

Relationships among climate, forests, and insects in North America: Examples of the importance of long-term and broad-scale perspectives

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Forest structure is strongly influenced by disturbance, agents of which can include fire, weather, mammals, annelids, fungi, insects, and increasingly with the advent of the Anthropocene, climate. Currently, climate change represents one of the broadest threats to natural systems, including forests, with the potential to directly alter forest structure and function through mechanisms such as drought induced tree mortality (Allen et al., 2010), changes in tree species distribution (Allen and Breshears, 1998; Neilson and Marks, 1994), density (Allen et al., 2010), and composition (Allen and Breshears, 1998; Mueller et al., 2005).

Although the direct effects of climate on trees often produce the most readily apparent changes to forested systems (i.e. tree mortality), climatic variation has the potential to indirectly alter forests by changing community interactions, including mycorrhizal associations (Gehring et al., 1998; Gehring and Whitham, 1994), insect outbreak dynamics (McCloskey et al., 2009; Otvos et al., 1979; Santos and Whitham, 2010; White, 1976), and arthropod community structure (Trotter III, 2008). Insects in particular provide an excellent opportunity to examine interactions among climate, forests, and the communities they support, as insect communities both structure (Eschtruth et al., 2006; Gandhi and Herms, 2009; Stadler et al., 2005) and are structured by (Trotter III et al., 2008) the forests

they inhabit. The extensive body of available research on forest insects, particularly economically important forest pests, further facilitates the study of these interactions in the context of anthropogenic climate change.

As work continues to evaluate the interactions between a changing climate and forest insects, it is critical that the discussion extends beyond simple increases in mean temperature. While the popular term ‘global warming’ captures the fundamental process of anthropogenic changes in the global climate (i.e. a net increase in mean global temperature), it represents a gross generalization of local manifestations of climate change, and oversimplifies the impacts climatic variation may have on forests and their associated insect communities. The 4th Assessment Report of Working Group 1 of the Intergovernmental Panel on Climate Change (IPCC 2007) summarizes some of the complex changes expected in the coming century. For example, northern regions of North America may experience an increase in precipitation, particularly winter precipitation, while central regions of the continent may become more arid. Changes in temperature are also likely to vary seasonally and geographically, including the potential for much warmer winters, and only slightly warmer summers (see IPCC Working Group 1, 4th Assessment Report, section 11.5.3 for additional information). Ongoing efforts to improve our understanding of the interactions among forests, insects, and climate must recognize

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the potential for complex, multidirectional interactions which extend beyond increases in insect development rate and winter survival, and increased heat stress resulting from warmer temperatures. Some of the complex responses insect populations may express due to projected changes in climate include:

- i) Changes in the geographic distribution of an organism's abiotic envelope, dispersal and/or colonization barriers, and climatic limits, as discussed by Williams and Liebhold (1995)
- ii) Changes in the length of the growing season, and concomitant shifts in voltinism (Hansen et al., 2001; Logan and Powell, 2001)
- iii) Changes in the Moran Effect (the tendency for large-scale processes to synchronize local events), as discussed by Williams and Liebhold (1995)
- iv) Changes in synchrony among hosts, predators, and parasites (Watt and McFarlane, 2002)
- v) Changes in the relative strength and/or importance of Allee Effects (the size below which populations tend to go locally extinct)
- vi) Changes in host-stress and defensive chemistry
- vii) Changes in seasonal cues for diapause, aestivation, and quiescence
- viii) Changes in disturbance regime (fire, flood, avalanche, or other mechanical disturbance)
- ix) Changes in nutrient availability, including carbon enrichment, nitrogen mobilization in plant tissues, etc. (White 1976)
- x) Changes in migration necessity, timing, and corridors
- xi) Changes in the distribution and abundance of host and herbivore genotypes, particularly those related to phenotypic plasticity and/or environmental tolerances.

Here, three examples of interactions between forests and herbivorous insects are described which include some of the above climatic influences. These examples include a foliage feeder, a wood borer, and a piercing-sucking insect, and represent both native and introduced species. Native forest herbivores such as the hemlock looper (*Lambdina*

fiscellaria) and *Dendroctonus* beetles offer the opportunity to evaluate interactions among climate, forests, and insects in the context of a long, shared evolutionary history. Invasive species such as the hemlock woolly adelgid (*Adelges tsugae*) offer a different set of research opportunities, as these organisms often arrive without their co-evolved communities, and as a consequence may operate under a set of ecologically simplified factors. Each of these examples highlights the challenges of addressing the multiple, interrelated and interacting factors such as those listed above, and demonstrate the difficulty of distinguishing cause-and-effect relationships from correlative patterns. These systems also highlight the importance of expanding the use of long-term perspectives (as provided by historical records and paleoecological reconstructions) and long-term studies and experiments to refine our understanding of these complex systems.

*Example 1: Native species and a long-term perspective, the hemlock looper (*Lambdina fiscellaria*) and the Holocene*

The hemlock looper, an herbivorous Geometrid moth with a broad geographic range, provides a particularly valuable opportunity to study long-term dynamics based on the discovery of head capsules found preserved in benthic sediments and peat in the boreal forests of North America (Anderson et al., 1986). Hemlock looper larvae feed on a variety of boreal species including fir (*Abies* spp.), spruce (*Picea* spp.), larch (*Larix* spp.), and hemlock (*Tsuga* spp.), and in the last century, numerous outbreaks of the hemlock looper have been documented in North America (McCloskey et al., 2009; Otvos et al., 1979). Some of these outbreaks have resulted in the defoliation and mortality of trees, leading to changes in forest structure (McCarthy and Weetman, 2007).

