

Surviving on the edge. Effects of climate warming on the common frog (*Rana temporaria*) population in the Montseny massif (NE Iberia). Present and future effects (#75330)

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Surviving on the edge. Effects of climate warming on the common frog (*Rana temporaria*) population in the Montseny massif (NE Iberia). Present and future effects

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The Montseny massif shelters one of the southernmost western populations of Common frogs (*Rana temporaria*) which experiences a Mediterranean climate that poses a challenge for the species persistence in warming temperatures scenario. We evaluated the effect of climate change in three levels. Firstly, we analyse if there has been an advance of onset spawn period due to warming temperatures. Second, we analyse the influence of climatic variables in the onset of spawn period and, third, how the distribution of these species could vary according to the predictions of temperature increase for the end of this century. From 2009 to 2021 we found an increase of temperatures of 0,439 °C/decade, more than 0,1°C of the estimates for the second half of previous century. We found an advancement of the onset of the reproduction of 26 days/decade during the period 2009-2022, more marked during the last eight years, when data were annually recorded. Minimal temperatures and the absence of frozen days from the previous week of onset spawning period determine the start of reproduction. Predictions of habitat suitability spawning 2021-2100 provided by climatic niche analysis supports a potential contraction of the species range in the Montseny and, remarkably, much isolation from the neighbouring populations.

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Abstract

The Montseny massif shelters one of the southernmost western populations of Common frogs (*Rana temporaria*) which experiences a Mediterranean climate that poses a challenge for the species persistence in warming temperatures scenario. We evaluated the effect of climate change in three levels. Firstly, we analyse if there has been an advance of onset spawn period due to warming temperatures. Second, we analyse the influence of climatic variables in the onset of spawn period and, third, how the distribution of these species could vary according to the predictions of temperature increase for the end of this century. From 2009 to 2021 we found an increase of temperatures of 0,439 °C/decade, more than 0,1°C of the estimates for the second half of previous century. We found an advancement of the onset of the reproduction of 26 days/decade during the period 2009-2022, more marked during the last eight years, when data were annually recorded. Minimal temperatures and the absence of frozen days from the previous week of onset spawning period determine the start of reproduction. Predictions of habitat suitability spawning 2021-2100 provided by climatic niche analysis supports a potential contraction of the species range in the Montseny and, remarkably, much isolation from the neighbouring populations.

Keywords: Climate change, *Rana temporaria*, Onset spawn, Phenology, Habitat suitability

Introduction

Climate change due to increases of human greenhouse gas emissions from the beginning of the industrial revolution to the present is now considered one of the major threats to biodiversity in the twenty-first century underlying several reported extinction events (Thomas et al. 2004; Parmesan 2006; Thuiller et al. 2011). Climate is rapidly changing and the same trend towards ~~the-increases of~~ global temperatures is forecasted for the next decades (IPCC, 2021; Seneviratne, et al. 2014). Understanding how species respond to increases of temperatures and changes in precipitation, both at a population and species level, is one of the most important questions to answer. Regarding the amphibians, Sheridan et al. (2017) indicate - - that changes in body size and breeding phenology are the two major ecological consequences of climate change in the wood frog (*Lithobates sylvaticus*), but it is unclear how temperature rise interacts with these variables. Reading (2007) reported in the common toad (*Bufo bufo*) a reduction of survival, body condition, size, and egg laying, and Blaustein et al. (2010), reported changes in developmental rates of eggs and larvae.

Changes in temperature or precipitation have the potential to influence timing of amphibian reproduction (Blaustein et al 2010). An earlier onset of spring breeding behaviour correlated with a warming climate has been observed among various pond-breeding frogs and toads in Europe (Beebee, 1995; Tryjanowski et al., 2003; Scott et al., 2008) and Asia (Kusano & Inoue, 2008; Primack et al., 2009). However, other species may exhibit either a trend towards later onset of spring breeding or no trend at all (Todd et al., 2010; Klaus & Loughheed, 2013). While & Uller (2014) and Ficetola & Maiorano (2016) after meta-analysis with published phenological data of amphibians around the world concluded that this group is strongly influenced by climate change, but we do not have a clear pattern of how climate influences important parameters of amphibian populations, such as abundance, survival, breeding success and morphology. Both authors coincided in the low importance of rainfall changes in the effects on offspring of climate change and the high relation of advance of onset spawn with rising temperatures. However, 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). Shifts in phenology due to climate change have been observed by many authors in several species (Beebee, 1995; Parmesan, 2006; Walther et al., 2002; While & Uller, 2014; Ficetola & Maiorano, 2016), founding evidence for earlier breeding with shifting climate and Chadwik et al. (2006) showed trends towards earlier breeding associated with shifts in climate in *Triturus* species. However, findings from several independent studies reveal that the impacts of a changing climate on

breeding times may be more complex. ~~However,~~ related to **Common Frog**, the most recent studies found a close relationship between warming temperatures and advanced reproduction date (While & Uller, 2014; Ficetola & Maiorano, 2016; Bison, 2021).

