

RESEARCH ARTICLE

Once and future changes in climate and phenology within the Adirondack uplands (New York, USA)

J. Curt Stager^{1*}, Brendan Wiltse^{1,2}, Skylar Murphy¹

1 Natural Sciences, Paul Smith's College, Paul Smiths, New York, United States of America, **2** Adirondack Watershed Institute, Paul Smith's College, Paul Smiths, New York, United States of America

* cstager@paulsmiths.edu**OPEN ACCESS**

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Abstract

Long-term monitoring of the spring and autumn phenology of five animal species, four plant species, phytoplankton communities, lake temperatures and ice cover on the Paul Smith's College Phenology Trail in the uplands of the Adirondack State Park (NY, USA) has produced time series spanning 1990–2020 for the biological and water temperature records and 1909–2020 for lake ice. In conjunction with climate records from three nearby weather stations these observations demonstrate that the ice on Lower Saint Regis Lake now thaws one week earlier, on average, than it did in 1909 while the region as a whole warmed by 1.7°C and received 19 cm more precipitation annually. Statistically significant warming trends between 1990 and 2020 were restricted to July and September and therefore contributed to a scarcity of temporal shifts in the spring phenologies of species and lake ice during that shorter time frame, but the lake surface warmed by 1.9°C on average in October. Although most of the phenological records displayed no statistically significant directional change within the 1990–2020 time interval they revealed strong correlations between phenology and monthly air temperatures that are of predictive value. Together with projections from regionally down-scaled climate models these relationships suggest that the phenologies of the species and ice dynamics in question could shift by ca. 1–3 weeks by 2100 depending on the analytical approach used and the magnitude of fossil fuel emissions during this century. As Adirondack winters become shorter and milder before potentially losing snow and ice altogether over the longer term, the unique cultural ecology of the region's human residents will face profound existential challenges along with the ecosystems and species around them.

Introduction

Global climate change driven by human activity is both well documented and well under way [1–3], but its influences on local to regional scales are less thoroughly understood. Although overviews of climate change in the northeastern United States have been published previously [4, 5], fewer such studies have focused on distinct sub-regions of the Northeast. Even less

frequently documented are the long-term effects of climate change on the seasonality of natural phenomena ("phenology") within such sub-regions despite some exceptions [6–8], particularly during seasons other than spring [9, 10].

We focus here on the nature and phenological impacts of climate change in the Adirondack State Park of northern New York, a mountainous sub-region of the Northeast that is of national and international importance. The Adirondack Park is part of a UNESCO Biosphere Reserve, the site of numerous major winter sport competitions, the largest park in the contiguous United States (2.4 million ha), and a unique mosaic of human communities on a largely undeveloped wild landscape. Apart from lake ice records [11–13] and paleoecological investigations [14–17] little information is currently available regarding the effects of climate change on species and ecosystems in the Adirondacks [12, 18, 19]. Evidence from elsewhere in North America indicates that future warming is likely to cause spring phenology dates to advance earlier [6–8] and that differing responses among species to such warming could lead to "ecological mismatches" between, for example, flowering plants and the pollinators upon whom they depend [8, 20–22]. The scarcity of such information regarding the effects of past and future climate on phenology in the Adirondacks is particularly unfortunate in this context because modeling studies anticipate substantial warming in that sub-region during this century [4, 5, 12].

In this paper we document temperature and precipitation variability from 1900 to 2020 as recorded at three stations within the United States Historical Climatology Network (USHCN) that are located in the uplands of the Adirondack State Park (Fig 1A and 1B). We also present three decades worth of observational data from a study of terrestrial and lake phenology on the campus of Paul Smith's College (PSC) in Paul Smiths, NY (Fig 1C) from 1990 to 2020.

Together, these observations enable us to address the following questions: (1) has climate changed in the Adirondack uplands during the last century? (2) did the phenology of plants,

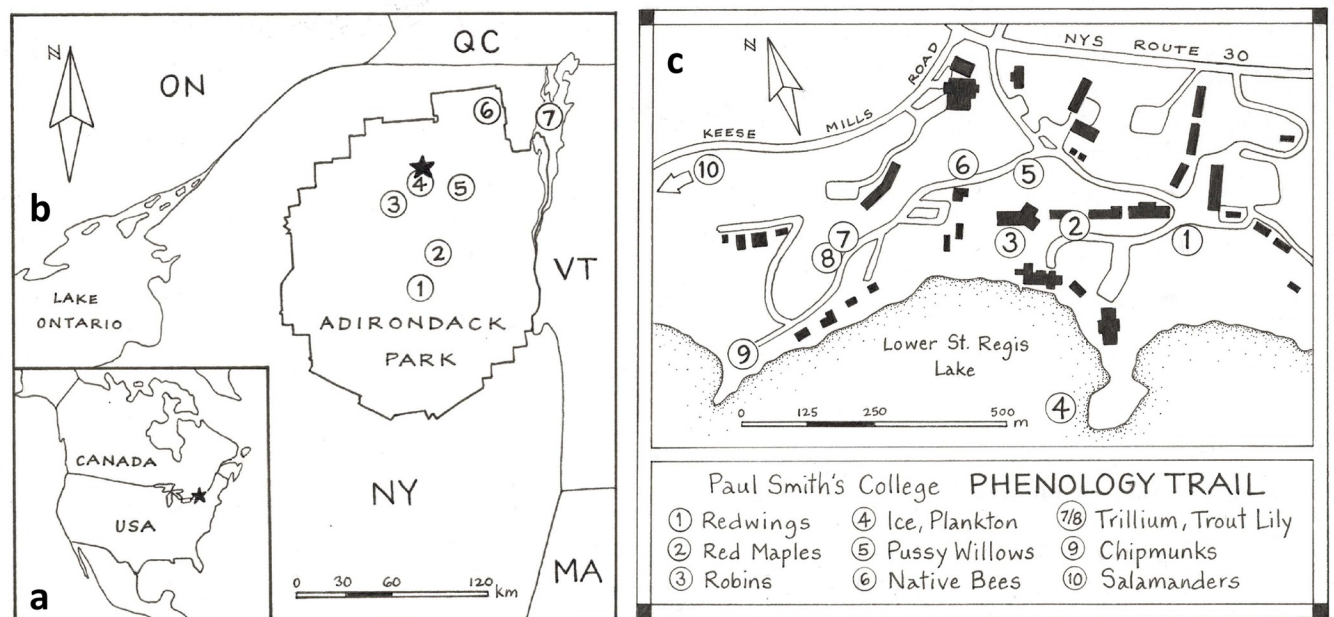


Fig 1. Site maps. a. Adirondack State Park (star). b. Regional map with study sites and weather stations indicated. (star) Paul Smith's College and Lower Saint Regis Lake. (1) Indian Lake station. (2) Adirondack Ecological Center, Newcomb. (3) Tupper Lake station. (4) Lake Clear. (5) Lake Placid and Mirror Lake. (6) Dannemora station. (7) Lake Champlain. c. Map of the Phenology Trail on the campus of Paul Smith's College. Buildings are indicated in solid black and monitoring locations are indicated by numbers.

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animals, or the lake ecosystem at PSC change between 1990 and 2020? (3) does climate variability influence phenology in the Adirondacks?, and (4) how are climate and phenology in the Adirondack uplands likely to change in the future?

Materials and methods

The PSC campus (44°26'09"N, 74°15'10"E) is located on a sandy glacial outwash plain at 488 m elevation on the northern shore of Lower Saint Regis Lake (Fig 1C). The lake formed following deglaciation 13,000 years ago after which the site was occupied by a long succession of Indigenous peoples, a wilderness resort (Paul Smith's Hotel, 1859–1930), and most recently PSC (1946–present) [23–25]. Mean annual temperature and precipitation in the vicinity of Paul Smiths since 1900 have been 4.8°C and 111 cm, respectively, with the greatest monthly precipitation totals occurring during June–August and the least in January–March [26].

Field observations

Most of the phenological data in this study were collected from the central portion of the PSC campus (Fig 1C). Informal monitoring of spring terrestrial phenology at PSC was begun by the first author (JCS) in 1990. In 2019, the terrestrial monitoring was formalized by the establishment of the Phenology Trail for which PSC students help to make the observations. Since 1990, lake surface water temperatures and plankton community composition have also been monitored in autumn from the "Picnic Point" site (Fig 1C, site #4) by JCS in conjunction with students and faculty in the Biology 101 laboratory course at PSC.

Dates upon which Lower St. Regis Lake froze over in late autumn to early winter were also monitored by JCS since 1990, building upon observations by other PSC faculty and staff that began in 1985. However, the record of spring thaw dates (i.e. "ice-out") was much longer than the other phenological records, having originated with an annual ice-out contest conducted by employees of the former Paul Smith's Hotel from 1909 to 1945 [23]. The contest was resumed in 1970 by faculty and staff at PSC and replaced with personal observations by JCS since 2005.

Terrestrial phenology (1990–2020). The spring phenology of five animal species was monitored on the Phenology Trail between 1990 and 2020. The arrival of redwinged blackbirds (*Agelaius phoeniceus*) and American robins (*Turdus migratorius*) was documented as first appearance on or near the campus (Fig 1C, sites #1 and #3, respectively). First emergence of native solitary bees (*Colletes inaequalis*) from their burrows was monitored on the south-facing grassy slope of Essex Hill (site #6). First emergence of Eastern chipmunks (*Tamias striatus*) from their overwintering burrows was monitored on a wooded esker ridge adjacent to Essex Hill (site #9). Migration of spotted salamanders (*Ambystoma maculatum*) from their subterranean habitats to vernal breeding pools was observed on the first three miles of Keese Mills Road beginning at the main entrance to the campus (site #10).