Paleoecological evidence suggests these documented, large-scale hemlock declines are not unprecedented. In the mid-Holocene, beginning around 5500 yrs BP (14C years Before Present, Present = 1950) hemlock populations underwent a major reduction in both density and distribution (Allison et al., 1986; Anderson et al., 1986; Bhiry and Filion, 1996b; Foster et al., 2006; Haas and McAndrews, 1999; Lavoie et al., 2009). Early studies describing

this decline cited pathogens as a likely mechanism (Davis, 1981), based on similar patterns of abruptly reduced pollen deposition observed for both hemlock in the mid-Holocene, and in modern times, the American chestnut (*Castanea dentata*) following the introduction of chestnut blight (*Cryphonectria parasitica*) (Allison et al., 1986). Later studies of this decline, however, documented macrofossils of lepidopteran (Hemlock looper, and spruce budworm *Choristoneura fumiferana*) head capsules and hemlock foliage with damage indicative of feeding by the hemlock looper (Anderson et al., 1986; Bhiry and Filion, 1996b) preserved in peat and benthic deposits.

The discovery of these macrofossils has provided a window into the history of herbivory, particularly the hemlock looper, in portions of North America through much of the Holocene (Anderson et al., 1986). Radiocarbon dating (^{14}C) places the hemlock looper head capsules and herbivore damaged hemlock foliage at the time of the hemlock decline, roughly 4,910 $\pm$ 90 yrs BP (Bhiry and Filion, 1996b). In addition to the damaged foliage and head capsules, two hemlock stems were found preserved in the peat, and have been successfully cross-dated to ~5,000 years BP. Both fragments show reduced ring growth preceding tree death (Bhiry and Filion, 1996b), a pattern known in other systems to be an indication of herbivory (Fritts and Swetnam, 1989; Swetnam and Lynch, 1989; Trotter III et al., 2002).

The combination of hemlock looper head capsules, damaged foliage, and tree rings suggesting herbivory, coincident in time with the mid-Holocene hemlock decline suggests the hemlock looper may have played a role in the reduction of hemlock abundance in North America 5000 years ago. This potential link is supported by historical records in which documented outbreaks have directly changed forest structure (Otvos et al., 1979). This possible paleo-outbreak of a defoliating insect, and the simultaneous change in forest structure raises several questions that are challenging to answer. What drove the decline in hemlock distribution and abundance? What caused the apparent increase in hemlock looper populations in the mid-Holocene? What are the cause and effect relationships between the looper outbreak and the hemlock decline?

Reconstruction (via inference) of the mid-Holocene climate of eastern North America by Rolland et al. (2008) suggests the period from roughly 5500 to 4400 yrs BP was characterized by warm August temperatures, and analyses by Yu et al. (1997), Calcote (2003), Shuman et al. (2004), and Zhao et al. (Zhao et al., 2010) have shown that the mid-Holocene experienced a dry period relative to previous centuries. The increase in summer temperatures in combination with increased water-stress may have exceeded the physical tolerances of hemlock, or may have shifted the competitive advantage towards more xeric species. As a consequence, climate may have led directly to increased hemlock mortality, reducing its abundance and distribution at a landscape scale. Climate has frequently been cited as a direct driver of biogeographic change in biotic systems (Neilson and Marks, 1994), and there are numerous examples of changes in forest boundaries and structure driven directly by climatic variability (Allen and Breshears, 1998; Mueller et al., 2005).

Although some of the literature suggests climate drove the mid-Holocene hemlock decline, there exists growing evidence that climate acts in concert with biotic (and abiotic) mechanisms (Allen et al., 2010), and there has been some recent discussion of an over-reliance on climate as the presumed sole mechanism of biogeographic shifts (Crainel and McLauchlan, 2004). Climate (or its more proximate form, weather) has been shown to both facilitate (McCloskey et al., 2009) and synchronize (Fauria and Johnson, 2009; Williams and Liebhold, 1995) population cycles of herbivorous insects. Recent studies linking herbivory, climate, and changes in forest structure have documented the importance of interactions between these factors (Breshears et al., 2009; Santos and Whitham, 2010). Evidence for an interaction among climate, hemlock, and the hemlock looper can be found in early work by Otvos et al. (1979), which used historical records of hemlock looper outbreaks and weather records to show that hemlock looper populations may benefit from warm, dry growing seasons. More recently, research by McCloskey et al. (2009) has identified links between warm, dry conditions and historical outbreaks of the hemlock looper in the Pacific Northwest. Combined, these

studies provide a link between the paleoecological patterns of increased temperatures and decreased moisture, which in combination with an abundance of hemlock may have fostered increased herbivory by the hemlock looper (Anderson et al., 1986; Bhiry and Filion, 1996b). These populations may in turn have led to the synchronous (via the Moran Effect) defoliation and mortality of hemlocks, driving their decline at a landscape scale. Based on the projections of McCloskey et al. (2009), it is possible that the stage is set for a repeat performance of the mid-Holocene hemlock decline.

Ultimately, the most parsimonious explanation for the mid-Holocene hemlock decline may be the combined effects of both climatic and herbivorous pressures acting at a landscape scale. The question remains however, whether the looper was a secondary driver of hemlock mortality (i.e. the final straw for stressed hemlocks), or if the hemlock looper was simply benefiting from stressed (and already moribund) hemlocks, and was essentially along-for-the-ride. An example of this second process has been observed in pinyon pine (*Pinus edulis*) in the American Southwest, where extended drought stress (≥ 10 months below the zero carbon assimilation point) led to the death of trees through carbon starvation, brought about by the trees' efforts to maintain a constant leaf water potential by restricting stomatal conductance (Breshears et al., 2009). In the trees studied by Breshears et al. (2009), infestation by the bark beetle *Ips confusus* took place before tree mortality, but after 8 months below the zero carbon assimilation point, suggesting beetles may have been a "side effect" of drought stress, and the trees were already doomed.