One of the research areas of the effects of climate change on species is to measure the expected shift on its ranges they will experience in the future. Changes on geographic distribution can occur because climate change affects population growth and survival or the ability to colonise new areas (McCaffery et al., 2010) mediated by physiological adaptation of species to a range of environmental conditions (Greenberg & Palen, 2021). Modelling habitat suitability across time using current data is commonly used to predict how amphibian ranges will change shaped by effect of climate change (see for example García et al., 2013; Duan et al., 2016; Aguelo et al., 2019; Kim et al., 2021). However, the increase on data availability of species distribution gathered during the last decades, has recently shown shifts on the species ranges. For example, Enriquez-Urzelai, et al. (2019a) demonstrate that most of Iberian amphibians have changed ~~your~~ altitudinal and latitudinal distributions, moving up to the north or to higher altitudes in the last 20-25 years in response to rising temperatures.

The common frog (*Rana temporaria*) is widely found across the temperate and cold regions of Europe, from sea level to 2.700m a.s.l. reaching a latitude of 70° North, above to the Arctic Polar Circle. The southernmost populations of the species are placed in the Rodopi mountain range of Greece, in Eastern Europe (Kuzmin et al., 2009). The second most meridional edge of the common frog is found in Western Europe, in the Montseny massif, the southernmost foothill of the Transversal Catalan Range placed in Northeast Iberia (Figure 1). Common frogs breed in shallow, still, fresh water such as ponds, lakes or marshes. The onset spawning is variable depending on the altitude and latitude, between February to late June, but generally in March-April over the main part of their range. ~~However,~~ in the Atlantic region of Iberian Peninsula spawn occurs earlier, in November-December due to abundant rain and mild temperatures (Bea et al, 1986). Outside the breeding season, common frogs live a solitary life in damp places near ponds or marshes or in long grass.

Although climate in the Montseny is typically Mediterranean, the altitude of the massif and the north and east exposure of the main hillsides provide humid and temperate conditions (Panareda-Clopés, 1979), thus allowing the persistence of populations of this cold-adapted species. Thus, this massif harbours rear edge population of the Common Frog, where the species experiences small temperature buffer in comparison with most of its range, making these populations a good model to study the effects of climate change on temperate amphibians (Hampe & Petit, 2005; Habibzadeh et al., 2021).

Furthermore, the models of climatic change (González-Hidalgo et al., 2009; Peñuelas et al., 2021) for the Mediterranean area forecast more irregularity in precipitation patterns, specifically more rainfall in autumn than in spring, and concentrated over a few days in some years, while in others, there will be heavy droughts. Air temperature is rising (Vicente-Serrano et al. 2014) and in the Montseny the variation of the average air temperature in Turó de l'Home (1712m a.s.l.) for the period 1950-1999 was 0,3°C/decade (Peñuelas & Boada, 2003), and Minuartia (2016), shows a rate of increase with similar trend (+0.24 °C/decade), for the period 1950-2014, with a higher average seasonal increase in spring and a lower one in autumn.

Our objectives were to understand how the environmental variables influence the onset of breeding phenology of the Common Frog last years, and explore the changes that this species face in the context of climate change in the edge of distribution in Montseny massif using niche modelling. Specifically we examined the following issues: i) we analysed whether the onset of breeding period has advanced in recent years as a consequence of global temperature rising. ii) how and which meteorological variables influencing this onset, and iii) whether the species will experience in Montseny Massif a contraction of its distribution range in the 2100 scenario as a consequence of global warming.

