Microclimatic effects of the loss of a foundation species from New England forests

MONIQUE N. LUSTENHOUWER, LIZA NICOLL, AND AARON M. ELLISON†

Harvard Forest, Harvard University, 324 North Main Street, Petersham, Massachusetts 01366 USA

Abstract. Foundation species have a major impact on biotic and abiotic processes and create a stable environment for many other species. Eastern hemlock (*Tsuga canadensis*), a foundation tree species native to North America, is currently declining due to infestation by an invasive insect, the hemlock woolly adelgid (*Adelges tsugae*). Loss of hemlock canopies can greatly alter the dark, cool, and damp microclimate of hemlock forests. We studied five years of microclimatic changes following logging or girdling (to simulate physical effects of adelgid) of hemlocks in a multi-hectare-scale experiment in a New England forest. Both logging and girdling of hemlocks caused large changes in light availability, air and soil temperature, and soil moisture. Even though the impact of logging was more rapid than the effect of gradual hemlock mortality after girdling, the microclimatic changes in these two canopy treatments converged over time. The microclimate in hardwood control plots, which represent the predicted forest composition 50 years after hemlock loss, was intermediate between the two canopy treatments and the hemlock control plots. Our fine-scale results were generally consistent with average microclimatic effects observed in comparative studies but revealed additional changes in variance and seasonal rhythms, and the importance of stochastic events such as ice storms. The variance in air temperature, but not in soil temperature, greatly increased after loss of hemlock. We also observed a striking saw-tooth pattern, consisting of a small peak before bud-break in temperature differentials between hemlock control and the two canopy treatments—likely due to the insulating hemlock canopy preventing snow from melting—followed by a larger difference in temperatures after bud-break. We expect the ongoing decline of eastern hemlock—due to both infestation and pre-emptive salvage logging—to greatly impact the microclimate of hemlock forests, as well as the many taxa that are associated with it.

Key words: *Adelges tsugae*; eastern hemlock; foundation species; hemlock woolly adelgid; invasive species; Massachusetts, USA; microclimate; New England; *Tsuga canadensis*.

† **E-mail:** aellison@fas.harvard.edu

INTRODUCTION

Biotic and abiotic processes in forest ecosystems often are strongly influenced by the structural or functional characteristics of certain tree species (Ellison et al. 2005a). Such foundation species (sensu Dayton 1972) create locally stable conditions for other species and control essential ecosystem processes. An important foundation species in eastern North America is the late successional conifer, eastern hemlock (*Tsuga canadensis* (L.) Carr.) (Orwig et al. 2002, Ellison et al. 2005a). When hemlock dominates a stand, it creates a unique forest environment with a cool and dark microclimate, and acidic, slowly decomposing litter atop nutrient-poor soils (Rogers

1978, Jenkins et al. 1999, Ellison et al. 2005*a*). Throughout the central and southern part of its range (from Massachusetts south to Georgia), eastern hemlock is currently declining as stands are infested by two non-native insects: the hemlock woolly adelgid (*Adelges tsugae* Annand) and the elongate hemlock scale (*Fiorinia externa* Ferris) (Preisser et al. 2008). In addition to morbidity caused by both the adelgid and the scale, and mortality caused by the adelgid, hemlock has also been cut and salvaged in anticipation of further expansion of the adelgid (Orwig et al. 2002, 2012). Because foundation tree species often define or control the local microclimate, major changes in abiotic conditions are expected as eastern hemlock declines and is replaced progressively by early successional hardwoods, including birches (*Betula* spp.), red maples (*Acer rubrum* L.), and oaks (*Quercus* spp.) (Orwig et al. 2002). These changes in abiotic conditions may be associated with changes in abundance of a number of animal species, including arthropods (Rohr et al. 2009, Sackett et al. 2011), birds (Tingley et al. 2002), and aquatic invertebrates (Snyder et al. 2002), as well as with changes in species interactions, successional pathways, and the rates of cycling of energy and nutrients (Orwig et al. 2008, Gandhi and Herms 2010).

Despite the importance of variance in abiotic conditions for the population, community, and ecosystem dynamics (e.g., Benedetti-Cecchi et al. 2006), most contemporary studies of forest ecology simply report overall means, for example in temperature or light availability (e.g., Lebrija-Trejos et al. 2011, Moore et al. 2011). Fine-scale temporal dynamics in abiotic conditions are rarely quantified, but time-series analysis may reveal particular or episodic events that have long-term, cascading effects on the system. Temporal changes in abiotic conditions also can provide important insights into the pace of succession or the recovery of systems following disturbance.

Here, we describe fine-scale temporal changes in microclimate in a multi-hectare-scale manipulation designed to study the response of forested ecosystems to the loss of eastern hemlock (Ellison et al. 2010). We studied in detail five years of changes in air and soil temperature, light availability, and soil moisture in forest stands in which hemlock was killed in place (to simulate death by adelgid) or removed (as in a salvage logging operation). We chose these variables because they often are tightly associated with changes in species composition and ecosystem dynamics. For example, changes in air and soil temperature, light environment, and soil moisture are associated with changes in increased ant species richness and abundance (Ellison et al. 2005*b*) but decreased abundance of eastern red-backed salamanders (Mathewson 2009) as hemlock stands decline and are replaced by hardwoods. Soil nitrogen mineralization and soil respiration rates (carbon flux) in many forest types, including hemlock forests, are directly related to soil temperature and soil moisture (e.g., Savage and Davidson 2001, Templer and McCann 2010, Brzostek and Finzi 2011).

Materials and Methods

Experimental design

The Harvard Forest Hemlock Removal Experiment (HF-HeRE; Ellison et al. 2010) has two types of canopy manipulation applied to 90×90 m plots; a girdling treatment that mimics slow death by HWA infestation and a logging treatment analogous to a pre-emptive salvage logging operation aimed at extracting income from a forest stand before the adelgid would have arrived. HF-HeRE is located in two experimental blocks at the Simes Tract at Harvard Forest, a Long Term Ecological Research Site (LTER) in Petersham, MA, USA (42.47° to 42.48° N, 72.21° to 72.22° W, 215–300 m a.s.l): a "Valley" block located on a gently sloping, low terrain, and a "Ridge" block located on a forested ridge (Fig. 1). Each block consists of four plots: the two aforementioned treatments (girdling, logging) and two control plots: one dominated by hemlock, the other by young hardwoods (birches, maples, and oaks), which is the type of forest that is expected to develop after hemlock dies (Orwig et al. 2002). In the girdled plots, the bark and cambium of each hemlock (including small saplings) was girdled using a chain saw or knife. In the logged plots, all hemlocks >20 cm and all commercially valuable large white pine (*Pinus strobus* L.) and red oak (*Quercus rubra* L.) were cut and removed from the site with a skidder. Plots were located in 2003, pre-treatment obser-
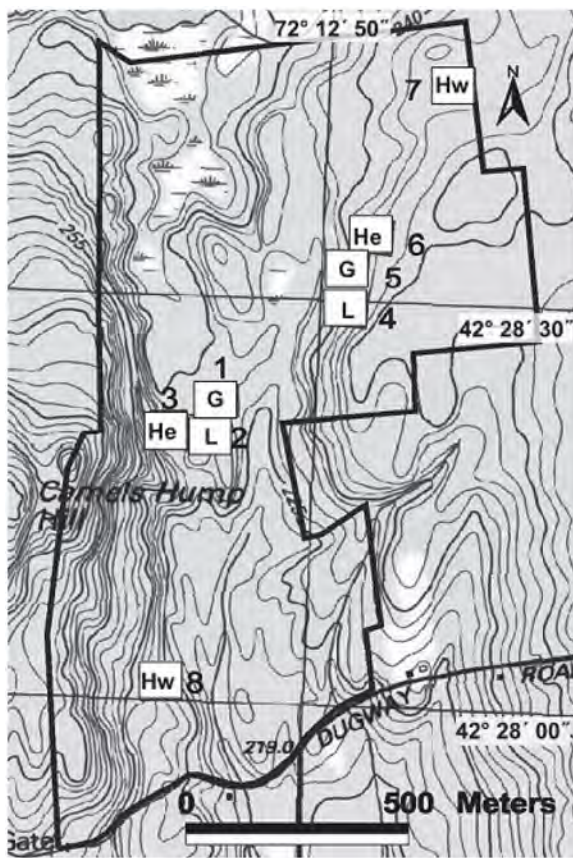
Fig. 1. Location of the logged (L), girdled (G), hemlock control (He) and hardwood control (Hw) plots within the Simes Tract at Harvard Forest. Plots 1–3 and 8 make up the Valley block and plots 4–7 make up the Ridge block.

