

# The Effect of a Warming Environment on Forest Pest Species: A Contrast Between Bark Beetles and Defoliators

---

**Matthew Huk**

**April 15, 2015**



## **Abstract**

Climate change has been the driver of diverse ecological changes worldwide. The effects of the warming environment have been observed among several forest insect species, and their host tree interactions. Insects are cold-blooded organisms, therefore, temperature is the key parameter determining timing and duration of lifecycle events, as well as their geographical distribution. Correspondingly, the warming environment is also affecting forest health, resilience and structure. Consequently, shifting herbivory rates, altered distribution of forest pests, and an increased unpredictability of trophic interactions have already threatened the integrity of several forest systems. This review contrasts the effects of climate change on bark beetles and European defoliators outlining the key mechanisms of altered population dynamics. Additionally two case studies are developed involving the spruce beetle and the larch bud moth (LBM) to illustrate the nuances between the systems.

## Introduction

A widely debated issue over the past several decades has been whether the rapid rise of greenhouse gas emissions has caused and continues to cause global warming. However, on-going research and empirical evidence substantiate that air and ocean temperatures have continued to rise at an unprecedented rate as atmospheric greenhouse gases accumulate (Environment Canada, 2014). The global carbon dioxide concentrations have now reached 400 parts per million, a phenomenon which has not occurred for 800 000 years (Thompson, 2014). As such, an increased rate of ice and snow melt has caused increased flooding, a rising sea level, altered precipitation patterns, and an increase in the frequency and severity of hazardous weather events such as hurricanes and heat-waves (IPCC, 2014). As altered climate patterns affect organisms differently, changing trophic interactions are threatening the integrity and resilience of many ecosystems, pushing some into new regimes as prior controls no longer function (Raffa et al., 2008).

The population dynamics of forest insects are particularly affected by the global average temperature increase. As cold-blooded organisms, temperature plays a vital role in determining the duration and timing of life cycle events, as well as their geographical distribution (Logan et al., 2003). Additionally, as several relationships between abiotic variables such as temperature and precipitation decouple under climate change, response mechanisms may no longer be adaptive resulting in reduced fitness of populations (Visser et al., 2000). These circumstances lead to high

selection pressures; however, many populations are able to persist, by dispersing to more climatically suitable areas, or changing their behaviour. Consequently, climate change has already driven several changes in population dynamics of insect species. The recent synchronous population outbreak of three North American bark beetle species - mountain pine beetle (*Dendroctonus ponderosae*), spruce beetle (*Dendroctonus rufipennis*) and the pinyon ips beetle, (*Ips confusus*) has largely been attributed to favourable conditions following climate change (Raffa et al., 2008). Conversely, the European defoliators - larch bud moth (*Zeiraphera diniana*) and the southern distribution of the winter moth (*Operophtera brumata*)- have been significantly disadvantaged to the point that outbreak population sizes may no longer be possible, despite a long history of regular outbreaks (Visser et al., 2000; Johnson et al, 2010). Despite each insect being subject to similar environmental changes, the different thresholds and controls acting on their systems have yielded different population dynamics. This review contrasts the effects of climate change on bark beetles and European defoliators outlining the key mechanisms of altered population dynamics. Additionally two case studies are developed involving the spruce beetle and the larch bud moth (LBM) to illustrate the nuances between the systems.

## **North American Bark Beetles**

Bark beetles are native insects to the forests of North America. Unlike most phytophagous insects (insects that feed primarily on plant matter), bark beetles require the death of their host to successfully reproduce (Wood, 1982). Selective

pressures during the co-evolution of bark beetles and their host trees have thus resulted in trees that are resistant to attack, as well as an increased behavioural complexity of beetles to better overcome tree defenses (Raffa and Berryman, 1983). Non-outbreak population levels are unable to overcome defenses of healthy trees, but bark beetles are ubiquitous in most North American forests due to their ability to colonize weakened or highly stressed trees (Raffa and Berryman, 1983). Periodically some bark beetle species can surpass the eruptive threshold, leading to positive feedbacks that amplify across multiple scales (Raffa et al., 2008). During the recent population explosions of the mountain pine beetle, spruce beetle and the pinyon ips beetle, a combination of host suitability and availability, conducive weather conditions, and sufficient escape from natural enemies, allowed for all three beetle species to reach densities that surpassed the stand level eruptive threshold. Additionally, each beetle expanded its range both elevationally and latitudinally into naïve ecosystems that were previously considered climatically unsuitable (Safranyik et al., 2010). Although the nuances of the outbreaks vary among the three systems, unusually high temperatures and drought conditions are thought to have been the catalyst for all three of the synchronous population eruptions, especially when considering the effects on host susceptibility (Raffa et al., 2008).