The spring phenology of four plant species was also monitored between 1990 and 2020. Blooming dates of red maples (*Acer rubrum*) were observed on mature trees distributed between the Freer Science Building and Pickett Hall (Fig 1C, site #2). Development of pollen on the catkins of pussy willows (*Salix discolor*) was monitored in a small wetland on the northern side of the library (site #5), and the sprouting and blooming dates of trout lilies (*Erythronium americanum*) and red trillium (*Trillium erectum*) were observed on the wooded western section of Essex Hill (sites #7 and 8).

Aquatic phenology (1990–2020). Monitoring of autumn lake temperatures and phytoplankton commenced in 1990 as part of the Introductory Biology laboratory curriculum at PSC. Under supervision by JCS and other instructors, students measured surface temperatures at Picnic Point (Fig 1C, site #4) with a hand-held thermometer and collected phytoplankton

with a plankton net for microscopic identification and tallying in the lab. Each of 20 students in 6–8 lab sections identified phytoplankton taxa and submitted their results for compilation by the instructor. These activities were repeated weekly from September until the lake froze in November or December. Some mismeasurements by individual students were inevitable but the combination of >150 such plankton observations per week minimized their impacts on the analyses considered here. The only student-generated data used in this aspect of the study were the surface temperatures and the dates of transition of phytoplankton dominance from easily identified cyanobacteria (*Anabaena*) to diatoms (mostly *Asterionella formosa*, *Aulacoseira subarctica*, *A. ambigua*, and *Fragilaria crotonensis*). These student activities were monitored and supplemented with additional documentation of temperature and plankton by JCS. A hiatus in the observations occurred from 1998 to 2006 when JCS was absent, and because measurements from early September were few in number due to scheduling issues this study focused mainly on data collected in October and November.

Ice phenology (1909–1945 and 1970–2020). The ice on Lower St. Regis Lake was considered "thawed" when the bay in front of the main campus was completely free of solid ice and "frozen" when ice was first present from shore to shore in the same bay. In years when new thin ice was subsequently broken up by wind or heating the final freeze dates were recorded as well, but only the first-freeze dates were used in this study (Fig 1C). Although ice-thaw dates were recorded since 1909 and freeze dates were recorded since 1985, we focused mainly on the ice records of the 1990–2020 interval for consistency with the time frame of the other phenological records.

Climatic reference sites (1900–2020)

Long-term records of monthly air temperatures and precipitation were not available in the immediate vicinity of PSC, so the climatic setting was inferred from weather records collected at USHCN weather stations nearby. Three upland stations were selected on the basis of proximity, similarity of elevation, and completeness of the dataset [26]. The Indian Lake station lies 73 km south of PSC, the Dannemora station lies 52 km north, and the Tupper Lake station lies 28 km to the west (Fig 1B).

The Dannemora station typically registered the warmest mean annual temperatures during the 1900–2020 period, presumably because of its lower elevation, but the Tupper Lake station's average was slightly warmer than that of Indian Lake despite its slightly higher elevation (Table 1). The Tupper Lake station also registered the most precipitation of the three stations. Correlations among the stations were strong for temperature ($R^2 = 0.9$, $P < 0.0001$) but less so for precipitation ($R^2 = 0.2$ – 0.3 , $P < 0.0001$) which is more spatially heterogeneous, particularly in a region with such complex topography. The weather records from the three sites were averaged together to produce composite time series of mean monthly temperatures and total precipitation (ADK3).

Statistical analyses

Although the focus of this study was primarily on the 1990–2020 interval, statistical analyses of climatic and ice-cover variability over two longer time frames were also conducted. For each time period, linear regression analyses were performed to test for significant trends.

Table 1. USHCN weather stations that were used to develop the ADK3 time series, with climate data from the 1990–2020 time frame.

Station	USHCN #	Latitude, Longitude	Elevation (m)	Mean T (°C)	Total P (cm)
Dannemora	301966	44.72°N, 73.72°W	408	6.3	110
Indian Lake	304102	43.76°N, 74.27°W	506	5.2	110
Tupper Lake	308631	44.23°N, 74.44°W	512	5.3	115

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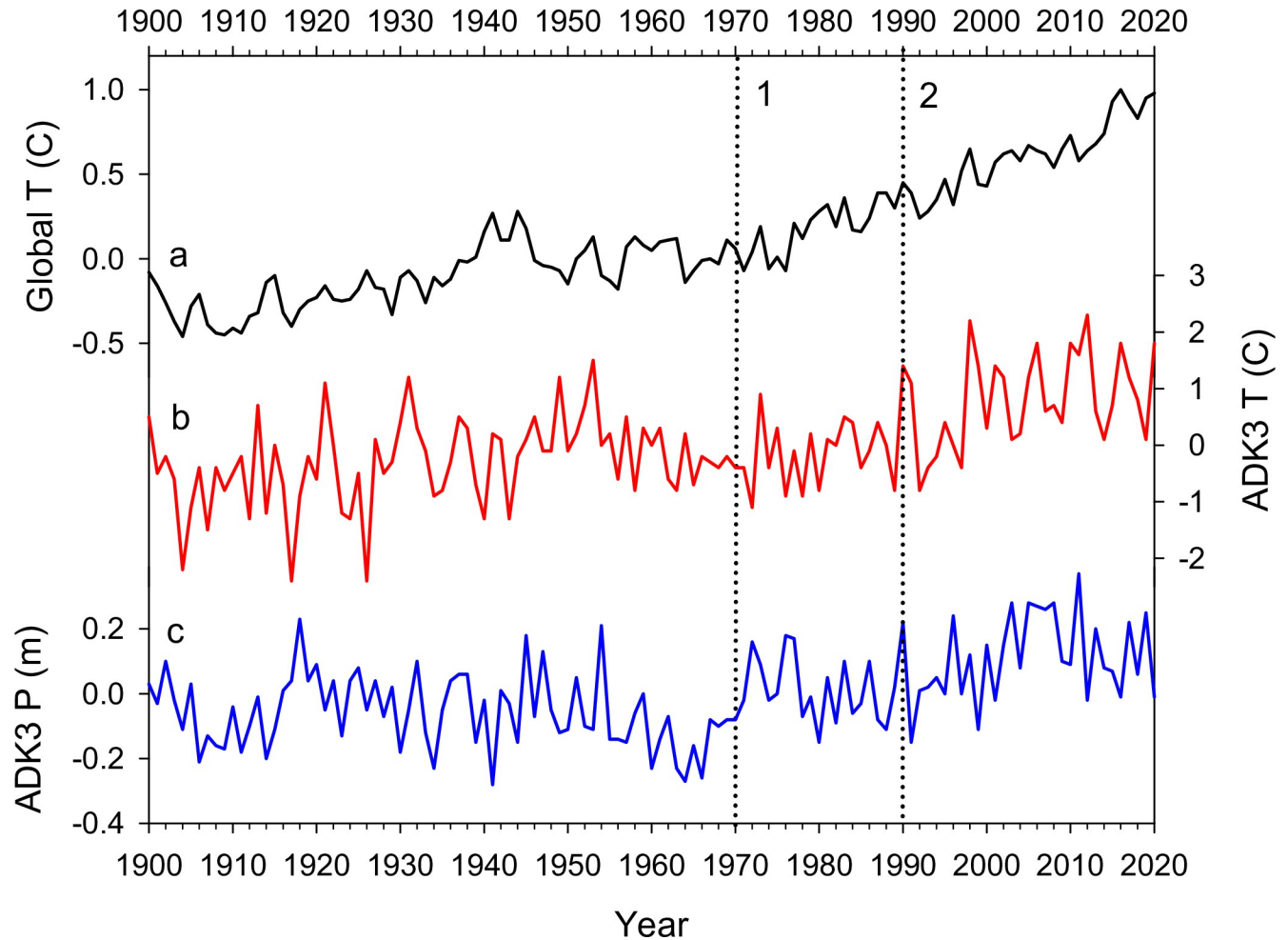


Fig 2. Global temperature anomalies (a) in comparison to ADK3 composite temperature (b) and precipitation (c) anomalies from 1900 to 2020. The global temperature data use the mean of the 1901–2000 period as the baseline [27]. The ADK3 series use the 1900–2020 base period. Dotted lines designate the three main time frames under consideration as referred to in the text: 1900–2020, (1) 1970–2020, and (2) 1990–2020.

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The century-scale period 1900–2020 ($n = 121$) was used for long-term perspectives on Adirondack climate and ice dynamics as well as for comparison to the global temperature anomaly record (Fig 2). The period 1970–2020 ($n = 51$) was examined because it encompassed the interval for which the PSC ice-cover records from Lower Saint Regis Lake were available. It also represented the time frame during which human influences on global climate have become most clearly prominent [1, 2], which provided a useful context for estimating future conditions as anthropogenic warming continues. The period 1990–2020 ($n = 31$) was selected because it approximated the standard 3-decade sliding time frame for determining current climate and because it matched the temporal framework of the phenological study.

For analyses of relationships among phenological and climatic variables, temporal gaps in the phenology time series required elimination of climate data from years in which phenology data were unavailable. No linear regression analyses were performed on the lake temperature and phytoplankton data due to a hiatus in the records from 1998 to 2006. Instead, one-tailed *t*-tests were performed to compare monthly mean temperatures and phytoplankton community transition dates within the 1990–1997 and 2007–2020 intervals.

Pearson product moment correlation coefficients were used to assess the relationships between climate records and each of the phenological variables. Analyses were performed using both current and prior year climate data in order to allow for the detection of potential interannual legacy effects on phenology. In addition to the correlation analyses that were conducted with a standard threshold of $P < 0.05$ as the primary test indicator of statistical significance, a Bonferroni correction was also applied to the alpha (0.05) to account for multiple correlations between the phenological variable of interest and the monthly climate variables ($n = 13$, $\alpha = 0.0038$). Applying the Bonferroni correction is a more conservative methodology when dealing with multiple comparisons [28], so although we relied on the correction to help identify strong, significant correlations and reduce the risk of Type I ("false positive") errors, we caution against basing determinations of the relevance of a correlation entirely on whether or not it is deemed "significant" in this particular kind of analysis.

