A phenological examination of terrestrial invertebrate abundance at H. J. Andrews Experimental Forest, Oregon

By:

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Abstract

Understanding the effects of climate change on forest ecosystems requires exploration of the relationships of different components of the system, such as the response of biota to local hydrology, temperature, precipitation, and elevation. The Long-term Ecological Research Program at the H. J. Andrews Experimental Forest, located in the Western Cascades of Oregon, has been exploring these relationships since the late 1940s in the search for a sustainable method of harvesting lumber. This study in insect phenology utilizes terrestrial insect samples collected in malaise traps from early April until early July of 2011 at 16 core sites in the Andrews that differ in elevation, slope, aspect, and stage of forest growth. Each site was sampled multiple times during the sampling period. Insect life cycles and activity are highly regulated by temperature. It was predicted that greater insect abundance, where abundance is the amount of insects captured, would occur at higher temperatures and lower elevations. Results demonstrated that higher abundances occurred at mid-temperature sites, which were also mid-elevation sites. Additionally, high-temperature sites took more cumulative degree-days for insect activity to achieve maximum levels. Preliminary examinations indicate that old growth forests have higher levels of insect activity; however, sample size was skewed and future research looking at insect activity as a function of forest structure would best be explored utilizing data from multiple years.

Introduction

Global climate change is a driver of phenological shifts observed in a variety of biological organisms (Forrest and Thomson 2011, Hodgson et al. 2011, Jepsen et al.

2011, Visser and Both 2005, Dunn and de Beurs 2011, Primack et al. 2009). Shifts can result in spatial and temporal asynchrony, creating potential ecological repercussions such as: phenological decoupling of interdependent organisms, local extinction of unadaptive species, and range expansion of potentially invasive species. As interest and concern over global climate change persists, biological information exploring fluctuating ecosystem dynamics will facilitate making future predictions of ecosystem shifts.

Plants and insects are sensitive to the seasonality of abiotic forces for regulating biological processes, and they make good primary indicators of climate change. Typically these organisms will experience advances in maturation time and range expansion into higher elevations with increases in temperature (Dingle 1972, Jepsen et al. 2011, Parmesan and Yohe 2003, Fremlin et al. 2011); however, delays in growth can also occur if a necessary period is unmet for plant vernalization or insect diapause (Forrest and Thomson 2011, Liu et al. 2011). Phenologically induced shifts of vegetation and invertebrates may affect higher trophic levels. For example, avian studies have observed asynchrony with food sources, either plant or insect, resulting in temporal shifts affecting breeding and migration in select species (Visser and Both 2005).

This study was based at the H. J. Andrews Experimental Forest in Oregon to examine insect activity responses to varying temperature, elevation gradients, and forest growth stage. It utilizes microclimate data for 2011, made available through the Andrews' database, as well as terrestrial invertebrate collections collected during spring.

The phenology sites ranged in elevation from 460 to 1,339 meters and vary in the age of the forest stand, allowing for microclimate variation across sampling sites. These variations in temperatures provide ranges that may demonstrate possible invertebrate differences in phenology.

It was expected that site differences in flying terrestrial invertebrate activity would correspond to changes in elevation gradients and temperature. As temperature likely decreases with increases in elevation, it was predicted that lower elevations would have higher temperatures. My study tested the hypothesis that insect activity would be greatest at lower elevations due to the higher ambient temperatures.

Study site

The H. J. Andrews Experimental Forest is a valuable research site for ecological studies due in part to the variable microclimates that represent the diverse topography of this western Cascades location (Fig. 1). Encompassing 6,400 hectares of the Lookout Creek Watershed in the Pacific Northwest, this area is characterized by warm, dry summers and cool, wet winters (Andrews Experimental Forest LTER 2011, McKee 2008, Frady et al. 2006). The Andrews was designated as an Experimental Forest by the U. S. Forest Service in 1948 and became part of the National Science Foundation's Long-Term Ecological Research (LTER) Program in 1980 (Greenland 1994). Climatological and ecological data have been amassed since the site was initiated, allowing for advanced studies in climate, forest, stream, and watershed dynamics. The phenology project has 18 core study sites, of which this study will utilize 16 because two sites, PC03 and PC06, were determined to have fewer plant species in common with the other sites.

The H. J. Andrews Experimental Forest was established for the improvement of forest harvesting methods towards sustainable production of timber (Berntsen and Rothacher 1959). As a result, the site is composed of young and old growth stands. Young growth forests were harvested through clear-cutting in the 1950s and are approximately 40 to 50 years old. These stands have denser canopies resulting in less understory growth. Old growth stands range in age from 240 to 550 years. Old growth stands have withstood natural disturbances such as fire and wind creating gaps in the canopy allowing for a more diverse understory and increased species diversity (Franklin et al. 2002, Andrews Experimental Forest LTER 2011, McKee 1998).

Methods

Invertebrate specimens were captured at each phenology core-sampling site utilizing malaise traps suspended between two trees with the base of the trap approximately 1.5 meters above the ground. Traps were placed within 50 meters of the center of the sampling site; they were further secured by attaching tags extending from the base and a corner of the trap to a fixed object to prevent spinning. The dates the traps were established, as well as the subsequent sampling dates, varied between sites due to weather conditions. Lower elevation sites were set in early April 2011, while those at higher elevations were not established until May 2011. Invertebrates were trapped in a solution of RV antifreeze containing a drop of unscented soap as surfactant. Samples were collected every six to nine days, depending on weather conditions, until July 12, 2011. The span of time from initial sampling until this final date was used as the "sampling period" for each site. Captured invertebrates were stored in ethanol for

laboratory analysis.

Laboratory processing consisted of filtering the samples through a 250-micrometer filter, rinsing with tap water, and transferring to a laboratory dish containing enough ethanol to submerge the invertebrates. Samples were separated into two groups: those with wings and those lacking wings. Each group was then counted and abundance was recorded. After processing, invertebrates were placed into centrifuge capsules containing fresh ethanol for storage.

Archived air temperature data for 2010 and 2011 for each of the sixteen sites was imported into Microsoft Excel and reduced to include temperatures from the period of October 20, 2010 through October 20, 2011. Data was recorded at fifteen-minute intervals. A loop for the statistical software R was created to determine average daily temperatures, reducing the data set to 366 values. To accommodate for missing temperature data resulting from gauge errors at sites PC09, PC16, PC17, and PC18, zeros were inserted as placeholders.

Cumulative degree-days were determined using average daily temperatures beginning on October 20, 2010 and ending on July 12, 2011, the last day of field collection (Fig. 2). Temperature values below 0 °C were changed to zero. The resulting values were added to produce cumulative degree-days at the individual phenology core sites.

One-way ANOVA, utilizing the statistical software R, was used to explore the relationships between temperature, forest growth, and invertebrate abundance at each site. Using PC-ORD5.19 software, cluster analyses was performed to examine

temperature similarities between phenology core sites. Visual aids using R and Microsoft Excel were constructed for observational analysis of the influence of degree-days on invertebrate abundance, as well as forest growth cover on invertebrate abundance (Maindonald 2008).

