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Dynamics of Phytophagous Insects and Their Pathogens in Alaskan Boreal Forests

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Introduction

Boreal forests support an array of insects, including phytophagous (plant-eating) insects, saprophagous (detritus-eating) insects, and their associated parasites, predators, and symbionts. The phytophagous species include folivorous leaf chewers and miners, phloeophagous cambial and sapwood borers, stem gallers, and root feeders. Biological diversity and distribution of insect species exhibit predictable patterns among vegetation types (Werner 1994a). In this chapter, we discuss how phytophagous species of insects differ among plant communities and how various populations of insects react to disturbances that alter forest stand composition and density.

Phytophagous Insects

The distribution of insects differs among plant communities depending on the ecosystem type and plant height (Table 9.1; Werner 1983, 1994a). Grasses, mosses, small tree seedlings, and other herbaceous plants located on the forest floor have the highest arthropod densities. Shrubs have the lowest densities, and trees are intermediate. The herbaceous layer is inhabited primarily by scavengers, predators, and saprophages but has few defoliators (Werner 1983). Taller shrubs contain more species of phytophagous insects than do herbs, but trees have the most species of phytophagous insects, parasites, and predators (Werner 1981, 1983). Few saprophages and scavengers (carabid beetles), however, occur on shrubs and trees (Werner 1986a).

Associations of plants and phytophagous insects in boreal ecosystems are similar to temperate assemblages in that insect species differ in the range of food plants

Table 9.1. Densities (per square meter of ground surface integrated through the canopy) of arthropods collected from three different vertical levels in five major vegetation types of the boreal forest ecosystem.

Vertical level	Balsam poplar	Aspen	Paper birch	White spruce	Black spruce	Average
Herb	2,901	3,093	1,593	1,117	12,538	4,248
Shrub	727	1,059	609	420	1,334	830
Tree	582	1,172	2,088	631	4,485	1,792
Average	1,403	1,441	1,430	723	6,119	

Source: Werner (1983).

that they utilize (Bernays and Minkenberg 1997, Futuyma et al. 1993, Thorsteinson 1960). Because of low plant diversity, however, many boreal phytophagous insects feed on several species of plants (Werner 198 1). For example, the spear-marked black moth, *Rheumaptera hastata* (L.), feeds primarily on paper birch, but during periods of high populations it also feeds on alder, willow, and rose species but not on poplar (Werner 1977, 1979). When population outbreaks of phytophagous insects deplete their preferred host plants, less desirable species are sometimes consumed or starvation occurs (Werner 1981, 1986a).

The biomass of phytophagous insects is greater on broad-leafed than on conifer trees (Werner 1983). Species of Coleoptera, Hemiptera, Homoptera, Hymenoptera, and Lepidoptera are common on broad-leafed trees, whereas only a few taxa of Homoptera, Hymenopera, and Lepidoptera are associated with conifers such as spruce or larch (Table 9.2; Werner 1983, 1994a). Species richness is greatest in early successional deciduous communities dominated by willow and aspen and lowest in black spruce communities (Werner 1986a, Werner and Ward 1976). Most plant species in boreal ecosystems have generalized defoliators, sap-feeders, and blotch and leaf miners, but white spruce and, to some extent, black spruce and larch are also inhabited by phloeophagous insects (Table 9.2; Werner 1986a, 1986b, Werner and Holsten 1984, Werner and Ward 1976).

Temperature is more important as a regulator of insect species composition at northern latitudes than elsewhere (Werner and Holsten 1985a). Species richness of scolytid bark beetles in Alaska is greatest where cumulative degree-day temperature sums are highest (Werner and Holsten 1984). For example, 27 species of bark beetles were found associated with white spruce in the Fairbanks area (latitude 64°37’N), where summer temperature is highest, compared to 22 species in the Brooks Range (latitude 68°15’N) in northern Alaska and 20 species in the Kenai Peninsula (latitude 60°37’N) in south-central Alaska (Table 9.3).

Folivorous Insects

Repeated defoliation by a variety of insects over several years has caused tree mortality of conifers and broad-leafed species. For example, infestations by two

Table 9.2. Biomass (g m^{-2}) of the major arthropod taxa in boreal forest ecosystems of Alaska.