vations began in summer 2004, and experimental treatments were applied between February and May 2005. In 2010, the adelgid colonized the site, changing the focus of the experiment from a comparison between treatment and controls to a comparison between the physical effect of girdling and the additive or interactive effects of the adelgid itself on forest dynamics. Ellison et al. (2010) provide a full description of the experimental design and analytical approach. Here we focus on the data collected prior to the arrival of the adelgid (2005–2009) to compare the initial response of the canopy manipulation plots to the hemlock and hardwood controls.

Light availability

Hemispherical canopy photographs have been taken twice yearly since 2005: in April before leaf bud-break by the deciduous trees ("leaf-off" condition), and in September, before the deciduous trees have dropped their leaves ("leaf-on" condition). Twenty-five photographs are taken in each plot on a 15-m grid. The photographs are taken with a Nikon 8-mm fish-eye lens, from a position 1–2 m above ground. From 2005 through April 2008, the lens was mounted on a Nikon F-3 film-camera body; from September 2008 onward the same lens has been mounted on a Nikon D-3 digital camera body. The canopy photographs were analyzed using the HemiView software, version 2.1 (Delta-T Devices, Cambridge, UK). For each photograph, we calculated the global site factor (GSF), which ranges from 0 to 1 and is the estimated proportion of (direct + diffuse) solar radiation reaching the camera (Rich 1989); here, GSF measures light available to the forest understory at 1–2 m above ground. Initial analysis found no evidence of spatial autocorrelation at the scale of the 15-m grid, showed that each of the 25 photograph locations within each plot showed similar patterns over time, and that differences among them were constant (A. M. Ellison and M. Levine, *unpublished data*). Thus, to compare the two canopy manipulations and the hardwood controls with the hemlock controls, we used the mean GSF value from all 25 photographs in a plot at each measurement time. Raw data, along with the digitized (from film) or digitally original canopy photographs are available from the Harvard Forest LTER data archive, dataset HF-107 (Ellison 2005b).

The GSF data were analyzed with a mixed model ANCOVA, using the lme function in the nlme package in R version 2.13.2 (Pinheiro et al. 2011, R Development Core Team 2011): GSF was the response variable and treatment entered the model as a fixed factor, with four levels corresponding to the four plot types. We used block as a random factor and time as a continuous covariate; the leaf-on and leaf-off data were analyzed separately and consisted of yearly measurements from 2005 to 2009. We included both the additive and the interaction term of time and treatment in the model. The main effects of the logged, girdled, and hardwood treatments were evaluated relative to the hemlock controls.

Air and soil temperature

Air and soil temperature are measured every minute using thermocouples located in the center of each plot. Air temperature sensors are located 1 m above the soil surface; soil temperature sensors are buried in the mineral soil, ~10 cm below the surface. Every hour the mean, maximum and minimum temperatures are stored in Campbell 21-X data loggers (Campbell Scientific, Logan, Utah, USA). We began collecting temperature data for the hemlock control, logged, and girdled plots in 2005. Temperature data collection in the hardwood plots started in July 2008.

Sporadic gaps (<5% of the data) in the data have occurred due to logger failure, lightning, damage by wild animals, and other stochastic events. Thus, all data were filtered for questionable data that seemed to be caused by data logger errors (Appendix). Average monthly air and soil temperatures were calculated from the mean hourly temperatures (raw data in Harvard Forest data archive, dataset HF-108: Ellison 2005*a*). Monthly data were used for three reasons. First, biotic changes and ecosystem dynamics in these plots are routinely measured seasonally or annually, and only occasionally monthly (Ellison et al. 2010). Thus, monthly data provide finer resolution than do biotic or ecosystem data, have enough signal relative to daily or weekly noise to be interpretable, and can also be scaled up (aggregated) when assessing impacts of a changing microclimate on overall (annual or decadal) ecosystem dynamics. Second, time-series analysis requires evenly spaced, regular data. There are consistently 12 months in a year, but there are not a regular number of weeks in a year, and leap years add additional temporal complexity. Thus, time-series analyses work most effectively with daily (or even finer-scale), monthly, or annualized data. We chose to use monthly data as it allowed us to deal with missing (daily) data in consistent ways (see Appendix).

We analyzed the data using time-series analysis, focusing on the monthly temperature differences between the hemlock control plots and the logged, girdled, or hardwood control plots. The monthly temperature differences were monthly averages of the hourly temperature differences between the hemlock control and each of the other three treatments. We also calculated the differences among treatments in the variance of all hourly measurements in each month. We decomposed the monthly time series into seasonal, trend, and residual components using STL, a decomposition procedure based on local regression ("loess": Cleveland 1979, Cleveland et al. 1990). First the seasonal component was estimated using loess smoothing; then a linear trend was fit to the data minus the seasonal component. We used the seasonal Mann-Kendall test to test for monotonic trends in the time series (Hipel and McLeod 1994). This test was specifically developed for monthly environmental data exhibiting seasonality and missing values. The test is implemented in the Kendall package in R.

We used phenological data that have been collected at Harvard Forest since 1990 (raw data in Harvard Forest data archive, dataset HF003: O'Keefe 2000) to identify the start and end of each year's growing season. On permanently tagged individuals at Harvard Forest, bud-break and leaf development were observed at 3–7 day intervals in spring, and leaf coloration and leaf-fall were observed at weekly intervals in fall. For this study, the period between 50% bud-break and 50% leaf-fall was used as an indicator of the growing season. We used data from four species—*Acer rubrum*, *Betula alleghaniensis* Britton, *Quercus rubra* and *Q. alba* L.—to calculate the mean bud-break and leaf-fall dates for the years 2005–2009.

Soil moisture

The percentage of moisture in the soil was measured in the hemlock control, logged, and girdled plots using a hand-held probe that was inserted vertically into the soil profile. Measurements were done 1–3 times a month during the summer months (June, July, and August) of 2006–2009. This method provides an estimate only of the relative differences in soil moisture among plots. Monthly averages of percent soil moisture were calculated for June, July and August of each year. The data were then analyzed in the same way as the light availability data using a mixed model ANCOVA, with the soil moisture percentage as the response variable and the year as a covariate. These data span only 2006–2009, no soil-moisture data were collected in 2005 (raw data in Harvard Forest data archive, dataset HF-130: Davidson and Savage 2009).