Results

Temperatures at Study Sites

Average daily temperatures for the period of October 20, 2010 through October 20, 2011 followed an overall sinusoidal curve, characteristic of seasonal fluctuations (Fig. 3). Temperature patterns for winter and fall months (October 2010 to March 2011) had greater variations in amplitude of extreme maximum and minimum temperatures, but between site differences were small. From March 2011 to September 2011, there was an overall increase in temperature with less variation in extreme temperatures (smaller amplitude). From approximately mid-March until late May at sites PC17 and PC18, the temperature gauge was covered by snow, resulting in ambient temperatures of approximately zero degrees Celsius. A second zone of temperatures depicted as zero in figure 2 represents gauge error occurring at sites PC09, PC16, PC17, and PC18. At each of these locations, the temperature gauge failed to record for twenty-five to twenty-seven days, leaving a gap in the temperature data.

Cluster Analysis grouped the phenology core sites into three groups with similar average daily temperatures: High Temperatures (PC01, PC02, PC04, PC05, PC08), Mid Temperatures (PC07, PC10, PC11, PC12, PC14, PC15, PC16), and Low Temperatures (PC13, PC17, PC18) (Fig. 4). Because of the missing data from sites PC09, PC16, PC17,

and PC18, the cluster analysis was performed twice, with the first cluster using data from October 20, 2010 through June 12, 2011 (Fig. 4a) to capture the trend going into the period of missing data, and the second cluster from July 16, 2011 through October 20, 2011 to capture the trend following the missing data (Fig.4b). Differences between these three groups are visible in a temperature plot that codes for each of the temperature categories, particularly from March through June (Fig. 3). Between the two time intervals used for the Cluster Analysis, relationships shifted a little, but PC09 was the only site to change groupings going from a mid-temperature group to a low-temperature group. As a result, PC09 was not included in further analysis that grouped by temperature.

Invertebrate Abundance

Invertebrate abundance, or capture, differed among the phenology core sites over the sampling period (1-way ANOVA, $F_{(15, 156)} = 4.253$, p-value < 0.05) with the greatest total abundance (11,809) occurring at site PC09 and the lowest at site PC17 (1,217) (Table 1, Fig. 5). Because PC09 was nearly double the next highest abundance (6,509 invertebrates at PC10), the weight of PC09 may have affected the ANOVA results. When one-way ANOVA was performed excluding site PC09, results confirmed that mean abundance varied between the sites ($F_{(14, 147)} = 5.253$, p-value < 0.05) (Fig. 6). Although sites PC17 and PC18 (low-temperature sites) were three to four sampling periods shorter than that for PC04 and PC05 (high-temperature sites), they have greater variability in invertebrate capture over the sampling period.

Mean abundance of Low-, Mid-, and High-temperature groups differed significantly (Fig. 7, $F_{(2, 159)} = 9.3067$, p-value = 0.0002). Moreover, the rates of highest increase varied between these groups. The greatest increases in rate of capture at the high temperature group occurred from May 31, 2011 to June 14, 2011 (Fig. 8). In contrast, capture rates at low-temperature sites (PC13, PC17, and PC18) appeared to ramp up beginning in mid to late June into early July. Abundance at mid-temperature sites fluctuated from early June into early July, but had the highest overall capture rates of the temperature groupings. Of the six sites that could be sampled during late April and early May, PC07 was the only site not grouped as high-temperature (Table 1). Abundance at this mid-temperature site surged to >700 invertebrates from May 2 to May 10 which was about twice that of any high temperature site during that period (Fig. 5).

Graphical analysis of invertebrate abundance by cumulative degree-days, beginning on October 20, 2010 and ending on July 12, 2011, implied that more cumulative degree-days were required at high-temperature sites to achieve similar abundance levels than at mid-temperature sites (Fig. 9). Mid-temperature sites reached greater abundances at 400 to roughly 900 degree-days, whereas high-temperature sites achieved greatest abundance after 900 to 1200 degree-days. Sites PC09, PC16, PC17, and PC18 were excluded from this analysis because of the missing temperature data thus the low-temperature group is represented by only PC13. Insect activity at PC13 increased rapidly from 300 to 800 degree-days.

Sites differed in the age of tree cover and were designated as either "old" growth forest or "young" growth forest. A one-way ANOVA testing abundance of invertebrates as a function of forest growth over the sampling period of May 15, 2011 to July 12, 2011 provided evidence that abundance at old growth sites ($mean_{old}$ = 433.74 invertebrates) was higher than at young growth sites ($mean_{young}$ = 230.50 invertebrates) even when excluding PC09 due to extreme values (Fig. 10, $F_{(1, 116)}$ = 5.1547, p-value = 0.02503). Examining the data on a cumulative degree-day scale was less conclusive about the effects of forest cover on invertebrate abundance (Fig. 9). Among high-temperature sites, composed of two "old" growth and three "young" growth sites, PC08 ("old") and PC01 ("young") cumulative highest abundances over the sampling period differed by only 123 invertebrates. Due to the missing temperature data, the mid-temperature sites lost a site representing "young" growth, and low-temperature sites lost a "young" and "old" growth site, making inferences speculative.

Discussion

As temperature was higher at lower elevations at the H. J. Andrews Experimental Forest, insect activity was expected to be greatest at lower elevations. In this study, activity was defined by the total abundance of insects captured in malaise traps across the sampling season at each site. For the summer of 2011, insect activity at the Andrews tended to be greatest at the mid-temperature sites, but there was no definitive pattern of activity associated with elevation or temperature gradient. Greatest total abundances across the reduced time frame (Fig. 8) show that the four sites with the greatest levels of abundance were not high-temperature sites. The figure

also demonstrates the variability in insect capture between the remaining sites providing evidence that additional environmental factors influence insect activity.

Cumulative degree-days provide information about how seasonal cycles and their resulting temperature patterns affect an insect's physiology and development (Danks 1987). In this study, there were differences in the amount of cumulative degree-days needed to achieve maximum levels of insect activity between the temperature groups, as well as differences in the ranges of temperature during which insect activity occurs. It appears that the critical temperature needed for increased activity is different for each temperature group and could be a result of microclimate influences or physiological response of individual species. Additionally, it appears that as temperatures groups get cooler, the rate of insect activity occurs more quickly, possibly as a result of a shorter seasonal window of optimal ambient conditions than at high-temperature sites. Further understanding the response to cumulative degree-days might best be accomplished by identifying key species to observe direct differences between core sites.