### **Synthesis of Attack**

As each bark beetle generation emerges from its host tree, it must locate new hosts to reproduce and sustain the population. This is the result of the host-tree habitat becoming nutritionally exhausted following colonization and its death (Raffa and

Berryman, 1983). Pioneering beetles, those leading the attack, will land on trees at random and attempt to bore into the subcortical region of their host (Raffa et al., 2005). As they bore into trees, beetles exploit the hosts' terpenes by emitting aggregation pheromones, thereby signaling to other beetles to join the attack (Raffa et al., 2008). Each beetle vectors an array of symbiotic fungi and other microorganisms, which have varying effects on host resistance and beetle population dynamics, effectively contributing to the virulence of the attack (Raffa and Berryman, 1983). Additional attacking beetles help to overcome the tree's defensive mechanisms, which is a necessary component in the successful colonization of healthy trees. Following the depletion of host resistance, beetles cease the production of aggregation pheromones, and begin producing antiaggregation pheromones to limit the effects of intraspecific competition (Raffa et al., 2008).

### **Climatic Effects on Host Tree Defenses**

For beetle establishment within host trees to be successful, the critical defensive threshold of hosts must be surpassed (Raffa et al., 2008). Beetles must kill the living cells of the xylem and phloem, thereby preventing the tree from impeding beetle colonization (Raffa and Berryman, 1983). Mortality ensues shortly thereafter; however, conifers exhibit two main defensive mechanisms to impede beetle colonization (Raffa et al., 2005). Firstly, constitutive defenses are formed in the cambium as a part of regular growth. These ducts are the first defense of the tree and respond to mechanical wounding by releasing resin to create a toxic physical barrier (Raffa et al., 2008). Secondary induced responses commence shortly after, as

a response to the beetle fungal complex (Raffa et al., 2005). Consequently, trees trigger autonecrosis in an effort to rapidly confine the fungal complex. While other forms of mechanical damage are common in North American forests, selection pressures have been high for rapid tree recognition of colonization and subsequent mobilization of induced responses due to the high energetic investments associated with induced responses (Raffa and Berryman, 1983). Therefore, incidences of non-recognition are low, as nearly all trees will respond with necrotic lesions (Raffa et al., 2005). However, there is high variation in the rate and extent of response, tightly linked with the health and vigor of the tree (Raffa et al., 2008). This directly affects the tree's critical defensive threshold. Drought-induced stress has been directly linked to reduced defensive thresholds of host trees, as demonstrated by the pinyon ips outbreak in the Southern United States, pinyon-juniper woodlands (Floyd et al., 2009).

While periodic drought is not a new phenomenon, the higher temperatures caused by climate change have the potential to exacerbate the effects of drought on vegetation by contributing to reduced soil moisture regardless of changes in precipitation (Cai et al., 2009). Severe drought conditions also have the ability to mask density-dependent suitable host tree locations, thereby increasing the amount of suitable beetle habitat and subsequent tree mortality (Thomson and Shrimpton., 1984). As precipitation regimes continue to alter under climate change (IPCC, 2014), the resulting effect of the distribution and frequency of drought events is challenging to anticipate for individual locations. However, higher average



temperatures will likely contribute to increased physiological stress of vegetation on a broad scale (Aukema et al., 2007). Additionally, short-term drought followed by a return to normal (or above normal) precipitation could catalyze a population eruption, and subsequently facilitate positive feedbacks by increasing the supply of healthy, thick-phloem trees.

While warm temperatures and enhanced drought conditions contributed to a landscape of trees with a reduced defensive threshold, other factors can simultaneously inflict physiological stress on host trees. Two factors that have contributed to stand and landscape-level stress are traditional forest management and active fire repression (Taylor and Carroll, 2004). Historically, easily accessible areas were generally harvested first, but there were few standards regarding the size of clear cuts and the adjacency between these areas. Consequently, there was a high incidence of valley bottoms and low elevation sites that were converted from natural forest, with diverse species and age class distributions, to single-aged stands with a propensity for monocultures dominated by fast-growing early successional species such as lodgepole pine. Additionally, humans frequently inhabit valley bottoms and low elevation areas; therefore, many areas, in which fire was historically an integral part of the ecosystem, have experienced a high degree of fire suppression. Extensive areas of even-aged stands with low compositional and structural diversity are fairly common in managed landscapes. Furthermore, the absence of fire from these ecosystems may create conditions that subject trees to crowding, disease, and old age, all of which present physiological stresses to trees

(Floyd et al., 2009). Connectivity among forests exhibiting similar conditions has increased within the dispersal range of several bark beetles, resulting in conditions conducive for insect populations to increase and stand eruptive thresholds to be met and surpassed (Taylor and Carroll, 2004).