While the task is challenging, there is an urgent need to identify the cause-and-effect relationships within this system. The paleo-outbreak of the hemlock looper remains one of the only documented instances of a large-scale, prehistoric herbivore outbreak, and the spatial scale of the event shows the potential for current climate change to dramatically alter systems. By improving our understanding of both the direct and indirect drivers of this event, we may be better positioned to develop adaptive management strategies for a changing environment. To be applicable across systems, it will be

necessary to build this understanding on a foundation of sound ecological theory.

Several ecological paradigms, including the Plant Vigor (Price, 1991) and Plant Stress (White, 1976) Hypotheses provide structure for predictive models of the relationships between herbivores and their hosts. In the context of the hemlock looper, McCloskey et al. (2009) noted that hemlock outbreaks may follow warm dry summers as a result of stressed hemlocks providing better nutritional quality, a pattern indicative of a Plant Stress response. Generalizing these processes, however, remains difficult. Communities of herbivores can include species expressing both positive and negative responses to host stress (Trotter III et al., 2008), and it seems likely that even individual species may exhibit both responses under varying conditions. Studies to identify a link between hemlock stress and hemlock looper impacts remain to be carried out. One approach might be the use of common garden studies in which hemlocks could be experimentally water-stressed, and subjected to herbivory by the looper. The inclusion of stress gradients (rather than simply the extremes) would further strengthen the study by identifying the optimum conditions for looper development, which may be at some "intermediate" stress condition.

Additional studies of the paleoecological record may also provide evidence of the cause and effect relationships between climate, hemlock, and the hemlock looper. For example, the peat used to study the hemlock decline (Bhiry and Filion, 1996a; Bhiry and Filion, 1996b; Lavoie et al., 2009). Bhiry and Filion (1996b) noted the presence of oak (*Quercus* spp.), a non-host species for the hemlock looper, and Filion and Quinty (1993) found white pine and larch wood in the peat material they studied. If wood of cross-datable quality can be found for both hemlock non-host species, it may be possible to determine whether the decline in hemlock radial growth observed by Bhiry and Filion (1996b) was the result of a shared environmental factor (such as climate), or a factor shared by susceptible species (the hemlock looper). Methods for this approach have been described by Fritts and Swetnam (1989), and the use of a non-host species avoids problems that result from interactions

between herbivore and climate signals extracted from the same dendrochronological series (Trotter III et al., 2002). While finding the necessary wood fragments may be difficult, work by Fillion and Quinty (1993) has shown it may be possible.

Overall, this example illustrates how the combined use of long-term monitoring and paleoecological studies can identify the cause-and-effect relationships between a major forest herbivore and a dynamic climate. By combining these research approaches, a stronger foundation of understanding can be built for the development of both ecologically sound forecasts and environmental management strategies.

*Example 2: The population dynamics of the mountain pine beetle (*Dendroctonus ponderosae*) in contemporary forests.*

While the paleoecological record provides historical examples of large-scale changes in forest structure and distribution related to populations of herbivorous insects, these events are also evident in contemporary forests. The mountain pine beetle (*Dendroctonus ponderosae*) provides what may be the most dramatic (and heavily studied) case-study in North America. This bark beetle is native to western North America where populations naturally cycle between outbreaking and endemic densities. Since the late 19th century, the mountain pine beetle has undergone numerous outbreaks in both the U.S. and Canada (based on records provided by direct observations and dendrochronological reconstructions), including 5 major outbreaks in British Columbia in the last century (Alfaro et al., 2004; Taylor et al., 2006).

Between outbreaks, populations of the mountain pine beetle tend to be low, concentrated primarily in isolated groups of a few stressed pines (typically lodgepole, *Pinus contorta*) of 80 to 160 years of age (Amman, 1978; Taylor and Carroll, 2004). Under suitable forest structure and climatic conditions however, these incipient populations can rapidly expand, resulting in large-scale pine mortality (Allen et al., 2010; Raffa et al., 2008; Safranyik and Carroll, 2006). An outbreak of this type is current-

ly underway in western North America, and although there have been many excellent treatises on this system, including those by Carroll et al. (2004), Fauria and Johnson (2009), Logan and Powell (2001), Safranyik and Carroll (2006), Taylor et al. (2006), and Williams and Liebhold (2002), no discussion of the interaction between forest insects and climate would be complete without a short description of this ongoing, forest-restructuring event.

Although some of the previous documented mountain pine beetle outbreaks have been large, the current outbreak is unprecedented in the historical record (Taylor et al., 2006), and has resulted in the loss of millions of hectares of pine. In 2004 (the most severe year of the current outbreak) the mountain pine beetle was responsible for the loss of an estimated 141 million m³ (59.7 billion bf) of pine in Canada alone (Walton et al., 2008). From 1998 to 2006, the mountain pine beetle killed an estimated 542 million m³ of pine (Walton et al., 2008) in Canadian forests. To put this volume in perspective, Canada exported approximately 50.7 million m³ (21.5 billion bf) of softwood in 2005 (<http://www.international.gc.ca>), suggesting that from 1998 to 2006, beetles killed a volume of pine roughly equal to the volume exported. In addition to the high intensity, the current outbreak has grown to cover an unprecedented scale, including higher elevations and ranges farther to the north and east than observed in previous outbreaks (Ayres and Lombardero, 2000; Carroll et al., 2004; Logan and Powell, 2001). This expansion has brought the mountain pine beetle to the edge of the boreal forest and major populations of Jack pine (*Pinus banksiana* Lamb.), forests which have not historically been subjected to intense mountain pine beetle herbivory. This contact raises the specter of potentially large impacts on a widely distributed and susceptible (Cerezke, 1995) pine. The mechanisms driving both the current and previous outbreaks can be grouped into two categories, host suitability and favorable climatic conditions.

