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Climatic conditions for emergence and flight of mountain pine beetle:
implications for long-distance dispersal

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Abstract: A significant shift in the mountain pine beetle range has been attributed to long-distance dispersal from the observed spatiotemporal patterns of beetle infestations in the recent outbreak in Western Canada. However, long-distance dispersal is still the least understood aspect of mountain pine beetle ecology. In particular, the mechanisms responsible for the three major phases of long-distance dispersal, the ascent, transport, and descent, are poorly known. In this study we used the North American Regional Reanalysis (NARR) meteorological data (1999 – 2010) to determine climate conditions under and above the forest canopy during mountain pine beetle emergence and flight at the landscape scale. We found that climate conditions are distinct during emergence and flight. They provide an ideal underlying environment to facilitate the potential long-distance dispersal. Climate conditions are unstable under the forest canopy during emergence, which would help loft beetles above the forest canopy to initiate long-distance dispersal. The first direct evidence from wind directions above the forest canopy suggests that atmospheric transportation of mountain pine beetle in the Planetary Boundary Layer (PBL) is aided by wind.

Key words: climate conditions, emergence, long-distance dispersal, mountain pine beetle, outbreak, planetary boundary layer

39 Introduction

40 Mountain pine beetle is a native disturbance agent in the pine forests of western North
41 America (Safranyik and Carroll 2006; Negron and Fettig 2014). The recent outbreak in British
42 Columbia is unprecedented in recorded history and started in the late 1990s (Aukema et al. 2006;
43 Chen 2014). It has rapidly spread northeastward and surpassed the mountain pine beetle
44 geoclimatic barrier of the northern Rocky Mountains (Robertson et al. 2009; de la Giroday et al.
45 2012; Chen 2014), successfully invading the jack pine forests in northern Alberta (Cullingham et
46 al. 2011). Such a significant shift in the mountain pine beetle range has been attributed to long-
47 distance dispersal from the observed spatiotemporal patterns of beetle infestations (Robertson et
48 al. 2009; de la Giroday et al. 2012; Chen 2014), which was recently confirmed in a genetic study
49 of beetle infestations (Samarasekera et al. 2012).

50 Dispersal is required for adult beetles to locate new hosts to produce broods (Safranyik and
51 Carroll 2006). It is an important driver of beetle population dynamics at local and regional scales
52 and plays a critical role in generating spatial synchrony and in facilitating shifts of population to
53 epidemic levels (Liebhold et al. 2004; Aukema et al. 2008; Raffa et al. 2008). Two modes of
54 dispersal have been identified in mountain pine beetle: short-distance dispersal and long-distance
55 dispersal (Safranyik et al. 1992; Safranyik and Carroll 2006; Robertson et al. 2007). The former
56 is most likely driven by pheromones after the initial flight exercise of beetles (Safranyik and
57 Carroll 2006; Safranyik et al. 2010; Lundquist and Reich 2014) and usually occurs within 50 –
58 100 m of the emergent tree under the forest canopy (Robertson et al. 2007), while the later is a
59 wind-driven event and occurs within the Planetary Boundary Layer (PBL; the zone in which the
60 earth's surface has a direct effect on the atmosphere) above the forest canopy over longer
61 distances (Murphy et al. 2004; Jackson et al. 2008). In contrast to short-distance dispersal, which

has received considerable attention (Gray et al. 1972; Safranyik et al. 1989, 1992; Robertson et al. 2007; Evenden et al. 2014), long-distance dispersal is the least understood dispersal mode in mountain pine beetle ecology. Specifically, little is known about the mechanisms responsible for the three major phases of long-distance dispersal: the ascent, transport, and descent (Gatehouse 1997; Murphy et al. 2004; Jackson et al. 2008; Bauer et al. 2011).

Mountain pine beetles have been directly observed to fly several hundred meters above the forest canopy during the recent outbreak using radar observation and aerial capture in British Columbia. Beetles may travel 30 – 110 km day⁻¹ and are likely to be congregated in sufficient numbers over the course of long-distance dispersal to cause epidemic infestations when beetles land in a new remote area (Jackson et al. 2008; Ainslie and Jackson 2011). A genetic study also confirmed that mountain pine beetles in northern Alberta were mainly from northern British Columbia, most likely travelling there by long-distance dispersal (Samarasekera et al. 2012).

Emergence is a key stage of the mountain pine beetle life-cycle (Safranyik and Carroll 2006). Mountain pine beetle emergence is strictly temperature dependent (Logan and Bentz 1999; Logan and Powell 2001). Weather conditions during, and immediately following emergence have a critical influence on dispersal after beetle emergence, particularly long-distance dispersal (Gatehouse 1997; Reynolds et al. 2005; Bauer et al. 2011; Chapman et al. 2015). Murphy et al. (2004) determined synoptic climate conditions during the emergence and flight of mountain pine beetle in British Columbia. They found that, in addition to increased air temperature, the peak emergence is generally associated with increasing 500 hPa geopotential height, decreasing mean sea level pressure, relative instability in the lower atmosphere, and lower relative humidity. In the long-distance dispersal cases documented by Jackson et al. (2008), the PBL in which beetles

84 are transported was well-mixed and convective. The PBL depth ranged from 997 to 1179 m
85 above sea level.