Taxon	Balsam poplar	Aspen	Paper birch	White spruce	Black spruce	Average
Noninsects						
Araneida	0.1186	0.1238	0.1510	0.1025	0.0846	0.1161
Acari	0.0400	0.0650	0.0742	0.0408	0.0996	0.0640
Other	0.0123	0.0126	0.0128	0.0057	0.0057	0.0098
Insects						
Coleoptera	0.0966	0.0838	0.1981	0.0820	0.1003	0.1122
Collembola	0.0153	0.0139	0.0121	0.0161	0.0378	0.0190
Diptera	0.0162	0.0704	0.0971	0.1100	0.0615	0.0710
Hemiptera	0.0397	0.0504	0.1284	0.0463	0.0423	0.0614
Homoptera	0.0351	0.0440	0.2810	0.0382	0.0307	0.0858
Hymenoptera	0.1061	0.0836	0.1757	0.0626	0.0331	0.0922
Lepidoptera	0.0750	0.0391	0.0482	0.0564	0.1016	0.0641
Mecoptera	0.0072	0.0062	0.0038	0.0058	0.0006	0.0047
Neuroptera	0.0052	0.0316	0.0072	0.0102	0.0178	0.0144
Pscoptera	0.0035	0.0018	0.0072	0.0064	0.0064	0.0051
Thysanoptera	0.0097	0.0151	0.0151	0.0139	0.0109	0.0129
Other	0.031I	0.0208	0.0933	0.0325	0.0221	0.0400
Total	0.6805	0.7196	1.4164	0.6364	0.6583	0.8222

Source: Werner (1983).

species of budworm, *Choristoneura fumiferana* (Clem.) and *Choristoneura orae* Freeman, covered 219,125 ha of interior Alaska white spruce forests from 1990 to 1994 and 259,855 ha from 1995 to 1999 (Table 9.4; U.S. Department of Agriculture 1995, 1999). In 1993, the spruce coneworm, *Dioryctria reniculelloides* (Mutuura and Munroe), was competing for the same buds and foliage as the spruce budworm, and competition for food resources was evident (U.S. Department of Agriculture 1995, Werner 1995). White spruce trees that were defoliated for three or more years exhibited terminal shoot and upper crown mortality, loss of reproductive potential (no cones produced), and reduced vigor and growth. These trees were stressed to the point where they became susceptible to attack by the northern engraver beetle, *Ips perturbatus* (Eichhoff) (Werner 1988, 1995). All sizes of spruce from two-year-old seedlings to mature trees were defoliated. Mature trees survived the continued defoliation after the budworm populations declined, but seedlings and young saplings did not recover.

Several species of folivorous insects occur chronically in stands of larch (*Larix laricina*) in interior Alaska. From 1975 to 1979, a species of larch bud moth, *Zeiraphera* sp. completely defoliated 238,773 ha of larch (Table 9.4) in interior Alaska, including stands in the Bonanza Creek Experimental Forest (Werner 1980). These trees were subsequently infested by eastern larch beetle, *Dendroctonus simplex*

Table 9.3. Diversity of scolytid bark beetles inhabiting white spruce at three sites in Alaska, 1977–1979.

Species	*Total number of beetles caught*[a]		
	Kenai Lake 900 degree-days[b]	**Fairbanks 1225 degree-days**[b]	**Brooks Range 1100 degree-days**[b]
Carphoborus andersoni Swaine	0	3	8
Carphoborus carri Swaine	0	21	6
Carphoborus intermedius Wood	0	5	0
Cryphalus ruficollis ruficollis Hopkins	68	4	3
Crypturgus borealis Swaine	0	163	6
Dendroctonus punctatus LeConte	0	3	3
Dendroctonus rufipennis (Kirby)	311	115	40
Dryocoetes affaber (Mannerheim)	87	655	88
Dryocoetes autographus (Ratzeburg)	36	206	15
Hylurgops rugipennis rugipennis (Mannerheim)	2	6	2
Ips borealis borealis Swaine	24	228	77
Ips perturbatus (Eichhoff)	348	3,141	43
Ips tridens tridens (Eichhoff)	954	433	6
Orthotomicus caelatus (Eichhoff)	0	274	4
Phloeosinus pini Swaine	0	2	6
Phloeotribus piceae Swaine	8	20	11
Pityophthorus bassetti Blackman	0	5	0
Pityophthorus murrayanae Blackman	14	0	0
Pityophthorus nitidulus (Mannerheim)	77	206	0
Pityophthorus nitidus Swaine	27	117	12
Pityophthorus opaculus LeConte	20	33	21
Polygraphus convexifrons Wood	3	6	15
Polygraphus rufipennis (Kirby)	128	353	634
Scierus annectans LeConte	6	103	6
Scierus pubescens Swaine	23	0	0
Scolytus piceae (Swaine)	0	752	233
Trypodendron lineatum (Olivier)	185	681	42
Trypodendron retusum (LeConte)	12	152	0
Xylechinus montanus Blackman	2	10	0
Total	2,335	7,697	1,281

[a] Beetles were caught in pheromone-baited sticky traps.