RESULTS

Light availability

In the logged plots, between 60% and 70% of the stand basal area was cut and removed, whereas in the girdled plots, the hemlocks died over the course of 30 months (Ellison et al. 2010). Regrowth in the understory of the logged and girdled plots became apparent around 2006, but did not reach the height of the canopy-photograph cameras until 2009 (Fig. 2). During the growing seasons (i.e., leaf-on conditions), there was a significant time × treatment interaction in light availability ($F_{3,40} = 11.59$, $P < 0.001$; Fig. 3). We observed a gradual increase in light availability at the forest floor as the hemlocks died ($t = 2.97$, df = 31, $P = 0.006$; Fig. 3). In contrast, we observed in the logged plots an abrupt increase in light availability at the forest floor followed by a decrease in light availability as regrowth commenced ($t = -2.93$, df = 31, $P = 0.006$; Fig. 3). There was no significant change in GSF in the hardwood control plots over time ($t = -0.12$, df = 31, $P = 0.91$; Fig. 3). Overall (across time), the hardwood and hemlock control plots had nearly identical GSF ($t = 0.12$, df = 31, $P = 0.91$; Fig. 3), but GSF in both the logged and the girdled plots were significantly higher than those in the hemlock control plots (logged: $t = 2.94$, df = 31, $P = 0.0061$; girdled: $t = -2.96$, df = 31, $P = 0.006$; Fig. 3).

During leaf-off conditions (autumn, winter, and early spring), there was also a significant time × treatment interaction in light availability ($F_{3,40} = 6.41$, $P = 0.002$; Fig. 3). However, only the girdled treatment showed a significant change in light availability through time, as it gradually increased ($t = 2.29$, df = 31, $P = 0.03$; Fig. 3). The girdled treatment also was the only treatment that differed significantly from the hemlock controls ($t = 2.29$, df = 31, $P = 0.029$; the girdled plots were brighter).

Air and soil temperature

The average monthly differences in air temperature between the canopy treatments and the hemlock controls ranged from approximately -0.4 to $+2.6°C$ in the logged plots and from -0.1 to $+2.3°C$ in the girdled plots (Fig. 4). The soil temperature differences were slightly greater, ranging from -1.1 to $+3.1°C$ in the logged plots

and from -1.5 to $+2.4°C$ in the girdled plots (Fig. 4). The magnitude of the temperature differences changed over time; in general, the temperature deviations in the logged plots decreased through time, whereas the temperature deviations in the girdled plots increased through time. An exception is the soil temperature on the Ridge, where the difference between the logged plot and the hemlock control also increased over time. By 2009, the air and soil temperature deviations of the logged and girdled plots had converged in both blocks (Fig. 4). The slopes of six out the eight trends were significantly different from zero; although consistent in direction with the other treatments, in the Valley block, neither the air temperature deviation in the girdled plot nor the soil temperature deviation in the logged plot changed significantly over time ($P > 0.05$, seasonal Mann-Kendall test).

There were clear seasonal patterns in the temperature deviations of the canopy treatments from the hemlock controls (Fig. 5). Both the logged and the girdled plots were warmer than the hemlock controls in summer and colder in winter. The amplitude of the seasonal pattern was greater in the logged plots than in the girdled plots, and greater on the Ridge than in the Valley. In general, the temperature deviation from the hemlock controls started increasing before bud break, reached a peak within the growing season, and then decreased until it reached its minimum in winter. An additional striking observation was a clear saw-tooth pattern in the air temperature deviations in the Valley, consisting of a small peak before bud break followed by a larger peak after bud break (Fig. 5). This pattern was weaker on the Ridge and was almost absent in the seasonal patterns of soil temperatures. We could not seasonally decompose the hardwood control data because of the short time frame of data collection in those plots (1.5 years), but a graphical inspection of the seasonal plots suggests that the peak deviations of the hardwood plots relative to the hemlock controls occurred before the peak deviations of the girdled and logged plots relative to hemlock controls (Fig. 5).

The monthly variance in air temperature was much greater in the logged and girdled plots than in the hemlock control plots (Fig. 6). The difference between the logged plots and the
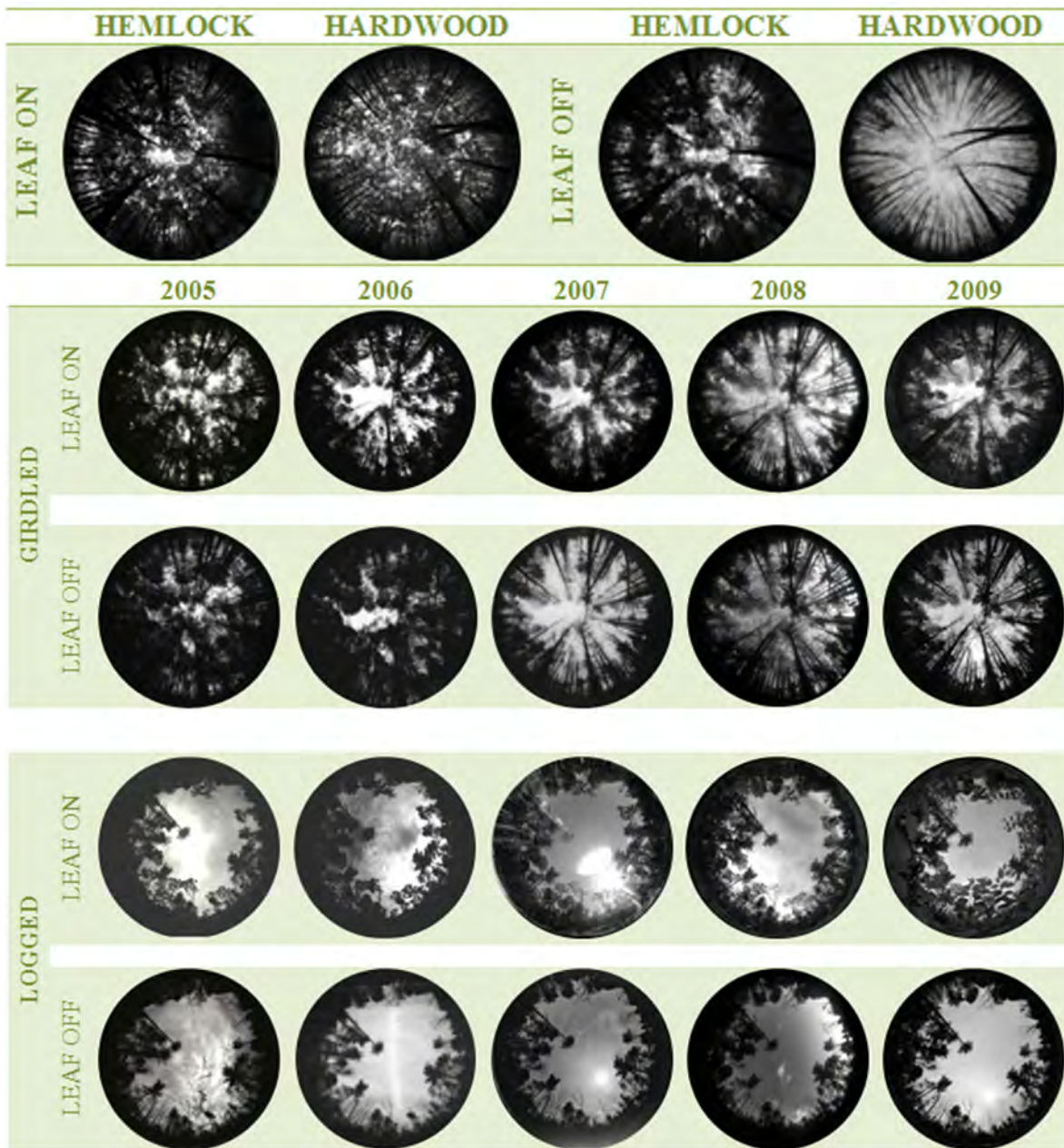
Fig. 2. Canopy photos taken in the hemlock and hardwood control plots in 2009 (top) and in the girdled and logged plots from 2005–2009 (bottom), during leaf-on (September) and leaf-off (April) conditions. Each of these photos was taken at a single location in the Valley block; we chose locations that represented the average canopy in each plot.

