

Pivotal effect of early-winter temperatures and snowfall on population growth of alpine *Parnassius smintheus* butterflies

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Abstract. Geographic range shifts in species' distributions, due to climate change, imply altered dynamics at both their northern and southern range limits, or at upper and lower elevational limits. There is therefore a need to identify specific weather or climate variable(s), and life stages or cohorts on which they act, and how these affect population growth. Identifying such variables permits prediction of population increase or decline under a changing climate, and shifts in a species' geographic range. For relatively well studied groups, such as butterflies, geographic range shifts are well documented, but weather variables and mechanisms causing those shifts are not well known. The Holarctic butterfly genus *Parnassius* (Papilionidae) inhabits northern and alpine environments subject to variable and extreme weather. As such, *Parnassius* species are vulnerable not only to long-term changes in average conditions but especially to short-term extreme weather events. We use population growth estimates for the alpine butterfly, *Parnassius smintheus*, from 21 populations in the Rocky Mountains of Canada over a 20-yr interval combined with techniques of machine learning (randomForests) and parametric modeling to identify the important weather variables determining population growth. We do this to determine the seasons and life stages of *P. smintheus* most affected by climate change. Extreme minimum and maximum temperatures in November, in combination with November snowfall, affect annual population growth most, more so than do mean temperatures in November, and more so than weather at any other time of year. Populations decline both in years with low extreme minimum temperatures in November and especially in years with high extreme maximum temperatures in November, indicating that overwintering eggs are particularly vulnerable to early-winter weather. Snowfall ameliorates the negative effects of extreme temperatures, particularly for extreme warm events. Results provide insight into biological mechanisms by which overwintering eggs might be affected by early winter weather. Short-term extreme weather in November, acting on a single pivotal life stage (egg) is a far better predictor of population change of alpine *P. smintheus* butterflies than is the general index of climate, the Pacific Decadal Oscillation.

Key words: alpine; butterfly; climate change; population dynamics; prediction; randomForests; regression trees; Rocky Mountains; snow; weather extremes; winter.

INTRODUCTION

One of the challenges of relating climate change to animal population dynamics is the need to identify the components of weather and climate that have the greatest impact on population growth and persistence, whether they be general indices of climate such as the North Atlantic Oscillation (NAO) or Pacific Decadal Oscillation (PDO; Vandenbosch 2003, Ciuti et al. 2015, Pardikes et al. 2015), or combinations of shorter-term variables such as growing degree days (Pöyry et al. 2009), temperature, and precipitation (Portier et al. 1998, Badik et al. 2015). Whereas broad indices are relatively easy to obtain and integrate multiple weather variables, they lack the detail needed to identify biological mechanisms causing population change. Identifying such critical weather (or climate) variables is not only essential in identifying

biological mechanisms causing population change and geographic range shifts, but also affords the ability to predict population increase or decline in response to short-term weather variation, and shifts in a species' geographic range in response to longer-term, large-scale, changes in climate.

Butterflies, being relatively well-studied, short-lived ectotherms, provide some of the best examples of population responses to climate change, in particular geographical range shifts in latitude and altitude resulting from warming temperatures (Parmesan and Yohe 2003, Kharouba et al. 2009, Pöyry et al. 2009). The implication of such shifts is that populations can establish and increase in locations previously too cold (e.g., Bennie et al. 2013), and decline in locations that have become too warm. In addition to the effect of a warming climate in causing such shifts, increased variation in climate and more frequent weather extremes (the second component of climate change [e.g., Schär et al. 2004]), may result in dramatic changes in population size, including population collapse,

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and ultimately range shifts (Lynch et al. 2014). Identifying the interaction between individual life stages (egg, larva, pupa, or adult) of butterflies, and specific weather variables affecting population change among the myriad potential variables (e.g., Pollard 1988, Roy et al. 2001, Badik et al. 2015), is an important step in identifying and understanding the biological mechanisms underpinning population change and range shifts. Although analyses of butterfly range shifts have often focused on the effects of changing summers (e.g., Kharouba et al. 2009, Pöyry et al. 2009), weather in other seasons may be equally or more important. For example winter weather is increasingly recognized as pivotal in altering the dynamics of lepidopteran populations (e.g., Hunter et al. 2014) and in causing shifts in their geographic range (e.g., Lynch et al. 2014).

Individual weather variables such as mean winter temperature (Radchuk et al. 2013), total winter rainfall (McLaughlin et al. 2002), or date of snow melt (Boggs and Inouye 2012) can be strongly related to butterfly population growth, but combinations of weather variables may be more important (e.g., Badik et al. 2015). Furthermore, although mean temperature and/or precipitation can be related to butterfly population growth, relatively short-term extreme events may be equally or even more important in causing population decline, collapse, or local extinction (e.g., Piessens et al. 2009, Lynch et al. 2014), and provide opportunities for populations to colonize and grow in previously uninhabited sites (Bennie et al. 2013).

Identifying specific weather variables affecting vital rates of each life stage would be ideal, but for butterflies this can be logistically very difficult (but see Radchuk et al. 2013). Vital rates are especially difficult to determine for isolated species in extreme environments such as those inhabiting the alpine. Most population studies of butterflies use annual censuses of one life stage, usually the adults, and assess the effect of covariates on either abundance (e.g., Pollard 1988, Vandenbosch 2003) or, more preferably, on the annual rate of change of that life stage (e.g., McLaughlin et al. 2002, Roland and Matter 2013). If the mechanisms affecting population change are known, this approach can be successful with a relatively short time series (e.g., Boggs and Inouye 2012); when the crucial population processes are not known a priori, longer and spatially replicated time series are needed (Turchin 2003).

Previously (Roland and Matter 2013), we used a 15-yr time series (1995–2009) to determine that the greatest effect of general climate on population growth of alpine *Parnassius smintheus* Doubleday (Lepidoptera: Papilionidae) butterflies, in the Rocky Mountains of western Canada, was that occurring over winter. General climate was characterized using the PDO, which is well correlated with both temperature and precipitation in western and northern Canada (see Fig. 3 in Mantua et al. 1997). *Parnassius smintheus* populations increase when the mean PDO from November through March is intermediate in value (moderate temperatures and moderate amounts of snow), but populations decline at both highly positive values (warm winters with little snow) and at low

negative values (cold, snowy winters). Despite this general pattern, PDO did not provide a good prediction of population growth at a new extreme value seen in the winter of 2014–2015 (see *Discussion*), suggesting that more detailed weather effects need to be identified to understand the process of population change of alpine *P. smintheus*, particularly at new, extreme conditions such as those that will occur under climate change. Additionally, although *P. smintheus* ranges from New Mexico in the USA north to the Yukon in Canada (Layberry et al. 1998), PDO is only well correlated with temperature and precipitation in Canada and Alaska (Mantua et al. 1997); less so in the Rocky Mountains and Sierra Mountains of the United States. While some have argued that general indices of climate can better predict population change than would local weather (e.g., Hallett et al. 2004), it may be more useful to identify specific weather variables closely linked to biological processes, which would provide the ability to more directly compare their importance across a species' range.

Alpine butterflies inhabit a thermally variable and extreme environment. As such, *P. smintheus* provide an excellent system for understanding the effects of variable and changing weather and climate on butterfly population dynamics. Because winter weather can be extremely important for butterfly performance and survival (Williams et al. 2012, Radchuk et al. 2013), and because of the previous indication of its importance for *P. smintheus* population change specifically (Roland and Matter 2013), we were particularly interested in confirmation that winter weather (which variables, their timing, duration, and possible interactions) affects population growth most. The genus *Parnassius* is typical of alpine, montane, and fellfield habitats, characterized by generally dry conditions and extreme temperatures, with some species being either threatened or endangered (Välimäki and Itämes 2003, Auckland et al. 2004, Fred et al. 2006, Ashton et al. 2009, Roland and Matter 2013) with at least two members of the genus, *P. mnemosyne* (Pöyry et al. 2009) and *P. apollo* (Parmesan et al. 1999) showing northward shifts in their geographic ranges. Our goal here, using a 20-yr (1995–2014) time series of 21 subpopulations, is to identify specific weather variables related to the rate of population change of *P. smintheus*, providing insight into mechanisms causing that change and which might be relevant for other *Parnassius* species. We invoke a systematic statistical approach using machine learning [randomForests (RF)], regression trees, and parametric regression models to identify the most important among the myriad potential weather variables affecting annual population growth.