[b] Thirty-year average of cumulative degree-days above 5°C.

Source: Werner and Holsten (1984b).

LeConte, in 1977. Two successive years of defoliation may have reduced tree vigor and increased their susceptibility to beetle attack. The first reported outbreak of larch sawfly, *Pristiphora erichsonii* (Hartig), in Alaska occurred in interior Alaska from 1993 to 1999 and killed most of the larch on 651,100 ha (Table 9.4; U.S. Department of Agriculture 1999). Many of the defoliated trees were stressed and subsequently attacked by eastern larch beetle as had occurred following outbreaks of the larch bud moth (Werner 1986b). Many river bottom sites previously occupied by black spruce and larch are now devoid of larch, showing the impact of insect folivores on forest composition.

Table 9.4. Total number of hectares of Alaska boreal forest ecosystems infested by folivorous and phloeophagous insects, 1955 – 1999, as detected by annual aerial surveys.

Species	1955–64	1965–74	1975–79	1980–84	1985–89	1990–94	1995–99
Spruce beetle (*Dendroctonus rufipennis*)	20,235[a]	10,039	284,505	744,989	595,725	1,114,587	1,265,364
Engraver beetles (*Ips perturbatus*)	404,700	0	4,452	1.667	12,020	13,345	14,081
Larch beetle (*Dendroctonus simplex*)	0	52,611	522,063	8,134	0	1,214	1,226
Spruce budworm (*Choristoneura fumiferana*)	0	0	121	4,452	907	219,125	259.855
Larch sawfly (*Pristiphora erichsonii*)	0	0	0	0	0	45,540	651.099
Larch bud moth (*Zeiraphera* spp.)	202,350	4,047	238.773	0	36,018	4,087	651,099
Spear-marked black moth (Rheumaptera hastata)	2,347,260	526,110	1,092,690	159.452	32.552	4,832	0
Large aspen tortrix (*Choristoneura conflictana*)	0	2,590,080	19,426	54,877	261,367	60,379	24,036
Hemlock sawfly (*Neodiprion tsugae*)	0	16.997	0	54,027	17.807	10,045	6,609
Western black-headed budworm (*Acleris gloverana*)	2,306	39,054	2.287	10,805	66,780	209,823	18.327
Leaf beetles (*Chrysomela* spp.)	0	0	41,927	5,463	10,103	25,116	9,932
Leaf miners (*Micrurapteryx salicifolliela, Phyllocnistis* spp.)	0	0	247,271	4.856	607	5,180	146,721
Aphids (*Adelges, Cinara, Elatobium* sp.)	0	47,350	186.162	19,764	14,974	1,077	13,605
Leaf rollers (*Epinotia, Euceraphis* spp.)	0	202,350	445,777	5,969	32,990	65,892	5,017

[a] Total ha for each five-year period.

Historical records of folivorous insects indicate that populations of spear-marked black moth occurred at IO-year intervals, and high populations of the large aspen tortrix, *Choristoneura conflictana* (Wlk.), occurred at 12-year intervals (Werner unpublished data). The most recent outbreak populations of spear-marked black moth occurred in 1975 to 1979 and of large aspen tortrix from 1985 to 1989 (Table 9.4). Average annual temperatures have increased since 1980 in interior Alaska (Chapter 4; Barber et al. 2000), which may contribute to the decreased outbreak frequency. Other species of folivorous insects, such as the eastern spruce budworm, spruce coneworm, and larch sawfly, had negligible populations prior to 1990 but since then have defoliated thousands of hectares of white spruce and larch, respectively, in interior Alaska (Table 9.4). Why were some populations maintained at low levels while others exploded beyond expectations? Is atmospheric warming a factor? Barber et al. (2000) suggest that temperature-induced drought has reduced the growth of white spruce. This could predispose trees to infestation by phloeophagous species.