### **Case Study: The Spruce Beetle**

The spruce beetle has recently undergone a population outbreak, causing wide-scale mortality of spruce forests synchronously throughout its range, while seemingly expanding its range into naïve ecosystems. A warming environment has altered the biology of spruce beetles, significantly contributing to their eruptive capacity. While spruce beetles are known to have a univoltine life cycle on warmer sites, the two-year semivoltine life cycle is predominant throughout most of its range (Hansen et al., 2001). In a typical two-year cycle, eggs tend to hatch near the end of summer, and larvae feed gregariously for the first two instars (Figure 1). Third and fourth instars construct individual feeding galleries where they overwinter (Holsten et al., 1999). The following summer, beetles will generally pupate at the end of their larval galleries, and up to 95% of adults will emerge from the tree and bore into the bark at the base of the tree where they will overwinter once again (Miller, 1987). Moving to the base of the tree thereby acquiring insulation from the snowpack is a behavioural mechanism to avoid overwinter mortality (Holsten et al., 1990).

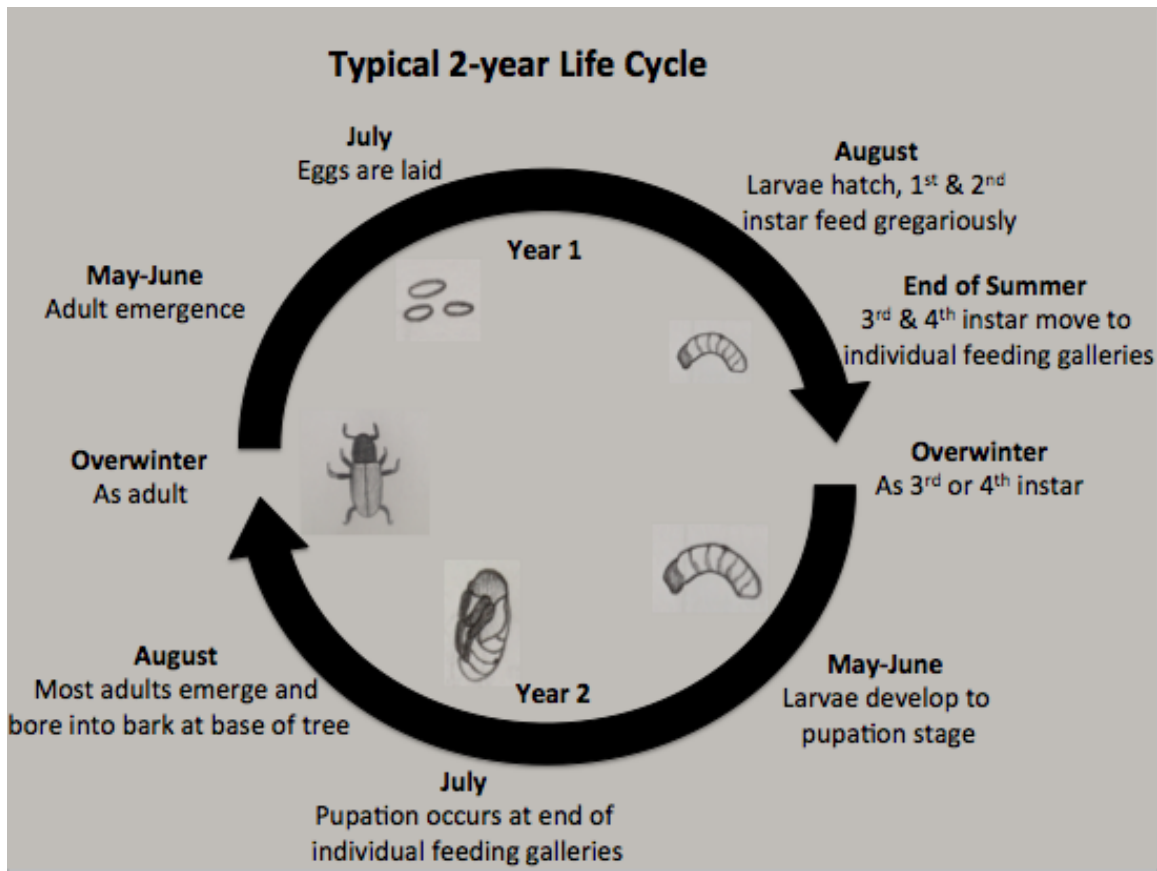


Fig. 1. Typical two-year lifecycle of spruce beetle considered predominant throughout its range.