86 Considering the size and flying speed (0.43-0.54 m/s, Evenden et al. 2014) of mountain pine
87 beetle in comparison with the wind speed above the forest canopy reported in this study (above 2
88 m/s on average - Figs S1 and S2), its movement in the PBL above the forest canopy may be
89 entirely passive and directly controlled by the wind as reported for other insects (Gatehouse 1997;
90 Reynolds et al. 2005; Bauer et al. 2011; Chapman et al. 2015). It is believed that, during clear
91 days usually associated with emergence (particularly the peak emergence), the PBL becomes
92 convective as the surface is rapidly warmed by solar radiation, leading to convective thermals
93 that may aid carrying beetles into the PBL where they can be transported by the wind (Gatehouse
94 1997; Reynolds et al. 2005; Jackson et al. 2008). Although previous studies (Murphy et al. 2004;
95 Jackson et al. 2008) have identified synoptic climate conditions during the emergence and flight
96 of mountain pine beetle, these studies were only conducted in one location and mainly focused
97 on climate conditions above the forest canopy.

98 Mountain pine beetle emergence varies in time and space (Safranyik and Carroll 2006). We
99 have demonstrated that a heating cycle defined and determined by an ambient temperature time
100 series represents a reliable window of potential beetle emergence (Chen and Jackson 2015) and
101 proposed a heating cycle approach to map potential beetle emergence spatially and temporally at
102 the landscape scale (Chen et al. 2015). In the present study, we determine climate conditions
103 both under and above the forest canopy during the mountain pine beetle emergence at the
104 landscape scale, addressing the following research questions: (1) What are the climate conditions
105 during emergence? (2) Do climate conditions during emergence favor potential long-distance
106 dispersal? (3) Do climate conditions change through the emergence peak (before, during, and

after) and period cycle (emergence, periods immediately before and after emergence, and periods between emergences)? (4) Are there distinct climate conditions during emergence favoring potential long-distance dispersal for the phases of the ascent and descent? (5) Do wind directions during emergence support potential movements of beetles during long-distance dispersal? The answers to these questions will provide insights to understand the key mechanisms of mountain pine beetle long-distance dispersal.

Materials and methods

Study area and data

The study area (Fig. 1) only encompasses mature pine areas (i.e., forest stands with pine older than 60 years) in the whole province of British Columbia, which were delineated based on the provincial forest inventory data compiled from the British Columbia Land Resource Data Warehouse (LRDW).

The North American Regional Reanalysis (NARR) meteorological datasets for the two summer months in which mountain pine beetle emerge (July and August) (Safranyik and Carroll 2006; Chen et al. 2015) over the period of 1999–2010, were first downscaled into a grid of 658,399 cells (1200×1200 m) that cover the whole province and used to derive climate variables both under and above the forest canopy. NARR is a long-term, consistent, high resolution (32 km horizontal) and frequency (8 times daily data) 3-dimensional meteorological dataset for the North American domain, covering the period from 1979 to present (Mesinger et al. 2006). The temperature was downscaled using the elevation-based approach (Chen and Jackson 2015) and other variables using bilinear interpolation. A heating cycle was defined as a temporal

window of at least three consecutive days with the maximum daily temperatures between 24 °C and 30 °C (Chen and Jackson 2015; Chen et al. 2015) and represents a period of potential mountain pine beetle emergence. The time window surrounding a heating cycle called a non-heating cycle was defined as three days before (called head) and after (called tail) a heating cycle. The gap time window represents the part of time series between the tail of one heating cycle and the head of the next (Fig. 1). Potential mountain pine beetle emergence was determined spatially and temporally using the heating cycle approach. For each mature pine cell (a total of 353, 920), climate variables were derived over three windows of time series (potential mountain pine beetle emergence, non-heating cycle, and gap) and at three times of a day (11 am, 2 pm, and 5 pm local pacific daylight time, PDT) (Fig. 1).

Climate conditions under the forest canopy are represented by seven NARR mono-level variables, which correspond to climate conditions at or near the ground (Table 1). Climate conditions above the forest canopy are represented by six NARR multi-level variables interpolated to about 400 m above the terrain (Table 1), an average elevation at which beetles undergoing long-distance dispersal were found by aerial capture (Jackson et al. 2008). The NARR multi-level variables are measured at 29 atmospheric pressure levels (1000 to 100 hPa; 1000 hPa is the approximate pressure at sea level and since pressure decreases with altitude, 100 hPa is at about 16 km above sea level). However, only 13 (1000 to 700 hPa) of the 29 pressure levels were used to derive climate variables above the canopy because they are sufficient to cover the target height of 400 m above the terrain. Climate variables above the canopy were produced with a linear interpolation approach using the NARR geopotential height of each pressure level (Fig. 2). Since consistent trends were observed for climate variables over the three windows of time series at the three times of a day (Figs S1 and S2), only climate variables

derived at 2 pm PDT were used in the analysis of this study because most emergences occur around this time of a day (Reid 1962; Carroll and Safranyik 2004; Jackson et al. 2008).