Phloeophagous insects

Insects can exert markedly different impacts in different regions, even when the underlying insect and tree biologies are quite similar (Werner 1986a). The spruce beetle, *Dendroctonus rufipennis* (Kirby), is distributed throughout all regions of Alaska that contain spruce and colonizes all spruce species within its range (Werner et al. 1977). Like other bark beetles, the spruce beetle carries a variety of wood-colonizing microorganisms, such as bacteria, molds, yeast, and stain fungi. The saprophytes apparently have no effect on beetles, but sapstain fungi have the potential to play a major role in beetle-host tree interactions (Illman et al. unpublished data, Reynolds 1992, Werner and Illman 1994a, 1994b). The spruce beetle typically colonizes severely stressed or dying trees but also (depending on the region) may undergo intermittent population eruptions, which kill most healthy mature spruce trees over areas encompassing several million hectares (Holsten 1990, Werner 1994a). These natural disturbance events have pronounced landscape-level effects: accumulation of fuels, release of early succession species such as willow, poplar, birch and aspen, improved or decreased habitat for some birds, mammals, and other subcortical insects, and changes in nutrient cycling.

The same spruce beetle-host tree interaction exerts markedly different impacts at the landscape level in south-central Alaska than it does in interior Alaska. In contrast to south-central Alaska, western Canada, and the Rocky Mountains, the same insect rarely, if ever, undergoes outbreaks in interior Alaska. Spruce beetles in interior white spruce forests sometimes colonize severely stressed or dying trees on fringes of fires (Werner and Post 1.985) and in areas periodically inundated with water. Thus, spruce beetles in interior Alaska might play an important role in canopy thinning and gap formation but do not exert ecosystem-level effects. The underlying reasons are poorly understood and are somewhat paradoxical. The major factors appear to be complex interactions involving abiotic and biotic influences, particularly moisture and temperature effects on translocation of defensive compounds and host suitability to the spruce beetles and to competitors such as *Ips* engraver beetles.

There are several factors that we initially hypothesized might explain the lack of outbreaks of spruce beetle in interior Alaska, including regional differences in climate, the genetic composition of beetle populations, differences in microbial associates, and different levels of natural enemies or competitors. Not only does weather fail to provide a simple explanation, but also the dichotomy between the existence of landscape-level impacts in south-central Alaska and the presence of only site-level impacts in interior Alaska is not easily explained by the relationships among phloem temperature, beetle phenology, and population dynamics. Spruce beetles exhibit facultative diapause, so a single generation can require either one or two years, depending on temperature (Werner and Holsten 1985a, 1985b). The predominant pattern in south-central and southeast Alaska is a two-year cycle. Warm temperatures, however, can favor complete brood development within one year. This has been identified as a major factor in the epidemic of the late 1980s and 1990s. In contrast, the warm summers of interior Alaska typically foster the one-year cycle (Werner and Holsten 1985a). Thus, on the basis of strictly temperature considerations, interior Alaska should be more. not less, prone to outbreaks. Likewise, lightning can play a crucial role in some bark beetle population dynamics by killing trees and making them suitable for beetle development (Coulson 1979). Lightning is more frequent in interior Alaska than in south-central Alaska, which again would generate predictions opposite to observed patterns.

One possibility for regional differences in spruce beetle population levels is that there could be genetic differences between interior and south-central Alaska populations. However, molecular (Bentz and Stock 1986, Cronin 1994) and behavioral analyses (Wallin and Raffa 2004) do not support this view. Likewise, beetles might show regional differences in their fungal complements that correspond to different population patterns. Again, we see no evidence for this possibility (Haberkern et. al. 2002, Illman et. al. unpublished data, Aukema et al. 2005). Furthermore, spruce beetles in the Great Lakes region, where forests are not susceptible to outbreaks or landscape-level infestations, carry fungal complements similar to those found in populations in south-central and interior Alaska (Haberkern et al. 2002). The increased frequency of a relatively pathogenic stain fungus has been proposed as a contributing factor to outbreaks of the European spruce beetle, *Ips typographus* L., in Norway (Krokene and Solheim 1998). The effect of fungal inoculation levels on the south-central and interior Alaska populations of spruce beetle is not known.

