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Earlier Snowmelt Advances Breeding Phenology of the Common Frog (*Rana temporaria*) but Increases the Risk of Frost Exposure and Wetland Drying

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The alarming decline of amphibians around the world calls for complementary studies to better understand their responses to climate change. In mountain environments, water resources linked to snowmelt play a major role in allowing amphibians to complete tadpole metamorphosis. As snow cover duration has significantly decreased since the 1970s, amphibian populations could be strongly impacted by climate warming, and even more in high elevation sites where air temperatures are increasing at a higher rate than at low elevation. In this context, we investigated common frog (*Rana temporaria*) breeding phenology at two different elevations and explored the threats that this species faces in a climate change context. Our objectives were to understand how environmental variables influence the timing of breeding phenology of the common frog, and explore the threats that amphibians face in the context of climate change in mountain areas. To address these questions, we collected 11 years (2009–2019) of data on egg-spawning date, tadpole development stages, snowmelt date, air temperature, rainfall and drying up of wetland pools at ∼1,300 and ∼1,900 m a.s.l. in the French Alps. We found an advancement of the egg-spawning date and snowmelt date at low elevation but a delay at high elevations for both variables. Our results demonstrated a strong positive relationship between egg-spawning date and snowmelt date at both elevations. We also observed that the risk of frost exposure increased faster at high elevation as egg-spawning date advanced than at low elevation, and that drying up of wetland pools led to tadpole mortality at the high elevation site. Within the context of climate change, egg-spawning date is expected to happen earlier in the future and eggs and tadpoles of common frogs may face higher risk of frost exposure, while wetland drying may lead to higher larval mortality. However, population dynamics studies are needed to test these hypotheses and to assess impacts at the population level.

Our results highlight climate-related threats to common frog populations in mountain environments, but additional research should be conducted to forecast how climate change may benefit or harm amphibian populations, and inform conservation and land management plans in the future.

Keywords: breeding phenology, common frog (*Rana temporaria*), elevation, snowmelt, climate change, mountain, French Alps

INTRODUCTION

In mountain environments, species living at high elevation face strong constraints such as seasonal snow cover and low temperatures during the breeding season (Körner, 2007). Species must grow, reproduce and acquire resources during a shorter and colder growing season than at low elevations (Ryser, 1996; McCaffery and Maxell, 2010; Muir et al., 2014). In addition, for amphibian species, their full development is highly dependent on water availability in wetland pools, which itself depends on climate parameters as well as potential water storage in snowpack and glaciers (Carlson et al., 2020).

In high elevation alpine areas, air temperatures are warming at a higher rate than at lower elevations (Pepin et al., 2015, for the Alps: Rebetez and Reinhard, 2008; Gobiet et al., 2014), glacier mass and extent have significantly decreased (Huss et al., 2017; Gardent et al., 2014) and snow cover duration has significantly shortened since the 1970s (Durand et al., 2009a; Pellicciotti et al., 2010; Valt and Cianfarra, 2010; Klein et al., 2016; Beniston et al., 2018). As locomotion, growth, and reproduction of ectotherms such as amphibians are strongly influenced by environmental temperature, and given that water resources influenced by snowpack are essential for amphibians to complete metamorphosis, amphibian populations in mountain environments should be strongly impacted by climate warming, with pathways of impacts that may vary along elevation gradients.

Numerous studies have shown that climate change affects amphibian phenology at low elevation sites (Alford and Richards, 1999; Blaustein and Kiesecker, 2002; Beebee and Griffiths, 2005; Parmesan, 2006; Blaustein et al., 2010), but results indicate high heterogeneity in phenological responses across species and populations (Todd et al., 2010). In most cases, an earlier onset of frog breeding phenology caused by warming temperature has been observed (Beebee, 1995; Blaustein et al., 2001; Gibbs and Breisch, 2001; Oseen and Wassersug, 2002; Saenz et al., 2006; Klaus and Lougheed, 2013; While and Uller, 2014) while some others exhibited a trend toward later breeding or no trend at all (Todd et al., 2010; Klaus and Lougheed, 2013; Arietta et al., 2020). Meta-analysis showed that air temperature was the main physical parameter influencing frog breeding phenology (Ficetola and Maiorano, 2016), but in some cases, increasing precipitation could enhance phenological advancement (Timm et al., 2007; Todd et al., 2010; Green, 2017), especially in warm and dry areas where precipitation is a limiting factor (Ficetola and Maiorano, 2016). In regard to temporal trends, Prodon et al. (2019) emphasized non-linear phenological shifts over time related to the North Atlantic Oscillation (NAO) index, with earlier dates of Mediterranean amphibian breeding phenology in 1983–1997 followed by a stabilization or a delay in 1998–2013 (corresponding to the climate "hiatus," Trenberth and Fasullo, 2013), and again earlier dates after 2013. In this context, relatively few studies have explored the temporal trends and drivers of amphibian breeding phenology in high elevation temperate ecosystems. However, two studies indicate that later snowmelt leads to a delay of breeding phenology of amphibians (boreal chorus frog (*Pseudacris maculata*) in Corn and Muths, 2002, boreal toads (*Bufo boreas*) in Corn, 2003).