Data and statistical analysis

Wind direction and speed are determined from the U (west-east) and V (south-north) wind components at 10 m above the ground for the mono-level NARR data and at about 400 m above the terrain for multi-level NARR data. The wind direction in the present paper is the wind vector azimuth (i.e., the direction towards which the wind is blowing), not the meteorological wind direction (i.e., the direction from which the wind is blowing). The NARR multi-level wind speed data for the year 2004 are not used in the analysis due to the erroneous presence of extremely large values in the data.

Canonical discriminant analyses (CDAs) were used to distinguish climate conditions between heating cycles and non-emergence period (i.e., heads and tails of non-heating cycles, and gap, Fig. 1) by including and excluding the variable temperature in the analysis, because the heating cycle is defined based on the temperature. CDAs were also used to distinguish climate conditions over heating cycles between long-distance dispersal types, sink and source, for the whole province and for the target long-distance dispersal areas. The long-distance dispersal type of a cell of the working grid was determined based on the infestation dynamics conceptual model (Chen 2014) in which sink refers to new infestation cells while source to old infestation cells. Beetles fly to a sink from a source via long-distance dispersal. In this study, the four target long-distance dispersal areas identified in four specific years (2002, 2003, 2006, and 2008) were used in the analysis (Fig. 8). They represent the areas where the significant expansion movements of infestations via long-distance dispersal were clearly revealed from the spatiotemporal pattern

analysis of mountain pine beetle outbreaks (Chen 2014). For target long-distance dispersal areas, sinks and sources were determined based on core areas of morphological spatial pattern analysis of beetle infestations (Chen 2014). Sink cells were first determined and a buffer of 100 kilometers was then applied to sink cells to locate surrounding source cells. We assume that the landscape long-distance dispersal type, source, is associated with the ascent phase of mountain pine beetle long-distance dispersal while sink is associated with the descent phase.

To get a general picture of climate conditions over heating cycles, anomaly maps of climate variables were produced by subtracting average values of climate variables over heating cycles from average values over all days of the two summer months (July and August). We also produced standard deviation maps of climate variables over heating cycles. To examine trends in climate conditions throughout the peaks of emergence, moving averages of climate variables were first determined over all days of the two summer months using a window size of 7 days representing an average length of mountain pine beetle peak emergence from a field study (Bentz 2006). Time-lag cross-correlations were calculated between moving averages of climate variables and frequency distributions of heating cycles across the whole province, which were determined using an area-based approach (Chen et al. 2015).

CDAs were conducted with the R packages “candisc” v.0.7-2 (Friendly and Fox 2016) and “DiscriMiner” v.0.1-29 (Sanchez and Determan 2013), while the time-lag cross-correlation was calculated with the base module cross correlation function in R v.3.2.2 (R Development Core Team 2012).

Results

What are the climate conditions during emergence?

Climate conditions both under and above the forest canopy during emergence (i.e., during heating cycles) are distinct and can be differentiated from non-heating cycles and gap conditions (Fig. 3). Temperature is the most important factor among climate variables both under and above the canopy. Other important climate variables include relative and specific humidity and best 4 layer lifted index under the canopy, and 500 hPa geopotential height, specific humidity, and wind speed above the canopy (Fig. 3). Climate conditions under the canopy during emergence are characterized by increased temperature, mean sea level pressure, and specific humidity, and decreased precipitation, best 4 layer lifted index, relative humidity, and wind speed (Fig. 4, Figs S3 and S4). Climate conditions above the canopy during emergence are characterized by increased temperature, specific humidity, and 500 hPa geopotential height, and decreased vertical velocity, turbulent kinetic energy, and wind speed (Fig. 5, Figs S3 and S4).

Do climate conditions during emergence favor potential long-distance dispersal?

The lower best 4 layer lifted index during emergence indicates increased atmospheric instability under the canopy (Fig. 4, Figs S3 and S4). Decreased vertical velocity (in pressure coordinates where negative values indicate upward motion), which on average remained below zero for most of the years during emergence (Fig. S4), also indicates ascending air movement above the canopy during emergence.

Do climate conditions change through the emergence peak (before, during, and after) and period cycle (emergence, periods immediately before and after emergence, and periods between emergences)?

Climate conditions change through emergence peaks with consistent trends (Fig. 6). For climate variables under the canopy, temperatures start to increase before the emergence peak, reach the highest point during peak emergence, and then drop after the peak. This trend is

expected, since the heating cycles are defined using temperature. The same trend is observed for specific humidity. Mean sea level pressure increases before the emergence period and drops throughout peak and afterwards. In contrast, total precipitation, best 4 layer lifted index, relative humidity, and wind speed start to decrease before peak emergence, reach the lowest point during peak emergence, and then increase after the emergence peak. The trend in relative humidity is also expected, given its inverse relationship with temperature and the fact that temperature is used to define the heating cycles. Similar trends in climate conditions are also clearly observed throughout the emergence period (Figs S5 and S6).