METHODS

Study sites

Population studies of *P. smintheus* have been conducted in a network of alpine meadows at Jumpingpound and Lusk Ridges, Alberta, Canada (50°57' N, 114°54.3' W)

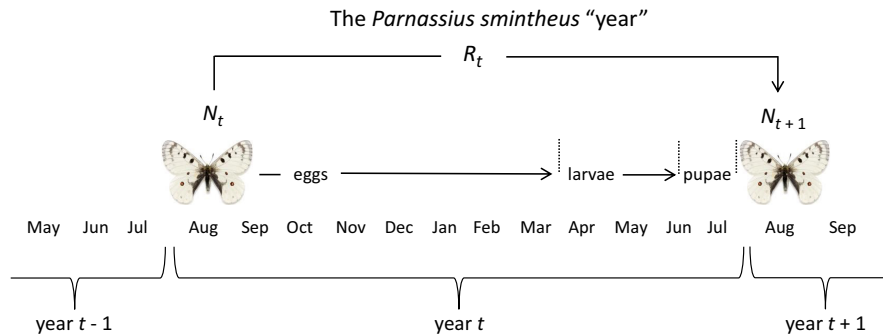


FIG. 1. Life cycle of *Parnassius smintheus* at Jumpingpound Ridge, Alberta, Canada, showing the phenology of emergence, timing of population estimation for years t (N_t) and $t + 1$ (N_{t+1}), estimation of rate of population change (R_t), and respective months in years $t - 1$ and t for which weather variables were related to population change.

since 1995 (Roland et al. 2000), where it is by far the most abundant alpine butterfly species. This network of generally south- and west-facing alpine meadows is located in the front ranges of the Rocky Mountains, ranging in elevation from 2100 to 2200 m. Meadows are characterized elsewhere (Roland et al. 2000).

At this site, larvae of *P. smintheus* are essentially monophagous on lance-leaved stone crop, *Sedum lanceolatum* Torr. (Crassulaceae), a perennial “succulent” plant growing on well-drained gravelly soils (van Ee et al. 2015). Caterpillars hatch after snow melt, usually in May, and pupate in the soil by late June (Fig. 1). Adults begin emerging in mid to late July, nectar-feed on a variety of plant species (Matter and Roland 2002), and fly through late August. Females oviposit single eggs on the ground or vegetation, near, but not on, the larval hostplant. *P. smintheus* overwinter as pharate first-instar larvae inside the eggs. Because eggs are laid off the hostplant, newly hatched caterpillars must move to locate and feed on hostplants after snowmelt in spring.

Population size and growth

Estimates of population size (N_t) were made for each of 21 subpopulations (meadows) in each year (t) using mark–release–recapture methods. Each butterfly was marked on the ventral hindwings with a three-letter individual identification code. Population size was calculated for each subpopulation for each year (1995–2014) using Craig’s Method (Craig 1953; additional details in Roland and Matter [2007]). For each subpopulation, the rate of change (R_t) in adult butterfly abundance from one summer (t) to the next ($t + 1$; Fig. 1) was calculated as $\log_{10}(N_{t+1}/N_t)$. To account for a few abundances of zero, a value of 0.5 was added to all estimates prior to log-transformation. Values of $R_t > 0$ indicate population increase between the two summers; values < 0 indicate decline. Population growth was estimated for the years 1995 through 2013, although a few sites were not sampled in some years. Population size ($\log N_t$) was included as a variable in all analyses of population growth (R_t).

Weather variables

Population estimates were of adults in August, and hence, population growth estimates are for the interval between two successive Augusts (Fig. 1). Although previous analysis (Roland and Matter 2013) indicated winter as the season affecting R_t , the most (likely via winter temperatures and snow amounts), we chose to step back and consider weather variables from all months of the year because short-term variation in other seasons may have additional important effects on population change in some years. Within years, the same values for weather variables were applied to all 21 subpopulations given that the study area spans a distance of only 12 km and all meadows are at similar elevation.

Continuous weather data are only available at our population study site, Jumpingpound Ridge, since 2010. Temperature and snow data spanning the 20 yr of population data were therefore obtained from a nearby weather station at Little Elbow, Alberta (50°42.3′ N, 114°59.3′ W, elevation 2,193 m) at treeline, also in the front range of the Rocky Mountains, and located 25 km from our study site at a similar elevation and aspect. This station monitors temperature and amount of snow hourly year round. Any gaps in temperature record at this site were supplemented with data from Nakiska Ridge, Alberta (50°56.5′ N, 115°11.3′ W) located 17 km from our population study site and 26 km from the Little Elbow weather site, again in the front range of the Rocky Mountains, but at a slightly higher elevation (2540 m). Temperature data are highly correlated among the three sites (Appendix S1: Fig. S1), and sites experience similar phenomena such as temperature inversions and warm, adiabatic “Chinook” winds, periodically through the winter.

We were interested in weather variables associated with estimates of R_t over the interval from August, when generation t emerges, through to the following July (just prior to emergence of generation $t + 1$, Fig. 1). Temperature variables we considered (Table 1) were the monthly mean, the mean of the daily minima for each month, the mean of

TABLE 1. Candidate annual and monthly variables considered for relating to rate of population growth (R_t) from 1995 through 2014.

Variables	Number of variables
Annual	
\log_{10} population size for each subpopulation	1
Maximum amount of snow (mm water equivalent) over the winter	1
Day of the year (where 1 Jan = 1) of snow melt in spring	1
Total rain for May through July in years $t - 1$ and t (mm)	2
Monthly	
Mean temperature for each month	12
Mean daily minimum temperature for each month	12
Mean daily maximum temperature for each month	12
Extreme minimum temperature observed in each month	12
Extreme maximum temperature observed in each month	12
Amount of snow (mm water equivalent) on the 15th of each month	12
Amount of snow (mm water equivalent) since the last month (September through April)	8
Rainfall (mm) for each of May, June and July in both years $t - 1$ and t	6

Note: There were a total of 90 candidate weather variables in addition to the estimates of population size for each subpopulation. Snowfall water equivalent in millimeters is generally related to snow depth by a factor of 10 (10 mm water equivalent \approx 10 cm snow).

the daily maxima for each month, and the extreme maximum and extreme minimum observed in each month (Appendix S1: Fig. S2). Monthly means were calculated from the hourly data; mean daily minima and daily maxima for each month were the average of the respective daily observations within each month.

Snow is monitored at Little Elbow by a “snow pillow,” located at treeline, which continuously records the water-equivalent (mm) of snow on the pillow (Appendix S1: Fig. S3). As such, snow pillow data do not provide a measure of snow depth in our meadows per se, but rather an indication of whether a specific year (or month within a year) is particularly snowy or snow-free compared to other years. We considered two monthly variables: (1) the accumulated amount of snow on the ground (pillow) on the 15th of each month and (2) the snowfall amount that had been added since the previous month, for September through April. We felt that this latter variable provides a better indication of short-term snow cover on the ridge-top meadows of our study area, which is subject to redistribution and loss of snow through the winter by wind and melting. In addition to the monthly snow variables, two annual snow variables were (1) the maximum amount of snow observed over the entire winter and (2) the date of snow melt standardized as the day of the year (where 1 January = 1) on which 150 mm water equivalent of snow

remained on the snow pillow in spring (Appendix S1: Fig. S3). The snow pillow melts out completely several weeks later than does snow in our meadows, so we standardized the date at 150 mm water equivalent simply to indicate whether snow melt in a year was generally early or late.

Rainfall records for each month were obtained from a manned weather station only 7 km from our network of meadows, but at lower elevation (1400 m) at Barrier Lake, Kananaskis (51°01.6' N, 115°02.1' W). Rainfall at this station was highly correlated with rainfall estimates at our butterfly study site (Appendix S1: Fig. S1). In our analyses, we included rainfall (mm) for each of the 3 months May through July, and the sum of those 3 months. We considered two potential effects of rainfall: (1) rainfall in year $t - 1$ (Fig. 1), which might affect flowering and phenology of nectar plants on which adults emerging in year t feed (Fig. 1), which in turn would affect fecundity of females maturing and laying eggs (Matter et al. 2009) and ultimately population size in year $t + 1$, and (2) rainfall in year t (Fig. 1), which might affect the larval host plant *S. lanceolatum* and hence larval development and survival. In both cases, we considered the individual monthly rainfall (May through July) and their summed value. Weather variables are summarized in Table 1.

Statistical analyses

The ultimate aim of our analyses was to identify specific weather variables that explain variation in population growth (R_t) from one summer to the next. One of the main challenges in this regard is the large number of potential weather variables that could be important given the different life stages of the insect through the year, and the fact that we do not know a priori what time of year the key weather variables occur, even though we do know that winter appears to be important (Roland and Matter 2013). For this reason, we used a combination of tree-based and linear regression techniques to systematically “winnow down” the large number of candidate variables to a few that suggest plausible mechanisms affecting population growth. Ultimately, we needed to account for random effects of the 21 subpopulations, and for any nonlinear pattern of population growth previously seen for the more general climate variable, PDO (Roland and Matter 2013). Any additional complex interactions among variables also needed to be considered and accounted for. Our goal was a final mixed-effects model explaining R_t based on population size and weather, for the 21 subpopulations.