hemlock controls remained constant over time, while the difference between the girdled plots and the hemlock controls increased over time ($P < 0.001$, seasonal Mann-Kendall test), converging towards the logged plots. The difference in air temperature variance was greatest in early spring and summer. In contrast, the differences in monthly variance in soil temperatures between the treatments and the hemlock controls were much smaller (Fig. 6). In the Valley, the devia-
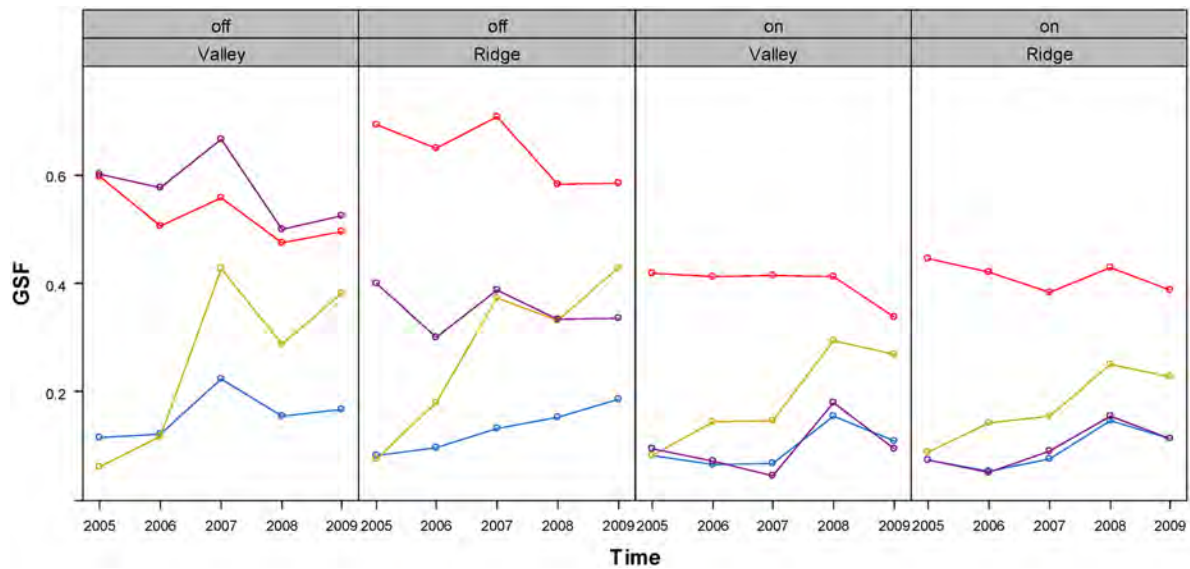
Fig. 3. Mean global site factor (GSF) per plot in the Valley and Ridge blocks, during leaf-on and leaf-off conditions, 2005–2009. GSF is the estimated proportion of (direct + diffuse) solar radiation reaching the camera at 1–2 m above ground. Different colors indicate different treatments; blue: hemlock control; red: logged; yellow: girdled; purple: hardwood control.

tions of the logged and the girdled plots from the hemlock controls converged over time (negative trend in the logged plots, $P = 0.006$; positive trend in the girdled plots, $P < 0.001$). On the Ridge, the differences between the treatments and the hemlock controls remained constant over time.

Soil moisture

There was no treatment × year interaction in the analysis of soil moisture data ($F_{2,69} = 0.39$, $P = 0.68$), but an additive model revealed significant effects of both treatment ($F_{2,69} = 6.92$, $P < 0.001$) and year ($F_{1,69} = 25.19$, $P < 0.001$). Both the logged and the girdled plots were significantly moister than the hemlock controls (logged: $t = 2.85$, $P = 0.006$; girdled: $t = 3.49$, $P < 0.001$), and in all plots the percent soil moisture decreased over time (Fig. 7). In the Valley, soil moisture was highest in the girdled plot, while on the Ridge, soil moisture was highest in the logged plot.

DISCUSSION

Microclimate influences rates of soil respiration (e.g., Savage and Davidson 2001, Brzostek and Finzi 2011), nutrient cycling (e.g., Templer and McCann 2010), and biomass production, among other ecosystem processes, as well as the distribution of many species (e.g., Ellison et al. 2005*b*, Mathewson 2009) in a wide variety of forests. Structural changes in the landscape can greatly alter microclimate (Chen et al. 1999), and loss of foundation species is a significant structural change. We observed large changes in both mean and variance of microclimatic variables after logging or girdling of eastern hemlock, a foundation tree species (Ellison et al. 2005*a*), to simulate the impacts of the hemlock woolly adelgid in the Harvard Forest Hemlock Removal Experiment (HF-HeRE; Ellison et al. 2010).

Hemlock mortality opened up the canopy and increased light availability in the girdled plots. These findings are consistent with both comparative (Orwig and Foster 1998, Jenkins et al. 1999, Orwig et al. 2008) and monitoring (Eschtruth et al. 2006) studies of infested and non-infested hemlock stands. We also observed a notable stochastic event that occurred during the data collection period: a severe ice storm that hit the northeastern United States in December 2008 (de la Crétaz et al. 2010). This singular event likely explains the increase in light availability observed in all treatments under leaf-off conditions
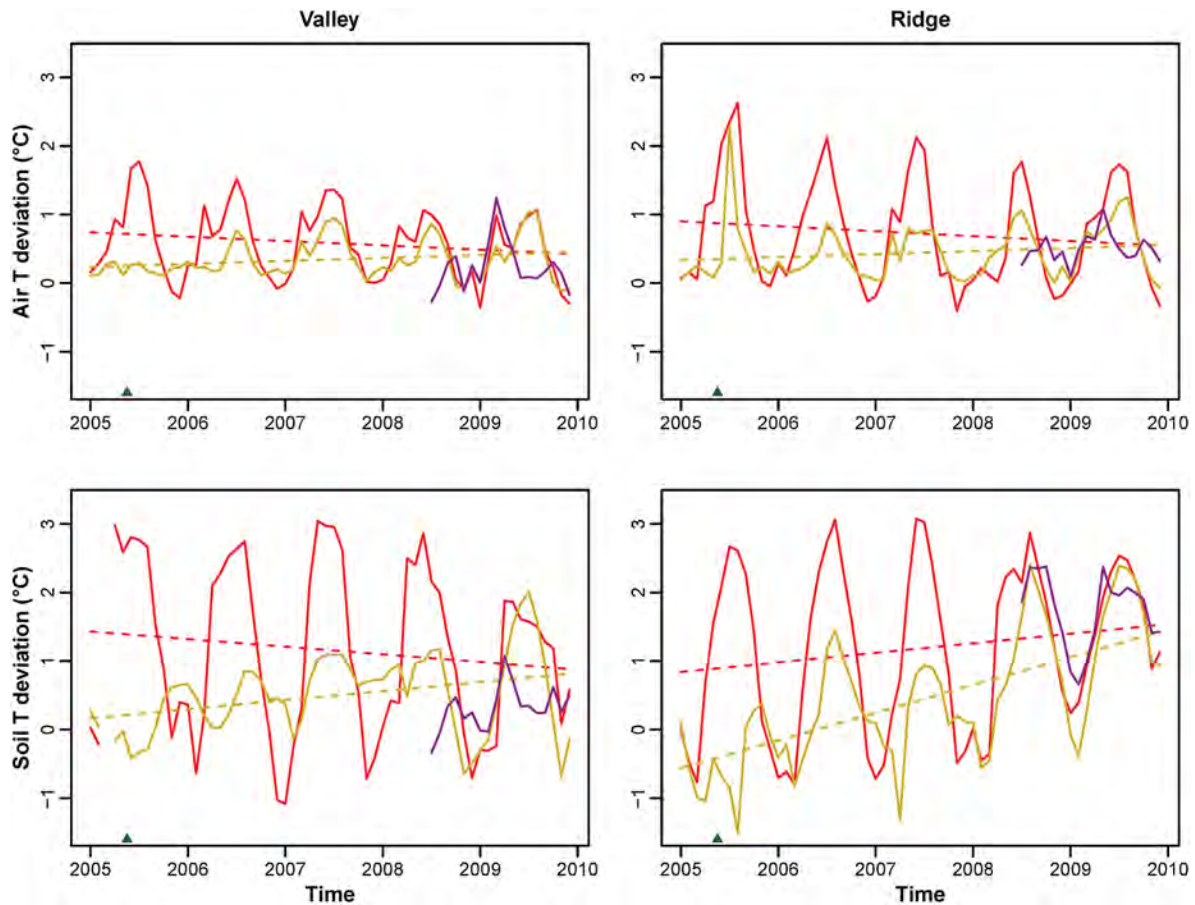
Fig. 4. Monthly means of hourly differences in air (top) and soil (bottom) temperature (°C) of the two canopy manipulation treatment plots and the hardwood control plots relative to the hemlock control plots, in the Valley (left) and Ridge (right) blocks, 2005–2009. Colors are as in Fig. 3. Solid lines are the monthly temperature deviations and dashed lines are linear trends estimated using STL decomposition. Green arrows indicate the completion of the logging and girdling treatments in early 2005.