Host Suitability: Host quality and suitability for the mountain pine beetle is determined by a variety of factors including: i) the ability of the pine to mount

a resin-based defense and ii) adequate phloem thickness for beetle development, determined in part by tree age. During endemic phases, mountain pine beetle populations may be limited to localized patches of stressed pines of 80-160 years of age (Amman, 1978) in areas with a suitable climate. Healthy pines defend against low-level beetle attack by “pitching out” the beetles, a defense based on either drowning the beetles in resin, or in some cases, physically forcing the beetles out of the tree (Amman, 1978; Cabrera, 1978; Shrimpton, 1978). Stressed trees may lack the resources needed to successfully pitch out attacking beetles, allowing smaller populations to overwhelm the tree’s limited defenses. During outbreak phases, large populations can shift to healthy pines where defenses are overwhelmed through mass attacks coordinated by aggregation pheromones. When a suitable host is located, an attacking female releases an aggregation pheromone, attracting both male and female beetles to the same tree. As additional beetles arrive they too release an aggregation pheromone until the tree is saturated, at which time the pheromone acts as an anti-aggregation cue. Once infested, the combination of cambial damage from boring and infection by blue-stained fungi (which disrupt water transport) vectored by the beetles compromises the tree’s ability to pitch out attacking beetles, and leads to the death of the tree, necessary for successful brood production.

Over the past century, the availability of suitable stands has increased (Taylor et al., 2006). Primarily as a result of fire-suppression, stand density has increased, and stand age structure has shifted towards demographics which favor beetle reproduction. Stand density has been shown to be related to water stress and resin production (Kolb et al., 1998), with increasing density being associated with decreasing resin production, and potentially, increasing susceptibility to bark beetle attack (though data from experimentally thinned stands has not always supported this premise, see Zausen et al. (2005)). Age structure in pine stands has also shifted towards a state which favors beetle populations (Taylor and Carroll, 2004; Taylor et al., 2006). Over the past century, the percentage of pine stands in British Columbia in age structures categorized as

susceptible to beetle attack has shifted from less than 20% at the beginning of the 20th century, to more than 50% (Taylor et al., 2006). This combination of increasing stand density and suitable age structure provides the first of the two conditions necessary for an outbreak of the mountain pine beetle.

Climatic Suitability: The second component necessary for rapid beetle population growth, a suitable climate, is provided through moderate winter temperatures which prevent winter beetle mortality, and growing seasons which facilitate univoltine generations. In northern regions and high altitude pines, populations of the mountain pine beetle have been regulated in part by winter lows which reduce or prevent beetle survival (see Safranyik and Carroll (2006) for an excellent phenology-specific summary). As poikilothermic animals, the development rate of mountain pine beetles is dependent on the temperature profile of its environment. Successful populations are bounded by the need for adequate warmth for univoltine development (see (Logan and Powell, 2001)), while avoiding summer temperatures high enough to result in a multivoltine population. A shift to multivoltinism could disrupt the synchrony of beetle emergence, reducing the potential for beetles to overwhelm tree defenses through coordinated mass attack (Logan and Powell, 2001)). With the end of the previous century came an increase in global temperatures (IPCC, 2001), and a concomitant expansion in the intensity and range of mountain pine beetle outbreaks (Ayres and Lombardero, 2000; Carroll et al., 2004; Logan and Powell, 2001).

Though this example shows the strength of potential climate/insect/forest dynamics and feedbacks, there are many questions that remain to be addressed. One of these factors, which has perhaps received less attention than it deserves is the potential for the beetle to adapt to changing environmental conditions. A study by Bentz et al. (2001) demonstrated the presence of heritable adaptive variation in development rate related to temperature regime. This genetic variability, in combination with the phenotypic variability in cold-hardiness observed in other studies (Safranyik and

Carroll, 2006) may interact with a changing climate to produce unexpected population dynamics. Other interactions may also vary temporally and spatially, for example, the roles and relationships between the multiple symbiotic fungi is known to vary as a function of temperature (Six and Bentz, 2007). Shifts in these relationships may also play a role in driving changes in the biogeographic distribution of the mountain pine beetle. Although past work has identified two key factors (the density and suitability of hosts, and climate) driving the population dynamics of this herbivore, these recent studies reveal additional complex factors that may play a role in structuring outbreak dynamics. Further work is needed to both identify and quantify these interactions in the context of a changing climate if we are to improve our understanding of the dynamics and impacts of this native forest herbivore.

Example 3: The invasive hemlock woolly adelgid: An (un)natural experiment in biogeography and climate

While taking a paleoecological approach to the study of interactions between forests, insects and climate provides a long-term perspective on these systems, paleoecological studies may not provide adequate detail to identify and model ecological interactions. Alternatively the use of species in their native, co-evolved habitats may result in systems which are inherently complex (genetic variability, roles of natural enemies, etc). In the middle, perhaps providing a bridge between these two extremes is the opportunity provided by invasive species. Invasive species often operate under ecologically simplified rules, for example, when an invasive species such as the Gypsy Moth (*Lymantria dispar*), the Asian Longhorn Beetle (*Anoplophora glabripennis*), or the Hemlock Woolly Adelgid (*Adelges tsugae*) is introduced to a novel habitat, it is often introduced without its co-evolved complex of predators, parasites, pathogens, and historical host, often lacking substantial genetic variation (founder effects). Without these biotic controls, invasive species are often limited by simplified factors such as the availability and quality of hosts, and the characteristics of the physical environment (such as temperature). This simplified ecological structure makes these systems well suited for evaluating the relationships among climate, forests, and

insects. Here we focus on one of these invasive species, the hemlock woolly adelgid.

