Insects and Diseases and Climate Change in Colorado Front Range Forests

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Introduction

Insects and diseases are major agents of change in forest ecosystems (Costello et al. 1995; Raffa et al. 2008). Their activities can result in scattered to extensive tree mortality across landscapes (Lundquist and Negrón 2000; Raffa et al. 2008). As natural components of forests, native insects, parasites, and pathogens contribute to shape forest structure and composition, contribute to nutrient cycling, and create habitat for wildlife species among other services (Negrón and Cain 2019). Innumerable species of insects, fungi, and other forms of life are part of the biological diversity of forests. There is a general consensus that abiotic disturbances such as fires and windstorms and biotic disturbances such as insects and diseases will increase in frequency and intensity as climate change manifests. Yet, there are still unresolved knowledge gaps, particularly on the effects of insect-associated organisms and interactions with their hosts (Jactel et al. 2019; Seidl et al. 2017). In this chapter, an overview of what is known about the general effects of a warming climate on pathogens and insects are presented followed by a general description of the most relevant insects and pathogens in the Colorado Front Range. Lastly, comments on how a warming climate may affect these organisms are offered.

General Effects of Climate Change on Forest Insects and Pathogens

Insects are poikilothermic organisms, meaning that they are not able to regulate body temperature and are, therefore, directly influenced by temperatures in their environment. Insects develop faster with increasing temperatures up to an optimal temperature with higher temperatures negatively impacting development. Insects exhibit differential life cycles and strategies to utilize their hosts and as a result effects of climate change on insects may vary in different ecosystems, habitats, seasons, and bioclimatic regions, among other factors.

In general, the literature supports the idea of increased frequency and intensity of forest insect activity under climate change. The predicted changes to insect presence and abundance under climate change may have the following effects: (1) potentially a higher number of generations and higher survival of overwintering stages with warmer winter temperatures; (2) weakened tree resistance mechanisms resulting from increased stress such as droughts; (3) increased breeding habitat such as blowdowns from increased storm activity; and (4) changes in food quality associated with elevated atmospheric carbon dioxide, particularly for defoliators (Jactel et al. 2019). However, a closer look reveals the complexity of these processes and that many other aspects of the interaction between hosts and insects under warming temperatures need to be considered. For example, increased temperatures can also increase mortality of some insects, and result in smaller insects with lower dispersal ability. A broader temperature variability can result in higher mortality. For example, extreme cold spells that happen

before an insect's supercooling period can kill overwintering bark beetle brood (Dooley et al. 2015). The effects of climate change on natural insect enemies such as parasitoids and predators remain largely unknown. In sum, a differential response by different insect species and guilds to climate change, novel interactions between insects and their hosts as they exhibit their own response, and changes in the frequency and severity of abiotic agents such as fires and windstorms make predictions about their individual responses challenging (see Jactel et al. 2019; Pureswaran et al. 2018 and references therein).

Climate change impacts on bark beetles and defoliators will affect range expansion or contractions (changes in geographical distribution), insect abundance, and outbreak patterns (Pureswaran et al. 2018). For example, range expansion of mountain pine beetle (*Dendroctonus ponderosae*) farther north in British Columbia and east into Alberta is well-documented (Cullingham et al. 2011; Safranyik et al. 2010). However, the occurrence of range expansion is not as well documented with defoliators. The processionary moth (*Thaumetopoea pityocampa*, not in Colorado) has shown both positive and negative behaviors in terms of range expansion (Battisti et al. 2006; Robinet et al. 2014). In terms of insect abundance, increased numbers could result in more intense outbreaks. For instance, the spruce beetle (*Dendroctonus rufipennis*) can transition from a 2-year life cycle to a 1-year life cycle under warm conditions providing their populations with the ability to rapidly increase in numbers (Hansen et al. 2001; Werner and Holsten 1985; Werner et al. 2006). In terms of outbreak patterns, the western spruce budworm (*Choristoneura occidentalis*) outbreaks are becoming more intense and frequent (Swetnam and Lynch 1989), and bark beetle outbreaks are expected to behave similarly (Seidl et al. 2017).

Plant pathogens, their hosts, and their interactions are also strongly influenced by environmental conditions; therefore, they will also be affected by climate change. Some effects will include changes in pathogen growth, rates of reproduction and infection, as well as variations in plant-host susceptibility. As a result of warming temperatures, changes in host tree distributions are expected, primarily contracting; however, migrations to areas with more suitable conditions are expected. Pathogens affecting drought-stressed hosts may increase where precipitation levels decline and temperatures increase. In addition, their life cycles may be affected; for example, fungal spore release and the life cycle of insect vectors may be affected (see Sturrock et al. 2011 and citations therein).

Ecology of Prevalent Forest Insect and Diseases on the Colorado Front Range

Important insects that interact with forests in the Colorado Front Range include various species of bark beetles such as the mountain pine beetle, spruce beetle, Douglas-fir beetle (*Dendroctonus pseudotsugae*), and the western balsam bark beetle (*Dryocoetes confusus*) (table 1). Notable defoliators include the western spruce budworm and the Douglas-fir tussock moth (*Orgyia pseudotsugata*). Although forest pathogens do occur in the Colorado Front Range, in general their impacts are less. The most important, perhaps, is dwarf mistletoes that affect several species of pines. White pine blister rust, an introduced disease, has become locally important causing tree mortality, reducing regeneration, and increasing susceptibility to mountain pine beetle (Cleaver et al. 2015).

Table 1—Forest insects and diseases acting as important disturbance agents in the Colorado Front Range. Modified from the Field Guide to Insects & Insects of the Rocky Mountain Region, RMRS-GTR-241 (Rocky Mountain Region, Forest Health Protection 2010).