Similarly, for climate variables above the canopy, temperature, specific humidity, and 500 hPa geopotential height shows the same trends in climate conditions, starting to increase before the emergence peak, reaching the highest point during peak emergence, and dropping significantly after the peak, while wind speed starts to decrease before peak emergence, drop to the lowest point during the peak, and increase after the emergence peak (Fig. 6). For vertical velocity and turbulent kinetic energy, the cross correlation function plots show a little different picture. Higher vertical velocity (i.e. downward motion) is significantly associated with emergence peaks and the period after emergence peaks, and lower vertical velocity is significantly associated with the period before emergence peaks. Although higher turbulent kinetic energy is associated with emergence peaks and the period before emergence peaks, this is not statistically significant. The temporal trends throughout the emergence period for vertical velocity and turbulent kinetic energy are not as distinct as for the other variables in which similar trends are observed as described above (Figs S5 and S6).

Are there distinct climate conditions during emergence favoring the potential long-distance dispersal for the phases of the ascent and descent?

At the provincial level, there is little difference in climate conditions both under and above the canopy between the phases of ascent (source) and descent (sink) during emergence (Fig. 7). However, for the target long-distance dispersal areas in 2003 and 2006, there are distinct differences in climate conditions under and above the canopy between sink and source (Figs S7b, c and S8b, c). For climate variables under the canopy, source areas have lower best 4 layer lifted index (i.e. a more unstable atmosphere) relative to sink areas for 2003 and 2006 (Figs S9c, S10c, S11c, and S12c). For climate variables above the canopy, source areas have higher vertical velocity (i.e. more downward motion) and turbulent kinetic energy compared to sink areas for the 2003 (Figs. S9i, k and S10i, k), while for the 2006 target long-distance dispersal area, the reverse trends were observed for these two variables between sink and source (Figs. S11i, k and S12i, k).

Do wind directions during emergence support potential movements of beetles during long-distance dispersal?

For the target long-distance dispersal areas, main wind directions above the canopy are consistent with the directions of detected long-distance dispersals (i.e., from source to sink) (Fig. 8). This consistency is supported by yearly changes of wind directions relative to the target year for the target long-distance dispersal areas (Figs S13 – S16).

Discussion

Long-distance dispersal above the forest canopy aided by wind in the PBL has been demonstrated in mountain pine beetle (Jackson et al. 2008) and other insects (Mazzi and Dorn 2012; Sturtevant et al. 2013; Chapman et al. 2015). This study is the first to describe climate conditions both under and above the forest canopy during the period of mountain pine beetle

emergence and flight spatially and temporally at the landscape scale in British Columbia. The canonical discriminant analysis (Fig. 3) and anomaly maps (Figs 4 and 5) clearly reveal that climate conditions both under and above the forest canopy are distinct during the period of beetle emergence and flight, which can be effectively differentiated from the conditions during non-emergence period (Fig. 3). The characteristics of climate variables under and above the forest canopy generally indicate warmer, more humid (but further from saturation), fair, and less windy but unstable weather conditions during emergence.

Distinct weather conditions during emergence demonstrated in this study is consistent with the synoptic climate of the region reported by Murphy et al. (2004). We observed a drop in mean sea level pressure during emergence (Figs S5 and S6) and the emergence peak (Fig. 6d) in this study, which was also reported by Murphy et al. (2004) and Jackson et al. (2008). This relatively increased mean sea level pressure and 500 hPa geopotential height a few days before the emergence peak (Fig. 6d and m) suggest the movement of an anticyclone (high pressure weather system) through the region just before emergence. Anticyclones are associated with fair weather and often have weak pressure gradients and winds. Murphy et al. (2004) even implied that the drop in mean sea level pressure, for example after passage of an anticyclone, could be another possible trigger like temperature to initiate emergence.

Distinct weather conditions during emergence would facilitate long-distance dispersal. Significant decreases in the best 4 layer lifted index during emergence relative to the non-emergence period (Figs S3 and S4), emergence peaks (Fig. 6), and average climate conditions over the study period (Fig. 4) all suggest increasingly unstable climate conditions developed near the surface during emergence, which will help the lofting of beetles above the forest canopy to initiate long-distance dispersal events. Many insects have developed specialized behavior

288 permitting them to ascend into the faster-moving airstream aloft (Thomas et al. 2003; Parry 2013;
289 Chapman et al. 2015). It is not clear if there is any behavioural factor involved in the ascent
290 phase of mountain pine beetle long-distance dispersal or if the take-off of beetles just passively
291 occurs by chance due to unstable climate conditions. Some studies (Amman 1988; Schmitz et al.
292 1989) implied that beetles may follow pheromone plumes lifted by convective updrafts and are
293 thereby drawn into the PBL above the forest canopy. Furthermore, wind speed both under and
294 above the forest canopy decreased during emergence (Figs S3 and S4) and emergence peak (Fig.
295 6), which is consistent with weaker pressure gradients causing lighter winds near an anticyclone.
296 Lighter winds will allow a more unstable atmosphere to develop near the surface. They may also
297 help congregation of small insects like mountain pine beetle in the PBL during their long-
298 distance transportation (Geerts and Miao 2005).

