill an economically or ecologically significant number of trees? Insect abundance per unit area, or population density, and what factors drive changes in population density over time are of critical importance to understanding and predicting the status of pest insects. The number of insects in a population at a given time (N_{t+1}) is determined by the number at a previous time (N_t, when the population was last measured) plus the number of new young ($B = births$), minus the number that perished ($D = deaths$), plus the number that migrated into the population ($I = immigration$), and minus the number that migrated out of the population ($E = emigration$).

$$N_{t+1} = N_t + B - D + I - E \tag{4.1}$$

A population can grow exponentially. If every female is replaced by two females in the subsequent time period (or generation), then the population is growing by a factor of two (i.e. the growth multiplier or finite rate of increase, λ, is two). This is often expressed as the natural logarithm of λ, and defined as the intrinsic rate of increase (r), which is "the rate of increase per [individual] under specified physical conditions, in an unlimited environment where the effects of increasing density do not need to be considered." (Birch 1948). Exponential population growth rate is described by

$$\frac{dN}{dt} = rN \tag{4.2}$$

where the change in number of insects at any given time $\left(\frac{dN}{dt}\right)$, is determined by the number in the population (N) multiplied by r per individual (Fig. 4.3a). A critical component of population growth rate, r is sometimes called the exponential rate of increase, the intrinsic rate of increase, the instantaneous rate of increase, or the Malthusian parameter (Price et al. 2011). The intrinsic rate of increase is defined as the number of females produced per female per unit of time (e.g. females/female/year).

4.6.1 The Environment Can Support a Finite Number of Insects

Insect populations in nature do not undergo exponential growth indefinitely. Rapid growth is curtailed as the population density approaches the carrying capacity, K, the theoretical limit for population numbers given the resources of a particular habitat. One resource is often scarcer than all others; typically, this resource is food. The
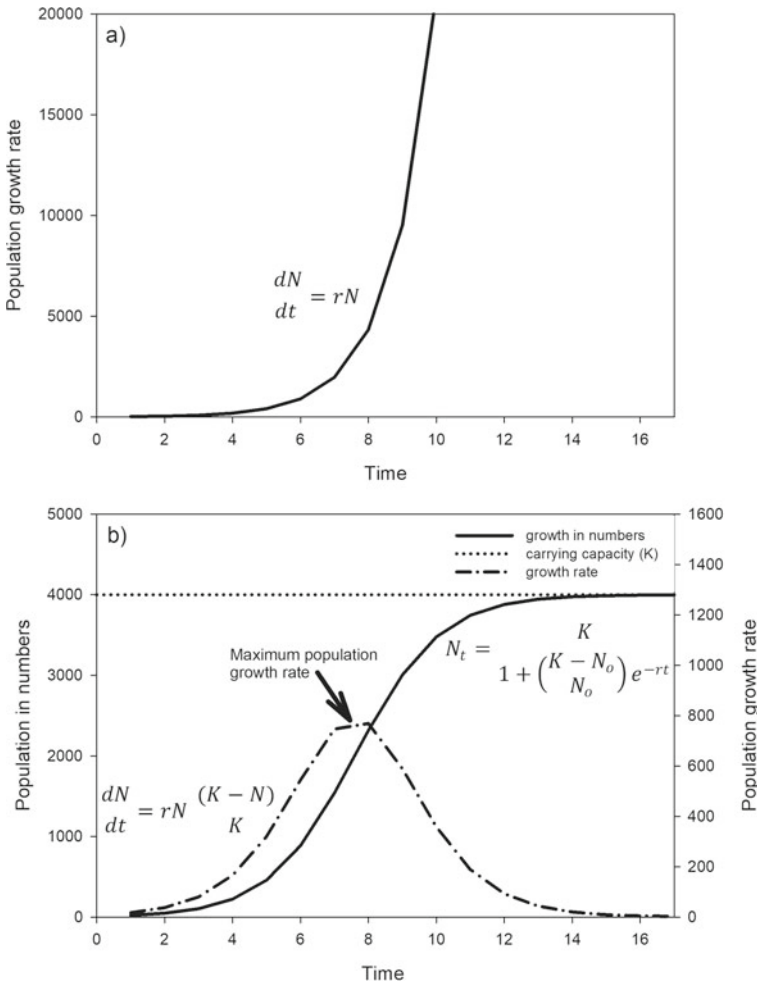
Fig. 4.3 Example of Exponential Population Growth and Population Growth Rate in an (**a**) Unlimited and a (**b**) Limited Environment According to Eqs. 4.2–4.4