Disturbance	Name	Primary host(s)
Bark Beetles	Mountain pine beetle	Ponderosa pine, Lodgepole pine, Limber pine
	Spruce beetle	Engelmann spruce, Blue spruce
	Douglas-fir beetle	Douglas-fir
	Western balsam bark beetle	Subalpine fir
	Pinyon ips	Pinyon pine
Defoliators	Western spruce budworm	Douglas-fir, Engelmann spruce, Blue spruce, White fir, Subalpine fir
	Douglas-fir tussock moth	Douglas-fir
Diseases	Mistletoes (parasitic plants)	Lodgepole pine, Limber pine, Pinyon pine, Douglas-fir, Bristlecone pine, Ponderosa pine
	Armillaria root disease	All common tree species and in all major forest types in the Rocky Mountain Region
	White pine blister rust	Limber pine, Bristlecone pine
	Sudden aspen decline / Cytospora	Aspen

Bark Beetles

Mountain Pine Beetle (Dendroctonus ponderosae)

This bark beetle is widely distributed across the western U.S. conifer forests. It attacks and kills about 15 species of pines but most of its activity is in ponderosa (*Pinus ponderosa*) and lodgepole pine (*Pinus contorta*) forests as these are the most abundant hosts in the Colorado Front Range. In the Colorado Front Range, the insect has a 1-year life cycle with emergence and dispersal occurring from late July through mid-August (McCambridge 1964; Negrón 2019; Tishmack et al. 2005; West et al. 2016). Mountain pine beetle prefers dense stands of larger-diameter trees. Data from the Colorado Front Range indicate that in ponderosa pine stands, the insect prefers stands with a ponderosa pine basal area > 74 ft^2/ac and trees with a d.b.h. > 7 inches (Negrón and Popp 2004). Data from the Sulphur Ranger District (RD) of the Arapaho-Roosevelt National Forests (NFs) indicate that in lodgepole pine forests, stands with a basal area > 59 ft^2/ac and mean d.b.h. of 7 inches are more likely to be infested. Increased mortality levels occur when lodgepole pine basal area is > 106 ft^2/ac (Negrón and Klutsch 2017). These levels are likely applicable throughout the Pike-San Isabel and Arapaho-Roosevelt National Forests (PSI-AR).

An extensive outbreak affecting ponderosa pine forests in the late 1970s affected about 2 million acres from the Colorado-Wyoming State line south to the San Carlos RD of the Pike-San Isabel NFs (McCambridge et al. 1982). A smaller outbreak occurred in lodgepole pine in the Sulphur RD of the Arapaho-Roosevelt NFs in the 1980s (Peltz and Smith 2012). A recent extensive mountain pine beetle outbreak occurred from the late 1990s to about the mid-2010s and extended from the southern Rocky Mountains north to British Columbia in Canada. In Colorado, 3.4 million acres were affected with mortality occurring primarily in lodgepole pine forests. Mortality was also observed to a lesser extent in ponderosa pine, limber pine (*Pinus flexilis*), and bristlecone pine (*Pinus aristata*). Klutsch et al. (2009), working in the Sulphur RD of the Arapaho-Roosevelt NFs, indicated mortality levels ranging from little to complete mortality in stands. Across the landscape, tree density and basal area were reduced by 62 percent and 71 percent, respectively, in infested stands and mean tree diameter was reduced by 53 percent.

Spruce Beetle (Dendroctonus rufipennis)

The geographic range of the spruce beetle is transcontinental from Alaska east to New Foundland, parts of the northeastern United States and the southern Rockies south to Arizona and New Mexico. All species of spruce are utilized as hosts, but in Colorado, Engelmann spruce (*Picea engelmannii*) is its primary host with some attacks also occurring in Colorado blue spruce (*Picea pungens*). It has also attacked and caused mortality to lodgepole pine (Mercado 2020 and references therein). The insect has primarily a 2-year life cycle but under warm conditions can complete its life cycle in one year. This has been the case during the extensive outbreaks in Alaska (Werner and Holsten 1985; Werner et al. 2006). Outbreaks of the insect are often associated with blown-down trees where populations can increase rapidly. A major outbreak in

Colorado occurred in the 1940s in the White River and Grand Mesa National Forests after a blowdown in 1939 (Massey and Wygant 1954). Another extensive outbreak occurred in the early 2000s after a large blowdown in 1997 in the Hanhs' Peak-Bear's Ears Ranger District of the Routt National Forest. Using tree-ring analysis, Veblen et al. (1991) suggested that another major outbreak occurred in western Colorado in the 1850s. According to Schmid and Frye (1977), in Colorado the most susceptible stands to spruce beetles are those in drainage bottoms with mean spruce d.b.h. > 16 inches, a live spruce component > 60 percent, and with basal areas exceeding 150 ft^2/ac. Extensive mortality occurred in the spruce-fir forests of the Canyon Lakes Ranger District since about the 2000s, killing most large-diameter trees.

Douglas-fir Beetle (Dendroctonus pseudotsugae)

This species of bark beetle uses Douglas-fir (*Pseudotsuga menziesii*) as its only host in Colorado. Its primary dispersal flight occurs towards the end of June (Negrón et al. 2011) and overwinters in the larval stage. Outbreak populations of Douglas-fir beetle can increase to epidemic levels when a precipitating factor occurs such as the availability of downed trees and trees with nonlethal fire injury. In Colorado, the primary precipitating factor has been defoliation events from western spruce budworm or the Douglas-fir tussock moth (Cole et al. 2022; Lessard and Schmid 1990; Negrón 1998; Negrón et al. 2014). Defoliation results in reduced carbohydrates compromising tree defenses against bark beetles facilitating successful beetle colonization (Webb 1981; Webb and Karchesy 1977; Wright et al. 1979). The Douglas-fir beetle also prefers large-diameter trees. The Douglas-fir beetle prefers stands with a high percentage of the basal area represented by Douglas-fir, high tree densities, and poor growth during the last 5 years prior to attack. Mortality levels are influenced by the initial host basal area (Negrón 1998).