The hemlock woolly adelgid is a small, aphid-like herbivore native to Asia and western North America (Havill and Foottit, 2007; Havill et al., 2006; McClure, 1996; McClure and Cheah, 1999). The first known documentation of this insect in eastern North America dates to the early 1950s (Gouger, 1971), when it was found on ornamental hemlocks near Richmond Virginia. Although the adelgid was known to be exotic, little attention was given to this species, and early discussions focused on its being a pest on landscape hemlocks. In the late 1970s and early 1980s however, this perception changed as the adelgid moved into natural stands of eastern hemlock (*Tsuga canadensis*), and began to spread rapidly up the east coast of the United States (data available at <http://na.fs.fed.us/fhp/hwa/infestations/infestations.shtm>). By the mid 1980s, the adelgid had expanded its range to include counties in Virginia, Pennsylvania, Maryland, New York, Connecticut, and Rhode Island. As the adelgid spread, it drove a decline in hemlock health with increased needle loss, branch die-back, and ultimately, high rates of hemlock mortality.

Since its initial spread into natural stands of both eastern and Carolina hemlock (*Tsuga caroliniana*), the two hemlock species native to eastern North America, the range of the hemlock woolly adelgid has expanded to include counties in at least 18 eastern states. The adelgid now infests roughly half of the distribution of hemlock in the eastern U.S. (Evans and Gregoire, 2007; Morin et al., 2009; Trotter III and Shields, 2009) and continues to expand its range, however this expansion has not been consistent either across space or through time (Evans and Gregoire, 2007; Morin et al., 2009). This variable pattern of spread makes the hemlock woolly adelgid an excellent model organism to study the factors that dictate the biogeography of an organism. Past studies of anisotropic expansion by the adelgid have identified heterogeneity in hemlock distribution and abundance (Morin et al., 2009), and climatic variability (Evans and Gregoire, 2007; Paradis et al., 2008) as key mechanisms.

Understanding the environmental factors that dictate geographic distribution of an invasive species is an important component to effectively manage its spread and impact. Several studies of the hemlock woolly adelgid have worked to measure the rates and directionality of its spread in the eastern U.S. Using infestation records from counties and townships for the period from 1990 to 2004 (inclusive), Evans and Gregoire (2007) estimated rates of adelgid spread to be 8.13 km/year towards the north, and 15.6 km/yr towards the south. Using a classification tree approach, they also found that infestation moved quickly or slowly, dependent in part on whether the region was warmer or cooler than the boundary between USDA plant hardiness zones 5B and 6A. Based on these findings, and those provided by laboratory studies (Parker et al., 1998; Parker et al., 1999; Skinner et al., 2003), Evans and Gregoire (2007) suggested low winter temperatures may have played a role in reducing rates of northward movement, a hypothesis supported by field measurements of hemlock woolly adelgid winter survival (Paradis et al., 2008; Trotter III and Shields, 2009).

Morin et al. (2009) also used county infestation records to evaluate patterns of hemlock woolly adelgid spread, focusing on quantifying the anisotropy

of adelgid boundary movement, and identifying the landscape variables driving that anisotropic behavior. Using infestation records spanning the full documented period of adelgid infestation (1951 through 2006), their findings suggested the movement of the hemlock woolly adelgid has been heavily influenced by the basal area of its hemlock host, and that rates of hemlock spread were only marginally ($p > 0.0774$) related to minimum January temperatures. Of perhaps equal importance, is their finding that this weak relationship between winter temperatures and adelgid movement was negative, with adelgid movement correlated with low (rather than high) winter temperatures.

Evaluating the relationship between the movement of adelgids and the climate of the landscape might seem to be muddled between two studies with inconsistent findings. However, two lines of evidence suggest these two studies are in fact consistent, and highlight the potential importance of climatic variation in structuring the historical spread of the hemlock woolly adelgid.

First, the two studies are dominated by two different phases of adelgid movement across the landscape. The hemlock woolly adelgid was initially introduced in the mild climes surrounding Richmond, Virginia, yet records of infestation indi-

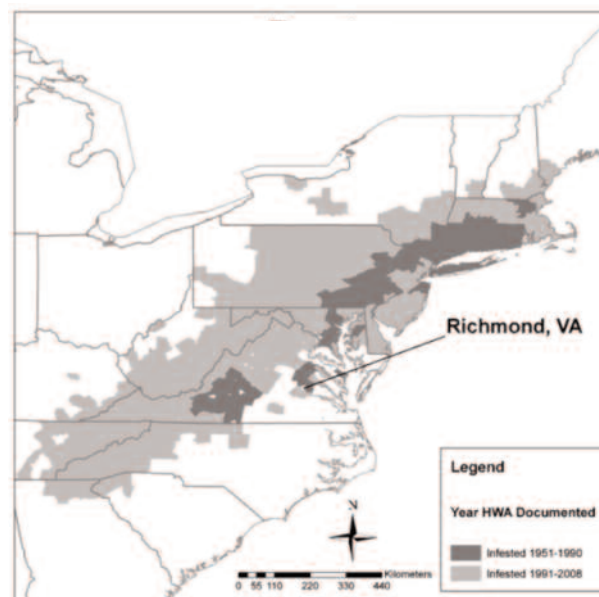


Figure 1. Hemlock woolly Adelgid expansion map. Although the hemlock woolly adelgid was first established near Richmond, VA, the first ~40 years of range expansion were towards the north and east into cooler regions.