in 2009 (Fig. 3). Overall, the girdled plots suffered more damage from the ice storm because the standing boles were already structurally unsound; data collection is underway to test this hypothesis (Ellison and Barker Plotkin 2009).

Air and soil temperature are very sensitive to changes in canopy cover; even small disturbed patches can have an increased temperature and a more variable microclimate (Mladenoff 1987, Chen et al. 1999). Adelgid infestation has been predicted to lead to an increase in soil temperature (Jenkins et al. 1999), and Orwig et al. (2008) found a strong correlation between soil temperature and the thinning of hemlock crowns. Our findings are consistent with these patterns, but

also highlight changes in variance and seasonal variability. For example, air and soil temperature differences between treatments and controls were greatest in summer, when the amount of solar radiation is highest. The amplitude of the seasonal pattern was greater in the more exposed logged plots and plots on the Ridge. The small peak in the saw-tooth pattern we observed in both the logged and the girdled plots (Fig. 5) occurred before the start of the growing season and we hypothesize that it is caused by the insulating hemlock canopy preventing snow from melting. Differences in air and soil temperatures between hardwood and hemlock controls also were greatest at this time. Although air and
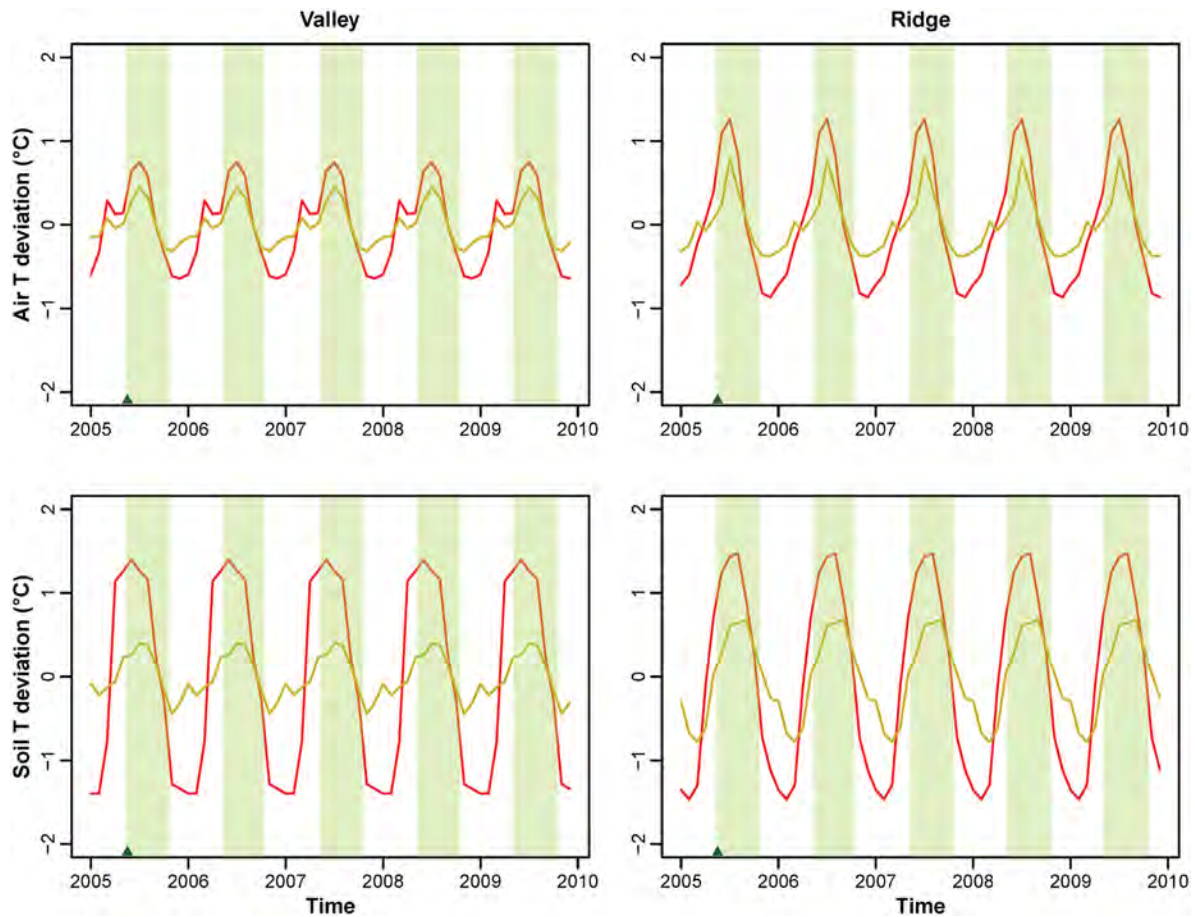
Fig. 5. Seasonal patterns, after detrending, in the deviation in air (top) and soil (bottom) temperatures (°C) of the two canopy manipulation treatment plots and the hardwood control plots relative to the hemlock control plots in the Valley (left) and Ridge (right) blocks, estimated using STL decomposition. Colors are as in Fig. 3. Green arrows indicate the completion of the logging and girdling treatments in early 2005. Shaded areas indicate the growing season: the period from 50% bud-break to 50% leaf-fall in each year.

soil temperature showed very similar patterns in mean monthly temperatures, only air temperature showed a large increase in monthly variance compared to the hemlock controls (Fig. 6), most likely due to the greater thermal inertia of the soil.