Western Balsam Bark Beetle (Dryocoetes confusus)

Although not adequately studied, over the past three decades, the western balsam bark beetle has caused high tree mortality of its primary host in Colorado, which is subalpine fir (*Abies lasiocarpa*). The only study on the biology of the insect in Colorado examined its life cycle, flight periodicity, and attack patterns in downed trees. The insect completes its life cycle in 1 year, overwintering in the larval stage, and emerges and disperses in mid-July. Preference for attacks is on the underside of downed trees, which is where populations usually increase (Negrón and Popp 2009).

Pinyon Ips (Ips confusus)

Pinyon ips is the primary bark beetle associated with pinyon pine (*Pinus edulis*) in Colorado and the southwest. Outbreaks occur during drought events. Although small outbreaks occur as a result of downed trees from logging operations, two major outbreaks across the Southwest, including Colorado, have coincided with major extensive severe droughts (Breshears et al. 2005; Shaw et al. 2005). Little is known about the basic biology of this insect. It has multiple generations per year, depending on geographic locations. The insect attacks all sizes of trees, particularly those with

dwarf mistletoe infections and in denser stands (Negrón and Wilson 2003). In general, pinyon ips beetles are favored by dry and warm climatic conditions. In addition, combined with an increased likelihood of pinyon ips infestation associated with higher pinyon dwarf mistletoe (*Arceuthobium divaricatum*) infections may result in pinyon ips populations increasing in relevance under climate change.

Defoliating Lepidoptera

Western Spruce Budworm (Choristoneura occidentalis)

Western spruce budworm is a major defoliator in western conifer forests in North America that utilizes various tree species as hosts. In Colorado, the preferred species are Douglas-fir and white fir (*Abies concolor*) and, to a lesser extent, subalpine fir and Engelmann spruce. Defoliation from the insect can result in reduced growth and height, top-kill, and mortality among other effects (Carlson et al. 1983; MacLean 1985). The insect has one generation per year with adults active in July–August. Egg laying takes place primarily on the underside of needles. The insect overwinters as a first instar larvae and the following spring begin feeding in new buds and young needles. Stand conditions preferred by the insect are multi-storied stands with high host tree densities. These conditions provide ample food and facilitate dispersal (Beckwith and Burnell 1982; Fellin et al. 1983; Hadley and Veblen 1993; Johnson and Denton 1975; Maclauchlan and Brooks 2009). Western spruce budworm outbreaks can trigger Douglas-fir beetle eruptions when larger trees are defoliated (Lessard and Schmid 1990; Negrón 1998).

Swetnam and Lynch (1989), using tree-ring analysis, estimated that about nine outbreaks of western spruce budworm have occurred between 1700 and 1983 in the Colorado Front Range. Reduced tree growth rates resulting from defoliation lasted for an average of 13 years while the return interval between outbreaks averaged 35 years. Outbreaks are hypothesized to be increasing in synchronicity because of changes in forest structure and species composition resulting from harvesting and fire suppression. These events have fostered the development multi-storied stands with high host tree densities (Swetnam and Lynch 1989)—conditions where western spruce budworm thrive as indicated above.

Douglas-fir Tussock Moth (Orgyia pseudotsugata)

Douglas-fir tussock moth is another major defoliator in western conifer forests. However, in Colorado, it has been historically more frequently found in urban environments with little and only localized activity in forested ecosystems. Since the early 1990s, outbreaks are occurring in forest lands in the Pike National Forest and surrounding areas (Negrón et al. 2014). The Douglas-fir tussock moth has one generation per year, overwintering in the egg stage in host tree foliage. Adults are active during summer and into the fall. Females are flightless so primary dispersion is by the first instar larvae which suspend on silken threads from the foliage, facilitating wind transport to other host trees, a behavior called “ballooning.” Outbreaks tend to be brief, most commonly up to 3 years, but can persist as long as 7 years. Outbreaks collapse

primarily by the pressure exerted by parasites, predators, and a nuclear polyhedrosis entomopathogenic virus. Defoliation by the insect can result in top-kill or tree mortality. Defoliation also results in tree growth reduction, although long-term growth rates may increase in surviving trees because of tree mortality of surrounding trees or increased nutrient availability, or both (Alfaro and Shepherd 1991; Wickman 1980). A study in the Pike National Forest indicated significant reductions in basal area caused by the Douglas-fir tussock moth in heavily defoliated stands compared to lightly defoliated stands. Douglas-fir beetle populations increased because of the outbreak but there were no differences in tree mortality between heavily and lightly defoliated stands. Douglas-fir tussock moth killed more trees < 6 inches in d.b.h. while Douglas-fir-beetle killed primarily larger-diameter trees (Negrón et al. 2014).

Balsam Woolly Adelgid (Adelges picea)

The balsam woolly adelgid is an invasive species of true firs that spread to the Interior West in the 1980s and into Utah in the 2010s (Davis et al. 2020). The insect is not present in Colorado but will likely spread into the Colorado Front Range in the future where subalpine fir occurs. Infestations can cause swelling at branch nodes (gouting) where feeding has occurred and can also occur in the main stem. Heavy infestations by the insect can kill trees of any age within 2 years by the sap-sucking activity of the insect to the stem, while lesser infestations cause a slow decline lasting several years by the gouting and stunted tree growth (Hrinkevich et al. 2016).