The unusually warm temperatures that began in the early 1990s allowed for a shift from semi- to univoltinism of spruce beetles (Raffa et al, 2008) (Figure 2). Two scenarios involving elevated temperatures result in univoltine broods (Werner and Holsten, 1984). The first scenario involves high temperatures in May to June that lead to early pupation and subsequent adult emergence (Berg et al., 2006). This allows the beetles to breed, attack a new tree, and lay eggs, thereby accelerating their life cycle by a year. The second scenario involves phloem temperatures reaching 16.5 °C during the first and second instars (Figure 3). This threshold is

based on empirical observations but the duration for which these temperatures needed to be sustained for univoltinism to occur was not quantified (Werner and Holsten, 1984).

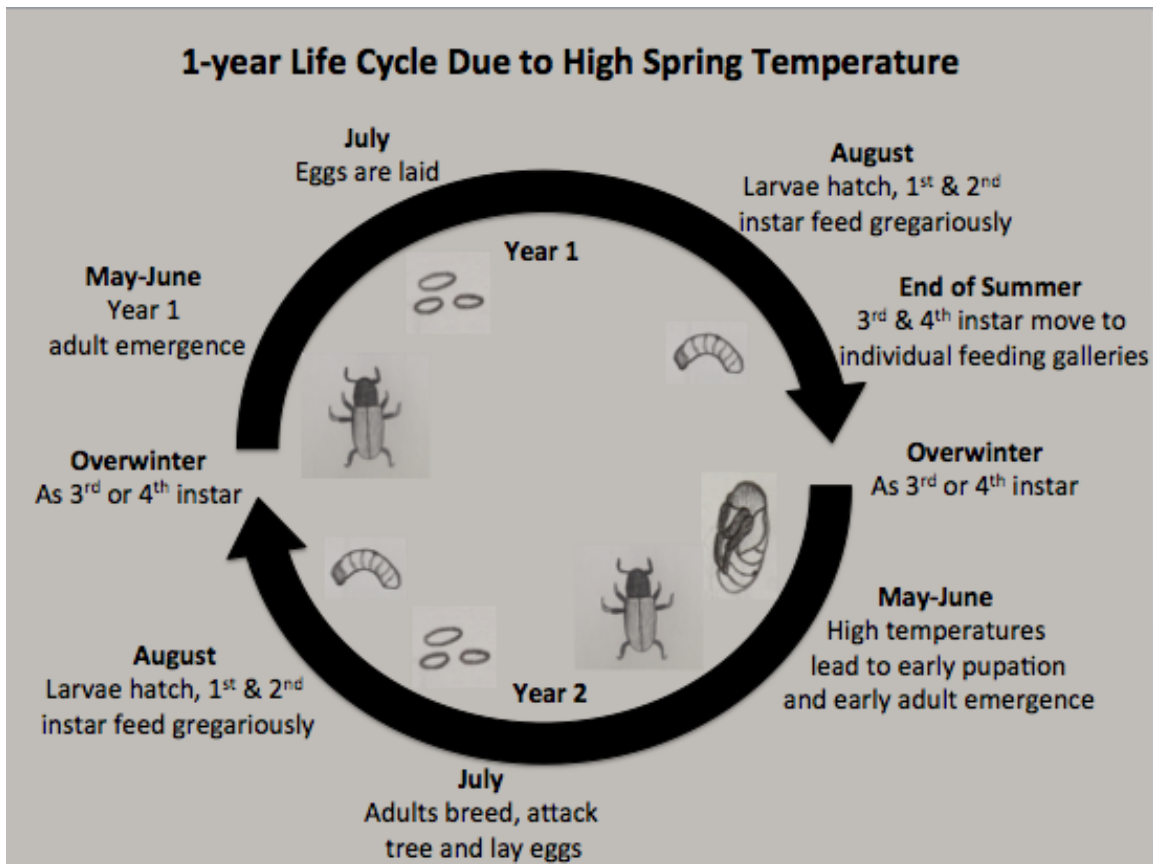


Fig. 2. One-year lifecycle as a result of high spring temperatures.