Projected changes in phenology by the end of this century were estimated for each species using two methodologies. One approach was to identify the strongest available relationship (R-value) between monthly temperature and the phenomenon in question, then use linear regression equations from those selected records to estimate future (2020–2100) phenological changes due to seasonal warming trends as previously determined from the ensemble means of 16 global circulation models that were down-scaled to focus on the Champlain-Adirondack watershed [12]. The other less quantitative approach was to apply the anticipated seasonal warmings to the mean monthly temperatures of the 1990–2020 interval and visually estimate temporal offsets of seasonal climatic conditions with which the phenological events are currently associated.

The seasonal temperature projections that we used [12] were constrained by the moderate (B1) and extreme (A2) scenarios of greenhouse gas (GHG) emissions, roughly equivalent to the more recently developed scenarios RCP 2.6 and 8.5 [29–31]. All of the regional projections anticipated warmer mean annual temperatures by the end of this century that increased with the intensity of GHG emissions. Projected warming in winter, spring, summer, and autumn between 2010 and 2099 was 2.0, 1.7, 1.9, and 1.7°C respectively in the B1 scenario and 4.7, 3.9, 4.0, and 3.6°C in the A2 scenario.

Results

In addressing the four primary questions of this study, we found that climatic conditions in the Adirondack uplands did change significantly over the last century and half-century, but less so during the recent 1990–2020 interval (question #1). Variability among the phenological records over the 1990–2020 interval was similarly muted and inconsistent (#2). Correlation analyses revealed strong relationships among climatic parameters and some but not all of the phenological records (#3), indicating that the responses of different species to anticipated future warming in the Adirondacks are likely to vary substantially, as well (#4).

Adirondack climate change since 1900

Over the long term, the climatic setting of the Adirondack uplands became significantly warmer and wetter between 1900 and 2020 (Fig 2, Table 2). The ADK3 composite series registered a rise in mean annual temperatures of 1.7°C at an average rate of 0.14°C/decade, and every month but January, March, and October experienced significant warming with the greatest rise in February and the least in July. During that same period the ADK3 precipitation record registered significant wetting trends in April, August, October, and December with maximum wetting in October and the least in December. A pronounced stepwise increase in precipitation occurred ca. 1970 following unusually dry conditions during the 1960s (Fig 2).

Table 2. Linear trends in temperature (left columns) and precipitation (right columns) for three time intervals in the ADK3 composite series.

Interval (months)	R ²	Slope (°C/yr)	P	Change (°C)	R ²	Slope (cm/yr)	P	Change (cm)
1900–2020								
2	0.139	0.029	<0.0001	3.6	-	-	-	-
4	0.067	0.014	0.0040	1.7	0.070	0.231	0.0034	2.8
5	0.079	0.014	0.0018	1.7	-	-	-	-
6	0.074	0.009	0.0025	1.1	-	-	-	-
7	0.058	0.008	0.0077	1.0	-	-	-	-
8	0.147	0.014	<0.0001	1.7	0.068	0.254	0.0038	3.1
9	0.071	0.011	0.0032	1.3	-	-	-	-
10	-	-	-	-	0.059	0.299	0.0071	3.6
11	0.104	0.018	0.0003	2.2	-	-	-	-
12	0.097	0.024	0.0005	2.9	0.035	0.150	0.0406	1.8
annual	0.307	0.014	<0.0001	1.7	0.170	0.002	<0.0001	19.4
1970–2020								
1	0.077	0.056	0.0489	2.9	-	-	-	-
6	0.080	0.022	0.0447	1.1	0.084	1.000	0.0374	5.1
7	0.124	0.027	0.0057	1.4	-	-	-	-
8	0.164	0.031	0.0032	1.6	-	-	-	-
9	0.372	0.060	<0.0001	3.1	-	-	-	-
10	0.153	0.047	0.0045	2.4	0.134	1.149	0.0083	5.9
12	0.086	0.058	0.0365	3.0	-	-	-	-
annual	0.373	0.036	<0.0001	1.8	0.161	0.035	0.0035	17.9
1990–2020								
7	0.240	0.069	0.0026	2.1	-	-	-	-
9	0.284	0.083	0.0020	2.6	-	-	-	-

Months in which significant trends occurred during each time frame are indicated numerically. Monthly trends that were not statistically significant ($P \geq 0.05$) are omitted or indicated with dashes.

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From 1970 to 2020 mean annual temperatures rose more rapidly ($0.36^\circ\text{C}/\text{decade}$, total of 1.8°C), and all months except February through May and November warmed significantly with the greatest increase in September and the least in June. The months with significant wetting trends were limited to June and October with the greater wetting in October.

The recent 1990–2020 interval saw no statistically significant trend in mean annual temperatures, and significant warming occurred only in July and September with the greater rise in September. No significant monthly wetting trends occurred over the 1990–2020 interval.

Changes in phenology (1990–2020)

The only significant phenological trend among the animal species during the 1990–2020 time frame was for robins, who arrived ca. 15 days earlier (Table 3). None of the botanical phenomena displayed significant temporal shifts in phenology.

Mean lake surface temperatures during October warmed by 1.9°C on average from the 1990–1997 interval to 2007–2020 (Table 4), and similar warming occurred during the first (1.9°C) and last (1.5°C) halves of October. Lake warming was also significant during late September (5.3°C), but observations for that month were far less numerous during the 1990–1997 interval ($n = 5$) than during the 2007–2020 interval ($n = 35$). There was no significant change among mean surface temperatures in November, the dates on which surface temperatures

Table 3. Temporal trends in phenology of species and lake ice on the PSC phenology trail over three time intervals.

Time frame & phenology	n	Min. date	Max. date	Mean date	R ²	Slope (days/yr)	P	Shift (days)
1990–2020								
Redwing	23	67	107	83.2	0.036	0.204	0.3889	-
Robin	26	70	102	87.0	0.208	-0.477	0.0192	-14.8
Chipmunk	18	64	117	83.4	0.064	0.399	0.3138	-
Salamander	23	84	118	103.2	0.141	-0.392	0.0770	-
Bee (M)	29	78	112	98.7	0.089	-0.285	0.1147	-
Bee (F)	16	92	118	106	0.217	-0.326	0.0689	-
Pussy willow	15	97	126	114.8	0.061	0.249	0.3743	-
Red maple	23	97	131	117.2	0.010	-0.099	0.6502	-
Trout lily (S)	23	102	124	114.3	0.029	0.127	0.4384	-
Trout lily (B)	11	116	132	124.9	0.060	-0.140	0.4667	-
Trillium (S)	18	105	124	117.3	0.047	-0.157	0.3867	-
Trillium (B)	14	114	136	126.4	0.011	-0.062	0.7251	-
Ice thaw	31	85	124	109.2	0.060	-0.265	0.1843	-
Freeze-up	28	319	369	337.9	0.010	-0.128	0.6218	-
1970–2020								
Ice thaw	51	85	132	110.4	0.080	-0.199	0.0447	-10.2
1909–2020								
Ice thaw	88	85	132	112.1	0.054	-0.066	0.0305	-7.4

(S): shoots of trout lilies and trillium. (B): blooming of trout lilies and trillium. Bee(M) and Bee(F): emergence of male and female *Colletes* bees, respectively. Absence of a clear temporal shift due to the lack of a statistically significant linear trend ($P \geq 0.05$) is indicated with dashes. Number of years sampled within the 1990–2020 interval is indicated by "n." "Shift" refers to the change in phenological date over the 1990–2020 time frame. All dates are given in Julian days.

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reached 4°C (generally in November), or the mean dates on which cyanobacteria were replaced by diatom-dominated phytoplankton communities (generally in mid-October).

There was no statistically significant shift in spring thaw or autumn freeze dates during the 1990–2020 interval. That short-term lack of consistent change was in contrast to the longer-term ice records (Table 3) in which the lake thawed one week earlier over the 1900–2020 period and thawed 10 days earlier during the 1970–2020 period.

Table 4. Mean monthly surface temperatures and autumn phytoplankton phenology at Lower Saint Regis Lake.

Time frame	n	Mean	Time frame	n	Mean	P
1990–1997			2007–2020			
lSept T (°C)	5	13.2	lSept T (°C)	35	18.5	<0.0001
eOct. T (°C)	25	13.6	eOct. T (°C)	29	15.5	0.0020
Oct. T (°C)	68	10.9	Oct. T (°C)	66	12.8	0.0008
lOct. T (°C)	42	9.4	lOct. T (°C)	35	10.9	0.0038
Nov. T (°C)	49	5.4	Nov. T (°C)	51	5.7	-
4°C date	6	315.8	4°C date	13	327.7	-
Cyan:Diat date	5	287.5	Cyan:Diat date	13	291.9	-

The time intervals of 1990–1997 and 2007–2020 were compared using one-tailed t-tests to identify significant differences in means ($P < 0.05$). Non-significant differences are indicated by a dash. lSept, eOct, and lOct. T = mean lake surface temperatures during the last half of September, first half of October, and second half of October, respectively. "4°C" indicates approximate date at which the lake surface temperature reached 4°C, a proxy indicator of seasonal lake turnover. "Cyan:Diat" indicates date of transition from cyanobacterial to diatom-dominated phytoplankton communities. All dates are given in Julian days. Data were not collected between 1997 and 2007.