Diseases

Dwarf Mistletoes (Arceuthobium spp.)

Dwarf mistletoes are parasitic plants that infect conifers in the Colorado Front Range including ponderosa pine, lodgepole pine, limber pine, pinyon pine, and Douglas-fir. Mistletoes use nutrients and water from their host trees. Infections can result in reduced growth, reduced seed and cone production, and mortality when infections are severe (Geils and Hawksworth 2002). In the Central Rockies, about 51 percent of surveyed forests exhibited infections with healthy stands comprising 1.5 higher volumes of mistletoe than infected stands (Tainter and Baker 1996). Infections can also make trees more vulnerable to bark beetle attacks and facilitate mortality of drought-stressed trees (Kliejunas 2011). Trees can be deformed and “witches’ brooms” are produced. These deformities are important for many wildlife species and other organisms, particularly insects, fostering biological diversity. Dwarf mistletoe seeds are produced in female plants and are released explosively. Once seeds fall in a new tree and germinate, a root is produced that penetrates the phloem and xylem of the tree, which is how mistletoe obtains resources from the host. Many species of dwarf mistletoes occur in the Colorado Front Range using a variety of host trees (table 2).

Table 2—Dwarf mistletoes and primary hosts in the Colorado Front Range. Modified from the Field Guide to Insects & Insects of the Rocky Mountain Region, RMRS-GTR-241 (Rocky Mountain Region, Forest Health Protection 2010).

Dwarf mistletoe (DM) species	Primary host
Lodgepole pine DM, *Arceuthobium americanum*	Lodgepole pine
Limber pine DM, *A. cyanocarpum*	Limber and bristlecone pine
Pinyon DM, *A. divaricatum*	Pinyon pine
Douglas-fir DM, *A. douglasii*	Douglas-fir
Southwestern DM, *A. vaginatum subsp. cryptopodium*	Ponderosa pine

Armillaria Root Disease (Armillaria spp.)

Armillaria root disease is the most widely distributed root disease in Colorado (Johnson 1984). In the Colorado Front Range, it occurs primarily in spruce-fir and mixed-conifer forests with higher mortality occurring in subalpine fir trees (Worrall et al. 2004). It is caused by various species of fungi, although *Armillaria solidipes* appears to be the most common. Armillaria root disease infects numerous hosts including all conifers in the Colorado Front Range. Infected trees often exhibit a flow of resin at the base of the tree and thinning of the crown. As the infections move through root contact and rhizomorphs, the disease can create disease centers where adjacent trees are killed, although this is not always the case. Species of *Armillaria* can be secondary agents of tree disease infecting stressed hosts, decomposing dead roots, or aggressive primary pathogens killing healthy trees (Kliejunas 2011; Wargo and Shaw 1985). Root diseases cause growth reductions, mechanical failure that can result in windthrow, and direct tree mortality (Shaw and Kile 1991). Root disease can also make trees more susceptible to bark beetle attacks (Geils and Hawksworth 2002; Tkacz and Schmitz 1986) suggesting that increases in root disease incidence could also exacerbate bark beetle infestations.

White Pine Blister Rust (Cronartium ribicola)

The white pine blister rust (*Cronartium ribicola*) pathogen was introduced from Asia into North America in the early 1900s (Bega 1978) and was first detected in Colorado in 1999 in limber pine in northern Larimer County (Johnson and Jacobi 2000). By 2003, infestations were detected in the Sangre de Cristo and Wet Mountains in limber and bristlecone pine (Blodgett and Sullivan 2004; Burns 2006; USDA FS 2013). The pathogen continues to move in limber to the south and east of the Rockies in Colorado and Wyoming (Jacobi et al. 2018). In combination with other stressors such as drought, and particularly the mountain pine beetle, high mortality levels have been reported for various species of white pines in locations across western North America (Kliejunas 2011). The disease is observed more frequently in limber pine than bristlecone pine although overall incidence is low (Burns 2006). Infections result in branch dieback and tree and sapling mortality (Kliejunas 2011). The rust requires two hosts for completion of its life cycle utilizing primarily *Ribes* spp. and a five-needle pine.

Sudden Aspen Decline and Cytospora Canker of Aspen

Sudden aspen (*Populus tremuloides*) decline was first observed in southwestern Colorado in the mid-2000s and by 2006 almost 150,000 acres were affected. It presents as a rapid synchronous branch dieback, thinning of crowns, and tree mortality at a landscape scale (Dudley et al. 2015; Kliejunas et al. 2009; Worrall et al. 2008). Aspen decline is related to drought conditions (Worall et al. 2010, 2013). Secondary factors such as western tent caterpillar defoliation and bark beetles may have exacerbated mortality levels (Dudley et al. 2015; Worrall et al. 2008).

Cytospora canker of aspen is a common bark disease caused by the fungus *Valsa sordida*. Infections occur primarily when the fungus enters the host through wounds on the bark surface and kills the cambium. It is also a stress pathogen as it occurs more commonly in stressed trees (McIntyre et al. 1996). Cytospora canker can cause dead branches but most importantly it can cause tree mortality of stressed trees, particularly by drought. Healthy trees can often limit colonization.