299 This study clearly suggests that the emergence and flight of mountain pine beetle are
300 associated with distinct climate conditions that are beneficial to initiate long-distance dispersal.
301 Long-distance dispersal would be much more likely to occur when beetle populations reach
302 epidemic levels due to local depletion of host resources (Safranyik and Carroll 2006). Jackson et
303 al. (2008) demonstrated that mountain pine beetles can fly long distances in the PBL above the
304 forest canopy. The present study provides the first direct evidence from the distribution of wind
305 directions above the forest canopy (Fig. 8), which not only supports significant expansion of the
306 recent outbreak via long-distance dispersal but also the widely held notion that atmospheric
307 transport of mountain pine beetle, like most other small insects, is aided by wind. This evidence
308 also suggests that mountain pine beetle may passively follow the mean wind during transport
309 without necessarily actively adjusting the direction of flight as observed in some large insects
310 (Chapman et al. 2015) although Jackson et al. (2008) suggested that behavioral factors may be

involved in reducing the height of the beetle flight when air temperature becomes too cold. Furthermore, the landscape wind directions above the canopy in this study revealed that wind generally blows toward the northeast at the provincial scale (Fig. S17). This is consistent with the observed pattern of mountain pine beetle spread and expansion toward the northeast (Aukema et al. 2006; Chen 2014), indicating that long-distance dispersal would be more likely to play an important role in the spread and expansion of the recent mountain beetle outbreak at the landscape scale.

Mixed results in climate conditions above the forest canopy during emergence conflict with the assumption of facilitating potential long-distance dispersal that significant ascending air movement indicated by more negative vertical velocity values and more turbulent convection indicated by larger turbulent kinetic energy should be expected above the forest canopy during emergence relative to the non-emergence period. Quite large areas in red color shown on the anomaly map of vertical velocity (Fig. 5b) imply descending air movement even though such movement is weaker during emergence compared to the whole study period. Furthermore, increased vertical velocity (downward motion) is associated with emergence peaks in the cross correlation function plot although drop in vertical velocity was observed before the emergence peaks (Fig. 6i). During emergence when atmospheric conditions above the forest canopy are convective due to observed increased temperature and clear weather, there are lots of updrafts and downdrafts at much finer scales. The NARR space/time average value of vertical velocity derived at coarse scales mostly results from the deflection of horizontal wind by topography and does not likely represent vertical velocity at finer scales arising from thermals in an unstable atmosphere, which is more relevant to the ascent process of beetle long-distance dispersal. This may explain the inconsistency observed in the patterns of vertical velocity. Turbulent kinetic

energy is related to both instability (negative lifted index) and wind speed. Decreased turbulent kinetic energy shown in large areas of the province on the anomaly map (Fig. 5d) likely results from decreased wind speeds observed during emergence.

For climate variables both under and above the forest canopy, no distinct climate condition could be statistically identified between sink and source during emergence (Fig. 7). This may be in part due to the coarse scale (32 km) of the NARR data used to derive climate variables relative to the scale at which beetles emerge from a source area and descend to a sink area.

Conclusion

Climate conditions under and above the forest canopy are distinct during mountain pine beetle emergence and flight compared with at other times during the summer. In addition to warmer temperatures during emergence and flight, the atmosphere is characterized by: higher specific humidity but lower relative humidity; less rain; lighter wind speeds; higher mean sea level pressure before the emergence; higher 500 hPa geopotential heights; and a more unstable lower atmosphere based on the best 4-layer lifted index. These conditions are consistent with the building up and passage of an anticyclone prior to- and during emergence periods. These conditions would facilitate the potential long-distance dispersal. In particular, more unstable atmospheric conditions in the lower atmosphere during the emergence period would help loft beetles into the PBL where they can be dispersed over long distances by the wind. Climate conditions evolve and change throughout the emergence period and peak. The observed decreasing mean sea level pressure and increased 500 hPa geopotential height during the emergence may be considered potential triggers like temperature to initiate beetle emergence.

The first direct evidence from wind directions above the forest canopy during emergence suggests that atmospheric transport of mountain pine beetle in the PBL is aided by wind. Mountain pine beetle may not need to adjust the flight direction by involving any behavioural factor.

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Table 1. Description of the NARR climate variables used in the study.