combined influence of limited resources will dictate the theoretical numerical value of K, which is determined by both abiotic and biotic variables including weather, natural enemies, and presence of disease. The following equation represents the continuous rate of population growth in a limited environment

$$\frac{dN}{dt} = rN\frac{(K-N)}{K} \qquad (4.3)$$

and the discrete numbers of individuals in the population at a particular time is given by the logistic equation:

$$N_t = \frac{K}{1 + \left(\frac{K-N_o}{N_o}\right)e^{-rt}}$$ (4.4)

As illustrated in Fig. 4.3a, population growth rate increases exponentially without limits. When limits to growth are considered, theoretical population growth rate (Eq. 4.3) and population numbers (Eq. 4.4) can be illustrated by the curves shown in Fig. 4.3b. In Fig. 4.3b, when N is low with respect to K, then rN is not affected, and population growth and growth rate appear exponential (both lines, left side of the figure). As N grows larger and approaches K, the population growth rate (rN) begins to slow (dashed line, middle of the figure), eventually approaching zero as the population approaches K (both lines, right side of the figure).

Below, we briefly examine factors that influence B, D, I, and E, how those factors affect population growth, and describe a useful way to measure them.

4.6.2   Births

Forest insect populations can grow exponentially in a short period of time (months or years), partly because insect generation times are short (relative to trees), and partly because females are highly fecund. Fecundity, measured by number of eggs, can be described as potential or realized. It is potential in regard to the total number of eggs a female can produce in her lifetime, and realized in regard to the number that she actually lays. Fecundity varies among and within species.

4.6.3   Deaths

There are a multitude of sources of insect mortality. Some important sources include natural enemies, intra- and interspecific competition, and failure to acquire necessary nutrients. Natural enemies (predators, parasitoids, and pathogens) kill herbivorous insects, and through negative feedback can regulate their population density. Biological control programs rely on the theory that natural enemies can effectively regulate populations of herbivorous insects by killing enough individuals to lower the population below a threshold that economically damages or kills plants. For example, in classical biological control it is thought that importation of natural enemies (which can include predators, parasitoids, and pathogens) from the native range of an exotic invasive pest will mitigate plant damage levels within the environment invaded by the pest (Hajek 2004). In practice, there are multiple factors that can limit the success of biological control efforts, yet many have been successful (Kenis et al. 2017). For example, winter moth, native to Europe, has twice been effectively controlled in North America by the introduction of two insect parasitoids, *Cyzenis albicans*

(Fallén) and *Agrypon flaveolatum* (Gravenhorst) that are effective mortality agents during specific stages of winter moth development (Roland and Embree 1995).

Competition for resources occurs among species (interspecific), but also within species (intraspecific), especially when population density approaches *K*. As resources become scarce, competition among individuals for limited resources can result in mortality and exponential declines in population size (see Chapter 5). Scarcity of food for the existing population density is often the primary cause of death among herbivorous forest insects. For example, there may be a limited number of trees in space and time that are nutritionally adequate or have depleted defenses against herbivory to support survival and development of enough insects for the population to grow.