Analysis was systematically done in four stages: (1) initial screening for important variables using randomForests RF (Breiman 2001, Liaw and Wiener 2002, Breiman and Cutler 2015), (2) identification of potential complex interactions using recursive partitioning regression trees (rpart; De'ath and Fabricius 2000), (3) identification of any nonlinear pattern of response using generalized additive models (gam; Wood 2006) and (4) linear mixed-effects (lme) models (Pinheiro and Bates

2000) to account for random effects among the 21 subpopulations and to estimate parameters that could be used for prediction. All analyses were done in R (version 2.13.1, R Development Core Team 2011).

Initial screening of variables using RF.—RF uses randomized subsets of the data to build individual regression tree models that identify which independent variables are most informative for grouping the dependent variable. In our case, subsets of the data with similar value of R_t are identified at the terminal “leaves” of the tree based on the variables that categorize R_t at each node. RF builds an ensemble of such regression tree models each based on a different subset of about two-thirds the cases in the data set. The other one-third of the cases are then run through these trees to be “classified” into groups with similar R_t based on the observed independent variables. The procedure compares each tree where the observed values of a particular variable have been run through the tree to the same tree where that variable has been randomized among cases. The percent change in mean square error (%MSE), and the increase in node purity between the observed values and the randomized values of each variable, averaged over all trees (the “forest” of 500 trees in our case), are used as the measure of the predictive value of that variable. RF has been used to successfully to predict, for example, levels of forest defoliation by spruce budworm based on forest stand characteristics (Candau and Fleming 2011), and small mammal distribution and diversity based on habitat characteristics (Baltensperger and Huettmann 2015). Although based on classification and regression tree analysis, RF does not produce a single “best” regression tree. For this, we used the variables identified as the best “splitting” variables in RF, and applied recursive partitioning regression tree (rpart) analysis to them.

Identification of interactions using regression tree (rpart).—Regression trees are particularly good at identifying complex interactions among variables in a manner not constrained by linear combinations of variables (De’ath and Fabricius 2000). Interactions are implicit in that a given variable may only appear in part of the tree, or in disjunct parts of the tree. Because of its ability to identify such interactions, we felt that it could be useful for identifying combinations of variables affecting population growth, and any variables being important only over a subset range of other variables, or in combination with a limited range of some variables. For example, it can only snow at certain temperatures, or density-dependent population effects may only be manifest in years without extreme weather perturbations.

Weather variables are typically highly correlated with each other, and although the analysis identifies the “best” variable for splitting at each node, it also provides an estimate of how well surrogate variables (other correlated variables) would also define the split. In this sense, the structure in the dependent variable (R_t) is provided

by the structure (nodes and leaves) of the tree, and indicates which variables contribute most to that structure. Other surrogate variables can be almost as good at providing a given split, and interpretation should therefore be made cautiously. Our intent is to use regression tree analysis to help identify interacting and minor variables for the final mixed-effects model beyond those identified from RF.

Accounting for nonlinearities (gam).—Nonlinearities between R_t and independent variables were identified using generalized additive models (gam; Wood 2006), using default thin-plate regression splines with a potential for three parameters (equivalent to the inclusion of a quadratic term in the model).

Mixed-effects models (lme).—Linear mixed-effects models (lme) were fitted based on the subset of variables identified from the RF and rpart analyses. We include random effects of subpopulations (intercepts only) and quadratic terms where indicated as appropriate in the gam analysis above. Best models were identified based on likelihood-ratio tests and the change in Akaike’s information criterion (Δ AIC; Burnham and Anderson 2002).

RESULTS

Twenty years of field studies on the 21 subpopulations produced 318 estimates of population growth of *P. smintheus*. Estimates were based on a total of 31,188 captures of 18069 individuals over that interval, providing time series of N_t from 1995 through 2014, and of R_t from 1995 through 2013, for each subpopulation (Fig. 2). We considered the effect of 90 candidate weather variables, in addition to that of population size ($\log N_t$), on R_t (Table 1), through the following series of analyses.

Initial screening of variables using RF.—Initial screening of all variables using RF indicated that only a small subset of the 91 candidate variables had strong effects on rate of population change (Fig. 3). The top eight variables (given the natural “break” in relative importance between the eighth and ninth variable, Fig. 3), were considered for subsequent analyses relating weather to R_t , with a view to identifying potential mechanisms affecting population change.

Population size ($\log N_t$) and all five November temperature variables (means and extremes), dominate in importance, but they are likely highly correlated with each other. December extreme maximum was also important, again indicating that population growth may be particularly sensitive to early winter temperatures. No temperature variable at any other time of year was identified as being related to annual population growth. Surprisingly, snow variables, as measured by the snow pillow, were unimportant, whether it be date of snow melt, amount of snow on the ground, or snowfall over the previous month. The above results support the general

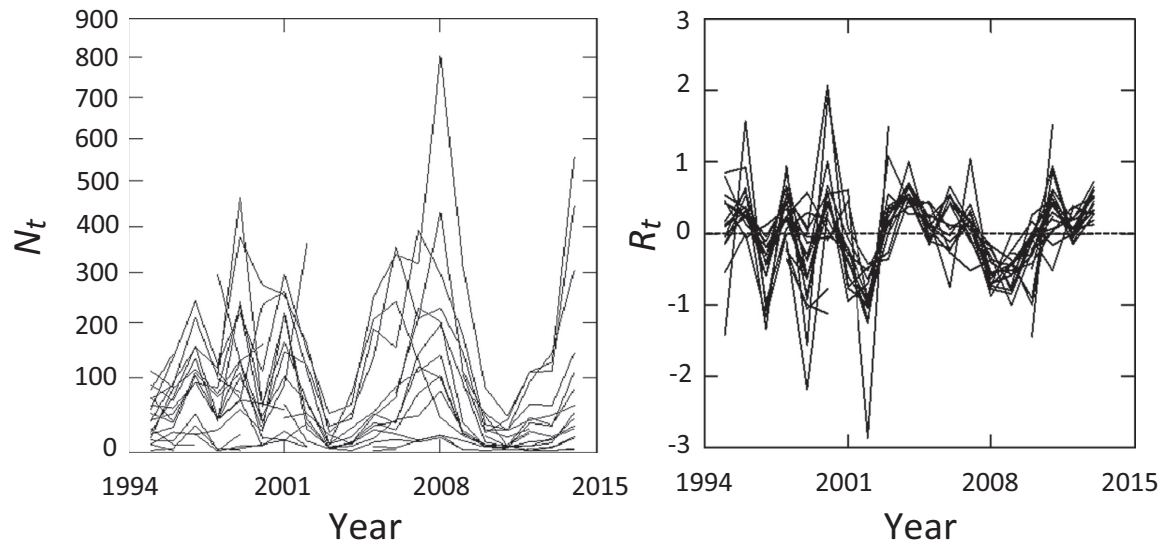


FIG. 2. Population size (N_t) and rate of population change (R_t) for 21 subpopulations of *P. smintheus* butterflies at Jumpingpound and Lusk Ridges, Alberta, Canada (1995–2014).

pattern for winter being the season with the greatest effect on *P. smintheus* population growth (Roland and Matter 2013), specifically early-winter weather in November. The one variable other than winter variables identified as being potentially important was July rainfall coincident with adult emergence and oviposition by females (July_{*t*-1}, Figs. 1 and 3).

Because of the dominance of November temperatures in the RF analysis, and because of our interest in winter weather generally, and known interactions between temperature and snow for other temperate insects (Sinclair et al. 2003, Bale and Hayward 2010, Williams et al. 2015), we ultimately did consider potential of interactions between November temperatures and snow for subsequent analyses. To do so, we reran RF with snow variables only (Appendix S1: Fig. S4). Short-term snowfall for any month was always a better predictor of R_t than was total snow up to that month (Appendix S1: Fig. S4). We therefore did include November snowfall as a variable in subsequent analyses in consideration of potential interactions with November temperatures for egg survival on the ground.

Identification of possible interactions using recursive partitioning regression trees (rpart).—To identify a “best” regression tree and potential interactions therein, we used the subset of the eight most important variables from RF plus November snowfall to build a regression tree using *rpart*. The four primary splits of the resulting tree (Fig. 4, nodes 1, 2, 3, and 7) are all determined by temperature variables, with left splits (lower population growth) being consistently associated with warmer temperatures; right splits (greater population growth) always associated with cooler temperatures. The greatest separation in population growth (R_t) was provided by mean November temperature, reflecting its general importance

as identified by RF. Warm Novembers with a mean temperature $> -4.6^\circ\text{C}$ (first left split in the tree, Fig. 4) are associated with the greatest population declines (mean $R_t = -0.56$, $n = 78$), and colder mean Novembers (first right split) are associated with modest population increases (mean $R_t = 0.16$, $n = 240$). Among the warmer years (first left split), those with even warmer Novembers ($\geq -2.7^\circ\text{C}$, furthest left split, $n = 14$) exhibit the greatest average population decline (mean $R_t = -0.99$). November extreme minimum was the next most important splitting variable (based on length of the branch), followed by November extreme maximum.