Materials & Methods

Study area

Phenological survey was conducted in the Santa Fe Valley situated on the eastern side of the Montseny massif (UTM31N 5524) at 1,100m a.s.l (Figure 1). At the study site, monthly mean temperature ranges from 3°C in January to 20°C in August and mean annual precipitation is approximately 1000 mm, occurring mostly as rain in autumn and spring, with occasional snow in winter. The valley is primarily forested with beech (*Fagus sylvatica*) and divided by streams that produce many wetlands and ponds. We have extended the study area to all the populations in the Montseny Massif to gather data for niche modelling analysis based on the known range that comprises the eastern side of the massif where the species lives associated with riparian and beech forests (Amat & Montori in press). Permits for fieldwork were granted by: Diputació de Barcelona (DIBA20140609, Servei de Fauna de la Generalitat de Catalunya: SF/0539/2019,

Onset breeding period

In 2009 and from 2014 to 2022 the day of the onset breeding period of *Rana temporaria* in Santa Fe del Montseny (Barcelona) was recorded. Other discontinuous data of reproductive success based on the observation of clutches or amplexus were obtained from reports, scientific publications, technicians and researchers of the Montseny Natural Park (Balcells, 1957; Pascual

& Montori, 1982; Montori & Pascual, 1987; Campeny, 2001; Roig & Amat, 2002; <http://ornitho.cat>; <https://siare.herpetologica.es> Martí Boada com pers. and unpublished data of the authors). However, these data are not included in the analyses of the climatic factors influencing the start of breeding period because they do not reference the day of the beginning of the breeding ~~success~~, but the day in which reproduction has been observed. They are only considered to describe the amplitude of the breeding period in Santa Fe del Montseny.

From 2009 to 2021, daily meteorological data have been obtained from “Viladrau Ws” Meteorological Station, located in Viladrau (Osona, Barcelona, at 953masl; 41.84008N; 2.41877E). Data of four weeks (28 days) prior to the spawning were taken in order to test how previous meteorological variables influence the onset of breeding period (Suppl. Mat. Table 1). We select four weeks because published studies reference the importance of the previous one to three weeks in the onset spawning (Bea et al. 1986; Tryjanowski et al, 2003; Loman, 2016; 2019; Bison et al. 2021). Nine meteorological variables have obtained: temperature (minimal, maximal and average in °C, relative humidity in %, rain in mm, maximum speed wind (in km/h), average of atmospheric pressure in hP, number of Days with temperature below zero <0°C and < 1°C, and Solar Irradiation in MJ/m² (Servei Meteorologic de Catalunya - <https://meteo.cat>).

To test the influence of meteorological variables in the onset spawning period, four weeks prior to the start of spawning were compared separately with ANOVA Kruskal-Wallis test using the period (week) as a grouping variable. These four periods: 1, 2, 3 and 4 correspond to 1-7, 8-14, 15-21 and 22-28 days before the start of reproduction. A non-parametric test was used in the univariate analysis since some variables did not fulfil the condition of normality (Kolmogorov-Smirnov test).

To observe if the last years the onset of Common Frog spawning ~~success~~ occurs early, we performed linear regression between the day of onset of reproduction (DOY: day of year) and the year. To determine which meteorological variables influence the onset of egg-spawning period Factorial Analyse, using Principal Components as extraction method. All statistical analyses carried out with Statistica 8.0 Software. Variables used in Factorial Analysis analyses are FD4, FD3, FD2, FD1 (Days with temperature below zero degrees in the four, three, two or one week before onset spawning period), TX4, TX3, TX2 (Average of Temperature in the four, three and two weeks before onset spawning period) and Tm4, Tm3, Tm2, Tm1 (Minimal Temperature in the four, three, two and one week before onset spawning period). Pluviometry, Maximal temperature and average of temperature on the first week previous to the onset of spawning has been not considered in the Factorial analyses due to low contribution to explained variance in a previous exploratory analysis.