Depending on the targeted amphibian species and study site, the effects of earlier onset of breeding phenology on survival and population abundance can be positive or negative—for example a longer snow-free season can be favorable for growth, reproduction and resource acquisition in energy-limited mountain environments (Carey and Alexander, 2003; McCaffery and Maxell, 2010). It can also be negative (Reading, 2007; Tomaševic et al., 2007; Blaustein et al., 2010; Todd et al., 2010; Garner et al., 2011; Wassens et al., 2013; Carter et al., 2018; Fitzpatrick et al., 2020), for instance if earlier breeding phenology increases the risk of exposure of embryos to cold air temperatures or drought (Loman, 2009; Benard, 2015). Hence, with the documented earlier onset of snowmelt occurring in response to warmer winter and spring temperatures in documented in the European Alps (Beniston, 2012; Hall et al., 2015; Klein et al., 2016), surface pond embryos may be exposed to a greater risk of frost, which in turn would influence embryonic survival (Beattie, 1987; Frisbie et al., 2000; Muir et al., 2014) and population dynamics. This phenomenon has been observed for plants (Inouye, 2008), where the change in last spring frost timing is slower than the shift in plant phenology, leading to higher plant mortality (Vitasse et al., 2018; Pardee et al., 2019; but see Klein et al., 2018 for evidence of consistent advances in snowmelt timing and last spring frost, leading to unchanged plant exposure to frost frequency and intensity).

In response to climate change, frog populations are also exposed to higher risk of wetland drying before completion of metamorphosis, leading to larval mortality (Ryan et al., 2014; Brannelly et al., 2019; Kissel et al., 2019). Alongside increases in mean air temperature, the frequency, intensity and length of summer heatwaves have increased in the French Alps, especially since 2000 (Corona-Lozada et al., 2019). Heatwaves have been shown to promote evapotranspiration and contribute to drier wetlands (Carlson et al., 2020). In parallel, the decrease of snow cover duration (Klein et al., 2016) and snowpack in mountain environments leads to a decrease in water supply (Hanzer et al., 2018) especially during the summer period. Hence, in mountain areas, the combination of heatwaves in summer and early snowmelt date—due to thin snowpack and/or high spring temperature—associated with early frog breeding phenology may increase the risk of recruitment failure in shallow ponds exposed to drought (McCaffery and Maxell, 2010).

Amphibians are declining at an alarming rate around the globe due to disease (Beebee and Griffiths, 2005; Briggs et al., 2010; Olson et al., 2013; Green et al., 2020; Muths et al., 2020), habitat loss and fragmentation (Cushman, 2006), and climate change (Blaustein and Kiesecker, 2002; Carey and Alexander, 2003; Beebee and Griffiths, 2005; Andrade, 2015; McCaffery et al., 2021). Here, we highlight the need to improve our knowledge of frog breeding phenology at different elevations in the context of climate change in mountain areas for which there is a lack of studies. First, we measured the temporal trends of common frog (*Rana temporaria*) breeding phenology and snowmelt date at two elevations (∼1,300 and ∼1,900 m a.s.l) near the Mont-Blanc Massif, in the northwestern Alps between 2009 and 2019. Second, we tested how environmental variables (snowmelt date, air temperature after snowmelt, rainfall, elevation) influenced egg-spawning date. As not only the egg-spawning date but also the egg-spawning duration (i.e., number of days between the onset and end of egg-spawning) can vary with elevation because of environmental constraints, we further quantified how egg-spawning duration differed between the two elevations. Finally, we assessed climate change-related threats to amphibian populations within our study area, and determined how these challenges varied with respect to elevation. We measured the relationship between the risk of spring frost exposure and egg-spawning date, and identified climate parameters associated with drying of wetland ponds and observed tadpole mortality. Given the general warming observed in alpine areas, we expected an advancement of the snowmelt date and of the breeding phenology of the common frog during the study period, with a stronger effect at the high elevation site. We hypothesized that egg-spawning date of the common frog depended on snowmelt date and rainfall and that warmer temperatures following snowmelt would shorten the duration between snowmelt and egg-spawning. In addition, we expected that elapsed time between snowmelt and initial egg-spawning, and the egg-spawning duration of the egg-spawning period, to decrease with elevation because of the temporal constraints imposed by a shorter growing season. Finally, we hypothesized that the risk of frost exposure and wetland drying increased with elevation as snowmelt date advanced and snow cover decreased strongly at high elevation.

MATERIALS AND METHODS

Field Survey of Common Frog Breeding Phenology

We collected common frog (*Rana temporaria*) breeding data from 2009 to 2019 (11 years) as part of a long-term phenology program initiated by the Research Center for Alpine Ecosystems (CREA Mont-Blanc). Respectively, two and four ponds were surveyed at 1,260 m (low elevation site, "LE") and 1,960 m (high elevation site, "HE") of elevation in Loriaz (46°1′N, 6°55′E), a mountain located near the Mont-Blanc Massif in the French Alps. The low elevation mountain pools are situated in the valley floor while the high elevation sites are located just above treeline (**Figure 1**). From March to August, ponds were visited weekly. Every week, at each pond, we recorded the number of egg masses in order to obtain the date of the maximum number of egg clusters (hereafter referred to as "egg-spawning date by pond," **Supplementary Figure 1** in ESM7). For each year and elevation (site), we averaged the date of the maximum number of egg masses (called "mean spawning date" hereafter). We also calculated the egg-spawning duration at each pond, i.e., number of days between the onset and end of egg-spawning. The years 2010 and 2011 were not included for egg-spawning duration calculation because the survey was not done using the same protocol compared to the other years. We also removed the duration measurement of one low elevation pond in 2014 for which there were already 210 egg-spawns at the first visit, indicating that we missed the onset date. From 2017 to 2019, ponds that dried out in summer were recorded. For each elevation, ponds were located close to each other (600 and 150 m between the two furthest ponds, respectively, at low and high elevation) in order to ensure comparable local environmental conditions. Average pond depth was 50 cm at low elevation and 24 cm at high elevation.