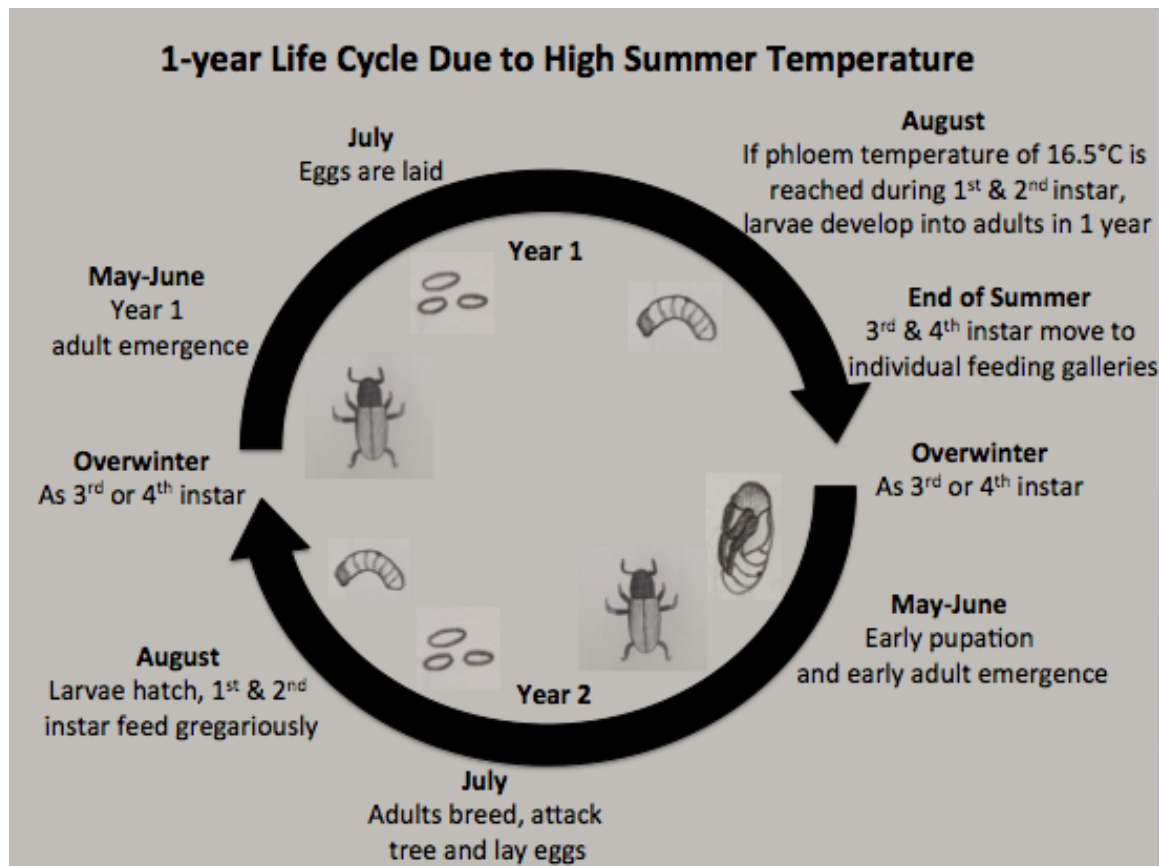


Fig. 3. One-year lifecycle as a result of high summer temperatures during 1<sup>st</sup> and 2<sup>nd</sup> instars.

Assuming equal brood survival and fecundity, univoltine beetles can effectively double their population size in each generation relative to their semivoltine counterparts (Hansen et al., 2001). This was likely the main contributor to population densities reaching the critical threshold beyond which positive feedbacks manifested and the resulting widespread outbreak throughout its range (Raffa et al., 2008). Consequently, millions of hectares of spruce forests experienced high rates of mortality, affecting forest structure and fire behaviour, while incurring direct financial losses for the forest products industry (Berg et al., 2006).

## European Defoliators

Defoliators are classified as insects that consume leaves or needles of trees.

Depending on the density and feeding intensity of the insects, they can cause direct tree mortality, or predispose trees to subsequent insect or pathogenic attacks

(Forest Health Protection, 2011). However, many tree species are able to survive even complete defoliation, and many defoliating species play integral roles in their ecosystems, as they contribute to nutrient cycling. The larch bud moth (LBM) and the winter moth are part of a group of defoliating pests that rely on precise synchrony of larval emergence with the bud burst of their host trees. Strong selection pressures have caused bud burst and egg hatching to respond to abiotic variables in the same way and with common thresholds so that synchrony may be maintained under varying climate conditions (Visser and Holleman, 2001).