Photoperiod and temperature are two abiotic characteristics that can have great impacts on invertebrate development and activity (Valtonen et al. 2010, Forrest and Thomson 2011, Hodgson et al. 2011, Danks 1987, Triplehorn and Johnson 2005). Photoperiod is considered to be a primary regulator in activation and termination of diapause in invertebrates of temperate areas (Dingle 1972). Temperature can also regulate dormant periods and has additional control over physical motility of the invertebrate. As invertebrates are cold-blooded organisms, to be capable of

movements such as flying, invertebrates have to achieve an appropriate internal temperature. Internal temperature increases could be a result of insolation, behavioral adaptations such as "pumping" or wing vibrating, or an accumulation of thermal days signaling sufficient warmth to emerge (Danks 1987). When thermal conditions are suboptimal, invertebrates are able enter a stage of hibernation when ambient temperatures are too cold or aestivation when the temperatures are too hot until more favorable conditions recur. In some species, such as the multivoltine codling moth (*Cydial pomonella*), sufficient thermal periods are needed in addition to photoperiod for the first generation to emerge. Secondary, *C. pomonella* generations respond to thermal accumulation of degree-days and are capable of emerging as adults in July if ambient temperature conditions are optimal, or they will enter diapause until the following season (Brunner 1993).

PC09 had the highest abundance captured over the sampling period, and it was the only site to change temperature groupings during the cluster analysis from a mid-temperature site to a low-temperature site. This suggests a unique temperature pattern may influence PC09's local environment. Capture was high in comparison to other sites, and 65.5% of capture occurred between June 13-27. Thirteen of the sixteen sites reached greatest abundance during the month of June, and eight of the thirteen peaked over the sampling period of June 21 – 29. These peaks occur around the summer solstice, indicating that a threshold in temperature, corresponding with increasing photoperiod, had been crossed. This combination likely stimulated an increase in invertebrate activity.

The low temperature sites (PC13, PC17, and PC18) reached their peak abundances late in the sampling period of July 4 – 12. These responses suggest that a combination of abiotic factors at higher elevations induce a delay in activity and emergence. In a reciprocal transplant experiment studying elevation and temperature influences on the phenologies of cavity-nesting Hymenoptera, Forrest and Thomson (2011) found that bees at higher elevations emerged an average of 18.2 days later than those at lower elevations (elevation difference of 350 meters), regardless of whether the nest originated at the lower elevation before the wintering.

Spatial arrangements of forest structure create highly diverse and variable microclimates that can influence penetration of solar radiation, relative humidity, temperature, and wind speed; all these factors can affect insect species distribution and activity (Andrews 2011). Climate modeling of the Pacific Northwest predicts that the forests will become warmer and drier in the future (Franklin et al. 1991). Shifts in vegetation and insect species composition could vary as a result of the surrounding microclimate and the physiological tolerances, susceptibilities, and evolutionary traits of the individual species; however, an overall shift to higher elevations is predicted (Parmesan and Yohe 2003). It was difficult to determine whether forest growth influenced insect activity over one season of sampling because of an unbalanced study design relative to forest age. Ten of the sixteen sites were located within old growth stands, and important forest properties such as density and composition surrounding the malaise trap was unknown. It appears that old growth stands have higher levels of insect activity, but further studies examining trends spanning a number of years within

H. J. Andrews Experimental Forest would be beneficial. Additionally, incorporating of variables associated with forest age would provide a more comprehensive understanding of forest structure influences.

Invertebrate activity is affected by a plethora of ecological parameters, such as: hydrology, food supply, habitat availability, moisture, temperature, and topography (Danks 1987, Dunn and de Beurs 2011). Temperate mountainous areas are known for their variability in microclimates (McKee 1998), which could account for the scattered variation in invertebrate activity over the phenology sampling sites. Long-term studies of Lepidopterans conducted in England and Finland indicated that individual species of butterflies and moths were affected differently by photoperiod and temperature (Valtonen et al. 2010, Hodgson et al. 2011). Often it was a combination of the two cues that influenced life cycles. Additionally, geographic variables of latitude, altitude, and vegetative corridors influence insect seasonal cycles at both a species level within a population as well as between populations (Parmesan and Yohe 2003, Valtonen et al. 2010, Thomas et al. 2004, Primack et al. 2009). Determining species composition within each sample, as well as identifying key species, would increase understanding of individual insect responses and help to understand phenological differences among core sites.

Addressing climate effects on a local scale with a limited amount of time has been shown to be less informative and accurate than global studies that cover extended periods of time (Thomas et al. 2004). Because biological data is inherently noisy, subtle climate changes can often be masked by confounding factors such as short-term

changes in habitats and landscapes. Incorporating all three years of existing invertebrate data (from 2009-2011), reviewing historical records of the H. J. Andrews, and creating models that compare abundance as a response to environmental and site variables such as slope, aspect, hydrology, forest composition and canopy density, would improve our understanding of climatic and geographical influences on insect phenologies in this forest ecosystem.

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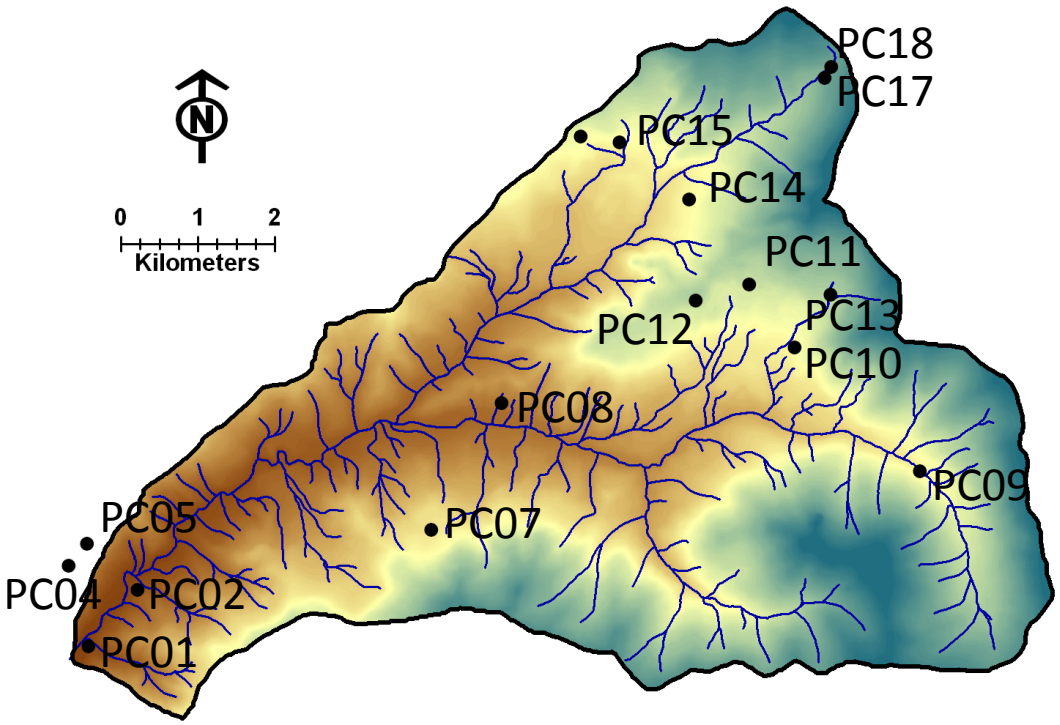

Figure 1. Phenology core sites. H. J. Andrews Experimental Forest occupies 6,400 hectares of the Lookout Creek Watershed located in the western slopes of the Cascade Range around 80.5 kilometers east of Eugene, Oregon. Brown represents low elevation and blue represents higher elevations.