Predators and competitors may contribute to, but not fully explain, differences in population dynamics between populations of interior and south-central Alaska spruce beetles. For example, there is some evidence that checkered beetles (Cleridae) such as *Thanasimus undatulus* and *T. dubius* are more abundant in interior than south-central Alaskan forests (Gara et a1. 1995, Werner 1993, 1994b). However, there are fewer clerids and other predators collected from colonized hosts or traps baited with spruce beetle pheromones in Alaskan spruce forests than elsewhere in North America (Haberkern 2001) and fewer than are commonly seen with other bark beetles (Weslien 1994, Reeve 1997, Erbilgin and Raffa 2002). Competitors of the spruce beetle include mostly *Ips* species, *Polygraphus rufipennis, Dryocoetes* *affaber*, Buprestidae, and Cerambycidae (Werner and Holsten 2002). These less aggressive colonizers can cause some reductions in spruce beetle populations (Poland and Borden 1998). However, interspecific competition is reduced somewhat by partitioning of the resource, based on a combination of tree vigor, height along the bole, and colonization of upper versus lower surface of downed trees. Moreover, there is no evidence that populations of competitors are consistently higher in interior than in south-central Alaska.

Host tree species appear to have some effect on beetle population dynamics, but these do not necessarily correspond to outbreak behavior. The Kenai Peninsula in south-central Alaska, a region of historically severe outbreaks of spruce beetles, contains a combination of white, Sitka, and Lutz spruce, *Picea x lutzii* Little, the latter a hybrid between white and Sitka spruce found only on the Kenai Peninsula. Lutz spruce is the most susceptible to attack, whereas white spruce is most suitable for development of the spruce beetle (Hard et al. 1983, Holsten 1984, Holsten and Werner 1990) and is typically associated with faster rates of development and more progeny. Sitka spruce is least susceptible to attack and is suitable for beetle development; it is found mostly in southeastern and coastal Alaska (Holsten and Werner 1990).

Biotic agents that predispose trees to colonization appear less important with spruce beetles in Alaska than elsewhere with other species of bark beetles. Large-scale defoliation of larch by larch bud moth in Alaska (Werner 1980), for example, is commonly followed by infestation of trees by the larch beetle (Werner 1986b). Defoliation of *Pinus banksiana* (Lamb.) by the budworm, *Choristoneura pinus* Freeman, is commonly followed by colonization of the tree by *Ips grandicollis* (Eichhoff) (Wallin and Raffa 1999, 2001), and defoliation of *Abies grandis* is usually followed by colonization of the host by *Scolytus ventralis* LeConte (Wright et al. 1984). Defoliation is less common in spruce in south-central Alaska. However, repeated defoliation by eastern spruce budworm of white spruce in interior Alaska can predispose trees to *Ips* engraver beetle attack (Werner 1995). Likewise, root insects such as *Hylobius* and *Hylastes* can be important predisposing agents for *Ips pini* colonizing pine in Wisconsin (Klepzig et al. 1991, 1995) and for the Douglas-fir beetle, *Dendroctonus pseudotsugae* (Witcosky et al. 1986a, 1986b), colonizing Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) in Oregon. By contrast, populations of root colonizing beetles do not appear high in spruce forests of Alaska (Werner et al. unpublished data). The following species of weevils were caught in pit-fall traps in stands of white spruce in the Bonanza Creek Long Experimental Forest from 1996 to 2003: *Lepidophorus lineaticollis* Kirby, *Pissodes rotundatus* LeC., *Dorytomus laticollis* LeC., *Magdalis gentilis* LeC., *Orchidophilus* spp., and *Grypus equiseti* (F.) (Werner et al. unpublished data). Likewise, root pathogens are important predisposing agents to subsequent bark beetle attack in many ecosystems (Filip and Goheen 1982). However, we see no evidence for a significant role in Alaska (Illman unpublished data). One biotic agent that may be more important in disposing trees to attack than elsewhere are black bears that feed on the cambium of tree trunks, a damage that is similar to girdling (Lutz 1951). To date, however, no correlation between black bear girdling and spruce beetle attack has been found.