Consequently, timing of egg hatch relative to bud burst should remain coupled given a temperature increase. However, insect development rates respond to temperature in an almost linear fashion (Raffa et al., 2008), while bud burst responds to multiple climatic variables non-linearly (Chuine, 2000). The high degree of environmental asynchrony experienced by LBM and the southern range of the winter moth suggests that the response mechanisms in their systems are no longer adaptive under the new temperature regime (Visser and Holleman, 2001, Johnson et al., 2010). Furthermore, rising temperatures may interact with other abiotic variables such as soil moisture, influencing host plant quality and host parasitoid interactions, further disadvantaging the defoliators (Johnson et al., 2010).

### **Climatic Effects on Bud Burst**

Budburst phenology is largely based on three variables: chilling period, photoperiod, and heat sum above a certain threshold (Hanninen, 1995). Thresholds vary among species and there is also a large potential for variation within species due to variations in phenology and microhabitat conditions. The interaction between generally warmer winters, warmer spring temperatures and altered cloud cover from changing precipitation patterns (which affects photoperiod) results in the non-linear response of budburst to climate change (Chinua, 2000). This has generally resulted in the earlier onset of budburst, especially in high elevation areas where climate warming is more pronounced (Johnson et al., 2010). Trees are thereby able to meet their heat sum and photoperiod requirements earlier in the year, beginning their growing season earlier.

### **Climatic Effects on Defoliator Phenology**

While responses of defoliating insects to climate change will be complex and varied among species, many will continue to exhibit threshold-like responses to changing abiotic factors in life cycle stages such as diapause and development rates (Bale et al., 2002). Climate change will also potentially influence insect distribution, as suitable habitat range is likely to change elevationally and latitudinally (Wagner et al., 1984). Other potential changes to phenology include altered voltinism, genetic variability and reproductive fitness, and increased winter survival, all of which will influence host plant exploitation and population densities (Bale et al., 2002, Jepsen et al., 2008).

### **Case Study: The Larch Bud Moth**

The larch bud moth (LBM) has exhibited regular periodic outbreaks every 8-10 years in the European Alps since A.D. 800 (Baltensweiler et al., 1977). While endemic populations persist, there have been no recorded outbreaks of LBM since the 1980s (Johnson et al., 2010). Prior to the current phenomenon, dendrochronological evidence suggests that infestations consistently originated in western Europe and spread eastward across the Alpine arc in the direction of prevailing winds (Baltensweiler et al., 2008). Throughout the 20<sup>th</sup> century, outbreak epicenters had also been moving upwards in elevational as a response to rising temperatures and the subsequent shift of optimal climatic conditions (Johnson et al., 2010). Prior to the disruption of LBM outbreak cycles, the optimal elevational zone for LBM was estimated to be near the larch timberline.

LBM's food source is the needle biomass of European larch (*L. decidua*). Larch is a relatively poor seed disperser and requires exposed mineral soil for successful regeneration. Despite climate change allowing for potential elevational range expansion of larch, the upward shift of larch has lagged behind the upward shift of the more mobile LBM (Johnson et al., 2010). Furthermore, available needle biomass decreases as elevation approaches the timberline due to harsher growing conditions yielding smaller trees (Matras and Paques, 2003). Now that the optimal elevational zone of LBM has reached the treeline, the smaller trees cannot supply enough biomass in order for LBM to reach the outbreak density threshold (Johnson et al., 2010). Additionally, as climate warming is most pronounced at high elevations, the



onset of budburst in high elevation larch trees is increasingly occurring earlier, contributing to a high incidence of environmental asynchrony between egg hatch and larch bud burst (Johnson et al., 2010). The combined effects of a reduced food source and environmental asynchrony make the recovery of this system unlikely given climate projections. While the effect of the collapse of the LBM is speculative, regular periodic outbreaks have played an integral role in the system for centuries. This may have negative impacts on LBM predators, who may be responsible for a myriad of other ecosystem processes. Additionally, reduced defoliation may contribute to altered forest structure, which can alter downstream water yield, as well as fire behaviour. The absence of LBM outbreaks may therefore indirectly cause future financial losses if fire mitigation or water supply become necessary.