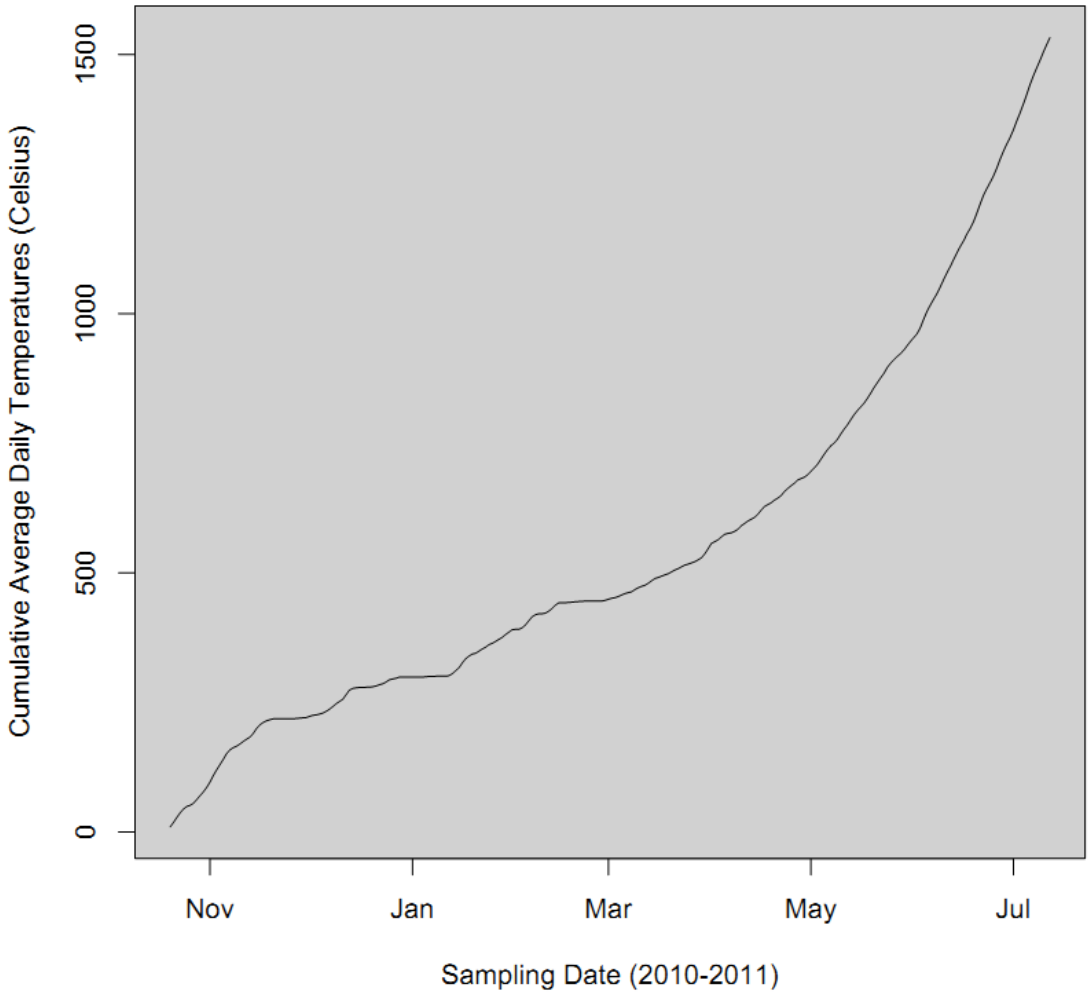

Figure 2. Cumulative degree-days at site PC01 determined using average daily temperatures from October 20, 2010 through July 12, 2011.

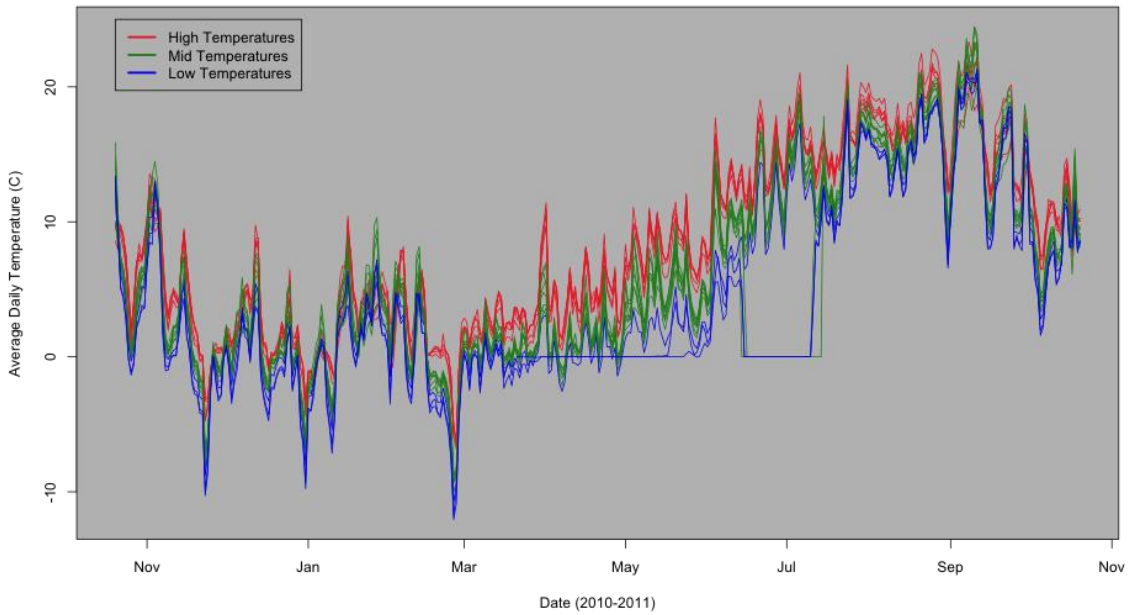

Figure 3. Average daily temperatures from October 20, 2010 through October 20, 2011 for 16 study sites. Colors represent temperature groupings. Snow covered sites PC17 and PC18 from mid-March through May. Temperature gauges at sites PC09, PC16, PC17, and PC18 malfunctioned between June 13 through July 11 when temperatures are expressed as zero degrees Celsius.