Effects of Climate Change on Colorado Front Range Forest Insects and Diseases

Climate change will have significant effects on insects as they are particularly sensitive to temperatures. Their short generation times and high biotic potential may lead to faster adaptations to new climatic conditions of higher temperatures compared to their hosts (Jactel et al. 2019). Climate change is anticipated to result in more intense droughts that can weaken trees and compromise their defenses making them more susceptible to insect infestation. More intense storms may facilitate the occurrence of blowdowns that can foster outbreaks of some bark beetle species. Increased atmospheric carbon dioxide will influence host physiology and interactions with associated insects; however, these interactions are not well understood. Finally, climate change will also influence the ecology of natural enemies of insects such as parasites, predators, and a suite of organisms associated with bark beetles such as fungi, mites, and nematodes. Changes in temperature and moisture will influence the life cycle, development, and infectivity of diseases. Effects on host tree physiology and migration will also influence the response of pathogenic organisms.

Bark Beetles

The most important effects of climate change on bark beetles will be manifested through increased temperatures (Bentz et al. 2010). Warmer temperatures will impact overwintering survival and developmental time. Other important effects will include how host trees respond to climate possibly affecting the relationship between beetle species and its host. Climate change will also impact a suite of organisms associated with bark beetles such as mites, fungi, nematodes, and other microorganisms that strongly influence insect development and population dynamics (Jactel 2019).

Cold winter temperatures are a major mortality agent for overwintering bark beetle populations (Bentz et al. 2010; Cole 1981). To survive cold winter temperatures, mountain pine beetle larvae begin the process of "cold-hardening," producing alcohols that protect the larvae from freezing. This begins as temperatures decline towards the winter (Bentz and Mullins 1999). While this adaptation fosters survival of the larvae, cold temperature can still result in mortality. An increase in winter temperatures will facilitate increased winter survival that can lead to higher populations and increased tree mortality. Mountain pine beetles begin attacking new trees in the early to mid-summer and "mass attack," that is, large numbers of beetles attack the tree to be able to overcome the defenses of the tree. For this to occur, mountain pine beetles need to emerge in synchrony. Mountain pine beetle exhibits differential developmental thresholds during its larval instars that fosters synchronous emergence. Warmer temperatures could increase this synchrony and enhance population success (Powell and Bentz 2009). However, warmer temperatures could also increase developmental rates causing the insects to enter winter as an adult, a cold-susceptible stage.

Warmer temperatures can also influence habitat suitability. For example, spruce beetle typically exhibits a 2-year lifecycle, but under warmer conditions they can complete development in 1 year. This change in developmental timing can result in faster buildup of populations and increased tree mortality (Werner and Holsten 1985; Werner et al. 2006). Models have indicated an increase in the probability of spruce beetle transitioning from a 2-year life cycle to 1-year life cycle (Bentz et al. 2010; Hansen et al. 2001).

Warming temperatures will also impact host trees. Changes in water availability to trees will result in physiological stresses that compromise trees' ability to maintain defenses such as resin production. However, elevated atmospheric carbon dioxide could also result in increased resin availability for defense and increased carbohydrates improving the nutritional quality of the host (see Jactel 2019).

In addition to the major bark beetles, pinyon ips may be an insect worthy of increased attention. In general, ips beetles are favored by warmer and drier conditions as they prefer to colonize trees under stress. In addition, the likelihood of infestations by pinyon ips increases with dwarf mistletoe infections (Negrón and Wilson 2003), which may also be exacerbated under climate change and are well distributed in the Pike-San Isabel National Forests (table 4). The combination of these two factors may elevate the importance of this insect in the Pike-San Isabel National Forests.

Mountain Pine Beetle Degree-Day Scenario

A mountain pine beetle scenario is presented as an example of the potential effect of climate change on the habitat distribution of mountain pine beetle in the Arapaho-Roosevelt National Forests. Pheromone traps catch data from several years in lodgepole and ponderosa pine stands indicate that peak flight occurs around the end of July to

early August (fig. 1). Data from several years of successive pheromone trap catches indicate that 898 is the mean number of degree days from peak flight in one year to peak flight the following year using a base temperature of 5.5 °C (Negrón, unpublished data).