Climate Data

Climate data were obtained using CREA Mont-Blanc climate stations located at 1,340, 1,915, and 1,970 m of elevation on the Loriaz mountainside (Mont-Blanc Massif). The stations located at 1,340 and 1,970 m of elevation are associated, respectively, with the ponds located at low and high elevation. They record soil and air temperature every 15 min with four sensors (5 cm under the ground, at ground-level, 30 cm and 2 m above the ground). We used the station records to (1) calculate the mean air temperature *via* the sensor located at 2 m in spring after snowmelt date and during summer; (2) to estimate the snowmelt date with the ground level sensor; (3) to identify the last spring frost date (LSF) with the sensor located at 30 cm above the ground, which more specifically reflected the habitat conditions of eggs and frogs (Kollas et al., 2014); and (4) to calculate the number of frost days using the sensor located 30 cm above the ground during the egg-spawning date range for each pond (**Table 1**). We completed our local temperature observations with daily time series of meteorological and snowpack parameters provided by the SAFRAN-Crocus coupled snowpack-atmosphere model (Durand et al., 2009a,b). For the duration of our study, we extracted daily values of snowpack height and precipitation (rainfall and snowfall) for 300 m elevation bands within the Mont-Blanc Massif (**Table 1**) to relate the risk of wetland drying with climate parameters not available from field stations. Data were downloaded from the open-access Aeries portal (Vernay et al., 2019).

Mean Air Temperature

Average daily mean air temperatures were calculated during the 2009–2019 period for each elevation. Calculations were done for daily datasets having less than 20% missing values within a day—climate stations record a maximum of 96 temperature

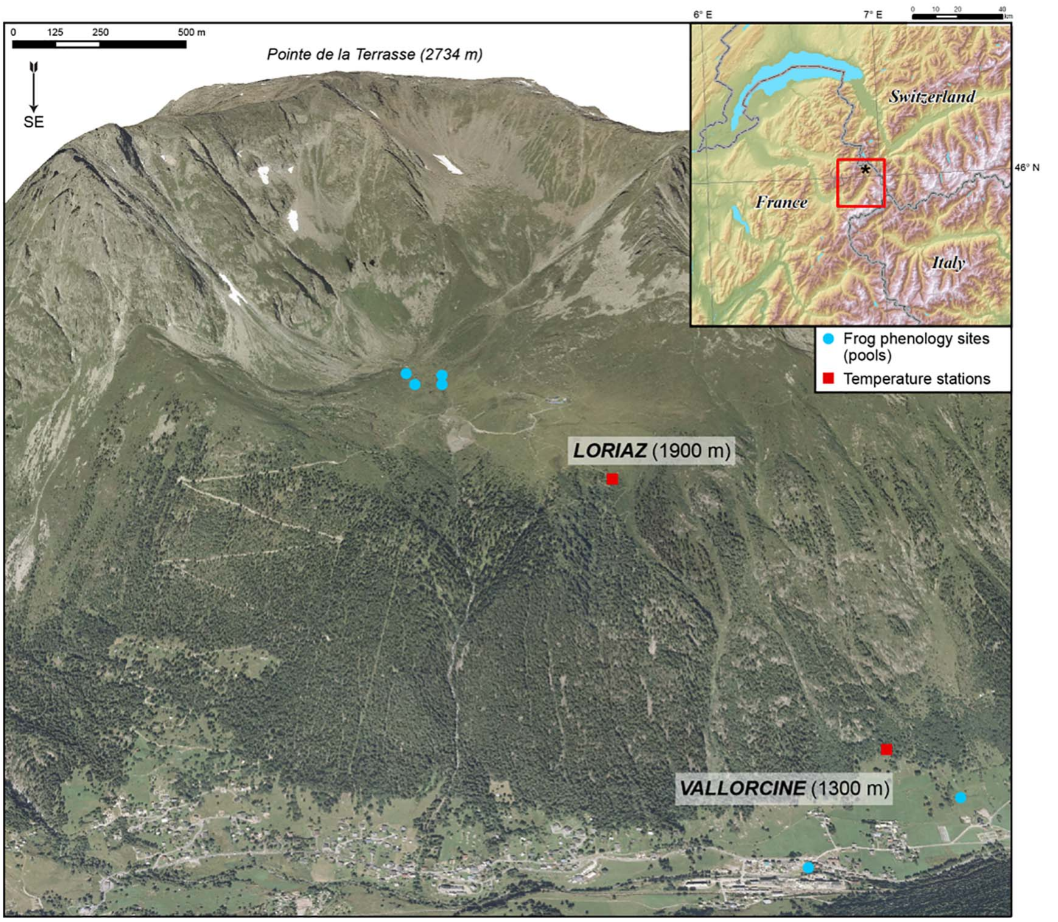

FIGURE 1 | Location map of the climate stations and the wetland pools used to survey breeding phenology of the common frog *Rana temporaria*. The red box situates the Chamonix valley in the French Alps.

measurements per day. Subsequent missing air temperature values were then estimated using nearby climate stations (ESM 1). In order to determine whether temperature influenced mean spawning date after snowmelt, we calculated mean air temperature at 2 m for the 30 days after snowmelt, for each year and elevation (30 days corresponded to the median duration between snowmelt date and spawning date). Maximum temperature, minimum temperature and growing degree days (above 5°C as in Muir et al., 2014) were also tested and gave the same conclusions as mean air temperature. Finally, to compare the risk of wetland drying during the larval development, we calculated the average summer air temperature at 2 m (June, July, and August) at both stations (1,340 and 1,970 m asl) for each year.

TABLE 1 | Climate data sources and associated variables.