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Climatic influences on phenology (1990–2020)

Analyses of the current- and previous-year climatic variables among the phenology records without the Bonferroni correction produced larger numbers of significant correlations (Table 5) due to the less restrictive threshold of statistical significance ($P < 0.05$ versus 0.0038). Several of the correlations, indicated by asterisks in Table 5, were obviously spurious because the timing of the relationships was unrealistic. For example, an apparent correlation between the spring migration dates of salamanders with temperatures in the following autumn that persisted even after the Bonferroni correction (Fig 3, Table 5) helped to demonstrate the limitations of statistical analyses alone in eliminating such Type I errors. In addition, the conservative nature of the correction eliminated otherwise significant correlations that were also clearly supported by the ecology or behavior of the phenomena in question ("false negative" Type II errors). We therefore used the full suite of significant ($P < 0.05$) correlations in Table 5 in combination with Fig 3 to identify climate-phenology relationships that were most informative and likely to be of predictive value.

With the Bonferroni correction, statistically significant correlations between terrestrial phenology and current-year monthly temperatures occurred only in March and April (Fig 3A). March temperatures were negatively correlated with dates of salamander migration and emergence of male bees as well as the blooming dates of maples and emergence of trout lily shoots. April temperatures were negatively correlated with the emergence of trout lily and trillium shoots and the blooming of willows, maples and trout lilies. These relationships were strong enough to produce significant correlations with annual temperature as well. No significant correlations among the terrestrial phenology records and precipitation were indicated (Fig 3B). Analyses of relationships among phenology and climatic variables during the preceding year using the Bonferroni correction (Fig 3C and 3D) yielded no significant relationships except for negative correlations with temperature for the emergence dates of trillium shoots and bloom dates of maples, both in relation to the preceding November.

Due to the availability of longer observational records for lake ice, we extended the time frames of correlation analyses to the 1909–2020 period for thaw dates and 1985–2020 for freeze dates. Lake thaw dates over the full 1909–2020 interval were negatively correlated with temperatures in February through April (Fig 3), and significant correlations with freeze dates over the 1985–2020 interval occurred for current-year temperatures in November and December (all positive). Without the Bonferroni correction we also found significant correlations between thaw dates and temperatures in the previous December and precipitation in March of the previous year (possibly spurious), and between freeze dates and temperatures in May and September in addition to total precipitation of the preceding year (Table 5).

Future changes in phenology

We applied projected 21st century warming trends [12] to temperature-phenology relationships in months for which the strongest correlations were obtained in order to estimate how seasonal warming is likely to influence animals, plants, and lake ice by 2100. The Bonferroni-corrected analyses (Fig 3) identified those strongest correlations in most cases but yielded no significant correlations for redwings, robins, chipmunks and female bees (potential Type-II error). In those latter cases, temperature-phenology relationships with a lower significance threshold of $P < 0.05$ (Table 5) were used instead for identifying the strongest correlations.

This approach yielded advances in spring phenology of less than one week for the terrestrial species in the B1 emissions scenario and 1–2 weeks in the A2 scenario (Table 6). One exception was a shift to later dates that was inferred for the chipmunks, the only non-migratory species whose spring phenology lacked strong correlations with March or April temperatures

Table 5. Correlation and linear regression analyses of plant and animal phenology at PSC with temperature (left columns) and precipitation (right columns) in the ADK3 composite series.

Phenology (months)	n	R ²	Slope (days/°C)	P	R ²	Slope (days/mm)	P
Redwing							
3	23	0.187	-1.785	0.0391	-	-	-
<i>p6*</i>	23	0.240	-4.577	0.0178	-	-	-
Robin							
<i>annual</i>	26	0.189	-4.527	0.0268	-	-	-
3	26	0.294	-1.894	0.0042	-	-	-
<i>p12</i>	26	0.168	-1.555	0.0376	-	-	-
Chipmunk							
2	18	0.305	3.469	0.0175	-	-	-
<i>p2</i>	18	0.364	2.753	0.0081	-	-	-
<i>p10</i>	18	0.221	4.182	0.0490	-	-	-
Salamander							
<i>annual</i>	23	0.387	-6.608	0.0015	-	-	-
2	23	0.252	-1.648	0.0073	-	-	-
3	23	0.478	-2.139	0.0003	-	-	-
<i>11*</i>	23	-	-	-	0.348	0.147	0.0030
<i>p8</i>	23	-	-	-	0.213	-0.100	0.0268
<i>p9</i>	23	0.247	-3.086	0.0160	-	-	-
<i>p11</i>	23	0.266	-2.028	0.0117	-	-	-
Bee (male)							
<i>annual</i>	29	0.273	-5.367	0.0037	-	-	-
2	29	0.176	-1.275	0.0236	-	-	-
3	29	0.366	-2.027	0.0005	-	-	-
<i>p2*</i>	29	-	-	-	0.140	-0.139	0.0462
<i>p8</i>	29	-	-	-	0.245	-0.113	0.0063
Bee (female)							
<i>annual</i>	16	0.479	-6.030	0.0030	-	-	-
3	16	0.261	-1.547	0.0426	-	-	-
<i>p1*</i>	16	0.289	1.400	0.0320	-	-	-
Willow							
<i>annual</i>	15	0.542	-7.535	0.0017	-	-	-
4	15	0.618	-3.266	0.0005	-	-	-
<i>p1*</i>	15	0.418	1.783	0.0091	-	-	-
Maple							
<i>annual</i>	23	0.579	-7.544	<0.0001	-	-	-
1	23	0.236	-1.534	0.0186	-	-	-
2	23	0.246	-1.459	0.0160	-	-	-
3	23	0.461	-2.255	0.0004	-	-	-
4	23	0.494	-3.666	0.0002	-	-	-
<i>p8</i>	23	-	-	-	0.263	-0.127	0.0123
<i>p11</i>	23	0.335	-2.320	0.0038	-	-	-
Trout lily (s)							
<i>annual</i>	23	0.447	-5.499	0.0005	-	-	-
1	23	0.187	-0.932	0.0391	-	-	-
2	23	0.259	-1.131	0.0131	-	-	-
3	23	0.416	-1.450	0.0009	-	-	-
4	23	0.377	-2.118	0.0018	-	-	-
<i>p10</i>	23	0.238	1.843	0.0182	-	-	-

(Continued)

Table 5. (Continued)

Phenology (months)	n	R ²	Slope (days/°C)	P	R ²	Slope (days/mm)	P
<i>p11</i>	23	0.179	-1.260	0.0442	-	-	-
Trout lily (b)							
<i>annual</i>	11	0.507	-5.354	0.0140	-	-	-
3	11	0.375	-1.298	0.0455	-	-	-
4	11	0.739	-2.156	0.0007	-	-	-
Trillium (s)							
annual	18	0.603	-5.602	0.0002	-	-	-
3	18	0.406	-1.365	0.0045	-	-	-
4	18	0.555	-2.505	0.0004	-	-	-
<i>p3</i>	18	-	-	-	0.222	-0.113	0.0481
<i>p8</i>	18	-	-	-	0.378	-0.093	0.0065
p11	18	0.632	-2.204	<0.0001	-	-	-
Trillium (b)							
4	14	0.552	-2.706	0.0023	-	-	-
<i>p2</i>	14	-	-	-	0.461	-0.153	0.0076
<i>p3</i>	14	-	-	-	0.401	-0.131	0.0148
<i>p8</i>	14	-	-	-	0.483	-0.113	0.0057
Lake freeze							
annual	33	0.343	8.314	0.0003	-	-	-
5	33	0.239	3.636	0.0039	-	-	-
9	33	0.146	3.251	0.0283	-	-	-
11	33	0.576	4.879	<0.0001	0.374	-0.222	<0.0001
12	33	0.271	2.080	0.0019	-	-	-
<i>pannual</i>	33	-	-	-	0.170	0.381	0.0171
p8*	33	-	-	-	0.256	0.179	0.0026
Lake thaw							
annual	88	0.347	-6.506	<0.0001	-	-	-
2	88	0.111	-1.239	0.0015	-	-	-
3	88	0.506	-2.903	<0.0001	0.052	0.0934	0.0327
4	88	0.457	-3.472	<0.0001	-	-	-
7*	88	0.107	-2.992	0.0019	-	-	-
<i>p12</i>	88	0.058	-0.896	0.0232	-	-	-

(s): shoots of trout lily (TRT) and red trillium (TRIL). (b): blooming of trout lily and red trillium. Bee(M) and Bee(F): emergence of male and female *Colletes* bees, respectively. Months in which significant ($P < 0.05$) linear trends occurred during each time frame are indicated numerically. Correlations that were not statistically significant are indicated with dashes. Monthly label with "p" indicates a month during the preceding year (e.g. p11 = November of previous year). Bold font indicates months with significant correlations as determined with Bonferroni correction in Fig 3. Italicized font indicates relationship with a P value between 0.05 and the 0.0038 threshold for inclusion in Fig 3. Asterisks indicate correlations that the authors consider most likely to be spurious.

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(Fig 3, Table 5). Like the freeze dates on Lower Saint Regis Lake that moved later in our inferred projections, the spring emergence of chipmunks also moved later in response to temperatures during the preceding autumn.