Although soil moisture tends to be relatively high beneath hemlock canopies because of hemlock's relatively constant but low transpiration rate, we expected that soil moisture levels would initially increase as hemlock dies and forest transpiration declines. Subsequently, soil moisture should decrease beyond initial conditions as hemlocks are replaced by deciduous species that transpire approximately twice as much water as hemlock (Catovsky et al. 2002, Hadley et al. 2008). Our results supported this hypothesis. Soil in the logged and girdled plots was consistently moister than in the hemlock controls (Fig. 7). Five years after the canopy manipulations, decreased evaporation due to hemlock loss still has a greater impact on soil moisture at our site than does increased evapotranspiration by new hardwood trees; similarly, Jenkins et al. (1999) and Orwig et al. (2008) found no difference in soil moisture between infested and non-infested stands. However, Kizlinski et al. (2002) found that much older, logged and adelgid-infested sites were dryer than recent harvest or undamaged sites. We note that our
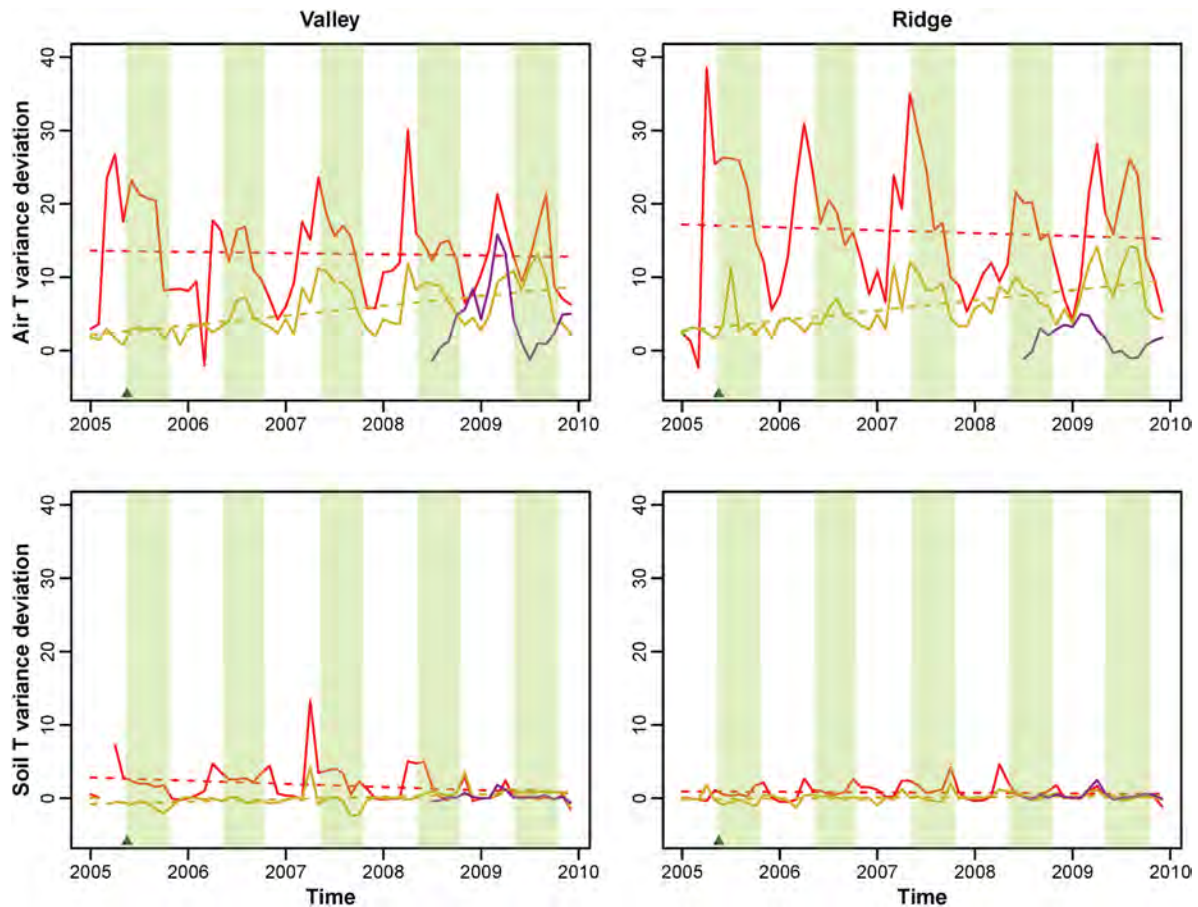
Fig. 6. Monthly variance in air (top) and soil (bottom) temperature of the two canopy manipulation treatment plots and the hardwood control plots relative to hemlock control plots in the Valley (left) and Ridge (right) blocks, 2005–2009. Solid lines are the monthly deviations and dashed lines are linear trends estimated using STL decomposition. Colors are as in Fig. 3, symbols and shading are as in Fig. 5.

soil moisture data were collected only during the summer months, and do not present a complete picture of changes in this important variable. Continued monitoring of the HF-HeRE plots, extension of data collection into other parts of the year, and linkages with available precipitation data at weather stations within 10 km (Boose 2001) all will allow us to better test our hypothesis that soil moisture levels should eventually decrease below initial levels under intact hemlock stands.

Overall, we observed a rapid change in microclimate in the logged plots and a slower change in the girdled plots, but over time the two treatments have converged in their responses. Although we had fewer data from the hardwood control plots, the microclimate of the hardwood plots appears to be intermediate between the canopy treatments and the hemlock controls. Continued monitoring of these experimental plots will reveal whether the logged and girdled plots will diverge again in the future, whether they will become more similar to the hardwood controls, and how these changes will impact biological diversity and ecosystem processes in these changing forests. As the spread of the adelgid continues (Fitzpatrick et al. 2012), it is necessary to make as complete an assessment as possible of the effect of the decline of eastern hemlock—our canonical foundation tree species—on forest ecosystems in eastern North America (Albani et al. 2010).
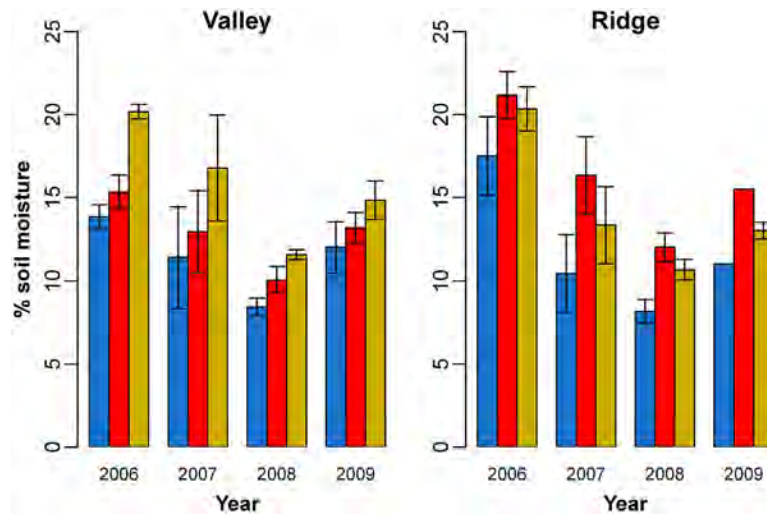
Fig. 7. Percent soil moisture of the logged, girdled and hemlock control plots in the Valley (left) and Ridge (right) blocks, 2006–2009. Plotted are means of June, July and August of each year ±1 SD. Colors are as in Fig. 3.