Data sources		Variables
CREA stations	Sensor at 2 m height	Mean air temperature in spring after snowmelt date and mean summer air temperature (June to August)
	Sensor at 30 cm height	Number of frost days and last spring frost date (tested thresholds: 0 and −2°C) obtained from the minimum air temperature data
	Sensor at the ground level	Snowmelt date
SAFRAN-Crocus		Mean snow depth (in March) and sum of summer precipitations (rainfall from June to August)

Last Spring Frost and Number of Frost Days

We found conflicting reports in the literature concerning the lower thermal limit of *Rana temporaria* embryos, varying from 2.8 to 8°C (water temperature, see Beattie, 1987 for references therein). For the species *Rana sylvatica*, Frisbie et al. (2000) experimentally showed that the freezing tolerance of embryos varied from −4.2 to −0.5°C (water temperature) according to the embryos' development stage, the position in the water column and the duration of cold exposure. Muir et al. (2014) demonstrated that just over half of the tadpoles of *Rana temporaria* survived after freezing experiment (water was gradually cooled until it became completely frozen and then rewarmed to 15°C). Loman (2009) reported considerable variation in the survival of eggs of *Rana temporaria* when temperature was below 0°C. For our study, in order to represent minimum air temperature experienced by frog embryos located at the pond surface during their egg-period, we tested two thresholds: 0 and −2°C (using −1°C did not change the final results). In order to assess the relationship between the number of frost days during the egg-spawning duration and the egg-spawning date, we calculated the number of frost days as the sum of days for which minimum air temperature was below 0 or −2°C during 28 days around the maximum egg-spawning date, according to the sensor 30 cm above ground. This period corresponded to the maximum egg-spawning duration in our study site (**Supplementary Figure 1** in ESM 6). As the average duration between first egg-spawning date and maximum egg-spawning date equaled 11 days, we defined the 28 day period around the maximum egg-spawning date as 11 days before plus 17 days after. Data in 2013 at the low elevation site and in 2018 at the high elevation site were removed from the analysis because of the high percentage of missing air temperature values during the target 28-day period.

Snowmelt Timing

We estimated snowmelt using the temperature sensor located at the ground-level of the station. When snow cover was present, we assumed ground-level temperature equaled zero, and otherwise expected that variation in air temperature above or below zero reflected snow-free air temperature (Gadek and Leszkiewicz, 2010). Snowmelt date corresponded to the last day of continuous snowpack. For each year, snowmelt date was defined as the first snow-free day following a minimum 40-day snow-covered period (∼6 weeks) from 1st of September until 31st of August, following the methodology used by Klein et al. (2016). Given the strong correlation obtained for 2 m height air temperature values between the two highest stations (1,915 and 1,970 m of elevation) and as there were some missing values for the date of snowmelt, we averaged the snowmelt date by year between the 1,915 and 1,970 m stations (**Supplementary Table 2** in ESM 2). In addition, we extracted mean snow depth in March from 2009 to 2019 from SAFRAN-Crocus in order to assess the risk of wetland drying during embryonic development.

Rainfall

We hypothesized that a short period of rainfall prior to the mean spawning date (i.e., 3 days) could enhance frog spawning while creating more suitable habitats for reproduction. For each year and each elevation, we summed up the daily rainfall provided by the SAFRAN-Crocus reanalysis during the 3 days before the mean spawning date. In addition, we summed daily rainfall during egg development from June to August, for years between 2009 and 2019 to better describe the climatic conditions during the study.

Data Analysis

First, we estimated the effects of elevation and year on egg-spawning date during the 2009–2019 period using linear mixed models with year and elevation as fixed effects and the pond as a random effect (egg-spawning date ∼ year*elevation + (1| pond). We assessed the effects of elevation and year on snowmelt date using linear models (snowmelt date ∼ year*elevation), where "*" denotes an interaction between year and elevation (i.e., different slopes for the year effect at the two elevations).

Then, to identify which environmental variable (snowmelt date, rainfall, mean temperature during 30 days after snowmelt) influenced mean spawning date, we performed a model selection based on AICc (Burnham and Anderson, 2002) from the full model tested on the period 2009–2019: mean spawning date ∼ snowmelt*elevation + rainfall*elevation + mean temperature during 30 days after snowmelt*elevation. We also quantified how egg-spawning duration differed between both elevations and across the study period (egg-spawning duration ∼ elevation).

Finally, as the variance of the pond random effect was estimated as 0 or very low values, and as the number of frost days was well approximated by a negative binomial distribution, we used generalized linear models instead of generalized linear mixed models to assess the relationship between the number of frost days during the egg-spawning period and the egg-spawning date (number of frost days ∼ egg-spawning date*elevation) for the period 2009–2019. Finally, in order to classify years with respect to inter-annual climate variability and to identify climate parameters related to the drying up of wetland pools and associated tadpole mortality observed in the field, we compared mean summer air temperature, sum of summer precipitation, mean snow depth in March and snowmelt date over the 2009–2019 period. Statistical analyses were carried out using R 3.6.1 (R Development Core Team, 2018).

RESULTS

Temporal Trends

From 2009 to 2019, the earliest egg-spawning date occurred on the 22nd of March, 2017 at low elevation and on the 5th of May, 2011 at high elevation. The latest egg-spawning date occurred on the 27th of April, 2011 at low elevation and on the 29th of June, 2016 at high elevation.

Over the 11-year period (2009–2019), year as a continuous variable was a significant predictor of egg-spawning date at high elevation, revealing an advancement of 1.4 days per year of the first spawning date at low elevation [$\beta = -1.4$, CI 95% (−3.1; 0.3), $P = 0.10$], and a delay of 1.7 days per year at high elevation [$\beta = 1.7$, CI 95% (0.3; 3.1), $P = 0.02$] (**Figure 2B**). Year was not a significant predictor of snowmelt date (**Figure 2A**), but an advancement of 1.6 days per year was observed at low elevation [$\beta = -1.6$, CI 95% (−4.8; 1.7), $P = 0.32$] whereas a delay of 2.8 days per year was observed at high elevation [$\beta = 2.8$, CI 95% (−0.4; 6.0), $P = 0.09$].