Discussion

The climate of the Adirondack uplands has become 1.7°C warmer and 19 cm/yr wetter on average since 1900 (Table 2), with a 0.14°C/decade mean warming rate that exceeded the

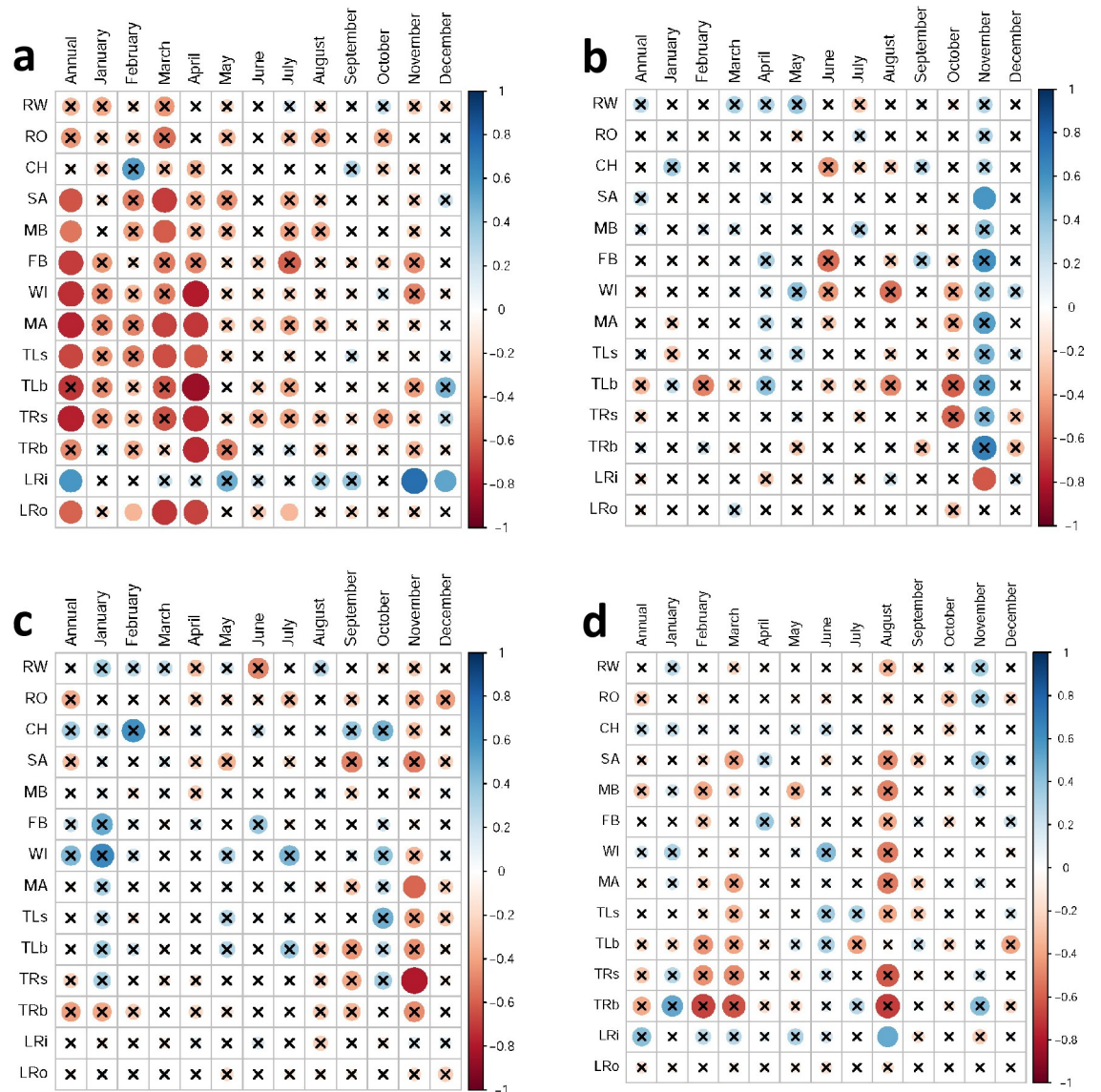


Fig 3. Correlations among the phenologies of plants, animals, and lake ice on the PSC Phenology Trail with (a, b) current-year and (c, d) previous-year monthly temperatures and precipitation, respectively, over the 1990–2020 interval as determined after application of Bonferroni correction [28]. RW = redwing arrival. RO = robin arrival. CH = chipmunk emergence. SA = salamander migration. MB = Male bee emergence. FB = female bee emergence. WI = pollen on pussy willows. MA = red maple blooming. TLs = trout lily shoot emergence. TLb = trout lily blooming. TRs = trillium shoot emergence. TRb = trillium blooming. LRI = freeze date for Lower St. Regis Lake. LRO = ice thaw date for Lower St. Regis Lake. "X" indicates lack of statistical significance at the 0.0038 level. Size and darkness of circle represents magnitude of positive (blue) and negative (red) correlation coefficients.

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global warming rate of 0.09°C/decade (Fig 2) [27]. The relatively rapid rate of change in this region is not surprising because higher latitudes in general are warming faster than the global average due in large part to the amplifying effects of declining snow and sea ice cover, particularly in the Arctic [3, 29, 30].

Although the climate of the Adirondack uplands has warmed over the long term, trends over shorter time frames varied substantially. The 1970–2020 interval saw a similar amount of warming but during the 1990–2020 period more variable temperatures flattened the upward trend while global mean temperatures continued to rise (Fig 2, Table 2). Short-term variability

Table 6. Linear relationships among monthly temperature and phenology series between 1990 and 2020, with applications to future projections.

Phenology Month	Rs _q	P	Slope days/°C	B1 (days)	A2 (days)
Redwing					
MarT	0.187	0.0391	-1.785	-3.0	-7.0
Robin					
MarT	0.294	0.0042	-1.894	-3.2	-7.4
Chipmunk					
OctT	0.221	0.0490	4.182	8.4	19.7
Salamander					
MarT	0.478	0.0003	-2.139	-3.6	-8.3
Bee (M)					
MarT	0.366	0.0005	-2.027	-3.7	-8.6
Bee (F)					
MarT	0.261	0.0426	-1.547	-2.6	-6.0
Pussy Willow					
AprilT	0.618	0.0005	-3.266	-5.6	-12.7
Red maple					
AprilT	0.494	0.0002	-3.666	-6.2	-14.3
TRT shoot					
MarT	0.416	0.0009	-1.450	-2.5	-5.7
TRT bloom					
AprilT	0.739	0.0007	-2.156	-3.7	-8.4
TRIL shoot					
AprilT	0.555	0.0004	-2.505	-4.3	-9.8
TRIL bloom					
AprilT	0.552	0.0023	-2.706	-4.6	-10.6
Lake freeze					
NovT	0.576	<0.0001	4.879	8.3	17.6
Lake thaw					
MarT	0.506	<0.0001	-2.903	-4.9	-11.3

"B1" and "A2" columns: inferred number of days of phenological date shift between 2020 and 2100 based on mean projected seasonal warming in the Champlain Basin under the moderate B1 and extreme A2 fossil fuel emissions scenarios, respectively [12]. TRT: trout lily. TRIL: red trillium.

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produced similar brief leveling of the long-term warming trend in 1960–1980 and 1970–1990 and is not likely to prevent the long-term trend from continuing upward during the remainder of this century [4, 12].

The scarcity of seasonal climatic trends in winter and spring between 1990 and 2020 was reflected in a lack of significant trends among the spring phenology records of that time frame with the exception of earlier arrivals by robins (Table 3). In contrast, the pronounced century-scale warming in July and September has continued into the present (Table 2). The mean lapse rate based on USHCN weather stations in and adjacent to the Adirondack uplands is 0.55°C/100 m of elevation, so warming of 2.1°C in July and 2.6°C in September during the 1990–2020 time frame could be equivalent to a drop of ca. 300–375 m in elevation (close to that of Elizabethtown, near Lake Champlain) during summer and early autumn.

Terrestrial spring phenology and climate

Although only one of the spring phenology records displayed a significant temporal trend, most of them exhibited strong sensitivity to March and April temperatures and, in some cases,

to temperatures during the preceding winter (Fig 3, Table 5). With the exception of chipmunk emergence dates all of the correlations with terrestrial phenology records were negative, meaning that warmer winter or spring temperatures were associated with earlier migration, emergence, sprouting, or blooming. No reliable correlations with current-year precipitation were apparent among the terrestrial phenology records, but several of them were negatively correlated with precipitation during the preceding August, suggesting that increased soil moisture and/or shading by cloud cover in summer might favor earlier phenology among salamanders, male *Colletes* bees, red maples and trillium during the following spring.

Many of the significant correlations among spring phenologies and monthly temperatures in Table 5 offer potential insights into the ecology or behavior of the species under consideration regardless of whether or not they remained following application of the Bonferroni correction (Fig 3). We examine here some of those relationships for individual species that are ecologically informative and likely to be of predictive value.

Animal species and climate. Redwinged blackbirds and robins overwinter in regions outside the Adirondack uplands so their migration habits are influenced by environmental conditions elsewhere as well as locally. The male birds normally appear at PSC ahead of the females in March (Table 3) when snow is still present, and the negative correlations between arrival dates and temperatures in both March and (for robins) the previous December (Table 5) suggest that warmer conditions in winter and spring favor earlier arrivals by speeding the retreat of snow cover that helps the birds to establish breeding territories and forage on exposed ground. The lack of a trend in the arrival dates of redwings is consistent with the lack of trends in March temperatures but why, then, did the robin migration shift to earlier dates? The latter advance is probably not a statistical artifact because it has been documented elsewhere in North America [32], so factors other than local temperature must account for it. Possibilities include weather conditions and food availability elsewhere within the geographic ranges used by the robins, particularly snow cover conditions along their migration pathways.

A positive correlation between emergence dates of chipmunks and temperatures during the previous October might be related to longer time frames available for food-storage due to warmer conditions in autumn that could allow the animals to remain in their burrows longer. The positive correlations with current- and previous-year February temperatures might be spurious because we presume that warmer winters should encourage emergence dates to shift earlier by encouraging the animals to end their subterranean torpor sooner. We hesitate to label them as such in Table 5 because the correlations are strong and occur within the same month, but in light of this uncertainty we chose to focus instead on the positive relationship to October temperatures in later analyses.