4.6.4 Movement

Immigration to and emigration of individuals from a population can change its size. Natural dispersal is the movement of an individual (or group of individuals) away from the natal population to another location where it (they) will reproduce (Schowalter 2006). Individuals in a population may disperse for many reasons. For example, if their habitats are very patchy or ephemeral in nature, insects may disperse if quantity or quality of resources (e.g. suitable trees for feeding or oviposition) becomes scarce and/or no mates can be found. Crowding or other stimuli may also be important. Dispersal may also occur randomly. Some foliage feeding caterpillars, such as spongy moth, climb to the top of the tree canopy and produce a small thread of silk that "balloons" them to a new tree on wind currents (McManus 1973). Strong winds or weather fronts could carry insects hundreds of miles, and authors have hypothesized this for several species (Frank et al. 2013; Furniss and Furniss 1972; Sturtevant et al. 2013), though it is difficult to determine for sure. Displacement of insect populations across vast areas with no suitable hosts or other methods of transport implies weather could have carried them. Insects may also be transported long distances by humans, as larvae in firewood (e.g. emerald ash borer), or as eggs or other life stages on nursery trees, lumber, household goods, or vehicles (e.g. European spongy moth).

4.6.5 A Tool to Measure Population Growth and Regulation

An effective way to determine how fast insect populations grow and what factors inhibit or allow their growth is to follow a cohort (a cohort is a group of individuals, usually of the same species, born within a defined period of time) or many cohorts, throughout development and document the sources of mortality. Life tables accomplish this task; they determine the identity, timing, and relative importance of mortality factors. For example, parasitism (*Trichogramma* spp. and unidentified

parasitoids), tree resistance (resinosis), and other (unknown) factors contributed to mortality during a generation of Nantucket pine tip moth, *Rhyacionia frustrana* (Comstock), in Georgia (Table 4.2). *Trichogramma* spp., parasitoids of tip moth eggs, were by far the most common mortality factor, responsible for 48.0% of all tip moth mortality during a generation. Though pupal mortality was high (49.7%) in relation to the numbers of pupae measured, it was low relative to the number of individuals present at the beginning of the cohort, a statistic termed real mortality. Real pupal mortality (10.7%) was much less than real egg mortality (48.0%). Generation mortality is the sum of all real mortality that occurred from the egg to adult stages, and indicates whether the population will be larger or smaller in the following generation (larger by 10.8% in this case).

A survivorship curve shows the number of individuals entering each successive life stage (Fig. 4.4), and is a simple way to examine mortality occurring through the different insect life stages. For the Nantucket pine tip moth, the precipitous drop in number of individuals between the egg stage and 1st larval instar shows that more

Table 4.2 Life Table of the 2nd 1979 Generation of the Nantucket Pine Tip Moth, *Rhyacionia frustrana*, in Oglethorpe County, Georgia, USA

Life stage (x)	No. entering life stage (l_x)	Mortality factor (d_xF)	No. dying during life stage (d_x)	Apparent mortality ($100q_x$)
Eggs	23,425	*Trichogramma* spp.	11,236	48.0
Instar 1	12,189	Resinosis	881	7.2
		Other	845	7.0
		Total	1,726	14.2
Instar 2	10,463	Resinosis	121	1.2
		Other	1,257	12.0
		Total	1,378	13.2
Instar 3	9,085	Resinosis	64	0.7
		Other	912	10.0
		Total	976	10.7
Instar 4	8,109	Unknown	881	10.9
Instar 5	7,228	Parasites	1,153	15.9
		Other	1,024	14.2
		Total	2,177	30.1
Pupae	5,051	Parasites	569	11.3
		Other	1,942	38.4
		Total	2,511	49.7
Moths	2,540			
Generation				89.2

Adapted from Gargiullo and Berisford (1983)