Factors Influencing Mean Spawning Date

The best model based on AICc described snowmelt and elevation as additive effects influencing mean spawning date (adj. $r^2 = 0.94$, **Table 2** and **Figure 3**). The second-best model also included mean

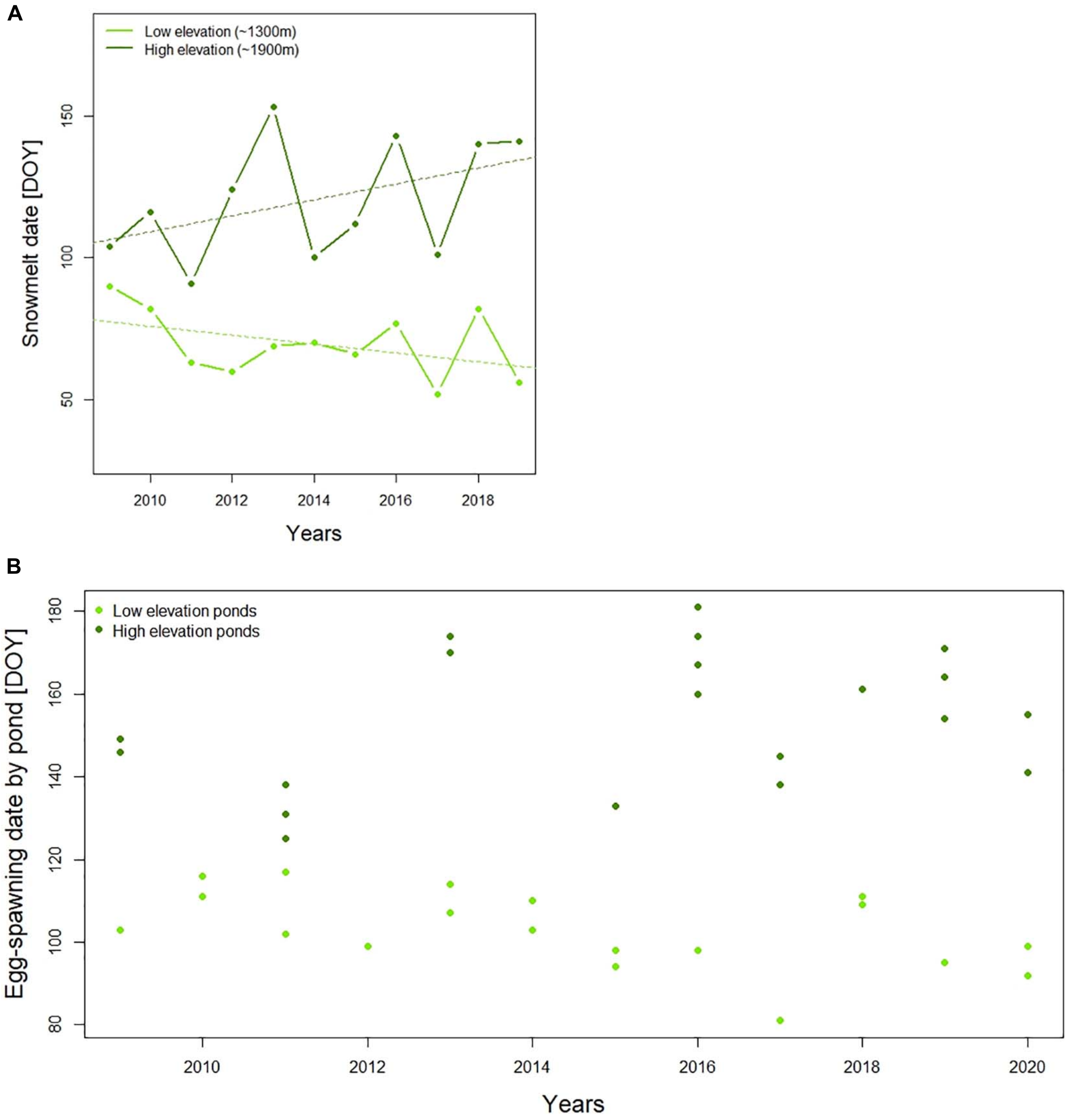

FIGURE 2 | Temporal trends of **(A)** snowmelt date, and **(B)** maximum egg-spawning date (called "egg-spawning date") of the common frog *Rana temporaria* during the period 2009–2019, near the Mont-Blanc Massif in the French Alps. **(B)** Every pond was surveyed except in 2010, 2012, and 2014 where no data were available in the high elevation site (∼1,900 m). A single point, for example in the low elevation site (∼1,300 m), means that both ponds were surveyed but they had the same maximum egg-spawning date. DOY means "day of the year".

temperature during 30 days after snowmelt as an additive effect, but as it did not improve the model (ΔAICc = 0.15, adj. $r^2 = 0.94$) and as its effect was not significant [β = −1.7, CI 95% (−3.9; 0.4), *P*-value = 0.10], we did not take this effect into account. Hence, when snowmelt was delayed by 10 days, mean spawning date was delayed by 5.8 days [CI 95% (3.7; 7.9)] at both elevations (**Figure 3**). For a given snowmelt date, mean spawning date took place 19.6 days later on average at the high elevation site.

We observed strong inter-annual variation regarding the lag between snowmelt date and mean spawning date (**Supplementary Figure 1** in ESM 5), and elevation had no significant effect on this duration [mean duration in days at low elevation: 32.3, CI 95% (25.8; 38.7), at high elevation: 29.6, CI 95% (22.0; 37.2)]. By contrast, over the study period, elevation had a significant effect on the egg-spawning duration, with a longer duration at low elevation than at high elevation [17.6, CI 95% (13.7; 21.5) days in low elevation site vs 7.9, CI 95% (5.4; 10.4) days at high elevation site].