Earlier migration dates for salamanders were correlated with warmer temperatures in February, March, and the preceding autumn that can reduce the depth or duration of frost in the forest soils within which the animals overwinter. Warmer winters also hasten the melting of snowpack that helps to produce the vernal pools in which the salamanders breed. Because February and March temperatures did not increase significantly during the study period the lack of a clear trend in migration dates (Table 3) is to be expected. Perhaps surprisingly, although the migrations tend to occur on warm, rainy evenings in April the migration dates were not significantly correlated with April temperatures or precipitation. The negative correlation with precipitation during the preceding August might reflect an influence of summer soil moisture on the salamanders that could carry over to the following spring.

Emergence of ground-dwelling *Colletes* bees was negatively correlated with temperatures in March and, for the males, in February as well. These relationships are probably related to thawing and warming of the soil that encourages the insects to emerge after having developed underground since the previous spring. The negative correlation with precipitation during the

previous August when the male bees lay dormant in moisture-resistant capsules several feet down in the soil may be spurious, particularly because no such relationship was apparent with the female bees. However, we hesitate to reject it altogether because several of the other phenology records displayed it as well (Table 5).

Plant species and climate. Onset of the production of pussy willow pollen was negatively correlated with temperatures in April, the month during which the pollen typically appears (Tables 3 and 5), meaning that the flowers tend to develop earlier under warmer conditions. The lack of correlations with precipitation is expected because the willows grow in a perpetually moist wetland habitat.

Of the species examined here red maples and trout lilies displayed the most numerous correlations with temperature. They mainly occurred during the four months leading up to late April when the maples bloom and trout lilies sprout in addition to the preceding November and, for trout lilies, the preceding October (Tables 3 and 5). Blooming dates of trout lilies were strongly correlated with their sprouting dates ($R^2 = 0.77$, $P = 0.0002$) as well as with March and April temperatures. These results suggest that shorter, milder winters that allow soils to thaw and warm earlier in spring encourage these species to flower and/or sprout sooner. The similarity of responses to temperature variability among these two species might also reflect the dependence of trout lily leaf growth on the brief and variable time frame between snowmelt and leafing out of the forest canopy [33] as well as mutualistic relationships between trees and understory plants through mycorrhizal fungal networks [34, 35]. The correlation of maple bloom dates with precipitation during the preceding August might reflect sensitivity of growth rates to summer drought [36], in which case a drier summer might contribute to later blooming the following spring by, for example, reducing photosynthetic carbon reserves.

Sprouting dates of red trillium were correlated with temperatures in March, April, and the preceding November, a pattern similar to that of the maple flowering record. As with the trout lilies, bloom dates were strongly related to sprouting dates ($R^2 = 0.73$, $P = 0.0018$), but the sprouting and blooming dates of trillium were also linked to precipitation during the preceding March and August. We have no ready ecological explanation for the relationships to precipitation, particularly because trout lilies displayed no such sensitivity, but the existence of significant correlations in the same two months for the sprouting and blooming dates of trillium suggests that they may not be statistical artifacts. We speculate that they might have something to do with the quality of the growing season that could influence carbohydrate reserves or with climatic effects on the insects, slugs, mycorrhizae or other organisms with whom the plants interact [34, 37, 38].

The reliability of such analyses is somewhat weakened by temporal discontinuities in the records, as none of our phenological records fully represent the 31 years from 1990 to 2020 ($n = 11$ – 29 years). Nonetheless, most of the patterns found among the terrestrial phenomena and spring climates are remarkably consistent among species. Together with the lack of concurrent warming in late winter and spring or precipitation trends between 1990 and 2020, these findings help to account for the general lack of temporal trends among the phenological records in recent decades.

Lake phenology

Lake surface temperatures warmed significantly in October (Table 4) along with regional warming in July through September (Table 2). We consider the large magnitude of the warming (5.3°C) calculated for September to be unreliable because only five measurements were available from September during the 1990–1997 period, but the general warming trend is probably real for that month as well. The lack of atmospheric warming in October and November during the

1990–2020 time frame contributed to the lack of significant trends in lake temperatures in November and the date at which the lake cooled to 4°C (typically in November).

Although the durations and intensities of thermal stratification and deep-water oxygen depletion in Lower Saint Regis Lake were not measured directly in this study, it is likely that they increased along with water temperatures in late summer and early autumn during the last three decades. The weakening of stratification in autumn triggers a re-organization of the phytoplankton community in which buoyant cyanobacteria (mostly *Anabaena*) are replaced by diatoms who tend to rely more on vertical mixing to keep them suspended in the euphotic zone. Considering the air and lake warming trends observed during early autumn we expected the mid-October transition from cyanobacteria to diatoms to be delayed as well, but no such change was indicated. We surmise that the lack of a shift in the transition date might reflect a lack of precision in methodology. The phytoplankton transition is a gradual process influenced by temperature, precipitation, and wind conditions, and the mean dates were calculated from transition periods ranging in duration from two days to two weeks.

The timing of ice thaw on Lower Saint Regis Lake advanced to earlier dates by about one week since record-keeping began in 1909 (Table 3), which is consistent with significant century-scale climatic warming in autumn, winter, and spring that can reduce ice thickness and strength (Fig 4, Table 2). From 1970 to 2020 the thaw dates also occurred earlier despite the lack of warming trends in spring over that time period, suggesting that warming in early winter is a likely cause. The lack of significant trends in thaw or freeze dates during the recent 1990–2020 interval is consistent with the scarcity of trends in winter and spring temperatures as well as the other phenology records during that shorter time frame.

The record of lake freeze-up dates in relation to temperature suggests that warmer conditions in May, September, November, and December can delay freezing, presumably by adding more thermal energy to the lake's annual heat budget (Tables 4 and 5). Earlier thaw dates during the preceding spring also appear to delay freezing ($R^2 = -0.35$, $P = 0.023$) through a similar process, as do warmer lake surface temperatures in November ($R^2 = 0.50$, $P = 0.013$). Negative correlations with precipitation in November and the year as a whole suggest that increased insolation from reduced cloud cover associated with dry weather might also delay freezing.

Applicability to the Adirondack region and elsewhere

Most of the variability in the ADK3 temperature record is comparable to that reported in the ClimAID study of New York State's climate as a whole [4]. ClimAID reported a warming of 2.4°F (1.1°C) between 1970 and 2010, somewhat less than the warming registered in the ADK3 series for that time frame (1.8°C). Our finding that the Adirondack uplands have warmed faster than the global average between 1900 and 2020 is consistent with a regional study of temperatures in New England that obtained similar results over the same time frame with the greatest mean seasonal warming in winter and the least in spring [40]. The relative flattening of the long-term warming trend seen in the Adirondack records during the last 2–3 decades is also apparent in much of New England [41, 42].

The ClimAID study reported no significant trend in precipitation over the state as a whole since 1900, but the ADK3 series displayed wetting trends from 1900–2020 and 1970–2020 that are also reflected in lake level records from the region [12]. Patterns of precipitation are typically less consistent over large geographical areas than temperature, and we tentatively attribute the differences among Adirondack and statewide averages to site-specific factors such as topography and lake effect precipitation downwind of the Great Lakes [43].

A record of plant phenology from the Adirondack Ecological Center (AEC) in Newcomb, NY (Fig 1B), is consistent the records from PSC. Previous analyses of bloom dates of red