Future distribution range contraction

We collected four-hundred georeferenced observations of *Rana temporaria* at high resolution in the northeastern Iberian range of the species (Figure 1). Nearly forty percent of localities we used ~~were placed in~~ the Montseny massif and were recorded from us during twelve years of the monitoring of amphibian populations in the natural park. We gathered nineteen bioclimatic variables at 30 seconds resolution from WorldClimateDatabase (Hijmans et al., 2005, <https://www.worldclim.org/data/cmip6/>) of current and future climatic conditions under the coupled model intercomparison project phase 6 (CMIP6). We used the CNRM-CM6-1 model for a short (2021-2040) and long term (2081-2100) based on the lowest (126) and highest (585) emission scenarios to estimate the species habitat suitability. We selected maximum entropy approach (Phillips et al., 2006) to model habitat suitability using MaxEnt 3.4.1. because this method only uses presence data, performing well even with low sample sizes providing reasonably accurate and interpretable models with good predictive power (Phillips & Dudík, 2008). We clipped raster layers to the same geographic extent covering the south westernmost margin of the Iberian Peninsula, including Montseny massif, Transversal Catalan Range and, Catalan Prepyrenean and Eastern Pyrenees. In order to minimise collinearity among bioclimatic variables, we used R usdm 1.1-8, to calculate variance inflation factor (VIF) and removed highly correlated variables performing a stepwise procedure. We checked the model performance using the size of the area under the receiver operating curve (AUC) which when exceed a threshold value of 0.75 (Pearce & Ferrier, 2000) indicated high model suitability. We performed fifty replicates training the model using the 25% of the presence data and quantifying variable importance using jack-knife. Predicted species geographic distribution based on climatic suitability under current and future scenarios was represented by means of using the logistic representation of probability of occurrence.

Results

The data of onset spawn of multiple years has been obtained from 1957 to 2022 from reports, databases and personal observations (Suppl. Mat. Table 2). This table ~~only presents~~ the earliest and latest date of registered spawn each year. During this period, the early amplexus was registered on February 5th, in 2021 and the latest amplexus was registered on March 27th, 1984 (Campeny, 2001). Then, the reproductive period of *Rana temporaria* in Sta. Fe del Montseny ~~occurs~~ between early February until the second half of March. However, some sporadic spawn could occur on April (1979, per obs.).

Onset breeding period

When analysed with a linear regression the DOY of onset spawning data recorded from 2009 to 2022 period, we found a pattern of advancement of the beginning of the reproduction (Figure 2). The onset of reproduction, quantified as day of year (DOY), was inversely correlated with the year. The linear model obtained was significant ($R = -0.7903$; $P = 0.0065$; slope = -2.5959 ; $SE = 2.4974$) and explained 62.45% of the total variation, reflecting that part of the fluctuation of reproductive onset have advanced over time in the last years. Between 2009 to 2022 the average of advanced onset of reproduction is 26 days/decade on average in the last 14 years (Figure 2). From 1997 to 2021 the average of maximal temperature has been raised $0.404^{\circ}\text{C}/\text{decade}$ (Suppl. Mat. Figure 1 and Suppl. Mat. Table 3). This value is higher than the values published by Peñuelas & Boada (2003) and Minuartia (2016) for the Montseny massif.

The results obtained in the Kruskal-Wallis test between periods (weeks) previous to onset breeding success from 2009 to 2022 related to meteorological variables analysed shows in Table 1. Only temperature, solar irradiation and the number of days with temperature below zero degrees were significant. However, multiple comparisons indicated that only significant differences exist between the first and fourth week. This could indicate that the previous week to onset spawn influences the date of onset breeding period. Pluviometry, relative humidity and atmospheric pressure had not significant differences in the previous for weeks to onset spawn.

The average and standard deviation for the four weeks previous to the start of reproduction showed that the last week had minimal temperatures greater than zero degrees and more uniform temperatures (Figure 3). The data indicated that the temperatures stabilized during the week prior to breeding, both minimum and maximum. The number of days with minimum temperatures below zero also decreased significantly and represent only one day in average for all the years analysed. Rainfall did not seem to be a determining factor (Figure 3 and Suppl. Mat Fig. 2). In fact, average minimal T^a for the previous week of onset spawning is 2.09°C ($STD = 0.88^{\circ}\text{C}$; $Max = 4.07^{\circ}\text{C}$; $Min = 0.9^{\circ}\text{C}$ -see meteorological data in Supplementary Material, Table 1-).

The same results offer the daily variation of the minimum temperature and the average of the interannual variance (Figure 4). In fact, the days prior to the start of reproduction, the minimal temperature stabilised and showed less variance than the previous weeks. Figure 5 shows the relationship between the DOY of spawning period and the last DOY with one or three consecutive days with temperatures below zero. Both correlations were significant and highlight the importance of not frozen days in the onset of reproduction.

Factorial analysis (Figure 6), confirmed that the variables best associated with the DOY were the number of days with temperatures below zero degrees in the previous weeks. In the

first factor (Table 2), the variables related to the number of days those temperatures remained below zero and temperatures would have more relevance, while in the second factor are the variables related to temperature and frozen days in the week previous to onset spawn. The two first factors explained 83.70% of the variance (Table 2), so these variables can be considered as indicative of the start of reproduction.