## **Conclusion**

While climate change brings many uncertainties regarding altered trophic interactions, several effects of warming environments have been observed in forest pest species dynamics in the past decade. As host and insect species are subject to thermal environments beyond their historic range of variation, there will be “winners” and “losers” depending on their complex ecological responses (Logan et al., 2003). Several North American bark beetle species have greatly benefitted because of rising global temperatures, while certain European defoliator species face a new regime in which eruptive populations may never again be reached. The ways trophic interactions are influenced by abiotic variables tend to be ecosystem specific and predicting the effect that rising temperatures will have on forest pests

in general is difficult to achieve (Bale et al., 2002). Given the varied responses among species and uncertainty in forecasting local-scale changes in climate, forest managers should be prepared for shifting herbivory rates, altered distribution of forest pests, and an increased unpredictability of trophic interactions between hosts, pests, and parasites (Logan et al., 2003). While the downfall of certain forest pest species may be economically beneficial in certain circumstances, they tend to play an integral role in highly adapted ecosystems, which can also adversely affect other species. Conversely, range expansion and population outbreaks of pests can have lasting economic and ecological impacts, and may even leave forests predisposed to subsequent infestations (Raffa et al., 2008). It is therefore extremely important to monitor forest health and structure, and to implement forest practices that reduce stand susceptibility on appropriate temporal scales. While uncertainties and budget constraints may be major hindrances in the short term, initiative must be taken in order to sustain biodiversity and ecological processes in the long term.

## References

- Bale, Jefferey, Gregory Masters, Ian Hodgkinson, Caroline Awmack, Martijn Bezemer, Valerie Brown, Jennifer Butterfield, Alan Buse, John Coulson, John Good, Richard Harington, Susane Hartley, Hefin Jones, Richard Lindroth, Malcolm Press, Ilias Symmioudis, Allan Watt, and John Whittaker. "Herbivory in Global Climate Change Research: Direct Effects of Rising Temperature on Insect Herbivores." *Global Change Biology* 8.1 (2002): 1-16. Web. 13 Apr. 2015.
- Baltensweiler, W., G. Benz, P. Bovey, and V. Delucchi. "Dynamics of Larch Bud Moth Populations." *Annual Review of Entomology* 22.1 (1977): 79-100. Web.
- Baltensweiler, Werner, Urs M. Weber, and Paolo Cherubini. "Tracing the Influence of Larch-bud-moth Insect Outbreaks and Weather Conditions on Larch Tree-ring Growth in Engadine (Switzerland)." *Oikos* 117.2 (2008): 161-72. Web.
- Cai, Wenju, Tim Cowan, Peter Briggs, and Micahel Raupach. "Rising Temperature Depletes Soil Moisture and Exacerbates Severe drought Conditions across Southeast Australia." *Geophysical Research Letters* 36 (2009): n. pag. Web.
- Chaine, Isabelle. "A Unified Model for Budburst in Trees." *Journal of Theoretical Biology* 207.3 (2000): 337-47. *A Unified Model for Budburst of Trees*. Web. 13 Apr. 2015.
- "Climate Change Science and Research." *Government of Canada, Environment Canada*. Environment Canada, 18 Sept. 2014. Web. 13 Apr. 2015.
- Floyd, M. Lisa, Michael Clifford, Neil S. Cobb, Dustin Hanna, Robert Delph, Paulette Ford, and Dave Turner. "Relationship of Stand Characteristics to Drought-induced Mortality in Three Southwestern Piñon-juniper Woodlands." *Ecological Applications* 19.5 (2009): 1223-230. Web.