Other minor interactions are indicated by the effects of November extreme minima, maxima, and of population size, in lower parts of the main right-hand split of the tree. In particular, population size ($\log N_t$) serves as a splitting variable (node 15) only under a subset of weather conditions. To visualize this interaction, we plotted R_t as a function of November extreme maxima and minima (Fig. 5), taking into account the cases for which R_t is determined mainly by abundance (those within node 15), and those for which R_t is not (all other cases in the tree). Population size is not an important splitting variable (open symbols in Fig. 5) when November temperatures are at their most extreme, both for minima (Fig. 5a) and maxima (Fig. 5b). This pattern indicates that weather perturbations can trump density-related effects on R_t . In contrast, in those years with benign Novembers, population size has a more important effect on R_t (solid symbols in Fig. 5). Although November snowfall had a minor effect in the regression tree, it had an interesting interaction with November extreme maxima. When November extreme maxima exceeded 6.9°C (left split at node 7), <44 mm water equivalent of snow (left split at node 14) resulted in population decline, whereas greater

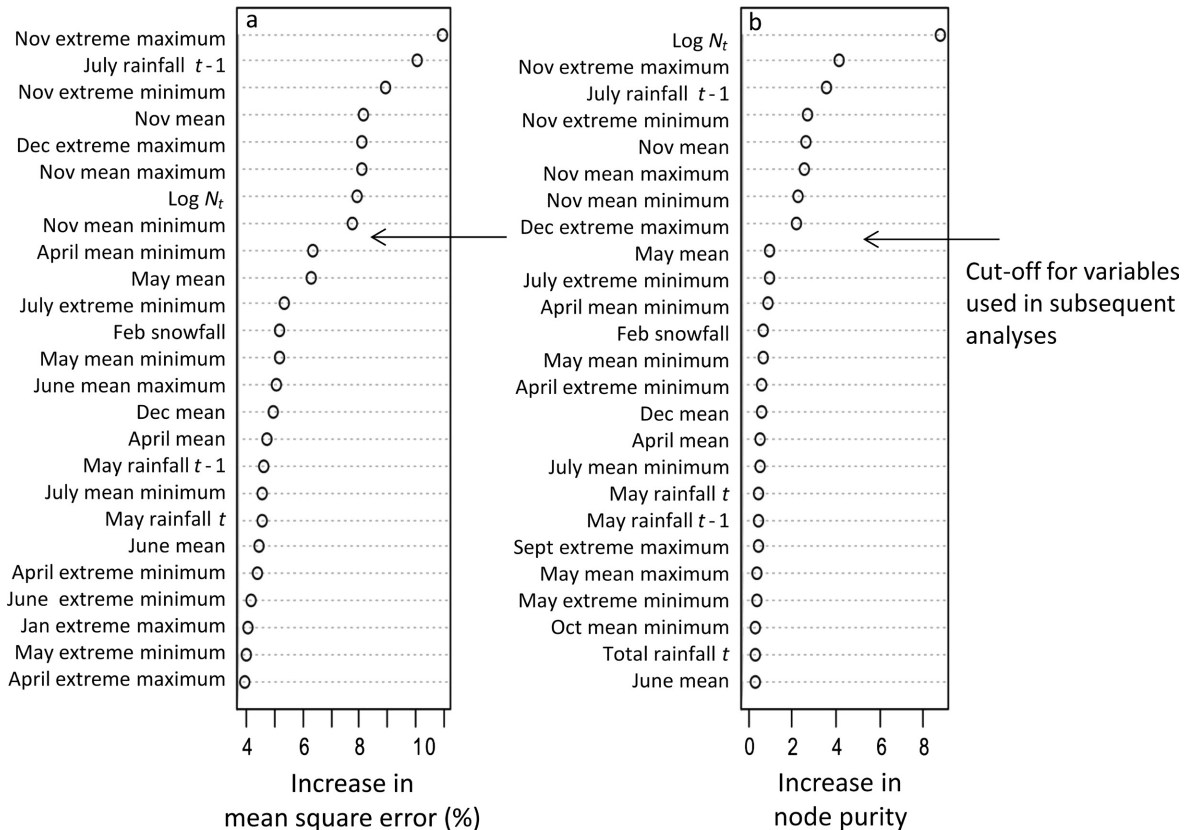


FIG. 3. Top 25 variables from randomForest analysis. (a) Mean square error difference between the randomized and observed values for each variable averaged across all 500 bootstrapped trees. (b) Increase in node purity when randomized values vs. observed values of each variable are run through the regression trees.

snowfall (more than 44 mm; right split at node 14) ameliorated the negative effect of unusually warm Novembers on growth. The robustness of these interactions is explored further in *Mixed-effects models (lme)*.

November mean minima and mean maxima were not important in the regression tree, despite their being identified as potentially important in RF analysis (Fig. 3). This is likely because, in RF, variables are assessed individually (and hence indicate possible importance on their own merit), but may be correlated with similar, but even more important, variables. November mean maxima and mean minima are in fact highly correlated with, and hence redundant to, mean November temperature ($r^2 = 0.97$ in both cases, $N = 20$ yr). Once November monthly mean temperature is in the rpart model, there is little additional information provided by either the mean maxima or mean minima. November mean temperature is, however, less well correlated with November extreme maxima ($r^2 = 0.28$) and extreme minima ($r^2 = 0.70$) indicating that the latter two provide additional information in explaining R_t , and possibly additional insight into mechanisms by which November weather affects survival.

The two other weather variables identified from RF (December extreme maximum temperature, and July_(t-1)

precipitation) were never dominant splitting variables in the regression tree, again reinforcing the over-riding importance of November weather on population growth.

Nonlinear effects (gam).—Variation in R_t was adequately described by a linear relationship with population size, $\log N_t$ (Appendix S1: Table S1, Fig. S5). Similarly, there were no additional nonlinear effects of November mean temperature on R_t (Appendix S1: Table S1, Fig. S5). However, the other temperature variables, extreme maximum and extreme minimum, had additional nonlinear effects indicating strong population declines at the extremes of their values (Fig. 6; Appendix S1: Table S1, Fig. S5), especially for extreme maxima above 6°C. GAM analysis supported models in which snowfall has an additional nonlinear effect on R_t , a pattern likely related to a similar curvilinear pattern of R_t relative to PDO (Roland and Matter 2013) where R_t was negative in cold, snowy years (negative winter PDO) and in warm, snow-free years (positive winter PDO), but was positive in intermediate years.

There was a marginally nonsignificant ($P = 0.07$) additional nonlinear effect of July_(t-1) precipitation, with a tendency for reduced population growth when July was very dry (<30 mm rain) just prior to, and coincident with,

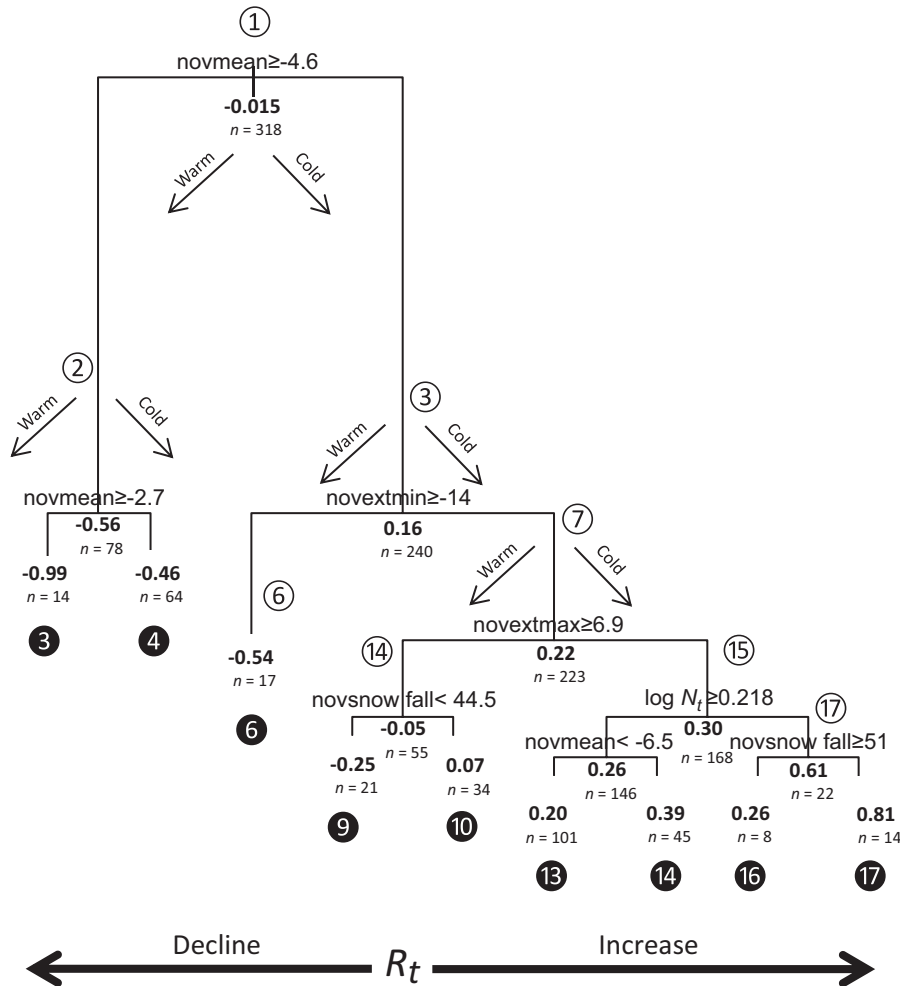


FIG. 4. Regression tree from rpart indicating variables that divide the population growth (R_t) data into the main groups. Splits to the left are “TRUE” for the condition at the node; those to the right are “FALSE.” November mean temperature (novmean) is the most important variable as indicated by the length of the split arms for a mean temp of -4.6°C . Numbers in boldface type are the mean R_t for that group with the associated sample size (n). Numbers inside open circles identify nodes; numbers inside solid circles identify terminal “leaves” as provided by rpart. Other variables are November extreme minimum temperature (novextmin), November extreme maximum temperature (novextmax), and November snowfall amount (novsnowfall).