cate populations spent the first ~40 years expanding primarily towards the north (figure 1). It was not until the 1990s that the adelgid moved into the western and southern range of hemlocks in the eastern U.S. When we compare the timing of these northward, then southward phases of adelgid expansion against the time-frames used by Evans and Gregoire (2007) and Morin et al. (2009), an interesting pattern emerges. Evans and Gregoire (2007) used records of spread limited to the years between 1990 and 2004 to avoid concerns about the temporal resolution of the records prior to 1990. Since 1990, range expansion has been biased towards the south (figure 1). Movement to the north during this recent expansion has, however, been quite slow, as described by Evans and Gregoire (2007). This decreased spread may be driven by the adelgid's proximity to what may be its northern population limits dictated by extreme cold (Paradis et al., 2008; Trotter III and Shields, 2009). Thus, the time frame used for their analysis is dominated by a period of southern boundary movement in regions with warmer temperatures. These data in

turn could drive the observed relationship between warm temperatures and rapid rates of adelgid spread.

Morin et al. (2009) however, used the full record of adelgid infestation, which begins in 1951. This time frame includes the early (pre-1990) phase of range expansion, which was biased towards northern regions. This northern movement into regions with high hemlock basal areas (and concomitantly cooler temperatures) could produce an apparent relationship between low temperatures and the rate of boundary movement, an issue discussed by Morin et al. (2009). Given these two apparent phases of adelgid range expansion, first to the north, and then to the south, and the documented negative relationship between adelgid survival and temperature (Paradis et al., 2008; Parker et al., 1998; Parker et al., 1999; Skinner et al., 2003; Trotter III and Shields, 2009), the question becomes, why did the adelgid initially expand towards the north?

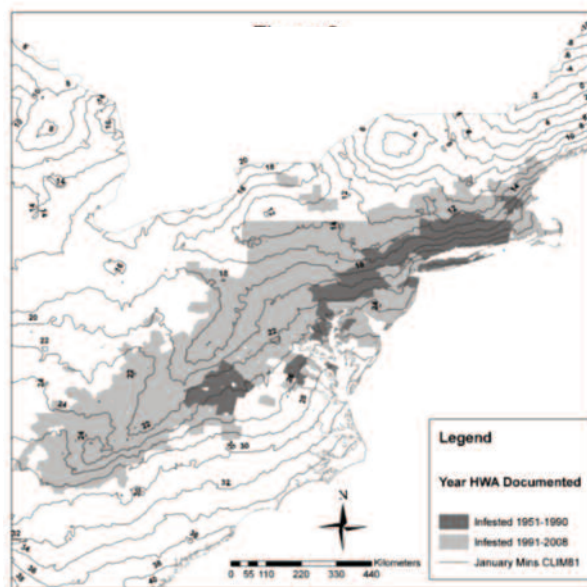


Figure 2. Hemlock woolly adelgid expansion map. The early northeastward spread of the hemlock woolly adelgid suggests the invasion front moved along a coastal corridor of more moderate climatic conditions. However, climate does not seem to explain the lack of southwestern movement, a pattern that may be related to the interplay between temperatures and the topography of the Appalachian Mountains.

The second line of evidence suggesting the two studies may be in agreement provides a potential answer to the question of why the adelgid may have initially moved north. The reasons for the northward movement may be as simple as a bias in the movement of the adelgid through regions with moderate temperatures, interacting with the importance of host density as discussed by Morin et al (2009). As figure 1 shows, until the mid 1990s, southern (and western) movement of the adelgid was limited, with most of the expansion occurring towards the northeast. By combining a map with the two phases of adelgid movement (pre and post 1990), with maps of landscape temperatures (based on interpolations of NOAA NCDC CLIM81 Normals), a potential corridor of moderate temperatures along the northeast coast becomes apparent (figure 2). As the map shows, the western edges of the pre 1990s adelgid population ran along the Appalachian Mountains, and these mountains, or more accurately, the low temperatures associated with the high elevations of the mountains, may have produced a barrier slowing western movement. Directly to the south and southwest of Richmond, Virginia, the landscape contains few

hemlock, however to the northeast, along a thin corridor of mild temperatures that follow the coast to Long Island and Connecticut, hemlock are more readily available. This combination of host availability and mild temperatures moderated by the proximity to the coast (and the influence of the warm Gulf Current) may have provided an “easy” path for range expansion.

This distribution of the adelgid (with some infilling) remained somewhat stable until the early to mid-1990s, when the adelgid crossed the “Appalachian barrier”, gaining access to southern hemlocks. This sudden and rapid range expansion over the Appalachian Mountains raises the question, what changed to allow the adelgid to cross this presumed geographic barrier? A potential answer is suggested by the nature of the barrier itself. The thermacelines shown on figure 2 are based on 30 year (1971-2000) temperature normals (averages). Actual temperatures at a given location, however, may vary greatly from one year to the next. Using annual temperature records from weather stations in the eastern U.S. (953-1740 stations for years 1960-1990, and 1507-1694 stations for years 1991-