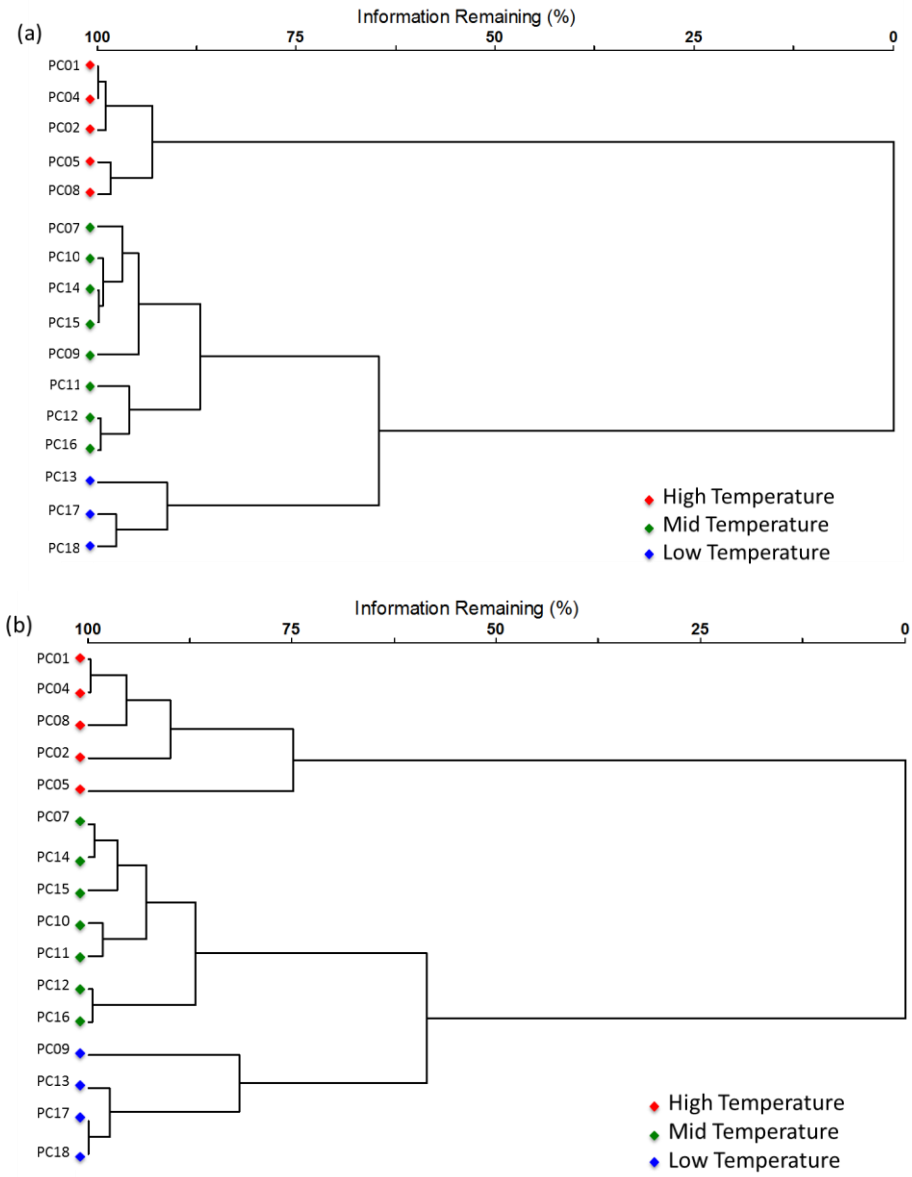

Figure 4. Cluster analysis of phenology core sites. Because of missing temperature data at sites PC09, PC16, PC17, and PC18, two analyses were (a) using average daily temperature data from October 20, 2010 through June 12, 2011 and (b) using average daily temperature data from July 16, 2011 through October 20, 2011.

Temperature Group	Site	Elevation (m.)	Total Abundance	Forest Stage
High Temperature	PC08	647	4610	Old
	PC01	460	4487	Young
	PC02	488	3236	Old
	PC05	644	2316	Young
	PC04	481	1382	Young
Mid Temperature	PC10	994	6509	Old
	PC07	903	6141	Old
	PC16	1030	4103	Young
	PC12	1082	3223	Old
	PC14	965	2937	Old
	PC15	971	2064	Old
	PC11	1116	1988	Young
Low Temperature	PC13	1178	3363	Old
	PC18	1339	1398	Young
	PC17	1301	1217	Old
Unclassified	PC09	979	11809	Old

Table 1. Total invertebrate abundance for the total sampling period at each of the sixteen phenological core sites, their corresponding elevations, designated temperature grouping, and forest cover. PC09 is listed as “unclassified” due to missing temperature data.