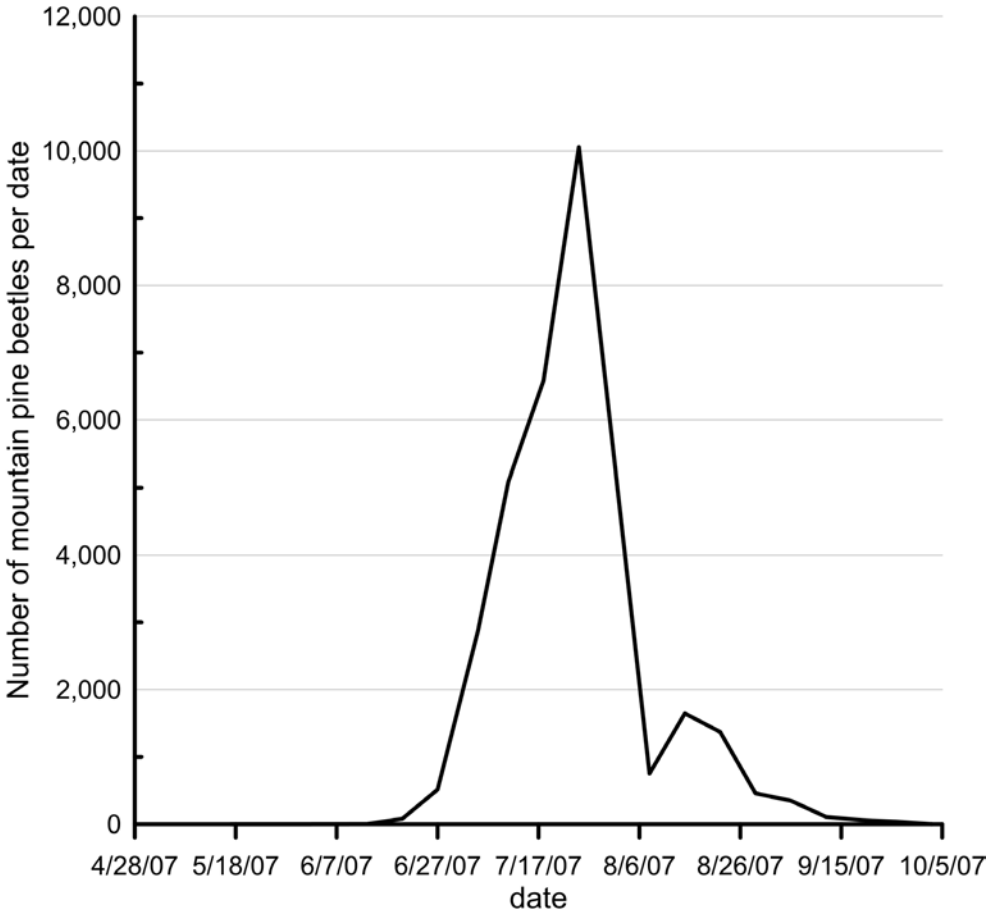

Figure 1—Example of typical mountain pine beetle flight periodicity at the Arapaho-Roosevelt National Forests using data from 2007. Note peak flight occurring at the end of July.

Matthews et al. (2018, 2019) examined signals of climate change across the United States including growing degree days (base 5 °C) and prepared maps comparing recent conditions to future projections under two scenarios of potential change (RCPs 4.5 and 8.5), and four different time periods. Data from the RPC 4.5 maps for the area comprised by the Arapaho-Roosvelt National Forests and plotting an isoline at 898-degree days indicate how the areas of biological suitability where mountain pine beetle can exhibit peak flight between successive years change (fig. 2). In brief, it can be seen how the suitability areas shrink over time, generally transitioning to higher elevations. It should be noted that this is a scenario that does not consider other effects of climate change of mountain pine beetle populations or host responses.

Balsam Wooly Adelgid

Balsam wooly adelgid is expected to continue to spread throughout the range of subalpine fir causing decline and mortality. Extreme winter and summer temperatures can compromise survival and spread. Predictive models of susceptibility to the insect for the Colorado Front Range were like those of forests in northern Utah where the species is now present and causing tree mortality (Hrinkevitch et al. 2016). Conditions associated with a warming climate may allow increased survival and spread of the insect. As the climate becomes hotter, it could further improve favorable conditions for the insect establishment, such as warmer September temperatures needed for the winter survival of the first instar nymphs. That, combined with climate that brings wet and cool spring conditions, especially in May, could incite mortality events (Hrinkevich 2016).