Climate variables	Description
Under the forest canopy: NARR mono-level variables (mostly at or near ground level within the canopy)	
Temperature	Air temperature at 2m above the ground and measured in kelvin (K).
Accumulated total precipitation	Total precipitation accumulated over a three hour period, including all types of precipitation from frontal activity, convection, orographic effects, and snow. It is measured in kilograms per meter squared (kg/m ²).
Best 4 layer lifted index	It measures the atmospheric instability within the canopy and planetary boundary layer. The lifted index is the difference between the temperature at 500 hPa and the temperature of a parcel lifted from within 180 hPa of the surface to 500 hPa. The most unstable lifted index of four layers within 180 hPa of the surface is used as the best lifted index, which is especially useful when the surface lifted index may not indicate the true instability (eg., during the morning). It is measured in kelvins (K). Its values can be used to explain the instability using the criteria: 6 or greater: very stable; 1 to 6: stable; 0 to -2: slightly unstable; -2 to -6: unstable; -6 and less: very unstable.
Mean sea level pressure	The atmospheric pressure extrapolated from the surface to sea level. It ensures that local geographic altitude does not affect atmospheric pressure readings since pressure values decrease with increasing altitude. It is measured in pascals (Pa).
Relative humidity	It is the ratio of moisture in the air compared to the amount of moisture in a saturated parcel of air at a specific temperature. The value is at 2m above the ground. It has no units and is measured in a percentage. Large values indicate air that is close to saturation.

Specific humidity	It is a humidity value at 2m above the ground. It is the ratio of the mass of water vapor relative to the total mass of a volume of air, expressed in units of kilogram kg(water)/kg(air).
Wind vector components (U and V)	Wind vector components are at 10m above the ground and are the wind components used to calculate the wind speed and direction. Positive U represents the wind component blowing towards the east while positive V indicates the wind component blowing towards the north. Wind vector components are measured in meters per second (m/s).
Above the forest canopy: NARR multi-level variables (pressure levels 1000 to 700 hPa) interpolated to about 400 m above the terrain	
Temperature	Air temperature taken at multiple pressure levels (100 – 1000 hPa) and measured in kelvin (K).
Vertical velocity (Omega)	It is the vertical velocity when pressure is the vertical dimension. It is measured as a change in pressure with time. Negative values indicate ascending air while positive values denote sinking air. It is measured in pascals per second (Pa/s).
Specific humidity	It is the same as the mono-level variable above and is measured at multiple pressure levels.
Turbulent kinetic energy	It is the mean kinetic energy per unit mass and represents the strength of the turbulence in the flow. It is strongly related to the wind shear and measured in joules per kilogram (J/kg).
Wind vector components (U and V)	It is the same as the mono-level variable above and measured at multiple pressure levels.
Geopotential height	It is the height of a pressure surface above mean sea-level. Low geopotential height indicates the presence of a storm or trough at mid-troposphere levels while high geopotential height indicates a ridge, and quiescent weather.

Over the time, decreasing geopotential height usually indicates an approaching or intensifying storm while increasing geopotential height suggests clearing weather for the period. It is measured in meters.

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Fig. 1. The study area and the approach to derive climate variables at three times of a day (UTC: Universal Time Coordinated; PDT: local Pacific Daylight Time) based on heating cycles. A heating cycle is a temporal window of at least three consecutive days with the maximum daily temperatures between 24 °C and 30 °C. Heads and tails of non-heating cycles refer to three days before and after heating cycles, respectively. The gap represents a temporal window between the tail of one heating and the head of the next. The cells in light green represent mature pine stands compiled from the provincial forest inventory data. For the better visualization, a larger size (approximately 12×12 km) of a cell was used on the map rather than the actual size of the working grid cell (1200×1200 m).

Fig. 2. The linear interpolation approach to derive climate variables above the forest canopy (i.e., 400 m above the terrain) using the NARR multi-level variables at 13 pressure levels (1000 – 700 hPa). E_w represents the elevation of a given cell. G_0 is the target geopotential height estimated from the target long-distance dispersal height above the terrain (i.e., 400 m) and elevation for a given cell. G_1 and G_2 are upper and lower limits of G_0 . N_0 represents the value of a specific climate variable to be estimated at the target geopotential height G_0 . N_1 and N_2 are upper and lower values of N_0 based on G_1 and G_2 through pressure levels, P_1 and P_2 .

Fig. 3. The canonical discriminant analysis of climate variables based on the heating cycle (HC) and non-heating cycle (NHC) that includes the gap and head and tail of a non-heating cycle (see Fig. 1) with the inclusion of temperature (left panels) and exclusion of temperature (right panels) in the analysis. Climate variables under the forest canopy include: temperature (temp), total accumulative precipitation (apcp), best 4 layer lifted index (lftx4), mean sea level pressure (prmsl), relative humidity (rhum), specific humidity (shum), and wind speed (wsp). Climate