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Supplemental Material

Appendix

Procedure for Filtering the Temperature Data

The air and soil temperature data were filtered for clear outliers that seemed to be caused by data-logger errors. The filtering procedure was carried out using R (R Development Core Team 2011); the R script along with the raw and filtered data files are available from the Harvard Forest LTER data archive, dataset HF-108 (Ellison 2005*a*). The raw dataset consists of hourly mean, maximum, and minimum air and soil temperatures in each of the eight plots. The difference between the maximum and minimum value of every hour was used as a method to detect outliers (Fig. A1). This difference was not allowed to be greater than a reasonable cutoff value or to be negative (see the R script for the exact cutoff values for each variable). All questionable data points detected by this filter were replaced with NAs.

An unusual amount of outliers was detected in the air and soil temperature data for the hemlock control, logged and girdled plots in the Ridge block in the winter of 2007/2008 (Fig. A2, top). Because the three plots share a data logger, this anomaly was most likely caused by data-logger failure. An additional, more thorough, filter was therefore applied to these data. Because of the nature of the data, different filters were applied to the air temperature and mineral-soil temperature data.

The filtering procedure for the mineral-soil temperature data was as follows (Fig. A3). First, the filter of (maximum minus minimum) values was repeated, but with a stricter cutoff value of 0.6°C. Next, values were filtered out that were too different from values in the corresponding plot in the Valley block (comparing the Ridge logged plot with the Valley logged plot, etc.). If the data point of the Valley plot was missing, the data point of the corresponding Ridge plot was kept. Finally, an extra filter was applied to the period between week 48 of 2007 and week 13 of 2008. Overall the temperatures were very constant with a low variance at this interval, but the mineral-soil temperature data from the hemlock control, logged and girdled plots on the Ridge contained many outliers in this period. The filtered data from winter 2007–2008 were then inserted into