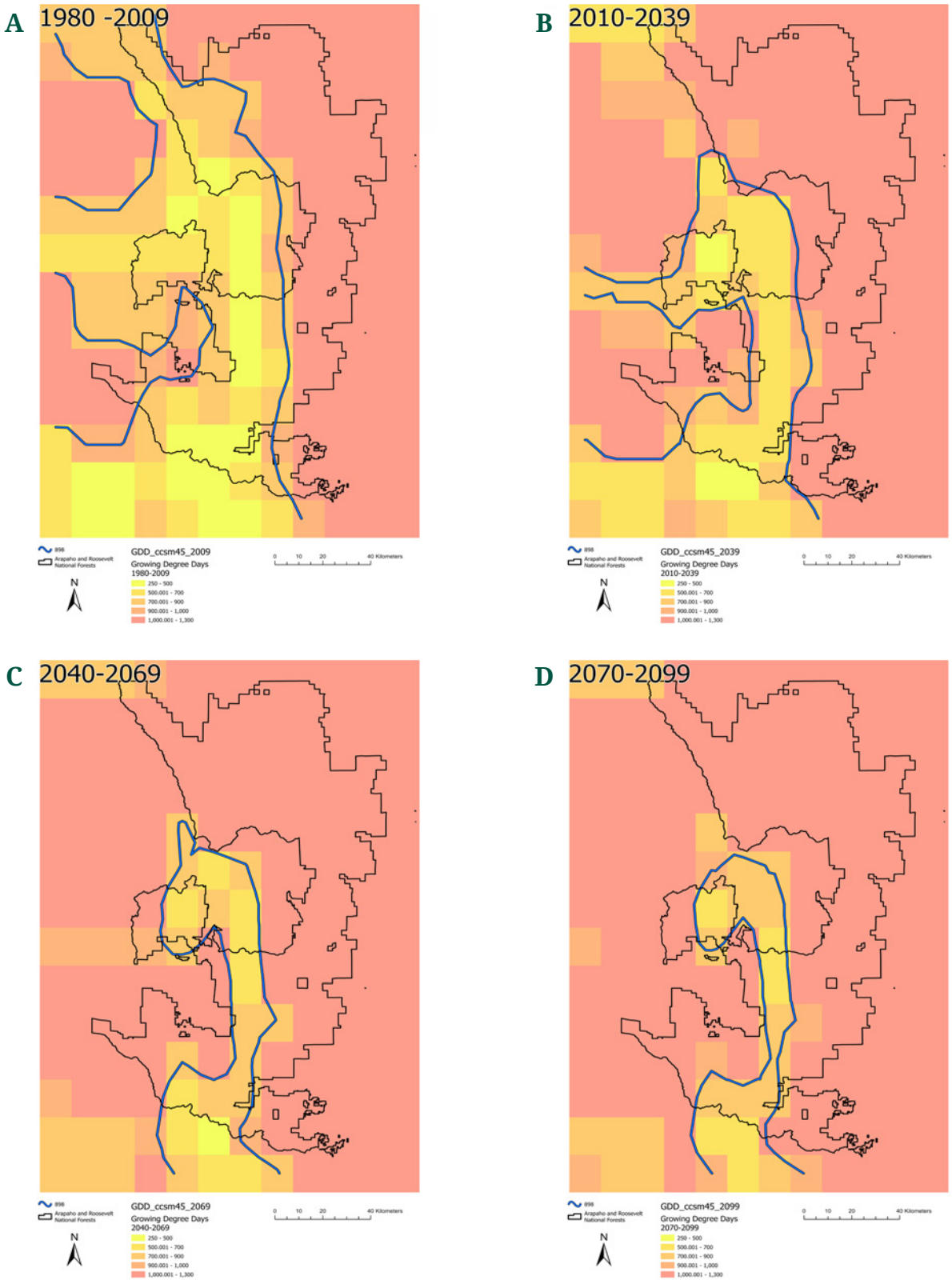

Figure 2—Recent and projected degree-day accumulations at the Arapaho-Roosevelt National Forests. Data come from projections by Matthews et al. 2018, 2019. Blue lines enclose areas of suitability for mountain pine beetle peak flight between successive years: (a) 1980–2009, (b) 2010–2039, (c) 2040–2069, and (d) 2070–2099.

Defoliators

Weather conditions govern many biological processes of defoliators and their interactions with their hosts. Although there is a paucity of information on the potential effects of climate change on defoliators in the PSI-AR, available knowledge on the ecology of these organisms can help answer some questions.

Climate change will influence western spruce budworm in diverse ways so it is challenging to portray what the future may look like. Western spruce budworm outbreaks have increased in duration, intensity, and extent. Historical land use and warming climate are considered as drivers (Gray 2008; Swetnam and Lynch 1993; Williams and Liebhold 1995) but causal mechanisms are poorly understood (Peltonen et al. 2002). Western spruce budworm outbreaks can cover large geographical areas and last decades (Swetnam and Lynch 1989, 1993). Temperature patterns and fluctuations and rainfall can affect development, dispersal, feeding, fecundity, and survival. Early spring temperatures help synchronize larval emergence with bud break. Warm springs can result in earlier emergence while cold temperatures can delay emergence decoupling synchronization; either way, it is maladaptive to the larvae by increasing exposure to natural enemies and limiting food quality. Warm temperatures in the fall and winter can result in increased metabolic expenditures by the larvae; colder temperatures can increase the risk of frost after emerging from their winter habitat; and dispersal limited by increased rainfall. Cool springs and early summer can reduce developmental speed making the larvae more susceptible to predation. (See Beckwith and Burnell 1982; Carlson et al. 1983; Chen et al. 2003; Johnson and Denton 1975; O'Connor et al. 2015; Régnière et al. 2012; Thomson 1979; Thomson and Benton, 2007).

Western spruce outbreaks in the southwestern United States have been associated with increased spring and summer precipitation, which may foster abundant and better-quality food resources (Flower et al. 2014; Ryerson et al. 2003; Swetnam and Betancourt 1998; Swetnam and Lynch 1993). On the other hand, several studies have related outbreak initiation with reduced moisture prior to the outbreak (Flower et al. 2014; Senf et al. 2017; Xu et al. 2019). The outbreak association with increased moisture has been documented in the San Juan Mountains of southwestern Colorado and in northern New Mexico while the association with reduced moisture prior to outbreaks is more typical of the Northwest and British Columbia (Flower et al. 2014; Senf et al. 2017; Xu et al. 2019)

It will be important to monitor western spruce budworm populations as climate change manifests. Tree-ring reconstructions in the southern Rockies, including the Colorado Front Range, suggest average outbreak return intervals every 35 years with a range of 14–58 years (Swetnam and Lynch 1989). Although an outbreak occurred in the Arapaho-Roosevelt NFs in the 1970s, populations are currently scarce (table 3). Western spruce budworm is currently well distributed in the Pike-San Isabel National Forests (table 4).

Table 3—Number of FIA plots by forest type in the Arapaho-Roosevelt National Forests with presence of dwarf mistletoe, root disease, or western spruce budworm. Note that dwarf mistletoe occurrence was widespread, with only small detections of root disease occurring mostly from lodgepole pine up to subalpine forests. Western spruce budworm was not detected. Data from FIA measurements from 2009–2018.

Forest type	FIA plots (number)	Dwarf mistletoe	Root disease	Western spruce budworm
Douglas-fir	14	50.0	0.0	0.0
Ponderosa pine	24	25.0	0.0	0.0
Engelmann spruce	17	5.9	5.9	0.0
Engelmann spruce/subalpine fir	47	17.0	2.1	0.0
Subalpine fir	16	18.8	0.0	0.0
Lodgepole pine	67	46.3	1.5	0.0
Bristlecone pine	1	0.0	0.0	0.0
Limber pine	5	0.0	0.0	0.0
Aspen	19	10.5	0.0	0.0

Douglas-fir tussock moth outbreaks are short-lived, and their duration is strongly influenced by the epidemiology of a nuclear polyhedrosis virus that regulates populations. It is unknown how the virus will respond to climate change; if negatively impacted, Douglas-fir tussock moth outbreaks may increase in duration. Warmer temperatures may increase the likelihood of outbreaks in drier sites.

Table 4—Number of FIA plots by forest type in the Pike-San Isabel National Forests with presence of dwarf mistletoe, root disease, or western spruce budworm. Note that dwarf mistletoe and western spruce budworm occurrence was widespread, with only small detections of root disease mostly occurring in subalpine forests. Data from FIA measurements from 2009–2018.