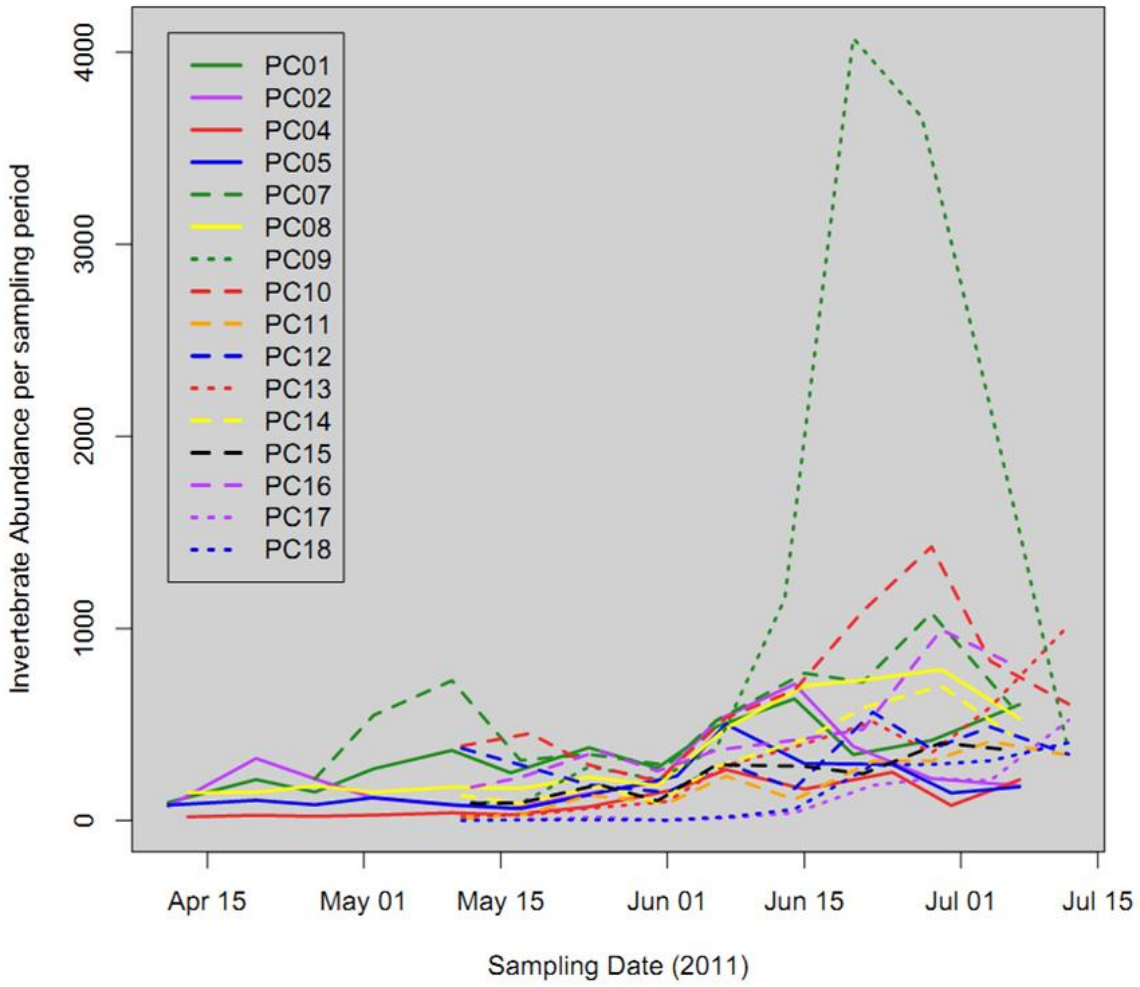

Figure 5. Invertebrate abundance per sub-sampling period at each phenology core site over the 2011 sampling season. Note that the sampling periods for each site may be different (i.e. early April into early May) due to site accessibility.

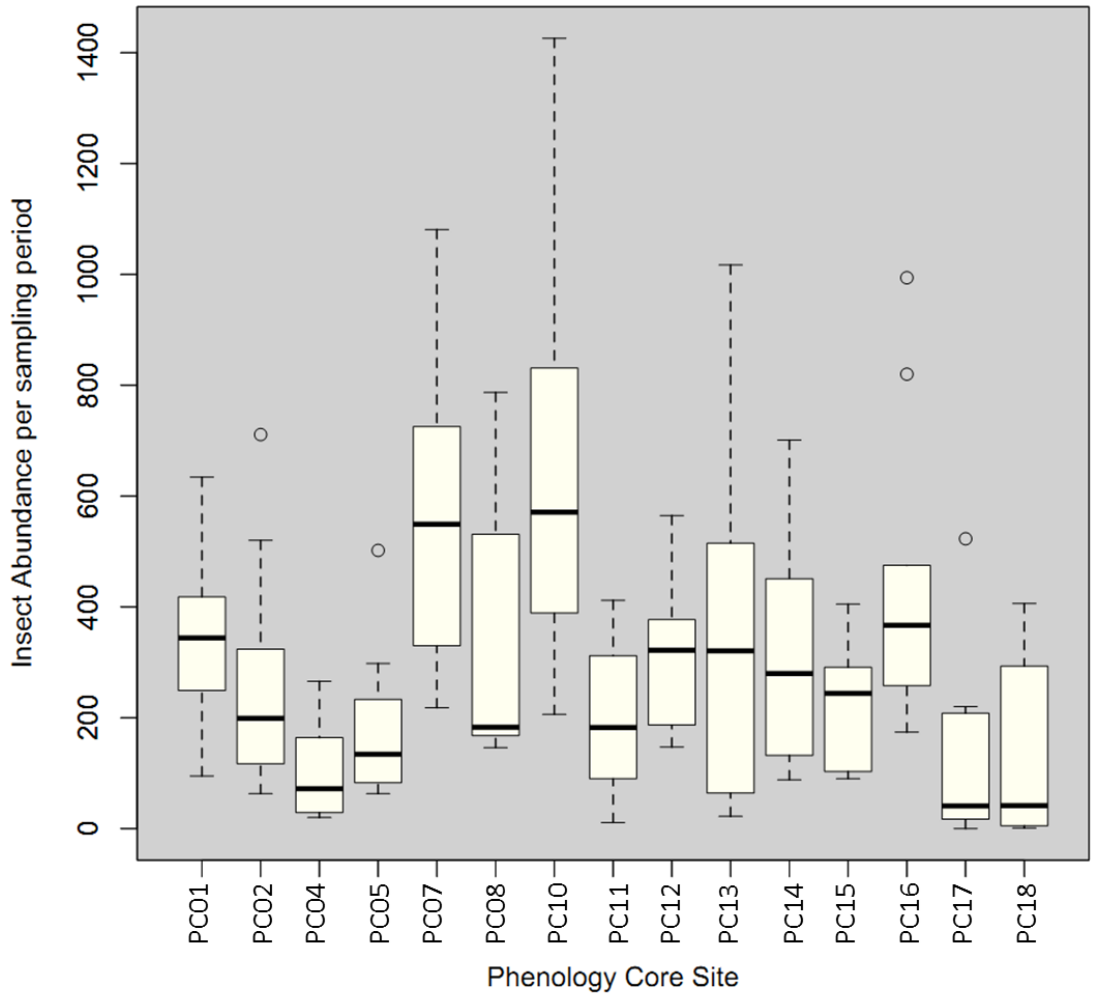

Figure 6. Insect abundance per sub-sampling period at core sites. Dark bars are the median abundance. The whiskers extend to the most distant point that is within 1.5 times the interquartile range from the end of the box. Sample sizes: n_{PC01}=13, n_{PC02}=13, n_{PC04}=13, n_{PC05}=13, n_{PC07}=11, n_{PC08}=13, n_{PC09}=10, n_{PC10}=10, n_{PC11}=10, n_{PC12}=10, n_{PC13}=10, n_{PC14}=9, n_{PC15}=9, n_{PC16}=9, n_{PC17}=9, n_{PC18}=10. PC09 is excluded because of the extreme values occurring in late June.