adult emergence (Appendix S1: Fig. S6). For these reasons, and because RF had indicated potential importance of July precipitation, we initially retained a linear effect of July precipitation in the mixed-effects models in the event that once random effects of the 21 populations were accounted for, its significance might increase.

Mixed-effects models (lme).—In fitting mixed-effects models, we considered linear effects of population size, November mean temperature and July_(t-1) rainfall, and also included quadratic terms for November extreme maximum and extreme minimum temperatures, and for November snowfall. July_(t-1) precipitation was not significant (Table 2, Model 1, $F_{1,288} = 1.40$, $P = 0.24$); dropping it from the model (Model 2) provided little support for keeping it in the model (Table 3, Model 1 vs. Model 2, $\Delta\text{AIC} = -0.58$). All other fixed-

effects were significant (Table 2, Model 1), including November snowfall, which if dropped from the model (Table 3, Model 3) produced a less well-supported model ($\Delta\text{AIC} = 12.38$).

Population size

Population size was the most important variable in all versions of the mixed-effects models (Table 2). This fact was reflected in the RF analysis in that $\log N_t$ provided the highest node purity and a large percent change in mean square error (%MSE) in determining R_t compared to the other variables (Fig. 3). Small populations tend to increase and large populations tend to decrease. Clearly, it is important to account for density-related effects on R_t , or at least to control for differences in abundance when assessing effects of weather variables. $\log N_t$ is the

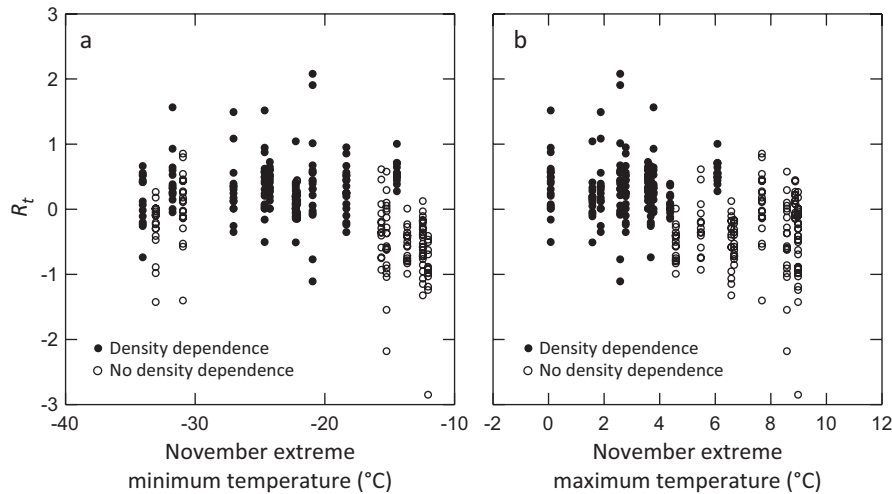


FIG. 5. Population growth (R_t) as a function of (a) November extreme minimum temperature and (b) November extreme maximum temperature. Solid symbols are cases in node 15 in the regression tree (see Fig. 4), i.e., all cases for which population abundance ($\log N_t$) is the most important splitting variable ($n = 168$); open symbols are cases in the rest of the tree ($n = 150$), for which abundance is not identified as the most informative splitting variable.

only independent variable that differs among meadows within a year, which may, in part, explain its dominance in this analysis (see *Discussion*).

Temperature

Among the subset of weather variables considered, November extreme maximum temperature was the most strongly related to R_t (Table 2, Fig. 6), with reduced population growth at higher extreme temperatures. Mean November temperature also had a strong effect on R_t , again with lower growth in years with warmer Novembers (especially when above -6°C , Fig. 6). Extreme cold in November was similarly important (Table 3), with the additional effect of lower annual growth when short-term extreme temperatures in November fell below -28°C (Fig. 6).

In order to determine the relative importance of mean November temperature vs. extreme temperature events in November on population growth, we compared the model with only significant weather variables (Model 2) to models where each temperature variable (along with its respective quadratic term) is dropped in turn, assessing ΔAIC in each case (Table 4). Dropping November monthly mean temperature from the model (Model 4, Table 4) lowered AIC only slightly ($\Delta\text{AIC} = -0.36$) indicating equally well-supported models. If either of the November extreme temperatures are dropped (Models 5 and 6, Table 4), AIC increased substantially, indicating that inclusion of extreme temperatures produced much better-supported models. These patterns suggest that short-term extreme temperature events in early winter may be as important as the monthly average in determining R_t . This exercise (dropping terms from the model) strictly considers statistical importance; the mechanism(s)

by which November temperature affects R_t no doubt involves November temperatures more generally. The three temperature variables are not only correlated with each other (see above), but likely cannot be separated from each other with respect to biological mechanisms affecting early-winter egg survival.

Snowfall

Despite the indication from the initial RF analyses that none of the snow variables were important, rpart analysis suggested there may nonetheless be interactions involving November snowfall effects on R_t that needed to be considered. Inclusion of snowfall improved the model substantially (Table 3, Model 3 vs. Model 1). We therefore also considered three additional alternative models that included interaction terms between November snowfall and the three respective November temperature variables (mean, extreme minimum, and extreme maximum) in turn (Table 5). Because models included a quadratic term for snowfall and for the two extreme temperature variables, models that considered these interactions needed additional terms to adequately account for those interactions: two for mean temperature and snowfall (mean temperature \times snowfall, and mean temperature \times snowfall²), and four for each of the extreme temperatures and snowfall (extreme temperature \times snowfall, temperature \times snowfall², temperature² \times snowfall, and temperature² \times snowfall²). Inclusion of interactions terms between snowfall and November mean temperature (Model 7) did not improve the model (Table 5). Inclusion of interaction terms between November snowfall and either extreme minimum (Model 8) or extreme maximum temperature

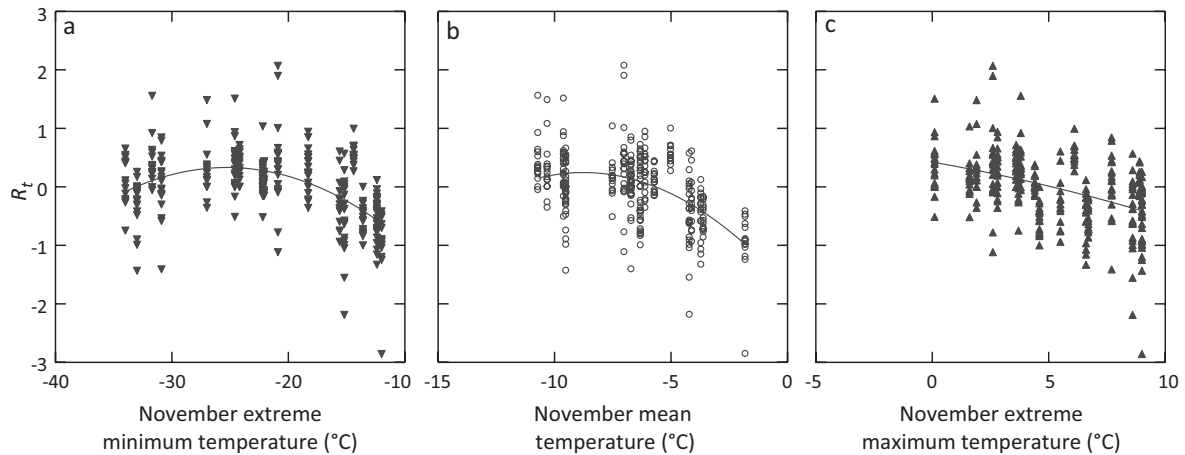


FIG. 6. Annual rate of population change (R_t) plotted against (a) November extreme minimum temperature, (b) November mean temperature, and (c) November extreme maximum temperature. Lines are quadratic smoother fits through each group.