Forest type	FIA no. of plots	Dwarf mistletoe	Root disease	Western spruce budworm
Pinyon-juniper woodland	13	15.4	0.0	0.0
Douglas-fir	64	14.1	1.6	26.6
Ponderosa pine	44	15.9	0.0	20.5
White fir	7	0.0	0.0	42.9
Engelmann spruce	59	0.0	3.4	11.9
Engelmann spruce/subalpine fir	14	7.1	7.1	14.3
Subalpine fir	2	0.0	0.0	0.0
Blue spruce	1	0.0	0.0	0.0
Lodgepole pine	31	32.3	0.0	3.2
Foxtail/bristlecone pine	5	20.0	0.0	0.0
Limber pine	12	0.0	0.0	8.3
Aspen	39	2.6	0.0	22.9

Pathogens

Dwarf Mistletoe

Dwarf mistletoe can cause tree mortality particularly when trees become stressed due to drought conditions (Kliejunas et al. 2009). Tree mortality caused by dwarf mistletoe is the result of declining growth rates in the long term, particularly when infections become severe towards the top of the tree (Hawksworth and Wiens 1996). For the most part, the geographic distribution of mistletoe species follows that of its hosts, but their range is limited by cold temperatures (Hawksworth and Weins 1996). This suggests that range expansion is possible under increased temperatures with mistletoes following host migration.

Stanton (2007), working with mature ponderosa pine, indicated that the growth rate of infected trees is more sensitive than those of uninfected trees and that moisture stress can exacerbate mistletoe infections. Increasing temperatures and drought frequency anticipated under climate change may have beneficial effects to mistletoe infections.

Dwarf mistletoe is currently widespread in both the Arapaho-Roosevelt and the Pike-San Isabel National Forests (tables 3 and 4), particularly in the ponderosa pine, lodgepole pine, and Douglas-fir forest types, indicating that it is one of the most important agents to monitor as climate change continues to manifest. Mistletoe infections in pinyon will make them susceptible to pinyon ips.

Armillaria Root Disease (Armillaria spp.)

Tree stress is a primary risk factor for Armillaria infection; therefore, increased stress of host trees associated with warmer temperatures and drought may result in increased levels of *Armillaria* (Kliejunas et al. 2009; Shaw and Kile 1991; Sturrock et al. 2011). In addition, increased levels of atmospheric carbon dioxide may foster increased root growth, which may increase the likelihood of an infection to move from one tree to an adjacent one through root contact (O'Neill 1994). Host distribution will also be key to the future distribution of *Armillaria*. While an increase in activity is expected, the area of climatic suitability for Douglas-fir, a primary host, may decrease (Klopfenstein et al. 2009).

Root disease is not widely distributed in either the Arapaho-Roosevelt or the Pike-San Isabel National Forests. However, it is present in spruce-fir stands of both Forests (tables 3 and 4). If the disease increases with tree stress, it may become a factor in these Forests.

White Pine Blister Rust (Cronartium ribicola)

White pine blister rust is considered a cool weather disease. Development, dispersal, and germination of rust spores are directly affected by environmental conditions (Kliejunas et al. 2009), and conditions for successful infection have been examined (Spaulding 1922; Sturrock et al. 2011; Van Arsdel 1956). The fungus requires high

humidity and temperatures below 68 °F. Reduced infection levels are expected under the high temperatures and dryer conditions anticipated under climate change (Kinloch 2003; Kliejunas 2011; Sturrock et al. 2011).

Sudden Aspen Decline and Cytospora Canker of Aspen

Both conditions are associated with stress conditions and drought and will likely increase under warming temperatures and more frequent droughts (Kliejunas et al. 2009; Worrall et al. 2013); however, interactions of these conditions with climate change have not been examined.

Concluding Remarks

Warming temperatures and changes in precipitation patterns associated with climate change will influence the biology and ecology of forest insects and diseases. In general, the literature suggests an increase in frequency and intensity of outbreaks, range expansions, and increases in population numbers will be affected by a warming climate. In the long term, effects will also be governed by how host trees respond to climate change as their distributions will change and species are expected to migrate. Changes in host distribution may have positive or negative effects on insects and diseases. Increased stress in hosts associated with drought may make trees more susceptible to some insects and diseases synergizing and influencing tree mortality in the most affected areas. The effects of climate change on associated organisms of insects and diseases, such as natural enemies and vectors, remain largely unknown. In sum, some insect and diseases will exhibit positive responses such as faster growth, larger insects, range expansion, and increased capability to successfully infest their hosts while others may exhibit negative responses such as decoupling host and insect phenology and fostering maladaptive life cycles.

While our understanding of these interactions necessitates additional research, a few general statements can be made. Outbreaks of mountain pine beetle may increase in frequency and intensity because of increased drought-induced stress in their hosts and increased winter temperatures that foster increased survival in insect overwintering populations. Spruce beetle outbreaks may also become more common as warmer temperatures foster 1-year life cycles, which support population growth along with increased stress in hosts caused by drought. Pinyon ips could increase as the insect prefers warmer and drier conditions and is exacerbated by dwarf mistletoe infections, which are also expected to increase due to host stress. Western spruce budworm populations will likely increase during periods of increased moisture. Armillaria root disease will likely increase in abundance in higher-elevation spruce-fir stands because of increased tree stress. At low elevations, mistletoe parasitism would be more prevalent and white pine blister rust may decrease as it is more successful under cooler wetter conditions. Continued monitoring of insect and disease populations should be increased by managers and practitioners as climate change continues to manifest and increased research efforts are needed to knowledge gaps.

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Acknowledgments

We would like to thank Seth Davis, Rebecca Stokes, Alison Foster, and Amy Birtwistle for their review of previous versions of this document, and Sharon Parkes for preparing the GIS maps.