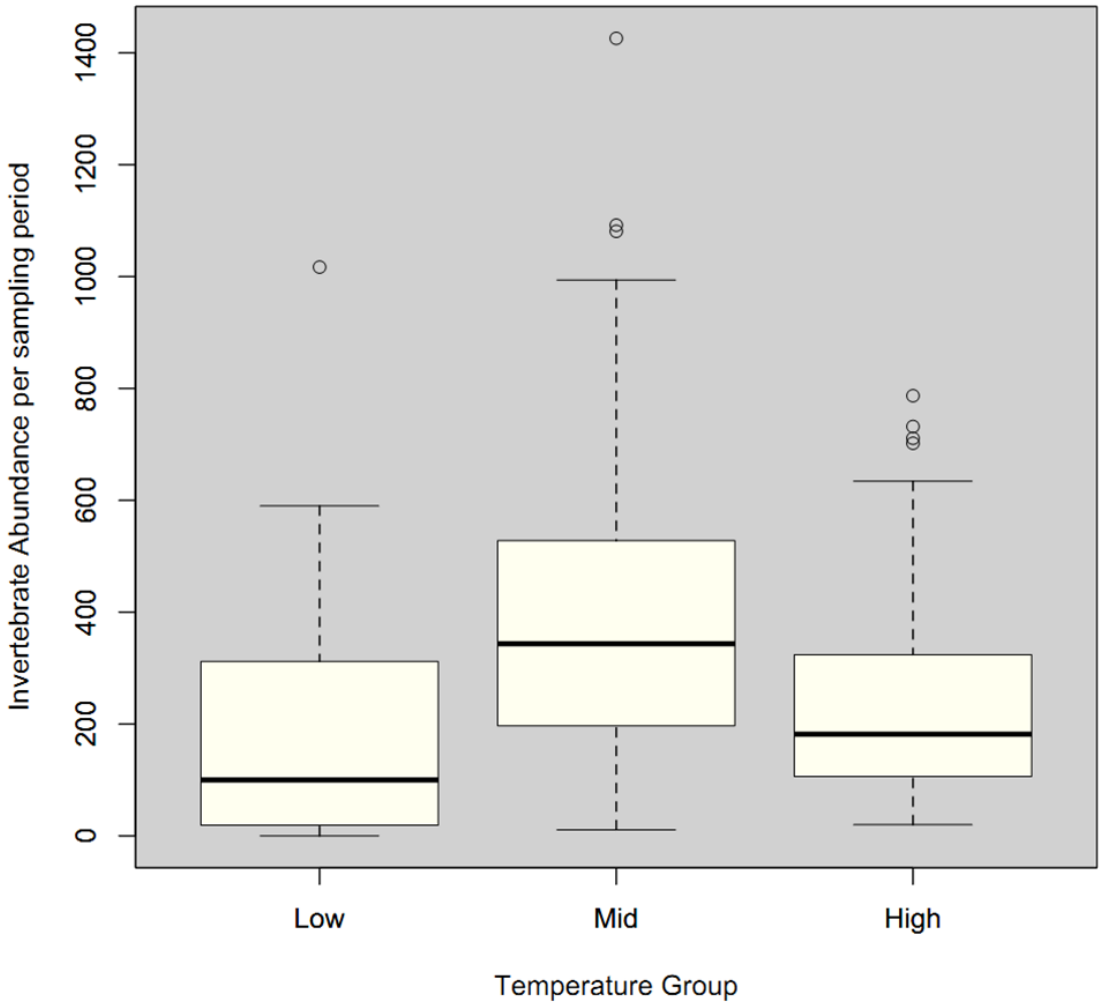

Figure 7. Mean insect abundances per sampling period for temperature groups during 2011 sampling season. Dark bars are the median abundances. The whiskers extend to the most distant point within 1.5 times the interquartile range from the end of the box. Sample size varies among sites (n_{High}= 65, n_{Mid}= 68, n_{Low}= 29).

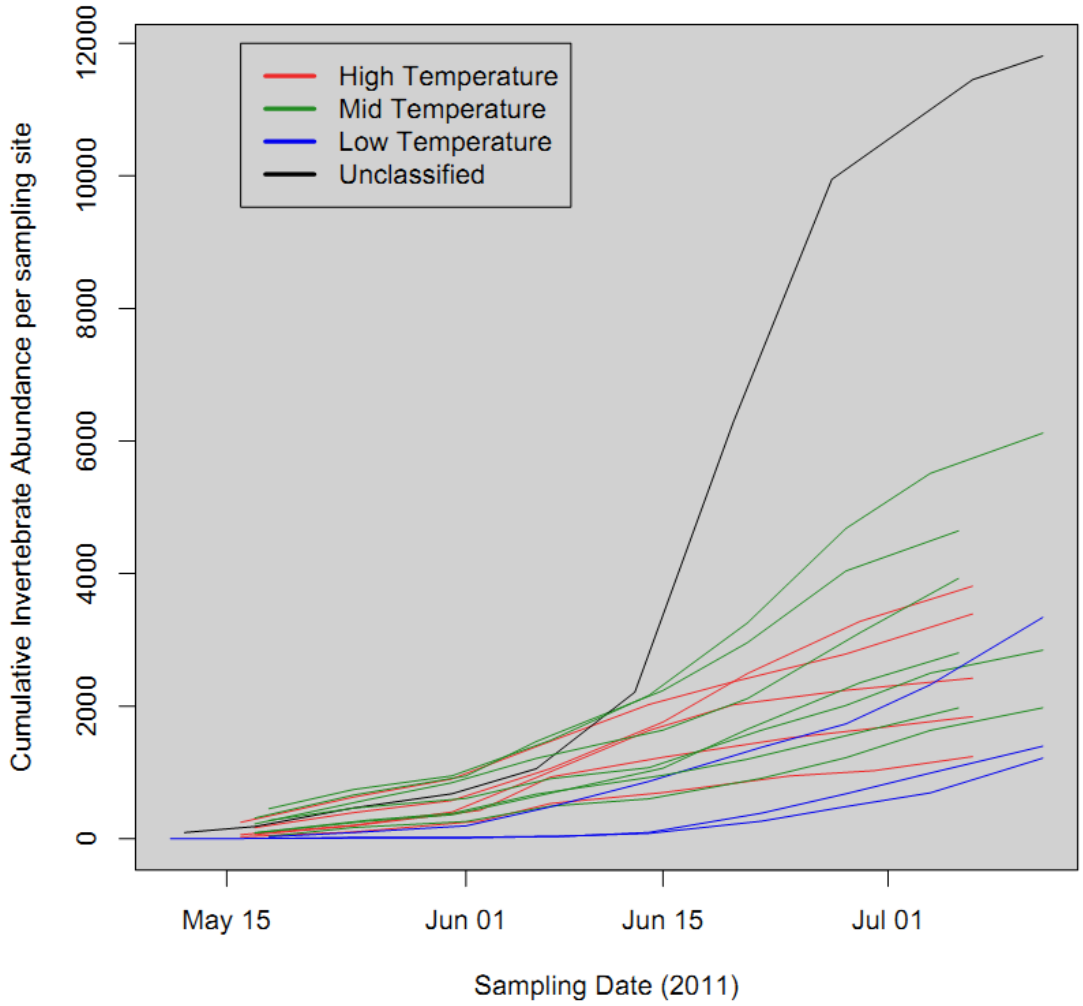

Figure 8. Cumulative invertebrate abundance over the sampling period when all sites were sampled.