Risk of Frost Exposure

The non-linear relationship between the number of frost days under 0°C and egg-spawning date was stronger at the high elevation site (**Table 3** and **Figure 4A**): for the same advancement of egg-spawning date at both elevations, the number of frost days during egg-development increased faster at high elevation than at low elevation. We did not observe a difference in relationships

TABLE 2 | Model selection including mean spawning date as the response variable.

Explanatory variables used in each model	Df	Adj. R^2	AICc	ΔAICc	Weight
Snowmelt + Elevation	4	0.94	136.5	0	0.32
Snowmelt + Temperature + Elevation	5	0.94	136.6	0.15	0.30
Snowmelt + Temperature	4	0.92	139.6	3.15	0.07
Snowmelt*Elevation	5	0.93	139.8	3.37	0.06
Snowmelt + Rainfall + Elevation	5	0.93	140.1	3.60	0.05
Snowmelt*Elevation + Temperature	6	0.94	140.1	3.64	0.05

**Only the sixth first models are presented here.*

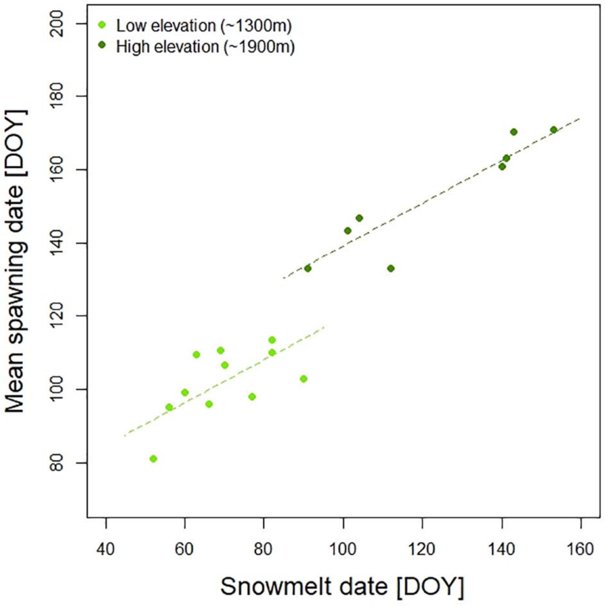

FIGURE 3 | Relationship between mean spawning date of the common frog *Rana temporaria* and snowmelt date near the Mont-Blanc Massif in the French Alps (selected linear model: mean spawning date ~ snowmelt + elevation). DOY means "day of the year" [adj. r-squared = 0.94, β = 0.58, CI 95% (0.37; 0.79)].

between low and high elevations when the threshold was lowered to −2°C (**Table 3** and **Figure 4B**). In addition, no significant differences were noted in the number of frost days when using a minimum air temperature threshold of 0 or −2°C for both elevations [5.2, CI 95% (3.4; 6.9) days below 0°C in low elevation site vs 3.1, CI 95% (1.8; 4.3) in high elevation site; 1.5, CI 95% (0.4; 2.6) days below −2°C in low elevation site vs 1.2, CI 95% (0.7; 1.7) in high elevation site].

Wetland Drying

Wetland drying was observed in 2017 and 2019 at the high elevation site at three ponds, which lead to larval mortality. During the duration of the study period, ponds never dried at the low elevation site. In terms of mean summer air temperature and snowmelt date observed during the study period, 2015 and 2017 were among the hottest years, and were characterized by early snowmelt at both elevations (**Supplementary Figure 1** in ESM6). At the high elevation site, summers 2018 and 2019 were similar in terms of temperature and snowmelt date, i.e., hot but with late snowmelt date (**Supplementary Figure 1** in ESM6). However, 2018 was characterized by an exceptionally deep March snowpack, and low summer precipitation, which was not the case in 2017 and 2019 (**Supplementary Figure 1** in ESM6).

DISCUSSION

Our objective was to understand relationships between environmental variables and the breeding phenology of the common frog (*Rana temporaria*) in a mountain environment, and assess the environmental stressors that this species faces in a climate change context. In agreement with previous studies, we identified a strong relationship between snowmelt date and mean spawning date at both elevations (Corn and Muths, 2002; Corn, 2003) confirming a high degree of plasticity in terms of breeding timing (Muir et al., 2014). In our study, the local climatic conditions such as snowmelt date led to opposite temporal trends between low and high elevation sites due to elevation-dependent effects of climatic environmental variables on frog habitat. These results concur with the high heterogeneity observed in the direction of the shift in different species (Todd et al., 2010), but also demonstrate that variation can occur between populations of the same species located in the same area but distributed along elevation gradients.

At low elevation, snowmelt occurred earlier during our study period, as found by Klein et al., 2016 [even though the effect is larger in our study site with an advancement of 1.6 days/year than in Klein et al., 2016, −0.5 (−0.7; −0.3) days/year since 1970 for stations under 1,500 m asl], which lead to the advancement trend of frog breeding phenology. At high elevation, however, we observed a delay in snowmelt in our study area and years, which is consistent with certain studies demonstrating decreased sensitivity of snow cover duration to climate warming above 2,000 m (Hantel and Hirtl-Wielke, 2007; Schoener et al., 2019). Consistent with the strong relationship between snowmelt and frog spawning, we observed a delay of frog breeding phenology at the high elevation sites. It is important to note that the snowmelt trend observed between 2009 and 2019 in the high elevation site did not call into question the general warming trend, particularly during the summer months (Easterling and Wehner, 2009; Li et al., 2015; Yao et al., 2016).

The model we used yielded a good fit to the data collected at the two elevations, but needs further calibration and validation

TABLE 3 | Outputs of the generalized linear models (negative binomial distribution), for the 0 and −2°C thresholds.