(Model 9) provided better supported models, especially for the latter (Table 5). Including both interactions (allowing snowfall to interact with both extreme minima and extreme maxima) provided the model best supported by the data (Model 10, Table 5).

Population growth declines as extreme cold in November approaches the freezing point of eggs, -28°C (Matter et al. 2011), indicated by the vertical line in Fig. 7a, particularly in the absence of snow (lower part of Fig. 7a). When snow is more abundant (upper part of Fig. 7a) there is little effect of extreme cold around the freezing point. Snowfall provides a much stronger interaction with extreme warm events in November (Tables 5 and 6, Fig. 7b) than with extreme cold. If there was little snow in November (lower part of Fig. 7b), unusually warm temperatures in November reduced R_t substantially, but if there was substantial snowfall in November (upper part of Fig. 7b), unusually warm temperatures (above 4°C) had little effect on R_t . Therefore, recent snowfall appears to ameliorate the negative effect of short-term extreme cold, and especially of extreme high temperatures in November, in causing annual population declines. Loss of November snowfall as a consequence of

climate change would render overwintering eggs more susceptible to early-winter temperature extremes which themselves are expected to become more extreme and more frequent.

DISCUSSION

The importance of winter

In temperate regions, butterflies are often thought of as summer insects, but of course at least one life stage is present at any time of year. Winters can in fact be the most critical season affecting annual population growth for moth (Hunter et al. 2014, Lynch et al. 2014) and butterfly (Forister and Shapiro 2003, Radchuk et al. 2013) species, with consequences for population dynamics (Crozier 2003, 2004, Radchuk et al. 2013, Roland and Matter 2013). November weather appears particularly critical for survival of *P. smintheus* butterflies as they overwinter in the egg as pharate larvae, and appears pivotal in determining annual population increase or decline. Such a pivotal point, wherein a specific life stage interacts with weather extremes, may not only determine

TABLE 2. Effect of population size and weather variables on population growth (R_t) in linear mixed-effects model (Model 1).

Factor	Coefficient	df	F	P
Intercept	-1.89	1,288	0.32	0.57
$\log N_t$	-0.34	1,288	138.70	<0.0001
November mean temperature	0.05	1,288	40.16	<0.0001
November extreme maximum temp	0.12	1,288	36.44	<0.0001
November extreme maximum temp ²	-0.015	1,288	10.72	0.0012
November extreme minimum temp	-0.209	1,288	18.88	<0.0001
November extreme minimum temp ²	-0.004	1,288	23.28	<0.0001
November snowfall	0.0084	1,288	14.69	0.0002
November snowfall ²	-0.00014	1,288	4.51	0.035
July rainfall ($t - 1$)	0.00096	1,288	1.40	0.24

Notes: $n = 318$, groups = 21; SD intercept = 0.210, SD residual = 0.417; Akaike's information criterion, AIC = 401.45. The method used was maximum likelihood.

TABLE 3. Alternative mixed-effects models for rate of population growth (R_t), assessed by dropping July precipitation and November snowfall from Model 1.

Model	df	AIC	Δ AIC	L.ratio	P
1) $\log N_t$ + Nov mean + Nov extreme max + Nov extreme min + Nov snowfall + July _{t-1} precipitation (all terms)	12	401.45	0.0		
2) $\log N_t$ + Nov mean + Nov extreme max + Nov extreme min + Nov snowfall (drop July _{t-1} precipitation)	11	400.87	-0.58	1.43	0.23
3) $\log N_t$ + Nov mean + Nov extreme max + Nov extreme min (drop November snowfall and snowfall ²)	10	413.83	12.38	16.38	<0.0001

Notes: Variables identified as having additional nonlinear effects in the gam analysis (November extreme maxima, November extreme minima, and November snowfall), are assessed with an additional quadratic term in each case. The method used was maximum likelihood. NULL model (random effects only), AIC = 566.33, df = 3.

annual population growth, but may also define geographic limits to distribution and the potential for range expansion or contraction under climate change (e.g., Lynch et al. 2014). For *P. smintheus*, generally warm Novembers and both short-term cold and short-term warm temperature extremes in November are associated with the greatest population declines. More moderate temperatures during this month are associated with population increase (Fig. 6). Susceptibility to warm November extremes could determine southern (or low-elevation) range boundaries; susceptibility to extreme November cold could determine northern (or high-elevation) bounds.

Snow does interact with temperature to affect physiology (Bokhorst et al. 2010) and phenology (Chen et al. 2015, Wheeler et al. 2015) of alpine plants and of overwintering vertebrates and invertebrates (Mani 1968, Bokhorst et al. 2012), by providing insulation at times of extreme cold and heat. Our analysis indicates that snowfall ameliorates the effects of extreme temperatures, in particular warm events in November. Other temperate Lepidoptera are similarly affected by late fall and early winter temperatures. Overwintering spruce budworm (*Choristoneura fumiferana*) larvae (Han and Bauce 1998), and gypsy moth (*Lymantria dispar*) eggs (Nealis et al. 1999) suffer from extreme cold in fall, and the effect of extreme cold on gypsy moth eggs is ameliorated by snow cover (Nealis et al. 1999). Extreme warm events in winter are particularly devastating to gypsy moth eggs (Andresen et al. 2001), but the potential for amelioration of these extremes by snow cover has not been considered.

Biological mechanisms

Late fall and early winter are critical times of year for insects preparing for successful overwintering (Sinclair 2015), and several biological processes could act to produce the above patterns of population change. First, an unusually warm early winter may increase respiratory energy demands of otherwise cold-adapted insects resulting in either increased mortality through starvation, or a trade-off with cryoprotection later in the winter (Sinclair 2015). Such a pattern is apparent for bees (Sgolastra et al. 2011) and for spruce budworm (*Choristoneura fumiferana*) (Han and Bauce 1998), for which overwintering mortality can result from failed diapause development, inadequate cold-hardiness preparation, and exhaustion of energy reserves, all influenced by pre- and early-winter conditions. *Parnassius smintheus* overwinter as pharate larvae within the egg and therefore rely on stored reserves not only to get through the winter, but also (because eggs are laid off of the hostplant) for newly eclosed larvae to successfully move, locate, and establish on the host plant in spring. Second, short-term warm extremes in November could cause individuals to hatch prematurely and subsequently die when colder normal winter temperatures resume. In a simple experiment in 2005, we found that of 124 eggs collected from 11 females in August, and held at 5°C, when transferred to 20°C on 24 November, 55 hatched within 1 d. Such rapid hatch, combined with the fact that air temperatures of 4–8°C in the alpine can easily generate ground temperatures of 20–30°C due to high insolation (Mani 1968),

TABLE 4. Alternative mixed-effects models for rate of population growth (R_t), assessing the respective effects of November mean temperature (°C) and November extreme minimum and maximum temperatures.

Model	df	AIC	Δ AIC	L.ratio	P
2) $\log N_t$ + Nov mean temp + Nov extreme max + Nov extreme min + November snowfall	11	400.87	0.00		
4) $\log N_t$ + Nov extreme max + Nov extreme min + November snowfall (drop November mean)	10	400.51	-0.36	1.64	0.20
5) $\log N_t$ + Nov mean temp + extreme max + November snowfall (drop November extreme minimum)	9	443.52	43.01	46.65	<0.0001
6) $\log N_t$ + Nov mean temp + extreme min + November snowfall (drop November extreme maximum)	9	421.92	21.05	25.06	<0.0001

Note: Models are compared by alternately dropping each term (and its respective quadratic term) from Model 2.

TABLE 5. Alternative mixed-effects models for rate of population growth (R_t), assessing the addition of interaction terms between November snowfall and November temperature variables to Model 2.