- Forest Health Protection. "Introduction to Defoliating Insects." *Forest Health Protection - Rocky Mountain Division* (2011): n. pag. Web.
- Hanninen, Heikki. "Canadian Journal of Botany." *Effects of Climatic Change on Trees from Cool and Temperate Regions: An Ecophysiological Approach to Modelling of Bud Burst Phenology* -. Canadian Journal of Botany, n.d. Web. 13 Apr. 2015.
- Holsten, E.H., Their, R.W., Munson, A.S., Gibson, K.E., 1999. The Spruce Beetle. U.S. For. Insect and Disease Leaflet 127, Washington , DC.
- Jepsen, Jane U., Snorre B. Hagen, Rolf A. Ims, and Nigel G. Yoccoz. "Climate Change and Outbreaks of the Geometrids Operophtera Brumata and Epirrita Autumnata in Subarctic Birch Forest: Evidence of a Recent Outbreak Range Expansion." *Journal of Animal Ecology* 77.2 (2008): 257-64. Web.
- Johnson, D. M., U. Buntgen, D. C. Frank, K. Kausrud, K. J. Haynes, A. M. Liebhold, J. Esper, and N. C. Stenseth. "Climatic Warming Disrupts Recurrent Alpine Insect Outbreaks." *Proceedings of the National Academy of Sciences* 107.47 (2010): 20576-0581. Web.
- Logan, Jesse A., Jacques Regniere, and James A. Powell. "Assessing the Impacts of Global Warming on Forest Pest Dynamics." *Frontiers in Ecology and the Environment* 1.3 (2003): 130. Web.
- Matras, Jan, and Luc Paques. *Forest Information: Trees: The European Larch: Larix Decidua*. Rotorua, N.Z.: Forestry Corporation, n.d. Web.
- Miller, L.K., and Werner, R.A. 1987. Cold-hardiness of adult and larval spruce beetles *Dendroctonus rufipennis* (Kirby) in interior Alaska. *Can. J. Zool.* 65: 2927-2930
- Raffa, Kenneth, and A. A. Berryman. "The Role of Host Plant Resistance in the Colonization Behavior and Ecology of Bark Beetles (Coleoptera: Scolytidae)." *Ecological Monographs* 53.1 (1983): 27-49. Web.
- Raffa, Kenneth F., Brian H. Aukema, Barbara J. Bentz, Allan L. Carroll, Jeffrey A. Hicke, Monica G. Turner, and William H. Romme. "Cross-scale Drivers of Natural Disturbances Prone to

- Anthropogenic Amplification: The Dynamics of Bark Beetle Eruptions." *BioScience* 58.6 (2008): 501. Web.
- Robinet, Christelle, and Alain Roques. "Direct Impacts of Recent Climate Warming on Insect Populations." *Integrative Zoology* 5.2 (2010): 132-42. - *ROBINET*. Web. 13 Apr. 2015.
- Safranyik, L., Carroll, A.L., Régnière, J., Langor, D.W., Riel, W.G., Shore, T.L., Peter, B., Cooke, B.J., Nealis, V.G., Taylor, S.W., 2010. Potential for range expansion of mountain pine beetle into the boreal forest of North America. *Can. Entomol.* 142, 415–442.  
doi:10.4039/n08-CPA01
- Santos, Maria J., and Thomas G. Whitham. "Predictors of Ips Confusus Outbreaks During a Record Drought in Southwestern USA: Implications for Monitoring and Management." *Environmental Management* 45.2 (2010): 239-49. Web.
- Tank, Albert, Matilde Rusticcucci, Lisa Alexandra, Stefan Broennimann, Yassine Charabi, Frank Dentener, Ed Dlugokencky, David Easterling, Alexey Kaplan, Brian Soden, Peter Thorne, Martin Wilde, Panmao Zhai, James Hurrell, Jose Orsini, Fredolin Tangang, and Pedro Viterbro. "Observations: Atmosphere and Surface." *IPCC: Fifth Assessment Report*. By Dennis Hartmann. Vol. 5. N.p.: IPCC, n.d. N. pag. Print.
- Taylor, S.W. and Carroll, A.L. 2004. Disturbance, forest age dynamics and mountain pine beetle outbreaks in BC: A historical perspective. Pages 41-51 in Shore, T.L., J.E. Brooks and J.E. Stone (eds)
- Thompson, Andrea. "CO2 Levels above 400 PPM Threshold for Third Month in a Row." *Scientific American Global RSS*. Scientific American, n.d. Web. 13 Apr. 2015.
- Thomson, A.J.; Shrimpton, D.M. 1984. Weather associated with the start of mountain pine beetle outbreaks. *Canadian Journal of Forest Research* 14: 255-258
- Visser, M. E., and L. J. M. Holleman. "Warmer Springs Disrupt the Synchrony of Oak and Winter Moth Phenology." *Proceedings of the Royal Society B: Biological Sciences* 268.1464 (2001): 289-94. Web.

Wagner, Terrence, Hsin Wu, Peter Sharpe, Robert Schoolfield, and Robert Coulson. "Modeling Insect Development Rates: A Literature Review and Application of a Biophysical Model." *Annals of the Entomological Society of America* 77.1 (1984): 208-20. *Modeling Insect Development Rates: A Literature Review and Application of a Biophysical Model*. Web. 13 Apr. 2015.

Wood, David L. "The Role of Pheromones, Kairomones, and Allomones in the Host Selection and Colonization Behavior of Bark Beetles." *Annual Review of Entomology* 27 (1982): 411-46. - *Annual Review of Entomology*, 27(1):411. Web. 13 Apr. 2015.