the main dataset (Fig. A2, bottom). The filtering procedure for the air temperature data was similar to the procedure for the mineral-soil temperature data. The cutoff values for the (maximum minus minimum) filter were between 2 and 5°C (the R script contains the cutoff values of all filters). No additional filter between week 48 of 2007 and week 13 of 2008 was applied to the air temperature data.
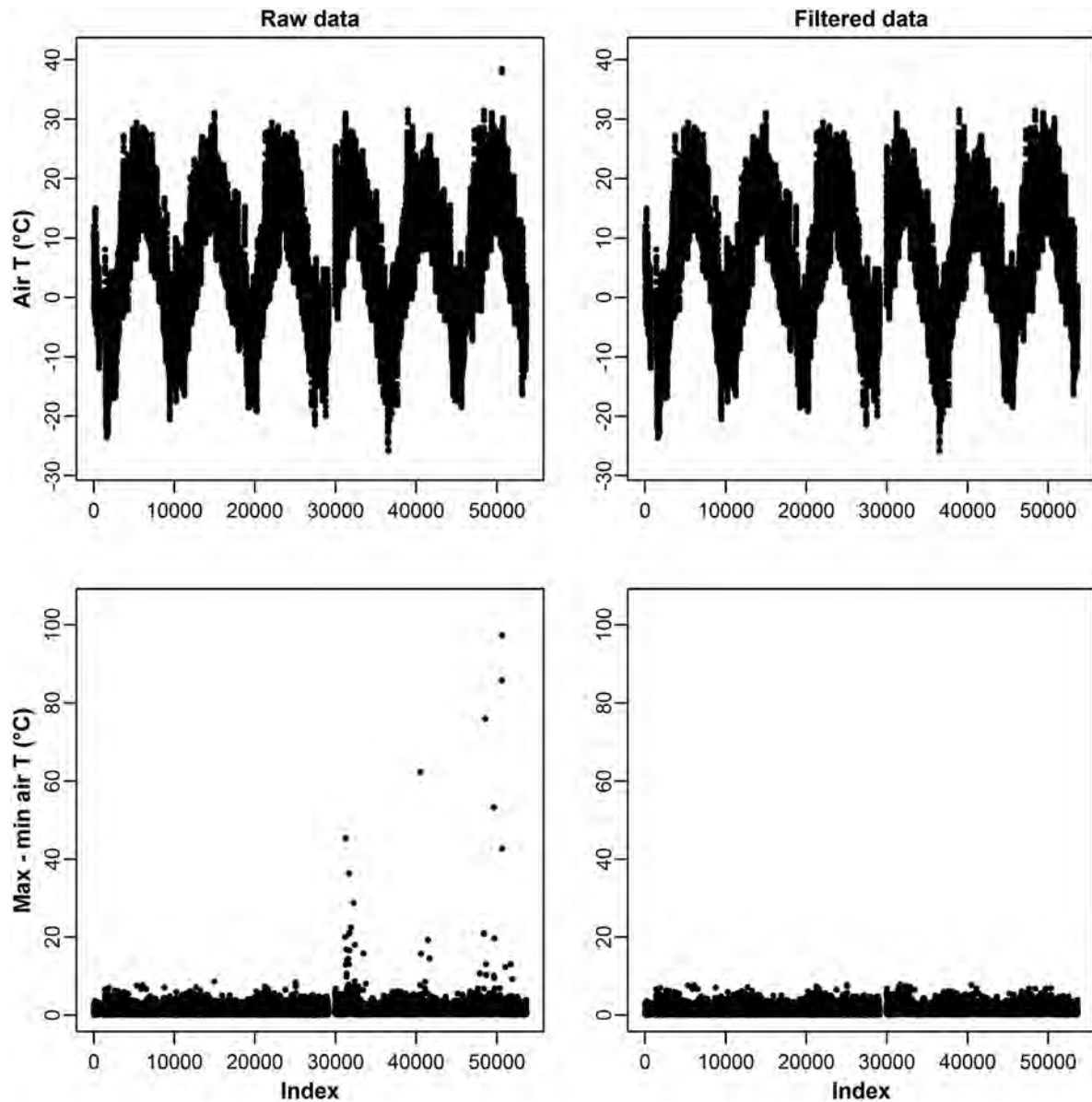
Fig. A1. An illustration of the main filtering method (here: air temperature data [°C] from the hemlock control plot in the Valley). Outliers in mean hourly temperatures (top) were detected by setting a cutoff value for the difference between the maximum and minimum temperature of every hour (bottom). Raw data are plotted on the left, filtered data on the right. The time frame illustrated here (16 November 2004 to 31 December 2010) is slightly longer than the time frame of the data we analyzed (1 January 2005–31 December 2009). The values on the x-axis are hours since 16 November 2004.
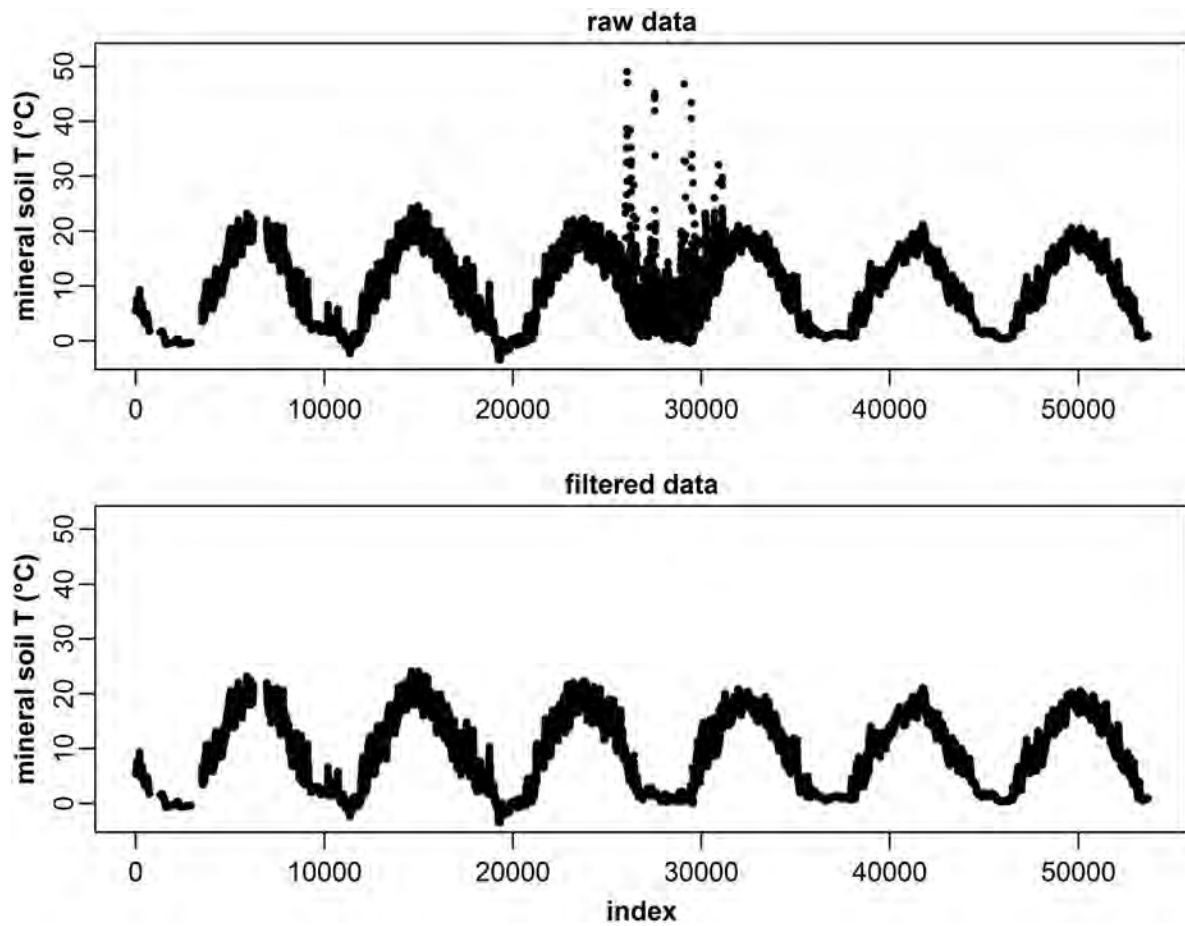
Fig. A2. Mineral-soil temperature data (°C) from the logged plot on the Ridge, before and after filtering. This plot, along with the hemlock control and girdled plots on the Ridge, contained an unusual amount of outliers in the winter of 2007–2008 that were probably due to data-logger errors. Additional filters were therefore applied. The time frame shown is from 16 November 2004 to 31 December 2010. The values on the *x*-axis are hours since 16 November 2004.
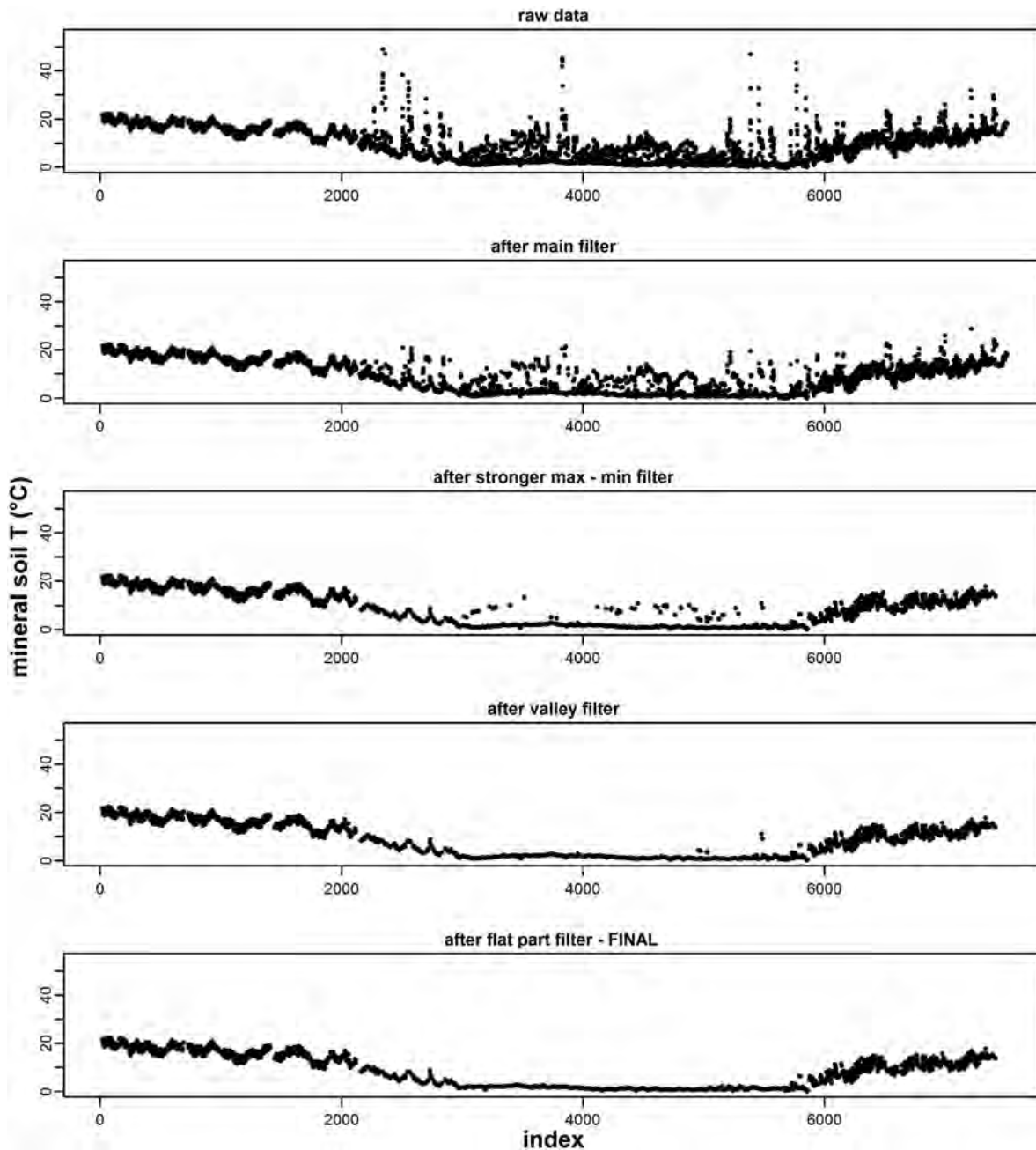
Fig. A3. An illustration of the additional filtering procedure that was applied to the mineral-soil temperature data (°C) from the logged, girdled, and hemlock control plots on the Ridge. The time frame of the figure is 1 August 2007 to 8 June 2008. The following filters were applied successively from top to bottom: the (maximum–minimum) filter, the same filter with a lower cutoff value, a filter that compared the data from the plot to the corresponding Valley plot, and a filter that was specified for the flattest part of the curve. The air temperature data from these plots were filtered in almost the same way, using different cutoff values and excluding the last step. The values on the x-axis are hours since 1 August 2007.