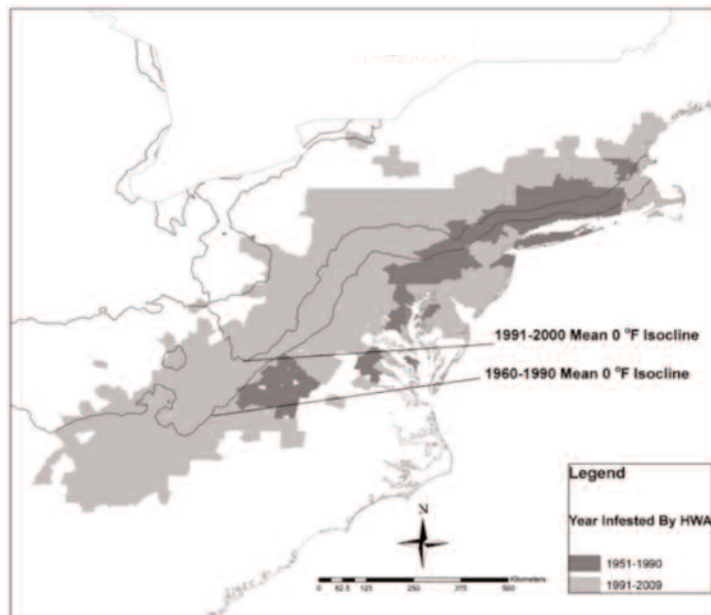


Figure 3. The 0 degrees Celcius thermocline for the period from 1960-1990 was further south than for the 1990s, suggesting the 1990s experienced warmer temperatures which may have facilitated the expansion of the adelgid distribution.

2000), it is possible to compare the distribution of the absolute minimum temperatures experienced in the eastern U.S. for the two periods of HWA range expansion. The results indicate that the temperatures between 1960 and 1990 were cooler than those of the 1990s. Figure 3 shows the same thermocline (0 °F) for the pre and post-1990 periods, demonstrating the northward shift in temperatures that occurred in the 1990s. This northward (and likely upward in elevation) shift was driven primarily by warm winters in 1991, 1992, and 1998. These warm periods in the Appalachians may have opened “windows” in the temperature barrier, allowing adelgids to expand west and south.

As temperature distributions are expected to change during the Anthropocene, understanding the role of these changes on the invasion dynamics of species such as the hemlock woolly adelgid will become increasingly important. Recent work by Paradis et al. (2008) highlights some of these potential changes. Using two variants (high and low carbon emission) of three different coupled ocean-atmosphere climate models, Paradis et al. (2008) show the northern limits of adelgid survival may move northward, expanding into areas that have, at least initially, resisted colonization by the hemlock woolly adelgid. If this northward expansion occurs, it may be the second time a climatic window of opportunity has facilitated the expansion of the hemlock woolly adelgid.

Some short comments on long-term research

Documenting the relationships and interactions among forests, insect populations, and climate change requires both a long-term paleoecological perspective, and a thorough analysis of contemporary patterns and processes. To quote the paleoecologist Julio Betancourt, “It is neither possible nor wise to assess man’s role in arroyo cutting, changing flood and fire frequency, shrub and tree encroachment of grasslands, and ultimately, global change, without historical context”. Simultaneously, studies based on direct, current observations can provide the high-resolution spatial and temporal perspectives necessary to evaluate the mechanistic interactions between factors such as climate, forests, and insects, at a resolution not available in

the paleoecological record. Generally, studies relating forests, climate, and insects can be placed in two broad (but overlapping) categories, long-term studies based on combinations of instrumental and calibrated proxy records, which can be multi-millennial in length, and shorter-term studies based on instrumental records and direct observations, often limited to the last century. Though each approach has limitations, the combination provides a broad perspective of forest-climate-insect systems, and can help accommodate the variable temporal and spatial scales relevant to each factor.

The hemlock looper, the mountain pine beetle, and the hemlock woolly adelgid provide three examples of interactions between forests, insects, and climate, at varying temporal and spatial scales. Each suggests the potential for insects to directly influence the abundance and distribution of a widespread host and alter forest structure and development. Yet, these are only three of many forest-insect systems yielding actual or potential changes in forest structure. Other species such as the spruce budworm (Volney and Fleming, 2000; Volney and Fleming, 2007), the gypsy moth (Williams and Liebhold, 1995), and the pine processionary moth (Netherer and Schopf, 2010), to name only a few, are known to interact with climate.

Whether evaluating the interaction of climate, forests, and insects at long or short time-scales, it is important to bear in mind that each of these three factors operates at multiple, interrelated temporal and spatial scales. Weather, for example, tends to be highly variable over short time periods, and may be of limited use in evaluating changes in climate when viewed myopically, despite the obvious dependence of climate on weather. Insect population dynamics can be conceptualized using a similar paradigm. Like weather, insect populations may be highly variable in their density and structure within or across a few generations, and this high frequency variation (which may appear stochastic) may mask long-term trends in population variability, and the links between those trends and complex factors such as climate. Reconciling the links between climate and insect dynamics will ultimately depend on adopting some of the approaches used for the study of climate change. Just as the study of climate change depends on both the long-term documentation of weather and the study of the mechanistic drivers of weather over long time periods, the

study of insects may depend on long-term monitoring and analysis of the mechanisms that drive insect populations, while recognizing the multiple time-scales involved in each of these processes. Insect life-histories, for example, are often measured in days or months, while the development history of a forest stand may be measured in decades or centuries, and both are subject to weather and climate, which can operate on scales ranging from minutes to millennia.

While the challenge of synthesizing climate-insect-forest relationships, while accounting for complex, multi-scale interactions with other biotic and abiotic factors remains a formidable task, advances are being made in the identification of those relationships. For example, Vehviläinen et al. (2007) suggest that changes in the diversity of a stand can have variable impacts on the intensity of herbivory within those stands, dependent on both the host species, and the insect feeding guild. By continuing and

expanding these types of studies, we can to identify coherent patterns and processes, as well as emergent system properties.