Interactions of abiotic and biotic environmental factors, particularly moisture with host plant physiology, could partially explain differences in eruptive spruce beetle behavior. First, the lower precipitation in interior Alaska results in phloem that has 20% less moisture than in spruce in south-central Alaska (Werner and Holsten 1985b). Spruce beetles perform poorly in dry tissue, whereas *Ips* beetles are more tolerant. The drier developmental habitat also appears to reduce the synchrony of beetle emergence, which is important for tree-killing bark beetles that overwhelm tree resistance by mass attack (Raffa and Berryman 1988, Bentz et al. 1991). Thus, interactions among precipitation, host suitability, host susceptibility, and interspecific competition may be important. There may also be interactions among temperature, host susceptibility, and beetle population dynamics. For example, in the mountainous areas of south-central Alaska, valley bottoms can remain cool well into the spring. Because the soil is cool, roots often do not begin translocation until after spruce beetle flight has begun (Hard 1987, Werner unpublished data). Thus, beetles can exploit trees that have low oleoresin flow rates, which is an important component ofconifer defense against bark beetles (Hard 1985, 1987, Lorio 1993). Associated stain fungi appear to play an important role in beetle-host relationships. Stain fungi induce an energy-requiring chemical defense response in phloem tissue (Werner and Illman 1994a, 1994b, Illman et al. unpublished data) that could weaken the tree's defenses against beetles. Additionally, stain fungi could lower tree resistance by colonizing xylem tissue and blocking water transport, as occurs in Norway spruce (Krokene and Solheim 1998). Beetle success at colonization of the host tree could be highly dependent on the abundance of associated fungi attacking the tree.

interactions with Disturbance

Disturbance factors such as wildfire, ice and wind storms, outbreaks of phytophagous folivorous insects, and timber harvest can cause fluctuations in populations of phloeophagous insects. For example, fringes of white spruce stands disturbed by wildfire or clear-cut and shelterwood harvests in the Bonanza Creek Experimental Forest had a direct impact on the diversity of species of buprestid and cerambycid wood-boring beetles and scolytid bark beetles (Table 9.5; Werner 2002). Fire and timber harvest are the two major disturbances that alter forest ecosystems of interior Alaska. Both types of disturbance provide habitats that attract wood borers and bark beetles the first year after disturbance. However, fire and clear-cutting timber significantly reduced the number of species of all three types of phloeophagous insects in stands of white spruce for 10 years following the disturbance. Shelterwood timber harvest had a less severe impact for 1 to 5 years after disturbance, but thereafter the number of species declined (Table 9.5).

Although major disturbances such as fire or insect outbreaks may appear to be independent events, they are often related (Showalter et al. 1981, Romme et al. 1986, McCullough et al. 1998). Insect outbreaks that are followed by fire can also effectively disrupt or redirect plant succession in forest ecosystems (Amman 1977, Geiszler et al. 1980, Showalter et al. 1981, Romme et al. 1986, Raffa and Berryman 1987, McCullough et al. 1998). For example, interactions among spruce beetle, species composition of spruce, and fire can determine the future composition of forest stands in south-central Alaska (Holsten et al. 1995).

Table 9.5. Average number of wood borers and bark beetles collected from stands of disturbed white spruce in the Bonanza Creek Experimental Forest at 1-, 5-, and 10-year intervals following disturbance.

	Buprestidae[a] *years*			*Cerambycidae* *years*			*Scolytidae* *years*		
Disturbance	1	5	10	1	5	10	1	5	10
Burned	7	0	0	1	0	0	9	0	0
Fringearea	14	8	0	4	3	0	14	11	4
Clear-cut	17	5	0	9	5	0	15	8	2
Shelterwood	22	17	0	11	9	0	18	15	12
Control	19	18	16	6	6	6	19	19	19

[a] Beetles were collected from pheromone-baited funnel traps and window flight traps from late May to early September in the respective years following disturbance.

Conclusions

Forest insects are intrinsic components of many boreal forest ecosystems. They contribute to the biodiversity of aboveground arthropods. Episodic outbreaks of phytophagous insects, including both folivorous and phloeophagous species, can affect succession, species richness, and plant and animal diversity at the landscape level. Folivorous insects can exert landscape-level effects, or they can predispose forest stands to attack by phloeophagous insects and decay organisms. Phloeophagous insects, in turn, can predispose forest stands to risk from tire by increasing fuel density and flammable ground vegetation. Changes in ecosystem health (e.g., drought stress) are associated with greater susceptibility of stands to damaging insect pests and disease organisms and can cause increases in outbreak intensity at the landscape level. Complex interactions among abiotic and biotic factors can determine whether insects such as spruce beetle exert either stand-level or landscape-level impacts.

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