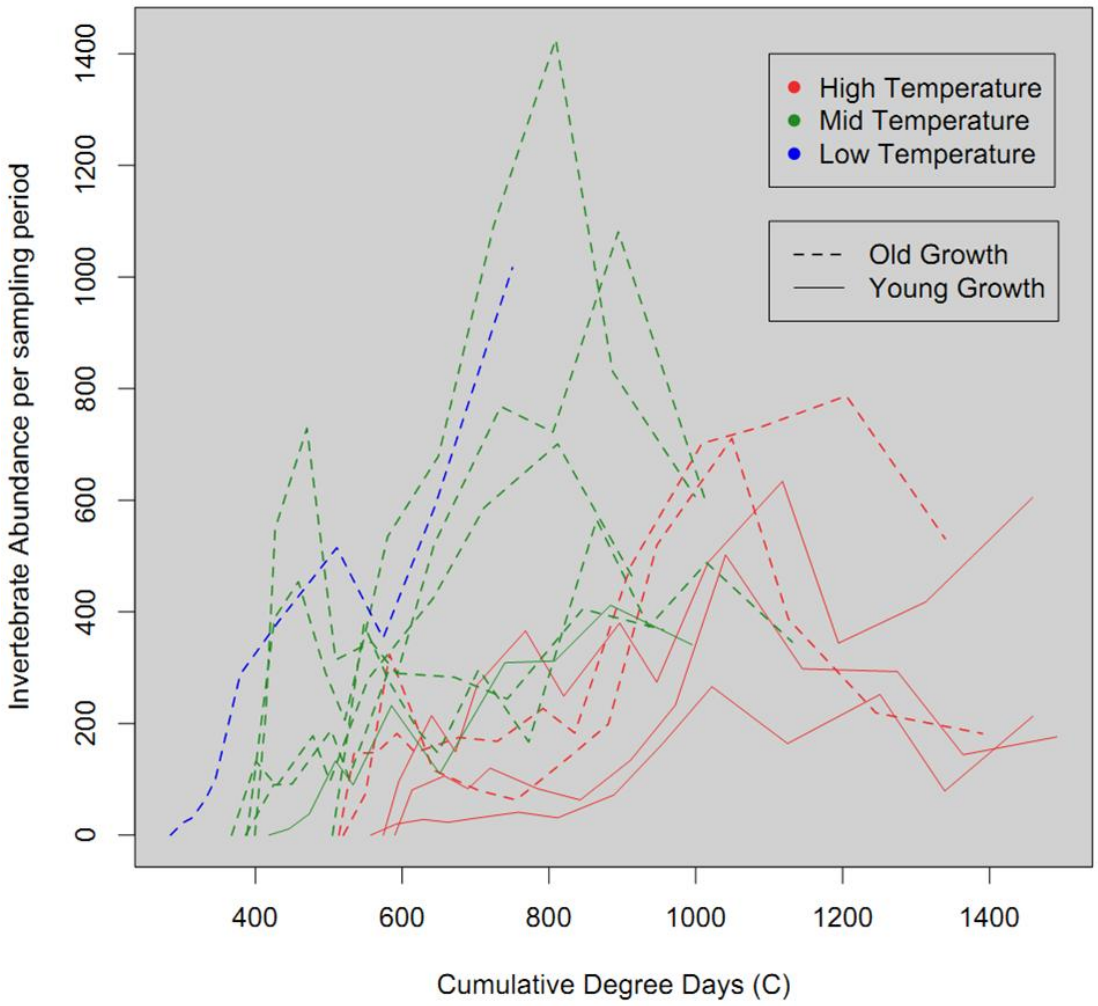

Figure 9. Invertebrate abundance by cumulative degree-days per phenology core site (excluding sites PC09, PC16, PC17, and PC18 due to missing temperature data). Cumulative degree-days begin on October 20, 2010 and extend to July 12, 2011. Temperature groupings are differentiated by color and forest growth differences are indicated by line segmentation.

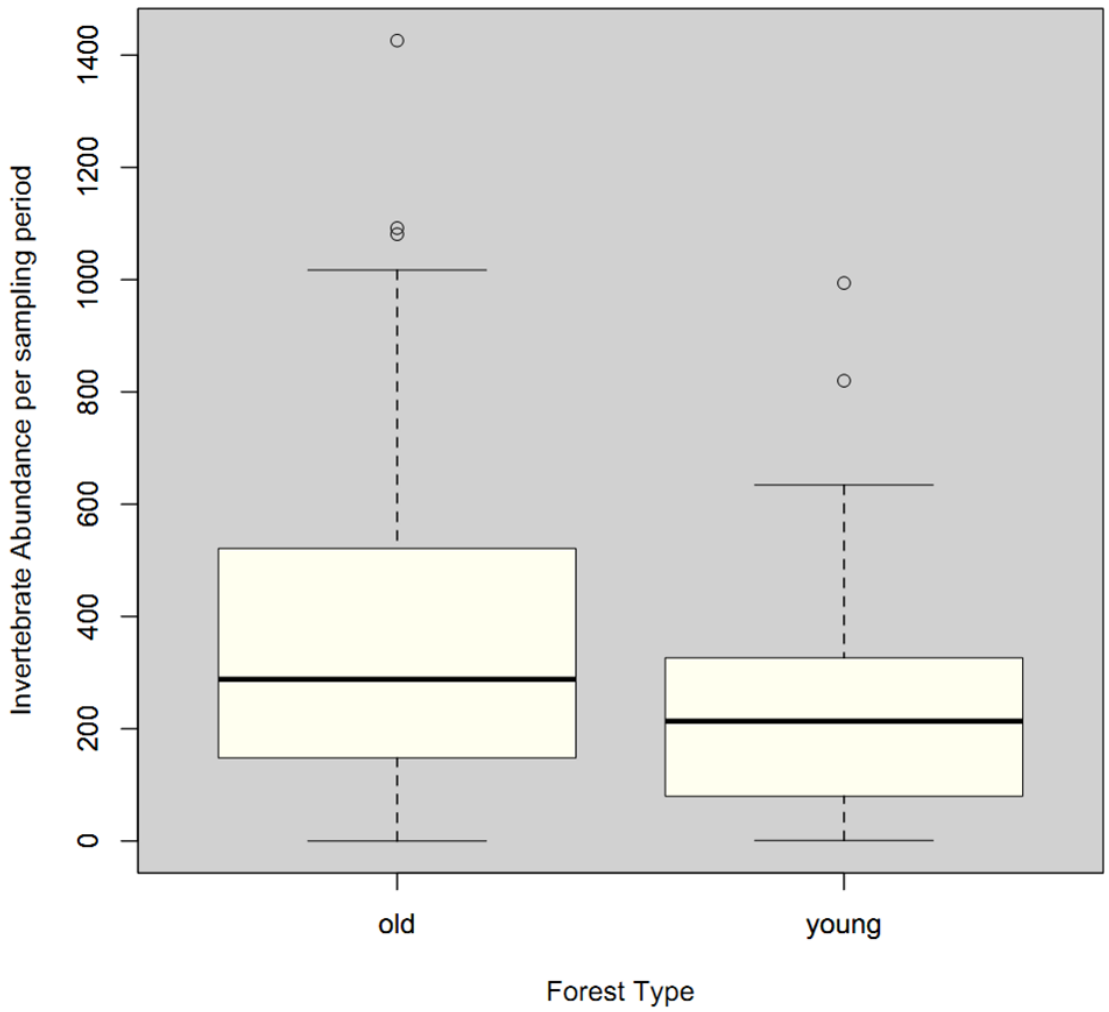

Figure 10. Insect abundance per forest cover group over the sampling period. Dark bars are the median abundance. The whiskers extend to the most distant point within 1.5 times the interquartile range from the end of the box. Sample size varies among sites (n_{old}= 94, n_{young}= 68).