Currently, the challenge to understand these interactions is being tackled using multiple approaches. First, there are efforts to synthesize and compile known information on individual host-herbivore interactions, and the role of weather (climate) in regulating those interactions. An example of this approach can be found in the Study on Impacts of Climate Change on European Forests and Options for Adaptation conducted by the European Forest Institute, and summarized in part by Netherer and Schopf (2010). Experimental forests provide a second, more systems oriented approach to study insect-forest interactions. The U.S.D.A. Forest Service maintains ~70 experimental forests in the U.S. (Figure 4), and many schools support research forests (ex. Yale, Harvard, University of Connecticut, University of Massachusetts, Cornell,

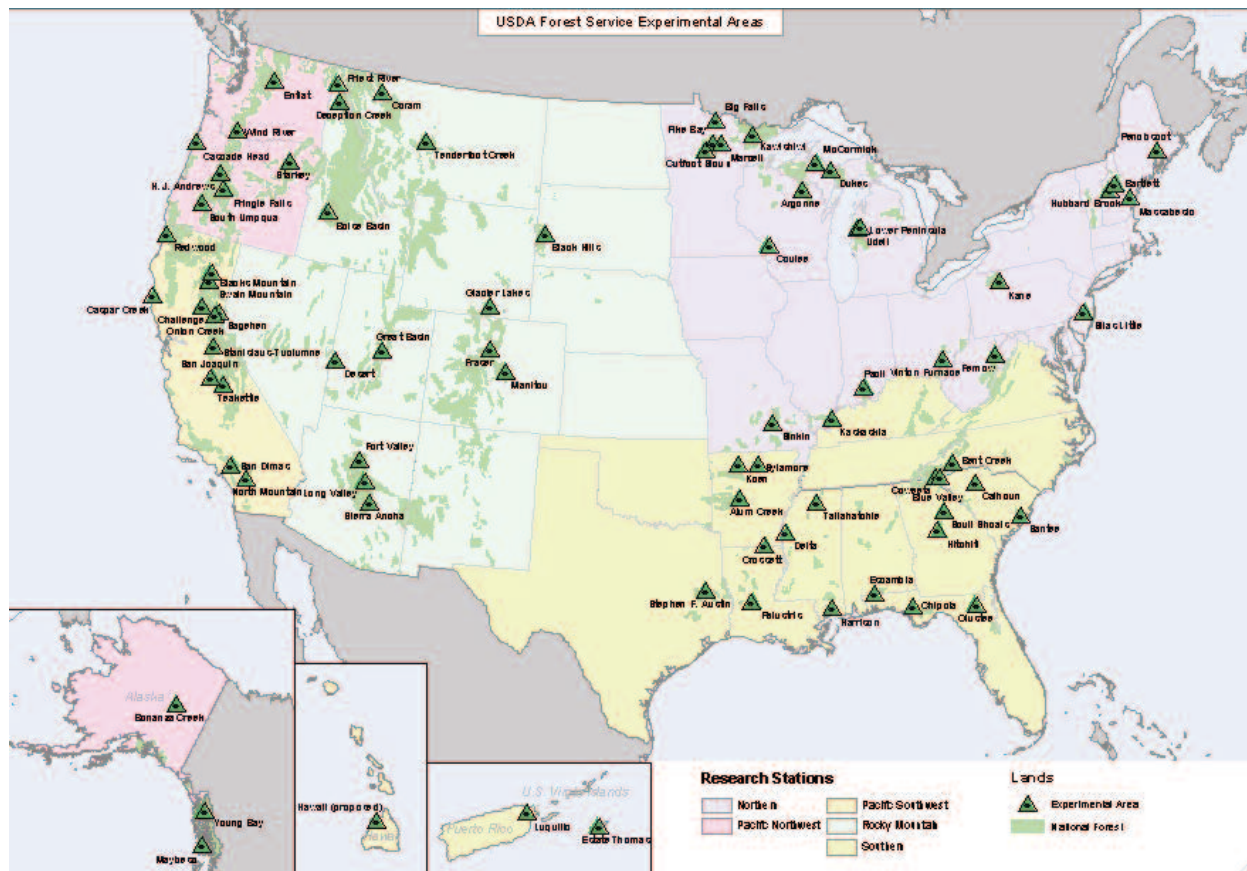


Figure 4. USDA Experimental Forests in the United States.

and even the Wausau School District in Wisconsin). These forested systems provide the opportunity to both establish new studies as well as mine existing datasets to identify links between climate variability and insect dynamics.

Simultaneous with the availability of these forests, new opportunities to pursue and support long-term and large-scale studies in forested systems are becoming available with the development of the National Ecological Observatory Network (NEON). Approximately half of the NEON domains fall within forested regions, with candidate core sites in domains 1 (Harvard Forest), 5 (Notre Dame Environmental Research Center), 7 (Walker Branch Watershed), 8 (Talledega National Forest), 12 (Yellowstone Northern Range), 13 (University of Colorado Mountain Research Center), 16 (Wind River Experimental Forest), and 19 (Caribou-Poker Creeks Research Watershed) being heavily focused on forested systems. The long-term (30 year) support for the NEON sites, in combination with extensive instrumentation make these areas excellent candidates for evaluating the relationships between climate, insects, and forests. With the potential for forest insects to not only respond to climate change, but to influence it by shifting some forests from carbon sinks to carbon sources (Kurz et al., 2008), the importance of long-term research and a long-term perspective becomes evident.

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Long-term Silvicultural & Ecological Studies

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