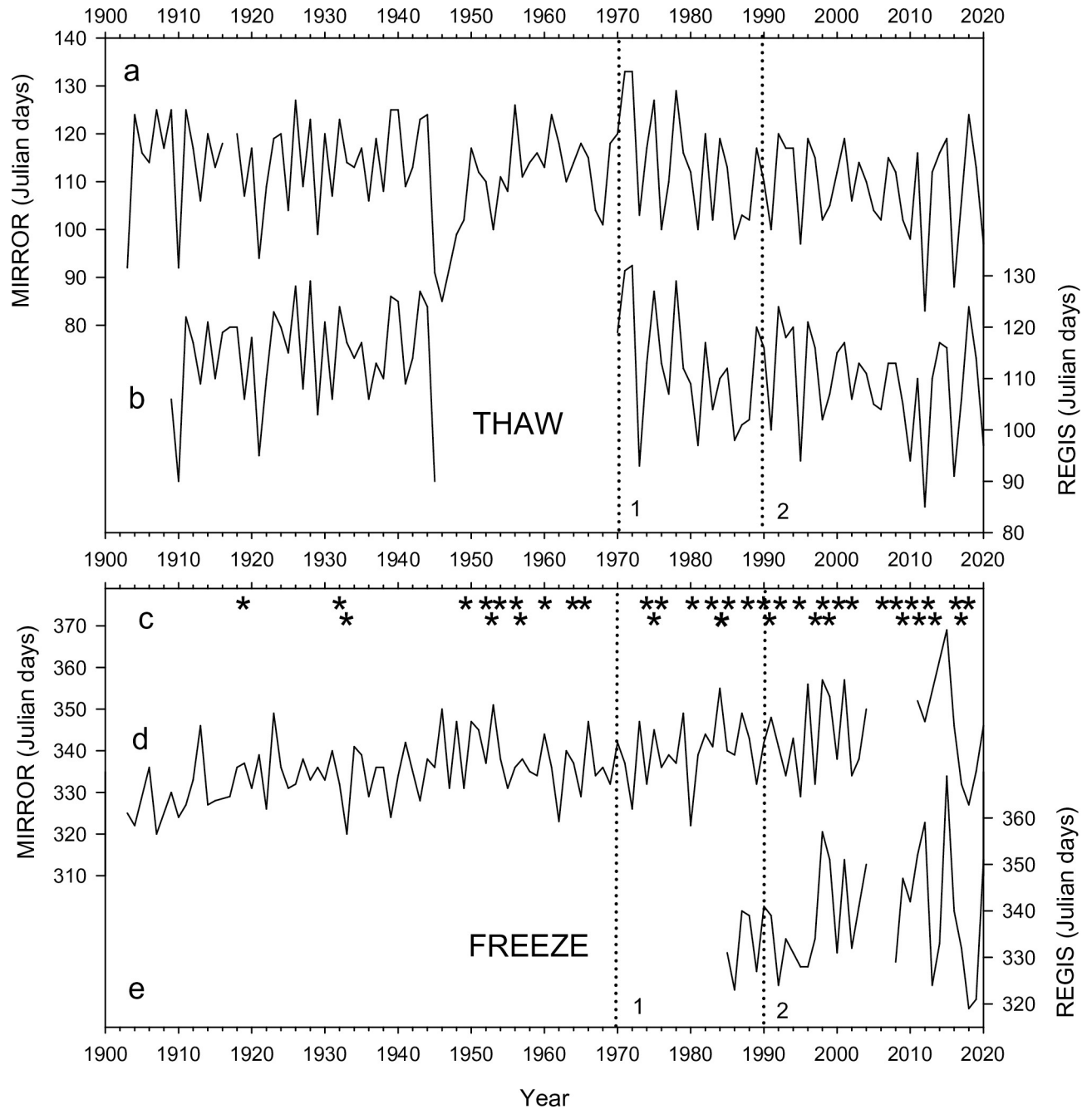


Fig 4. Records of ice thaw and freeze dates for Mirror Lake (a, d respectively) and Lower Saint Regis Lake (b, e). Asterisks (c) indicate years in which the main basin of Lake Champlain remained ice-free [39]. Vertical lines delineate time frames discussed in the text; (1) 1970–2020, (2) 1990–2020.

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trillium in Newcomb yielded a similar negative correlation with April temperatures ($R^2 = 0.42$, $P < 0.0001$) but no temporal trend over the 1975–2006 interval [18]. Unpublished bloom dates for red trillium recorded by master gardener Dana Fast in Lake Clear (Fig 1B) were also strongly correlated with April temperatures ($R^2 = 0.53$, $P < 0.0001$) and displayed no trend over the 1985–2006 period. Small sample sizes due to gaps in the records and short periods of overlap with the PSC series ($n = 5$) prevented reliable comparisons with trillium data from

those two sites, but the AEC and Lake Clear series were strongly correlated with one another ($R^2 = 0.83$, $P < 0.0001$).

Bloom dates for red maples at Lake Clear during the 1982–2007 interval, like those at PSC, displayed no significant trends and were correlated with April temperatures ($R^2 = 0.67$, $P < 0.0001$) as well as with bloom dates at PSC between 1992 and 2007 ($R^2 = 0.84$, $P < 0.0001$). Bloom dates of trout lilies at Lake Clear also displayed no trend (1982–2006) and were correlated with April temperatures ($R^2 = 0.50$, $P < 0.0001$) but the small sample size of the overlapping periods ($n = 3$) again prevented reliable analysis of correlations with bloom dates at PSC.

Median bloom dates for trout lilies, red trillium, and spotted salamanders near Mohonk Lake in southern New York displayed no significant change from the early 1930s to 1970 [6] but the dates were strongly correlated with temperature as was the case in the Adirondacks. The authors attributed the general lack of trends among most of the two dozen species studied to the mildness or absence of warming trends in spring when the observations were made and cited greater warming in winter and summer, findings that are consistent with our own.

These comparisons demonstrate that the records of terrestrial phenology at PSC reflect regionally coherent patterns that include strong sensitivity to spring temperatures and a scarcity of significant temporal trends in recent decades that reflects a short-term lack of climatic trends in late winter and early spring. The slopes of temperature-phenology relationships for the maples, trout lilies, and trillium generally increased from January to April, a pattern that is consistent with experimental evidence that sprouting dates for some forest plant species in the northeastern United States shift more in response to warming later in winter than earlier [44].

Unlike the terrestrial records, the ice records from Lower Saint Regis Lake were less clearly representative of the broader Adirondack region. Spring thaw and winter freeze dates for Lower Saint Regis Lake have covaried closely with those from Mirror Lake (Fig 4), located in the village of Lake Placid (Fig 1B) despite the mid-century hiatus in the former record. Thaw dates at those lakes from 1909 to 2020 were strongly correlated with one another ($R^2 = 0.86$, $P < 0.0001$) as were freeze dates from 1985 to 2020 ($R^2 = 0.62$, $P < 0.0001$). The increased frequency of ice-free conditions in the main basin of Lake Champlain in recent decades (Fig 4) [39] is also consistent with the trend toward later freeze dates in the uplands in addition to shortening of ice cover durations throughout the northern hemisphere [45].

In contrast, the short-term (1990–2020) ice records of Mirror Lake and Lower Saint Regis Lake were less consistent with those from the AEC where five lakes froze significantly earlier in autumn and thawed earlier between 1975 and 2007 [13]. The variability among these sites is not simply the result of analyzing different time intervals because thaw dates from Mirror and Lower Saint Regis Lakes displayed no significant trends over the 1975–2007 time frame either, and Mirror Lake freeze dates displayed no trends over the 1975–2004 interval. Similar geographic variability was documented among 65 ice records from New York and other Great Lakes states in which some Adirondack records displayed significant trends between 1975 and 2004 but others did not [11]. Those authors attributed the inconsistency to the multitude of factors that influence ice dynamics on lakes including wind activity, lacustrine heat budgets, and snow cover.

Pronounced warming of the surface temperatures of Lower Saint Regis Lake in early autumn represents one of the most prominent changes documented by the phenological records at PSC. Although we consider the magnitude of the rise in late September to be questionable due to small sample size, our evidence for significant lake warming then as well as in October is consistent with other records from the contiguous United States as a whole in which maximum warming due to climate change has generally occurred in summer and early autumn [46].

Adirondack phenology in a warming future

Although the lack of significant climatic trends in spring between 1990 and 2020 caused the phenology of organisms and ice to remain essentially free of trends as well during that time period, climate model projections anticipate pronounced warming in the Adirondack region by the end of this century [12]. The sensitivity of local phenology to temperature revealed in our analyses suggests that such warming could cause substantial phenological shifts during this century.

The effects of such warming on seasonal climates in the Adirondack uplands under both scenarios are illustrated in Fig 5, in which winter is defined as the period of sub-zero mean temperatures and the transition seasons of spring and autumn are periods during which temperatures range between 0 and 10°C. When the seasonal warmings determined for the Adirondack-Champlain basin [12] are applied to the current monthly mean temperatures (1990–2020), the transition seasons change mainly in terms of their positions on a sliding time scale because their temperature ranges are stable by definition. In Fig 5, for example, spring begins and ends roughly 1 and 3 weeks earlier by 2100 under the B1 and A2 scenarios, respectively, temporal shifts that are generally consistent with those listed in Table 6.

In contrast, winter and summer are likely to change in both duration and intensity. Using ADK3 temperatures of the 1990–2020 interval as a baseline and adjusting the time frame to 2020–2100, we find that winters become milder and shorten from today's mean duration of 16–17 weeks to 14–15 weeks (B1) and 11–12 weeks (A2) as summers become correspondingly longer and warmer (Fig 5). Because today's greenhouse gas buildups will continue to warm the planet far into the future [47] these findings suggest that reliably snowy winters in the Adirondacks could potentially cease to exist altogether, possibly before the end of the next century.

Ecological mismatches. We currently see little evidence of temporal mismatches in phenology developing during the 1990–2020 interval among mutually dependent species as has been documented elsewhere [8, 20–22], largely because we find few trends in the local climatic or phenological records over that time period. However, the differing relationships of individual species' phenologies to monthly temperatures suggest that ecological mismatches could arise in a warming future. We address this possibility for spring wildflowers and their pollinators here.

The differences in phenological advances projected for the bees (ca. 6–9 days earlier) and pussy willow pollen (ca. 13 days earlier) under the A2 scenario might become problematic as warming continues (Table 6). Female *Colletes* bees have a month or less after emergence in which to mate, dig burrows, and provision their eggs with pollen before they die, and at present the willows at PSC typically commence pollen production a week or so after the females emerge. A 1-week shortening of the ca. 2–3 week overlap period of pollen availability and pollinator activity could therefore represent an important reduction of reproductive potential for the bees as well as for other spring pollinators and the plants they service. The inferred 2-week advance in flowering dates for red maples could mean that an alternative source of pollen for *Colletes* [48] is also likely to undergo a similar reduction of availability to the bees during this century. During the process of publishing this study, we noticed that the spring phenology of the bees and flowers in 2021 and 2022 further highlighted the possibility of plant-pollinator mismatches developing in the near future. Adding those two seasons to the phenology records of 1990–2020 caused statistically significant temporal trends to emerge among the bees but not among the willows or maples.