	Estimate	Std Error	*Z*-value	*P*-value
Threshold: 0°C				
Intercept	2.00	0.18	10.86	< 2.0e-16
Egg-spawning date	−1.72	0.31	−5.51	3.69e-08
Low elevation site	−1.08	0.51	−2.11	0.035
Egg-spawning date*Low elevation site	1.03	0.51	2.00	0.045
Threshold: −2°C				
Intercept	−1.06	0.35	3.03	0.002
Egg-spawning date	−1.59	0.53	−3.00	0.003
Low elevation site	−2.95	1.09	−2.70	0.007
Egg-spawning date*Low elevation site	−0.49	1.00	−0.49	0.62

"" denotes an interaction.*

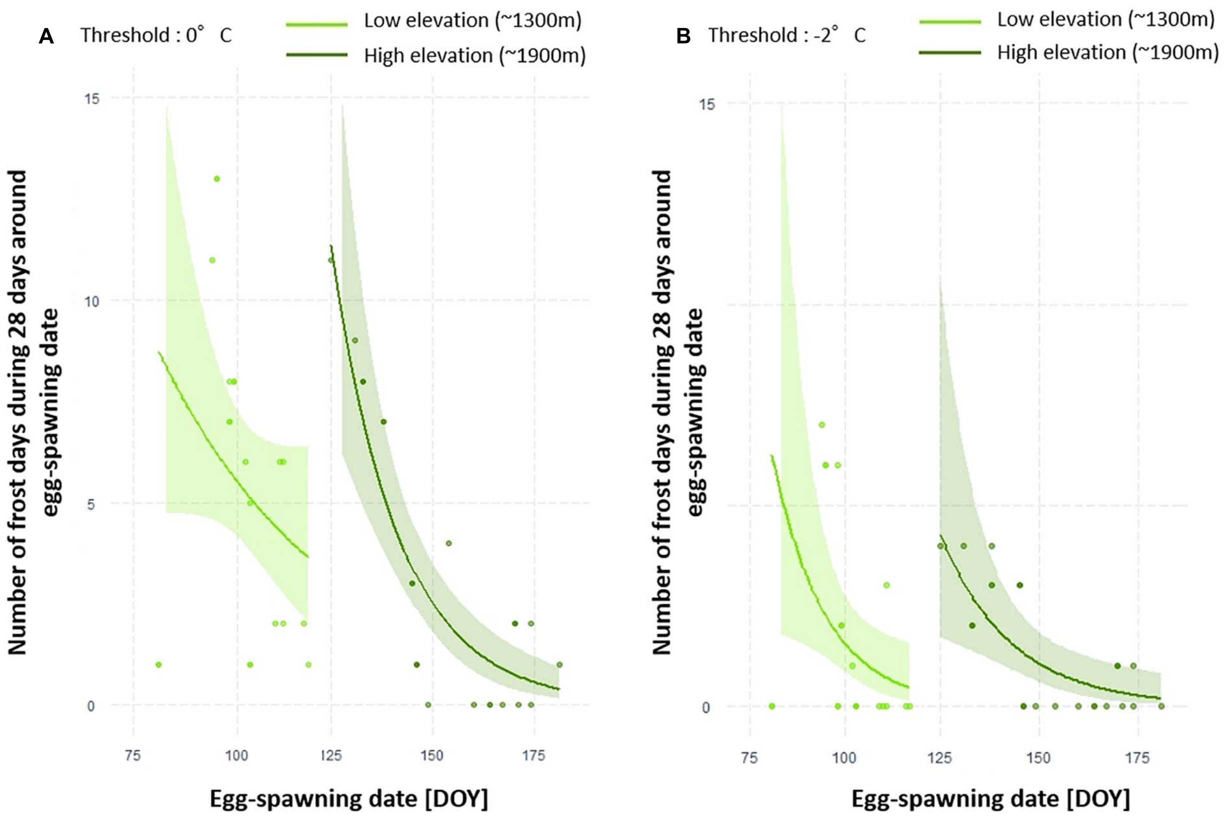

FIGURE 4 | Relationship between the number of frost days during 28 days around egg-spawning date and egg-spawning date of the common frog Rana temporaria, assessed with a generalized linear model. Number of frost days are calculated as the sum of days for which minimum air temperature was below **(A)** 0°C or **(B)**−2°C. Each dot corresponds to one pond. DOY means "day of the year".

across other alpine regions and at more elevations. Snowmelt date could be used to predict past and future egg-spawning dates in mountain areas, given the availability of future simulations of snowpack based on climate change scenarios (Verfaillie et al., 2018). Climate models predict that snow amount and duration will drastically decrease below 1,500–2,000 m of elevation by the end of the 21st century, in particular due to earlier snowmelt in spring (Beniston et al., 2003, 2018; Beniston, 2012; Castebrunet et al., 2014; Gobiet et al., 2014; Verfaillie et al., 2018). Furthermore, models predict increasing rainfall during the winter months as well as higher frequency of heavy precipitation events, which could contribute to a reduced and faster melting snowpack as well as more sporadic runoff regimes (Jacob et al., 2014). Changes in snowmelt dates between 1973–2013 and 2050 are projected to be −35 days at 2,000 m of elevation and −40 days at 1,500 m of elevation in the Mont-Blanc massif (south slope, RCP 8.5) (Cremonese et al., 2019). Given this climate projections, this would translate in egg-laying date being 20 and 23 days earlier, respectively, at both elevations. As we do not have snow measurements at the same sites earlier than 2009, the expected changes are somewhat less as snowmelt out dates have been later in the period 1973–2013 compared to 2009–2019. While earlier spring snowmelt will likely lead to an earlier onset of breeding at both low and high elevation sites, the risk of frost exposure may differ between elevations, with a stronger effect at high elevation as the number of cold days increased faster at high elevation when egg-spawning gets earlier than at low elevation.