Model	df	AIC	Δ AIC	L.ratio	P
2) $\log N_t + \text{Nov mean} + \text{Nov extreme max} + \text{Nov extreme min} + \text{Nov snowfall}$	11	400.87	0.00		
7) $\log N_t + \text{Nov mean} + \text{Nov extreme max} + \text{Nov extreme min} + \text{Nov snowfall} + \text{Nov snowfall} \times \text{Nov mean (snowfall interaction with November mean temperature)}$	13	402.70	1.83	2.17	0.34
8) $\log N_t + \text{Nov mean} + \text{Nov extreme max} + \text{Nov extreme min} + \text{Nov snowfall} + \text{Nov snowfall} \times \text{Nov extreme minimum (snowfall interaction with November extreme minimum temp)}$	15	369.34	-31.53	39.54	<0.0001
9) $\log N_t + \text{Nov mean} + \text{Nov extreme max} + \text{Nov extreme min} + \text{Nov snowfall} + \text{Nov snowfall} \times \text{Nov extreme maximum (snowfall interaction with November extreme maximum temp)}$	15	356.23	-44.64	52.65	<0.0001
10) $\log N_t + \text{Nov mean} + \text{Nov extreme max} + \text{Nov extreme min} + \text{Nov snowfall} + \text{Nov snowfall} \times \text{Nov extreme maximum} + \text{Nov snowfall} \times \text{Nov extreme minimum (snowfall interaction with both extreme maximum and minimum temps)}$	19	343.98	-56.89	72.89	<0.0001

Notes: Two terms are needed for the interaction between mean temperature and November snowfall (linear and quadratic), and four terms are needed for the interactions between extreme temperatures and snowfall (temperature and snowfall, temperature and snowfall², temperature² and snowfall, and temperature² and snowfall²). The method used was maximum likelihood.

make *Parnassius* eggs vulnerable to premature hatch even during short-term warm events of 4–8°C we observed in some Novembers (Figs. 5 and 6). Third, short-term cold extremes in November could cause larvae in the eggs to freeze and die. *P. smintheus* eggs freeze at -28°C (Matter et al. 2011), a low temperature often exceeded at our study site (Fig. 6; Appendix S1: Fig. S2). A combination of these three processes could produce the curvilinear pattern of population growth with respect to November temperatures (Fig. 6), a pattern similar to that seen for the more general climate variable, overwinter PDO (Roland and

Matter 2013), wherein both warm snow-free (positive PDO) and cold snowy (negative PDO) winters are associated with declines. It should be noted that, even in cold snowy years (negative PDO), snow can still be lost from our ridge-top meadows via redistribution by wind during and after snow storms, rendering eggs there vulnerable to extreme cold. Early winter temperature effects on physiology are known to alter dynamics of other insects, including mountain pine beetle *Dendroctonus ponderosae* (Regniere and Bentz 2007), spruce budworm (Han and Baucé 1998), and gypsy moth (Andresen et al. 2001).

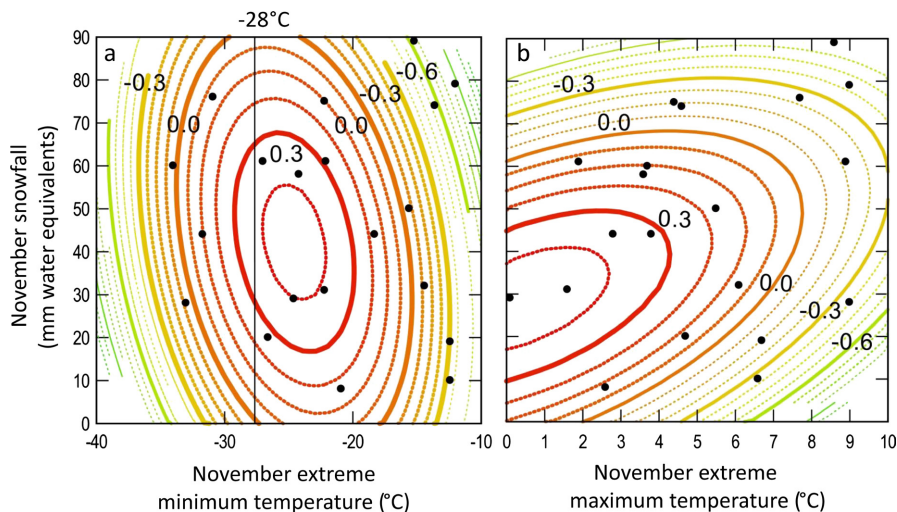


FIG. 7. (a) Contour plot of R_t as a function of November extreme minimum temperature (°C) and November snowfall (mm water equivalent) using a quadratic smoother in both dimensions. When there is little snowfall in November (lower part of the panel), R_t is reduced by extreme temperatures around the freezing point of eggs (-28°C, vertical black line), but less so when there is more snow (upper part of the panel). Numbers on contour lines indicate R_t values. (b) Contour plot of R_t as a function of November extreme maximum temperature and November snowfall. When snow is abundant (upper part of the graph), there is little effect of extreme warm Novembers. When there is little snow in November (lower part of the graph) there is a strong effect of November extreme warm temperature in reducing population growth. There are between 17 and 21 estimates of R_t (one for each meadow) at each indicated yearly data point. A color version of this Figure is available in the online version of the paper.

TABLE 6. Effect of population size and weather variables on population growth (R_t) in linear mixed-effects, Model 10.

Factor	Coefficient	df	F	P
Intercept	-22.95	1,281	0.21	0.65
$\log N_t$	-0.54	1,281	210.27	<0.0001
November mean temperature	-0.059	1,281	41.84	<0.0001
November extreme maximum temp	1.503	1,281	46.38	<0.0001
November extreme maximum temp ²	-0.086	1,281	14.58	0.0002
November extreme minimum temp	-1.929	1,281	26.32	<0.0001
November extreme minimum temp ²	-0.047	1,281	27.01	<0.0001
November snowfall	0.786	1,281	20.22	<0.0001
November snowfall ²	-0.007	1,281	5.58	0.0189
Nov extreme max temp \times Nov snowfall	-0.062	1,281	47.24	<0.0001
Nov extreme max temp \times Nov snowfall ²	0.00071	1,281	11.55	0.0008
Nov extreme max temp ² \times Nov snowfall	0.0037	1,281	3.46	0.064
Nov extreme max temp ² \times Nov snowfall ²	-0.000044	1,281	2.81	0.095
Nov extreme min temp \times Nov snowfall	0.060	1,281	6.05	0.015
Nov extreme min temp \times Nov snowfall ²	-0.0049	1,281	0.35	0.55
Nov extreme min temp ² \times Nov snowfall	0.00147	1,281	3.97	0.047
Nov extreme min temp ² \times Nov snowfall ²	-0.000012	1,281	9.72	0.002

Note: $n = 318$, groups = 21; SD intercept = 0.320, SD residual = 0.373; AIC = 343.98.

The two “extreme” temperature variables account for the greater statistical importance in the mixed-effects model (Table 2). Clearly, the fact that extreme minima account for almost all of the curvature in the relationship with R_t (Fig. 6), reflects a potentially strong effect of short-term extreme cold on egg freezing and survival, a pattern supported by laboratory experiments on freezing tolerance of *P. smintheus* eggs (Matter et al. 2011). The effect of short-term extreme maximum temperatures in November is less clear, since the potential mechanism of starvation through depletion of energy reserves would likely require a longer interval than one or a few days. However, short-term warm periods in autumn can void the effects of normal chilling in breaking diapause thereby altering phenology of hatch the following spring with consequences for fitness (Bradshaw and Holzapfel 2010). The apparent effect of extreme maxima could simply be due to the fact that all three November temperature variables are correlated with each other, especially at the warmer (more linear) part of the data range (Fig. 6). It is important to remember that the final model has mean temperature in it (and its statistical importance is evident in all four types of analyses); the effect of the other two November “extreme” variables may be in addition to that due to the November mean.

Few studies have explicitly considered the effects of winter weather on butterfly populations (but see Crozier 2003, 2004, Scriber et al. 2012). Interestingly, although vital rates of the butterfly *Boloria eunomia* are positively associated with higher spring and summer temperatures, as might be expected under climate change, they are negatively affected by warmer winters (Radchuk et al. 2013), and overwinter survival dominates predictions of the effect of climate change on its populations. For many temperate, alpine, and arctic butterflies, therefore, it may well be the effect of changing winters on overwintering life stages that are most important, and should be

considered more broadly, in particular in prediction of species’ range expansion or contraction.

Organisms such as alpine insects, faced with highly unpredictable environments, may be better able to deal with fine-scale spatial variation in microclimate (Huey and Tewksbury 2009, Sherrer and Körner 2010, Sunday et al. 2014) than are organisms in more benign environments. Unlike caterpillars (Weiss et al. 1988, Ashton et al. 2009) or adult butterflies (Buckley and Kingsolver 2012), which can move to select optimum microclimates to ameliorate extreme weather events, eggs cannot, and are hence more vulnerable to even short-term weather extremes. Ovipositing *P. smintheus* females (that always oviposit off of the larval host plant) could mitigate some of the microclimatic extremes. Females may “hedge their bets” on offspring winter survival by placing eggs over a greater range of possible temperatures and snow amounts than that offered by the microclimatic envelope occupied by their host plant. If *P. smintheus* oviposited on the host plant, it might be restricted to narrower subset of microclimatic conditions.

Snow

We were initially surprised that no snow variable by itself seemed important in determining population growth given that snow cover strongly affects temperature at ground level where eggs are overwintering. We previously (Roland and Matter 2013) showed that winter PDO is related to population growth, and is itself well correlated with both temperature and snowfall in this region of North America (Mantua et al. 1997). Date of snow melt has direct and indirect effects on multiple life stages of the alpine butterfly, *Speyeria mormonia*, in Colorado (Boggs and Inouye 2012), and on its dynamics, but neither total snow amount nor date of snow melt were important in determining *P. smintheus* population

growth. Short-term (monthly) snowfall was consistently more important, in particular in interactions with extreme temperatures. Snow pillow data indicate total amounts of snow, but do not provide any indication of how snow is actually distributed in the meadows. Because of the effects of wind, aspect, and slope on redistributing snow, we feel that more detailed data on amount and distribution of snow relative to oviposition sites by *P. smintheus* may be particularly enlightening. Such microclimatic detail may be especially important given the effects of short-term extreme minimum and maximum temperatures identified in the current study and how snow may ameliorate their effects. The resilience that such an ameliorating effect affords *P. smintheus* survival may be diminishing with climate change as the subnivium, as a habitat element, disappears from the alpine (Bale and Hayward 2010, Pauli et al. 2013). Mechanisms affecting egg survival still require direct experimental confirmation, and demonstration of their link to annual population change.