Future distribution range contraction

Habitat suitability of *Rana temporaria* in North-eastern Iberia after excluding the collinear variables was determined by five variables which had parametric correlations between 0.695 and 0.029. Specifically, the occurrence of the species was strongly restricted to temperate conditions during the warmest month, moderate precipitation seasonality and temperatures during the driest quarter. The average test AUC for the fifty replicates was 0.896 ± 0.009 (mean $\pm$ standard deviation) indicating a good fit of the model. The predicted range of common frogs in Northeastern Iberian Peninsula was sharpened by the terrain as revealed by high probabilities of occurrence in the mountain areas with low probabilities at lower altitudes (Figure 4). This led to the isolation of the populations placed in the southern edge of the range especially between the Montseny and Guillerics, and between this later and the rest of the Catalan Transversal Range. We predicted the presence of the species in the montane ranges of the Montseny except for the highest peaks of the massif. After controlling for redundancy, representing habitat suitability, analysis retained four-six variables (parametric correlations lower than 0.7). Models had AUC tests comprised between 0.867 and 0.887 indicating good performance. Jackknife test revealed that mean temperatures of the wettest and driest quarter, maximum temperatures in the warmest month, precipitation in the warmest quarter and precipitation seasonality were the most influential variables, followed by precipitation and temperature seasonality and isothermality. Models based on scenarios ssp128 and ssp 585 (Figure 8) considerably reduced the probability of species occurrence comparing the predictions achieved between 2040 and 2100. Our results highlighted the isolation between the populations in the southernmost edge, and between them and the Pyrenean ones. In the Montseny massif, the future predicted ranges in 2040 were similar than the currently occupied by the species, but occurrence probability drops and rejected an altitudinal shift towards the highest top mountains. The worst scenario, high level of emissions in 2100, predicts the species occurrence with low probability and only in the eastern side of the massif, suggesting the failure of its persistence in Montseny. Thus, all our predicted scenarios, low and high emission entailed a dramatic reduction of the habitat suitability in the Montseny massif within this century (Figure 8).

Discussion

Onset breeding period

The Common Frog in the Montseny Massif had advanced its spawn onset following the increase of temperatures due to global warming. Significantly, the four earliest dates of onset spawning period occurs in 2019, 2020, 2021 and 2022 (Figure 2). Between 2009 and 2022 the average of advanced onset reproduction is 26 days/decade (Figure 2). Our estimated advance of onset breeding season in Montseny Massif is high, but included within the range found by While & Uller (2014) for *Rana temporaria* (-28,1 days/decade).

Probably, the ~~extreme~~ Mediterranean climatic influence in the Montseny Massif, located in the southern limit of distribution of the species, associated with the increases of rising temperatures during the latest years (Minuartia, 2016), could be the causes of this great advancement. Supporting this data (Minuartia, 2016) estimates an increase in the average annual temperature of 0.7 °C for the decade (2012-2021) in the Coastal / Pre-coastal Region (Montnegre-Corredor Natural Park), to which the Montseny Massif is close.

This earliest onset reproduction date in amphibians has been pointed out by different authors. Beebee detected in 1995 an advance in the beginning of reproduction of some species related to global warming. Multispecies meta-analyses have suggested that amphibians are the taxa showing the strongest phenological advancement in response to global warming, with an average breeding advancement between 2.6 days per decade (Parmesan 2007) and 6.1 days per decade (While and Uller 2014). The mean advance in *Rana temporaria* onset spawn found by While & Uller (2014) was -5.95 day/decade (Stand. Dev.=11.92; Maximal advance; -28,1 day/decade). While & Uller (2014) has clearly shown that amphibian populations consistently anticipate their breeding periods, determined by trends of global warming, particularly at high latitudes.

Our results are in accordance with Ficetola & Maiorano (2016) who concludes that the temperature increase was the major driver of phenological advancement, while the impact of precipitation on phenology was weak. In fact, we didn't obtain any significant relation between rain and DOY of onset breeding (see i. e. Figure3 and Supplementary Material table1 and Figures 2 and 3).

For the end of the last century, other authors (Peñuelas & Boada, 2003; Minuartia, 2016), estimated an increase in air temperatures from 0.24 to 0.3°C per decade in the Montseny massif. However, the data obtained in this study from 1996 to 2021 in the same weather station indicate that this increase has accelerated to 0.404 °C/decade in average of maximal temperature (Supplementary Material Figure 1), according to the observations of Peñuelas &

Boada, (2003) which consider that the increasing of temperatures have accelerated last decades.