Fig. 4.4 Survivorship Curve Adapted from Life Table of the 2nd 1979 Generation of the Nantucket Pine Tip Moth, *Rhyacionia frustrana*, in Oglethorpe County, Georgia, USA. From Gargiullo and Berisford (1983)
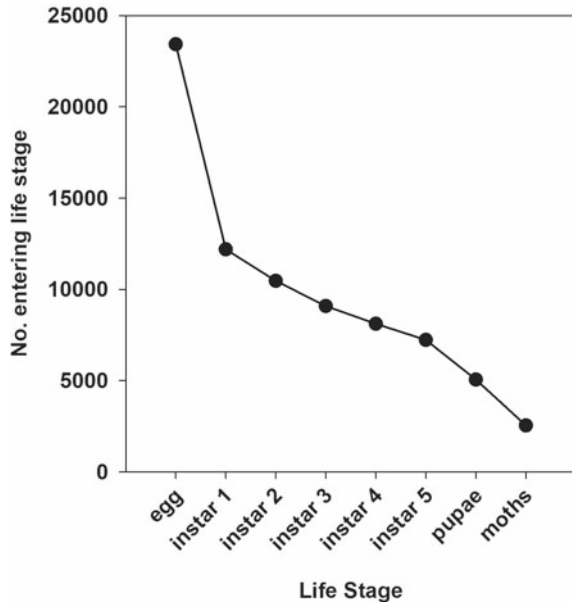
mortality occurred between these two life stages than any other successive stages (Fig. 4.4).

4.7 How Global Change Affects Insects in Forest Ecosystems

Any change in abiotic conditions (temperature, precipitation, extreme weather) will result in a change in insect growth and survival, because insects are poikilothermic organisms and because their food sources may also be affected by such changes. Forest insects have the capacity to adapt more quickly (short generation time coupled with high fecundity, mobility, and genetic plasticity) to environmental change than trees (long generation time and limited capacity for dispersal). As a result, with a warming climate, herbivorous insects may expand beyond their historical ranges to greater latitudes and altitudes where they will encounter new tree populations and species, potentially causing extensive tree mortality. All of this may disrupt the balance of energy and nutrient flow within those forest ecosystems.

Some of these changes have already begun. Warmer temperatures and longer growing seasons have allowed the mountain pine beetle to expand its range to higher elevations, as well as northward and eastward, where it has encountered populations of whitebark, lodgepole, ponderosa, and jack pine that lack a co-evolutionary history with the beetle (Logan et al. 2010; Safranyik et al. 2010). Similarly, the southern pine beetle has moved north beyond its historical range in the southeastern

US, encountering several pines (red, eastern white, jack, and scots pine) in New England that lack historical exposure to the beetle (Dodds et al. 2018). As the range of eastern spruce budworm expands northward, it will encounter greater prevalence of black spruce than it has in the past. Black spruce is considered a host for spruce budworm, yet historically budburst occurred too late in the season to support sufficient budworm survival (Pureswaran et al. 2015). Range expansion, combined with changes in phenology, and a low diversity of natural enemies in much of the boreal forest, will result in different impacts and outbreak dynamics of spruce budworm in decades to come (Pureswaran et al. 2015). Also, engraver beetles (*Ips* spp.), which have mostly been minor pests historically, may become serious pests in the future, because they can reach outbreak populations in hot and dry conditions (Negrón et al. 2009) and after windstorms (Gothlin et al. 2000).

Forest pests are transported to new forest ecosystems as people move forest products from one place to another. These introductions can have significant negative impacts on tree and forest health if the non-native pest is an aggressive one or there is no biotic resistance in the new habitat, from the trees or the community of natural enemies and competitors. Some invasive species are so aggressive that they threaten to completely or functionally eliminate a tree species, or genus, from a continent (e.g. emerald ash borer, hemlock woolly adelgid). Whether the threatened trees are foundation species for the ecosystem or not, the pest invasion will alter forest communities and functional relationships, e.g. Gandhi and Herms (2010). There are numerous examples of non-native forest insect invasions worldwide (see Chapter 23). In the US, each introduced species that has become a major forest pest has engendered a massive research, regulatory, and management effort to understand its biology, eradicate it, slow its spread, or elsewise mitigate its impact. As people continue to mobilize and engage in inter-continental trade, the problem of forest insect invasions is unlikely to recede.

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