variables above the forest canopy include: temperature (temp), vertical velocity (omega), specific humidity (shum), turbulent kinetic energy (tke), wind speed (wsp), and 500 hPa geopotential height (gh500). (A) Canonical scores of the first dimension discriminant function. The number in the parenthesis of the axis Y represents the percentage of variance, which indicates the discriminating power of the discriminant function relative to all variables. The number in the parenthesis of the axis X represents the accuracy of the classification with the discriminant function, indicating the percentage of the cells correctly classified into the given group. The box represents the inter-quartile range (IQR) and the heaving horizontal line the median. The lower whisker extends downward to the lower limit from the first quartile (Q1) (i.e., $Q1 - 1.5 * IQR$) while the upper whisker upward to the upper limit from the third quartile (Q3) (i.e., $Q3 + 1.5 * IQR$). (B) Standardized canonical coefficients of the first dimension discriminant function, which indicate the importance of each variable. The higher coefficients (i.e., larger absolute values) the more contribution of the given variable to the discriminant function. The arrows of up and down indicate positive and negative contributions of the variables in the discriminant function, respectively.

Fig. 4. Anomaly maps of climate variables under the forest canopy. “Anomaly” maps show the difference between the mean (HC_mean) of a given variable during emergence (i.e., over heating cycles) and the mean (ALL_mean) of a given variable over the whole study period (i.e., over two summer months, July and August) for a specific grid cell (or a location), that is, $HC_mean - All_mean$. “Std” maps show the standard deviation of a given variable during emergence for each cell. A special classification schema was used for the anomaly map of best 4 layer lifted index (c) because it has negative values when the atmosphere is unstable. In this schema, a code of -3 means that both the average atmosphere and the heating cycle are unstable but the heating

cycle is more unstable; -2 means that the average atmosphere is stable and the heating cycle is unstable; -1 means that both the average and the heating cycle atmospheres are unstable, but the heating cycle is less unstable; +1 means that the average atmosphere is unstable and the heating cycle is stable; +2 means that both the average atmosphere and the heating cycle are stable, but the heating cycle is less stable; +3 means that both the average atmosphere and heating cycle are stable, but the heating cycle is more stable. See Table S1 for the details.

Fig. 5. Anomaly maps of climate variables above the forest canopy. See the caption of Fig. 4 for the definition of “Anomaly” and “Std”. A special classification schema was used for the anomaly map of vertical velocity (b) because it has negative values when the atmosphere has upward motion. In this schema, a code of -3 means that both the average atmosphere and the heating cycle have ascending movements but the heating cycle has stronger ascending movements; -2 means that the average atmosphere has descending movements and the heating cycle has ascending movements; -1 means that both the average and the heating cycle atmospheres have ascending movements, but the heating cycle has weaker ascending movements; +1 means that the average atmosphere has ascending movements and the heating cycle has descending movements; +2 means that both the average atmosphere and the heating cycle have descending movements, but the heating cycle has weaker descending movements; +3 means that both the average atmosphere and heating cycle have descending movements, but the heating cycle has stronger descending movements. See Table S1 for the details.

Fig. 6. Time-lag cross-correlations between moving averages of climate variables and frequency distributions of heating cycles over all days of two summer months (July and August) across the whole province for the period of 1999 – 2010. The size of the moving window is 7 days which corresponds to the average length of mountain pine beetle peak emergence from Bentz (2006).

Positive lags mean that the patterns of climate variables (peaks) lead emergence (heating cycle) patterns (peaks) while negative lags indicate reverse trends. The dashed horizontal lines indicate 95% confidence intervals. Thus, significantly high cross correlation values beyond the confidence intervals at the lag of zero and at the lags close to zero indicate a strong match of two patterns.

Fig. 7. The canonical discriminant analysis of climate variables under the forest canopy (left panels) and above the forest canopy (right panels) by long-distance dispersal type (Sink: the cells of new infestation to which beetle fly from the source; Source: the cells of old infestation from which beetles disperse to the sink; None: cells of no infestation). See the caption of Fig. 3 for the definition of climate variable abbreviations and interpretation of the canonical discriminant analysis plots.

Fig. 8. The wind directions and speeds of the four target long-distance dispersal areas. These areas were identified based on the mountain pine beetle landscape infestation dynamics conceptual model and core areas of sinks and sources determined from the morphological spatial pattern analysis of beetle infestations (Chen 2014). Note that the indicated wind direction is the direction toward which the wind is blowing.

Fig. 1

Fig. 2

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Fig. 4

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Fig. 8

Table S1. The anomaly map schema for climate variables Best 4 layer lifted index (lftx4) and Vertical velocity (omega)

HC [*]	M [†]	DIF [‡]	Assigned code	The meaning of lftx4 difference (DIF) [§]	The meaning of omega difference (DIF)
-	-	-	-3	Unstable and more unstable during a HC	Ascending and stronger ascending movement during a HC
-	-	+	-1	Unstable but less unstable during a HC	Ascending but weaker ascending movement during a HC
-	+	-	-2	Unstable during a HC but stable on average	Ascending movement during a HC but descending on average
+	-	+	+1	Stable during a HC but unstable on average	Descending movement during a HC but ascending on average
+	+	-	+2	Stable during a HC but less stable than on average	Descending but weaker descending movement during a HC
+	+	+	+3	Stable during a HC and more stable than on average	Descending and stronger descending movement during a HC

^{*} Sign of climate variable mean values over heating cycles.