Although the risk of frost exposure may increase in the future (Vitasse et al., 2018; Lhotka and Brönnimann, 2020), this does not necessarily have a direct effect on the population dynamics of the common frog. Indeed, only the eggs located at the pond surface may be impacted by cold air temperatures, which do not concern the entire population. In addition, pre-metamorphosis stages have variable sensitivity to cold temperature (Moore, 1942; Herreid and Kinney, 1967; Muir et al., 2014; Wersebe et al., 2019). Earlier breeding increased the risk of frost exposure at both elevations, but this may also allow juveniles to reach larger size at metamorphosis and thus increase survival probability as adults (Altwegg and Reyer, 2003; Loman, 2009). Given the conflicting results regarding the lower lethal limit of water temperature for common frog eggs and tadpoles (Beattie, 1987; Loman, 2009; Muir et al., 2014), additional experimental and observational studies on larval common frog populations along an elevation gradient should be conducted. This would allow for more precise identification of physiological thresholds affecting the survival of embryos exposed to cold temperatures, as has been carried out for juvenile individuals (∼2 weeks after metamorphosis) of *Rana temporaria* in Enriquez-Urzelai et al. (2020). It would also be worthwhile to determine whether populations differ genetically in terms of freezing tolerance, and to quantify the risk of larval mortality to frost exposure, which is rarely considered in studies dealing with animal phenology and climate change.

Three shallow pools at the high-altitude site dried out in 2017 and 2019, 2 years characterized by high summer temperatures and shallow spring snow depth. In addition, early snowmelt in 2017 may have accentuated drying-up of wetland pools. Ponds that dried at the high elevation site are also characterized by low depth or are connected to a small stream with low water flow. Even though 2018 was also one of the warmest years within the study period, we found that the high snow depth in March allowed for sufficient water availability throughout the summer. On the contrary, ponds at the low elevation site remained wet during all summers, presumably because they are deeper and benefit from a larger upstream watershed and a more diverse water supply. In the future, we expect that the increase of summer heatwave frequency and intensity (Corona-Lozada et al., 2019) combined with a decrease in snow cover depth and duration (Klein et al., 2016) may lead to a higher probability of wetland pools drying out, especially in high elevation sites that are highly dependent on snowpack (Carlson et al., 2020). Analysis of the effects of snow depth and duration, precipitation, and temperature on the water regime of wetlands in mountain watersheds are consequently highly valuable to better understand the impact of climate change on these ecosystems and on frog populations (Carlson et al., 2020). It is known that amphibian populations can develop under wetland drying conditions (Laurila and Kujasalo, 1999) and that the upper thermal tolerance of juvenile frogs slightly increases with elevation (Enriquez-Urzelai et al., 2020). However, the shortened hydroperiod affects the rate of larval growth and development and alters post-metamorphic immune function (Brannelly et al., 2019). In the context of global warming, some model predict an increase of larval mortality due to pond drying and the decrease of adult survival given the decrease of summer precipitation associated with warmer winters (Kissel et al., 2019). Considering that climatic conditions are changing at a higher rate in mountain areas than in the Northern Hemisphere generally (Gobiet et al., 2014), and that high elevation populations are already constrained by a short growing season, further work is necessary in order to address the question of whether and how populations will be able to adapt quickly enough to ongoing climate changes, *via* plasticity or genetic variations (Enriquez-Urzelai et al., 2020).

Finally, as expected, the duration of egg-spawning was shorter at the high elevation site compared to the low elevation site, i.e., frog reproduction was more synchronized at high elevation. Indeed, the later the snow melts, the shorter the length of the growing season and the quicker frogs must reproduce in order for tadpoles to be able to complete their metamorphosis before the return of winter. Hence, in high elevation sites, threats evoked above (frost exposure and wetland drying) may have more pronounced negative effects on population dynamics, due to lower variability in phenological stages at a given date, which could lead to increased vulnerability to extreme events such as summer droughts. At the meta-population level, egg and tadpole mortality may be counterbalanced by a high diversity of available wetland pools and microhabitat structure, allowing for recruitment compensation and persistence of marginal populations in the face of climate change (McCaffery and Maxell, 2010; McCaffery et al., 2014; Enriquez-Urzelai et al., 2020). Indeed, in our study area, we observed wetland drying of only certain shallow pools and never observed drying up across all high elevation ponds.

Long-term surveys of population dynamics should be set up to understand how environmental (e.g., diversity of wetland pools), climate (e.g., temperature, snowmelt and snowpack, pond drying, precipitation) and density dependent (Kissel et al., 2020) variables influence mechanism of population change such as survival, recruitment and population growth rate at different elevations in this temperate mountain environment, in order to guide useful interventions.

CONCLUSION

In our temperate mountain study area, we showed that snowmelt regulated egg-spawning date regardless of elevation. As decreased snow cover duration is expected to cause earlier egg-spawning dates in the future, eggs and tadpoles of common frogs may face a higher risk of frost exposure and wetland drought, causing higher larval mortality. However, studies of population dynamics are needed in order to test how climate would impact abundance and population dynamics. Our results highlight climate-related threats facing common frogs in mountain environments, and underscore the need for further research in order to forecast how climate change may benefit or harm amphibian populations, and inform conservation and land management plans in the near future.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

MB, NY, AD, BC, GK, IL, and CV originally developed the idea. MB, BC, GK, and IL prepared the climatic database. CV and MB prepared the frog phenology database. MB and NY performed the statistical analysis. MB, NY, AD, BC, GK, IL, and CV wrote the first draft of the manuscript. All authors commented and approved the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.645585/full#supplementary-material

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