Heberling et al. [21] documented a greater temperature-sensitivity of tree leaf-out phenology relative to the flowering of understory plants who depend on high light levels in early spring. They concluded that this difference in responses might have led spring wildflowers in

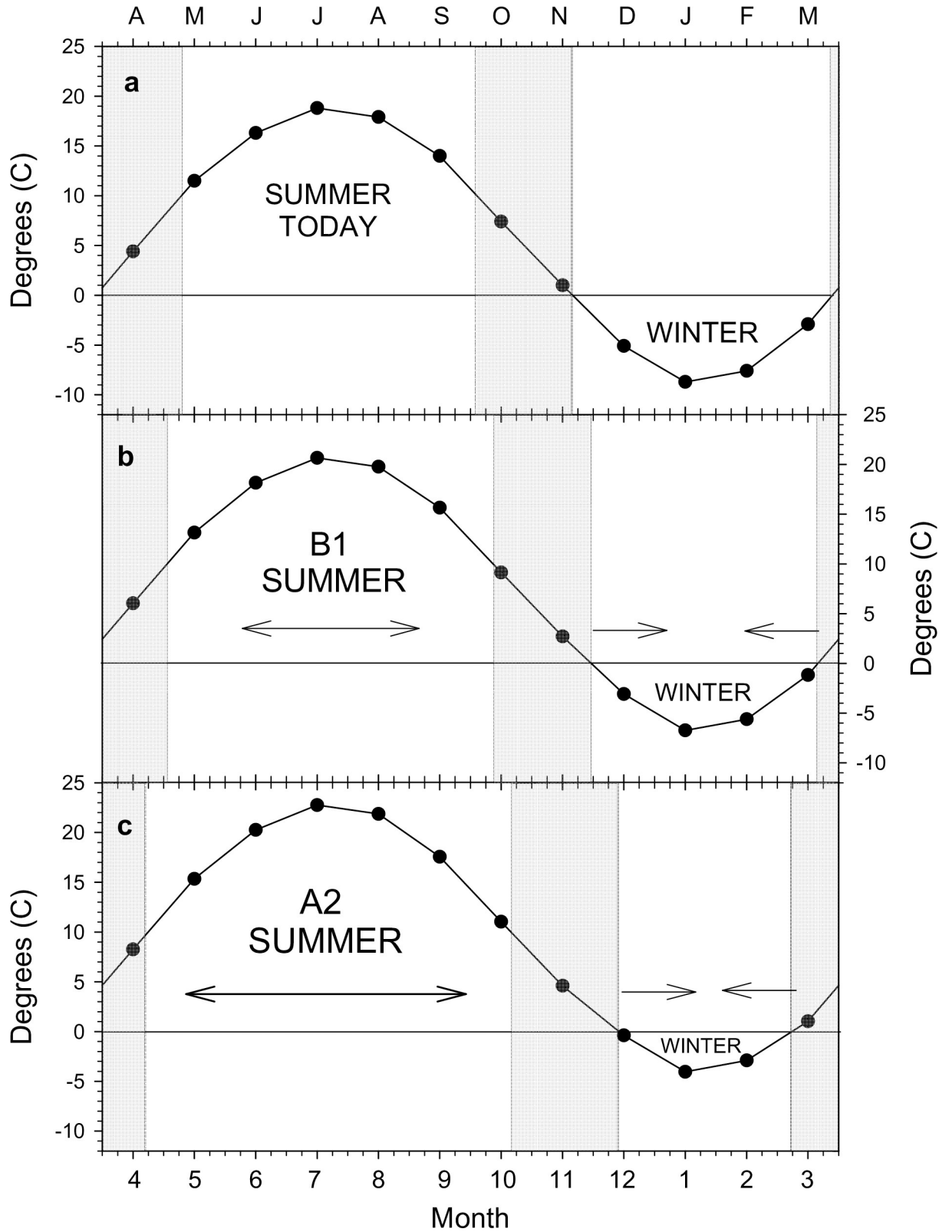


Fig 5. Seasonal temperature variability today and in two future scenarios based on the magnitudes of GHG emissions under moderate (B1) and extreme (A2) scenarios projected for the Adirondack-Champlain region [12]. Seasonal distributions of mean monthly temperatures in the ADK3 series are illustrated for (a) the 1990–2020 interval, and for year 2100 under the (b) B1 scenario and (c) A2 scenario. Grey bars indicate spring and autumn transition seasons as defined by the periods when mean temperatures range from 0°C to 10°C.

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the Northeast to experience a shortened window of light availability due to warming and earlier canopy leaf-out since the mid-19th century. The resultant decrease in the light environment is thought to have reduced the carbon budgets and overall fitness of spring wildflowers as a result. At PSC the red maples' relationships with winter and early spring temperature generally displayed stronger correlations and steeper slopes (days/°C) than those of trout lily shoots (Tables 5 and 6), and the projected temporal advances of maple flowering dates by 2100 are much larger than for trout lilies and trillium (Table 6). These findings suggest that ecological mismatches between forest canopies and understory flowers similar to those described by Heberling et al. [21] might develop in the Adirondacks as spring temperatures rise in the future.

Future lake conditions. Our statistical approach to anticipating phenological shifts indicates that freeze-up dates on Lower Saint Regis Lake could occur ca. 8–18 days later and thaw dates occur ca. 5–11 days earlier by 2100 (Table 6), estimates that are comparable to those suggested by the seasonal shifts in Fig 5. Both approaches demonstrate that the duration of ice cover on Adirondack lakes will shorten as warming continues and will shorten more under an A2 emissions scenario than under B1. Regardless of the GHG emissions scenario all Adirondack upland lakes will probably become ice-free in winter sometime after this century, a process that is already nearly complete on the main basin of Lake Champlain (Fig 4C).

Under such conditions, Lower Saint Regis Lake will experience correspondingly longer, more extreme thermal stratification as summers warm and extend well into September or early October, a trend that is already apparent in the water temperature data and that also affects other North American lakes [46]. Fig 5 suggests that summer's current mean duration of ca. 4.5 months in the Adirondack uplands is likely to increase to 5–6 months by 2100 under the A2 scenario. Summer warming and amplified thermal stratification, in turn, can encourage the development of cyanobacterial blooms in lakes that are potentially accompanied by toxicity, oxygen depletion, and restructuring of aquatic food webs [49, 50]. These trends could represent a serious challenge to cold-water fishes whose survival depends on the persistence of clean, cool, well-oxygenated refugia within the deepest portions of lakes during summer. In that context, Adirondack lakes with exceptionally large, deep basins will become increasingly important as climate refugia for cold-water species such as lake trout [51].

Cultural phenology and climate in the Adirondacks

Humans have been part of the Adirondack upland ecosystem for thousands of years, longer than most of the species of animals and plants found on the PSC Phenology Trail. As with other species their behaviors have long followed seasonal patterns, and today the economy of the region depends heavily upon the winter sports, outdoor recreation, and timber industries, all of which are strongly influenced by climate. The seasonal cycle within which the region's population organizes its activities creates a unique "cultural phenology" that distinguishes the social fabric of Adirondack communities from other mountainous regions farther south, and chief among those defining seasons is winter. The reliable annual return of deep cold has allowed to the region to host major sporting events including two Olympic Winter Games in Lake Placid, a Winter Carnival that has been celebrated annually in Saranac Lake since 1897, and a snowmobiling mecca in Old Forge. It is therefore appropriate to consider how shrinking winters and correspondingly longer, hotter summers could affect human residents of the Adirondacks.

Any complex ecosystem includes components that may experience benefits rather than harm from climate change. Milder, shorter winters can reduce heating bills and the use of road salt that pollutes water bodies and corrodes vehicles. Mild winters can increase survival of

white-tailed deer who are the focus of sport hunting, and concerns about the effects of warming on sugar maples in the Adirondacks [52] are tempered by the presence of healthy sugar maples and syrup harvesting far to the south in the Blue Ridge [47].

Conversely, poison ivy and disease-carrying black-legged ticks who are now largely restricted to the surrounding lowlands will likely spread into higher elevations as temperatures rise. The magnitudes of heavy downpours have also increased significantly over the last century in the region, bringing with them increased risk of damaging floods, more transport of algae-stimulating nutrients into water bodies, and costly replacements and upgrades of culverts and bridges [12].

Perhaps most importantly from a human perspective, economically and culturally important winter activities such as ice-fishing, snowmobiling, outdoor skating, and skiing depend on the reliable availability of frozen water, and thinning of ice due to warming threatens the safety of people engaging in such activities [53]. Frozen ground makes it easier for timber-harvesting equipment to move in forests, snow-plowing services provide supplemental income in this impoverished rural region, and ferry operators on Lake Champlain report that ice cover makes for smoother crossings during winter storms [54]. All of these activities will face major impacts from the waning of winter, and warming due to the high GHG emissions scenario could exclude national to international-level sporting events from the Adirondacks by the end of this century. For example, a recent study of climatic projections for 21 host cities of former Olympic Winter Games concluded that the extreme emissions scenario would make Lake Placid one of only four sites that still experiences climatic conditions suitable for the games by 2050, and that only Sapporo, Japan, would remain on that list by 2100 [55].

Today's annual crossing and re-crossing of the thermal threshold between solid and liquid water has profound effects on cultures and ecosystems alike [56], and the eventual loss of that transition—i.e. the demise of winter—could produce the greatest climate-driven changes in the region. Most Adirondack species will probably continue to exist farther north as temperatures continue to rise but the endemic place-based cultures of local human residents are not so mobile, particularly with an international border located a short distance to the north. As long-standing traditions associated with cold, snowy winters fade into the past, the cultural ecology of the human residents of the Adirondacks may well face the greatest existential challenges of all in a warming future.

Supporting information

S1 Fig. Trout lilies (*Erythronium americanum*) blooming in an Adirondack forest.
(TIF)

S2 Fig. Red maple (*Acer rubrum*) in bloom on the Paul Smith's College Phenology Trail.
(TIF)

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Author Contributions

Conceptualization: J. Curt Stager.

Data curation: J. Curt Stager.

Formal analysis: J. Curt Stager, Brendan Wiltse, Skylar Murphy.

Funding acquisition: J. Curt Stager.

Investigation: J. Curt Stager.

Methodology: J. Curt Stager, Brendan Wiltse.

Project administration: J. Curt Stager.

Resources: J. Curt Stager.

Software: Brendan Wiltse.

Supervision: J. Curt Stager.

Validation: J. Curt Stager.

Visualization: J. Curt Stager, Brendan Wiltse.

Writing – original draft: J. Curt Stager.

Writing – review & editing: Brendan Wiltse.

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