[†] Sign of climate variable mean values over the whole study period (i.e., July and August).

[‡] Sign of the differences of climate variable mean values between heating cycles and overall period, that is, mean of HC minus mean of overall period.

[§] The negative values of lftx4 reflect unstable climate conditions near the surface (see Table 1). The wording of this column represents climate conditions near the surface during heating cycles compared to the whole study period.

^{||} The negative values of omega reflect ascending air movement above the forest canopy (see Table 1). The wording of this column represents general air movement above the canopy during heating cycles compared to the whole study period.

Fig. S1. Climate conditions under the forest canopy by heating cycle type (HC: heating cycle; NHC: head and tail of non-heating cycle; XNHC: gap. See Fig. 1 for the details) at the three time intervals (Pacific Daylight Time) for the period of 1999 – 2010. The boxplots are defined as in Fig. 3.

Fig. S2. Climate conditions above the forest canopy by heating cycle type (HC: heating cycle; NHC: head and tail of non-heating cycle; XNHC: gap. See Fig. 1 for the details) at the three time intervals (Pacific Daylight Time) for the period of 1999 – 2010. The boxplots are defined as in Fig. 3.

Fig. S3. Overall climate conditions under and above the forest canopy by heating cycle type (HC: heating cycle; NHC: head and tail of non-heating cycle and gap; see Fig. 1 for the details) for the period of 1999 – 2010. The boxplots are defined as in Fig. 3.

Fig. S4. Yearly climate conditions under and above the forest canopy by heating cycle type (HC: heating cycle; NHC: head and tail of non-heating cycle and gap; see Fig. 1 for the details) for the period of 1999 – 2010.

Fig. S5. Overall climate conditions under and above the forest canopy by the whole heating cycle type (HC: heating cycle; H: head of non-heating cycle; T: tail of non-heating cycle; XNHC: gap; see Fig. 1 for the details) for the period of 1999 – 2010. The boxplots are defined as in Fig. 3.

Fig. S6. Yearly climate conditions under and above the forest by the whole heating cycle type (HC: heating cycle; H: head of non-heating cycle; T: tail of non-heating cycle; XNHC: gap; see Fig. 1 for the details) for the period of 1999 – 2010.

Fig. S7. The canonical discriminant analysis of climate variables under the forest canopy for the target long-distance dispersal areas (see Fig. 8 for locations of target sink and source areas). See the caption of Fig. 3 for the definition of climate variable abbreviations and interpretation of the canonical discriminant analysis plots.

Fig. S8. The canonical discriminant analysis of climate variables above the forest canopy for the target long-distance dispersal areas *i* (see Fig. 8 for locations of target sink and source areas). See the caption of Fig. 3 for the definition of climate variable abbreviations and interpretation of the canonical discriminant analysis plots.

Fig. S9. Overall climate conditions under and above the forest canopy for the target long-distance dispersal area in 2003 (see Fig. 8 for the location of the target area). The boxplots are defined as in Fig. 3.

Fig. S10. Yearly climate conditions under and above the forest for the 2003 target long-distance dispersal area for the period of 1999 – 2010 (see Fig. 8 for the location of the target area).

Fig. S11. Overall climate conditions under and above the forest canopy for the target long-distance dispersal area in 2006 (see Fig. 8 for the location of the target area). The boxplots are defined as in Fig. 3.

Fig. S12. Yearly climate conditions under and above the forest for the 2006 target long-distance dispersal area for the period of 1999 – 2010 (see Fig. 8 for the location of the target area).

Fig. S13. Yearly wind directions and speeds under and above the forest canopy for the 2002 target long-distance dispersal area for the period of 1999 – 2010 (see Fig. 8 for the location of the target area). Note that the indicated wind direction is the direction toward which the wind is blowing.

Fig. S14. Yearly wind directions and speeds under and above the forest canopy for the 2003 target long-distance dispersal area for the period of 1999 – 2010 (see Fig. 8 for the location of the target area). Note that the indicated wind direction is the direction toward which the wind is blowing.

Fig. S15. Yearly wind directions and speeds under and above the forest canopy for the 2006 target long-distance dispersal area for the period of 1999 – 2010 (see Fig. 8 for the location of the target area). Note that the indicated wind direction is the direction toward which the wind is blowing.

Fig. S16. Yearly wind directions and speeds under and above the forest canopy for the 2008 target long-distance dispersal area for the period of 1999 – 2010 (see Fig. 8 for the location of the target area). Note that the indicated wind direction is the direction toward which the wind is blowing.

Fig. S17. Wind directions and speeds under (A) and above (B) the forest canopy at the provincial level for the period of 1999 – 2010. Note that the indicated wind direction is the direction toward which the wind is blowing.