Within the meadows, the host plant, *S. lanceolatum*, is more abundant near treeline (Illerbrun and Roland 2011), where snow accumulation is more abundant and predictable than in open meadow (van Ee et al. 2015). Although *P. smintheus* do not oviposit on *Sedum* directly, they do tend to oviposit near the host plant (Fownes and Roland 2002), and by doing so likely ensure that at least some eggs are successful even in years with very little snow.

Why not rain?

Spring rainfall can have a large effect on butterfly populations through its effect on growth and senescence of the larval host plants, such as for butterfly species in Mediterranean climates generally (Forister and Shapiro 2003) and the Bay Checkerspot butterfly *Euphydryas editha bayensis* specifically (McLaughlin et al. 2002). We saw no indication of an effect of early summer (year t , Fig. 1) rainfall on alpine *P. smintheus* population growth via its larval host plant *S. lanceolatum*. Lack of an effect is perhaps not surprising given that *S. lanceolatum* is perennial, is a succulent, is very abundant at our study site (van Ee et al. 2015), and suffers little from feeding damage (Illerbrun and Roland 2011). As a succulent, *S. lanceolatum* can tolerate drought, and by preferring to grow on well drained gravel soils it is not prone to inundation due to heavy rain. Hence, *S. lanceolatum* may be an abundant and reliable resource for *P. smintheus* larvae irrespective of rainfall in early summer, even though *S. lanceolatum* distribution itself is affected by spatial variation in snow cover and distance above treeline (Illerbrun and Roland 2011, van Ee et al. 2015).

There was some suggestion (RF, Fig. 3), however, that July rainfall in year $t - 1$ can affect R_t potentially via nectar production for adults. When July rainfall is <30 mm coincident with adult emergence and flight

(year $t - 1$, Fig. 1), population growth is reduced (Appendix S1: Fig. S6). Reduced nectar abundance does lower fecundity of female *P. smintheus* (Matter et al. 2011) and renders a meadow less attractive to immigrants (Matter and Roland 2002). Although *P. smintheus* nectar feed on a number of flower species that could be affected by rainfall amount (Matter and Roland 2002), they also nectar-feed on the larval hostplant, *S. lanceolatum*, which, as we argue above, is largely insouciant to variation in rainfall. Nonetheless, there was no indication in the regression tree (rpart) analysis that July rainfall has an effect in even a subset of the population growth data, and it was non-significant in the mixed-effects models.

Allowing for among-meadow fixed effects

In our analysis, meadows (subpopulations) were treated as a random effect. Population size ($\log N_t$) was the only independent variable that differed among meadows within each year, which may, in part, account for its importance in all analyses. Greater population growth in smaller populations may reflect some unidentified density-dependent process such as a rapid-induced defense by *Sedum* (Roslin et al. 2008), or limited number of suitable microsites for oviposition (e.g., Konvička and Kuras 1999) or pupation. Alternatively, population size may be a surrogate for characteristics that differ among meadows, such as host-plant abundance and nectar-plant abundance (Matter and Roland 2002), and would therefore be confounded in our analysis. Meadows likely also differ with respect to characteristics related to temperature and snow cover, such as aspect, slope, topographic heterogeneity (Weiss et al. 1988), and edge effects of forest bounding each meadow, as well as meadow size and isolation (Roland et al. 2000). The effect of such meadow characteristics on R_t are considered in future studies and analyses.

Weather variables vs. PDO

Results here support our earlier analysis indicating the regional climatic variable PDO (averaged from November through March) was related to R_t , in particular with reduced growth at both the warm snow-free and cold snowy extremes of the range of PDO (Roland and Matter 2013). Results here also point to more specific biological mechanisms acting on overwintering eggs via the effects of temperature extremes in November in combination with variation in snowfall. Although PDO is well correlated with temperature and precipitation in Alberta (and further north), it is less well correlated further south in the Rocky Mountains (Mantua et al. 1997), such as in the Rockies of Colorado or the Tetons of Wyoming, where *P. smintheus* also occurs. Dynamics of *P. smintheus* in other regions may be similarly affected by temperature and snowfall in early winter, despite these variables being less well correlated with PDO in these regions.

Why might November weather be so critical? At this time of year, insects may not have adapted physiologically to oncoming winter, and may not be fully acclimated. Weather in November can be particularly unpredictable as the jet stream moves south relative to its position in summer, and as the polar vortex establishes its pattern across western North America. November is the first month in winter where temperatures go below -28°C , the super-cooling point for *P. smintheus* (Matter et al. 2011), yet is still subject to periods of very warm, snowless weather from the south and west. November is critically situated between stable warm summer weather and more predictable depths of winter in December through February. Also, early winter (November) may be particularly important because of its precedence relative to later-winter weather. For example, an extreme cold or warm event in February may have little additional population consequence if such an event had already occurred in the preceding November; November extremes may trump extremes later in winter.

Prediction using weather variables vs. PDO

Pacific Decadal Oscillation from November through March during the winter of 2014–2015 was the highest value recorded in the last 115 yr. We predicted (Matter and Roland 2015) the effects of this extreme value on *P. smintheus* population growth based on our earlier analysis relating R_t to PDO and population size (Roland and Matter 2013). A dramatic population decline was predicted, a prediction that failed miserably; all subpopulations increased rather than declined. Using the final model in the current analysis (Model 10, Table 6), and using population sizes in 2014, November temperatures, and November snowfall in 2014 (rather than PDO), produced predictions of R_t between the summers of 2014 to 2015 that are very similar to those observed (Fig. 8). In general, all populations increased by an amount very similar to that predicted (Fig. 8), and those predicted to increase the most, did so. Clearly, specific weather variables identified through the four analyses in the current study provide very good prediction of population change, suggesting that mechanisms related to egg survival dominate annual population growth of *P. smintheus*.

Although each life-stage of butterflies is affected by the timing and severity of a range of weather variables, our analyses indicate the dominance of extreme winter temperature, especially extreme warm temperature in winter, on the dynamics of the alpine butterfly, *P. smintheus*. Overwintering eggs appear to be an especially vulnerable life stage of this insect, particularly since winters will likely continue to be warmer, have more extreme warm events, and less snow cover (Brown et al. 2007, Pauli et al. 2013). As such, winter egg survival may provide a tipping point (Lynch et al. 2014) for the dynamics and distribution of *P. smintheus*, and potentially for congeners in similar habitats.

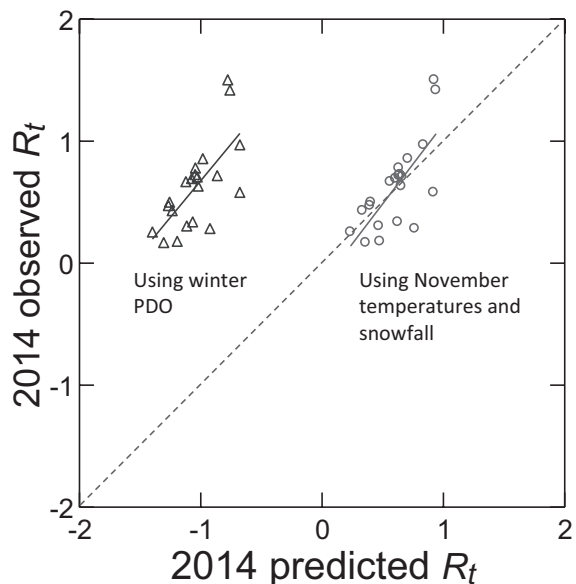


FIG. 8. Predicted and observed estimates of R_t between summer 2014 and summer 2015 for the 21 subpopulations on Jumpingpound and Lusk Ridges, Alberta, Canada. Predicted growth was based on (1) model using 2014 population sizes and mean Pacific Decadal Oscillation, $\text{PDO}_{(\text{Nov-Mar})}$ for the winter of 2014–2015 (triangles; Matter and Roland 2015) and (2) model using 2014 population sizes and November 2014 temperatures and snowfall (circles; Model 10, Table 6). Observed R_t is calculated from population estimates from mark–recapture studies in 2014 and 2015. Dashed line is the 1:1 line of equality for predicted and observed R_t .

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecm.1225/supinfo>

DATA AVAILABILITY

Data associated with this paper have been deposited in Dryad: <http://dx.doi.org/10.5061/dryad.tp324>