This advancement demonstrates a great plasticity in spawning dates in front climate change. However, Phillimore et al. (2010) in Britain observe that although all populations exhibit a plastic response to temperature, spawning earlier in warmer years, between-population differences in first spawning dates are dominated by local adaptation. Climate change projections for Britain in 2050-2070, will require first spawning date to advance between 21 and 39 days, but Phillimore et al. (2010) indicate that plasticity alone will only enable an advance of 5 to 9 days, and need microevolutionary and gene flow challenge to advance first spawning date between 16-30 days over the next 50 years. However, our data demonstrates that from 2009 to 2022 the advance of onset spawning has been 26 days, more than data shown by the other authors. Perhaps, living and surviving in the edge have been favoured and selected more plastic individuals due to the suboptimal and higher variability of environmental conditions. According to this hypothesis, Lesbarrères et al. (2007) in the Nordic limit of distribution of *Rana temporaria* found that metamorphic size was positively correlated with individual heterozygosity and fitness. These results suggest that genetic variability may be an important component of individual fitness in Common Frog (Lesbarrères et al. 2007). Ruthsatz, et al. (2022) found that *R. temporaria* has high acclimation capacity in the temperate populations, which could reflect an adaptation to increased thermal variability to enable survival in heterogeneous or suboptimal environments, especially during the larval stage. Generally, wide-ranging species, like *R. temporaria*, exhibit a greater capacity for thermal acclimation of upper thermal tolerance than narrowing-ranging species, suggesting that selection for acclimation ability may have been a key factor enabling geographic expansion into areas with greater thermal variability (Markle & Kozak, 2018). These authors demonstrate that young larvae of *R. temporaria* are the most temperature sensitive life stage and highlights that early life stages might define the climate change vulnerability of amphibian populations. Given that this widely distributed species possesses a high capacity for developmental, morphological, and physiological plasticity. In this sense in the Montseny Massif, *R. temporaria* has selected through the years the week with positive minimal temperature to onset spawn (Average minimal T^a for the previous week of onset spawning = 2,09°C; STD=0.88°C; Max=4,07; Min= 0,9), with a great variability in DOY between years (Figure 2) but low variability in spawn environmental conditions.

Enriquez-Urzelai (2018) indicates that tadpoles of *Rana temporaria*, are an eurythermal organism and thermal niches vary across latitudinal and altitudinal clines. Furthermore, at both extremes of the latitudinal gradient, plasticity is maximal. Enriquez-Urzelai et al. (2020a) indicate

that mixed signals of niche evolution and conservatism at the species level and generalized conservatism in thermal niches at the population level indicate that the pace of niche evolution in *R. temporaria* might be too slow to compensate climate change (mainly among terrestrial life cycle stages) according to Phillimore et al. (2010).

Previous studies identified a strong relationship between snowmelt date and spawning date (Corn and Muths, 2002; Corn, 2003; Bison et al, 2021) confirming a high degree of plasticity in terms of breeding timing (Muir et al., 2014). Bison et al, (2021) observe in *Rana temporaria* relationship with the DOY of snowmelt and DOY of middle spawning success. In our case, the location of the Montseny Massif in the southern limit of distribution where the climatic conditions are Mediterranean, makes impossible to determine the snowmelt day because not all the years the snow is present and the pluviometry in the firsts month of the year is very scarce. In consequence, to compare the DOY of onset snowmelt with the theoretical snowmelt, we use the DOY of the last one or three days with temperatures below zero. Our results confirm one highly and significant relation with the DOY of spawn and DOY of the last frozen days (Figure 5) according to the results obtained by Bison, et al. (2021).

Enriquez-Urzelai et al. (2020a) indicate that high-elevation populations had slightly wider tolerance ranges driven by increases in heat tolerance but lower potential for acclimation. Plausibly, wider thermal fluctuations at high elevations could be extrapolated to distribution limits like Montseny populations. Then, extreme events could have more unpredictable effects in populations living in the edge of its distribution like Montseny populations. Increases in air temperatures and more frequent extreme events (e.g., heat waves) due to climate warming will produce changes in pond temperatures (Enriquez-Urzelai, 2019b). Species could respond in situ by increasing upper thermal limits through genetic adaptation or phenotypic plasticity. However, the potential for adaptation and plastic responses to shift thermal tolerances seems limited in ectotherms, relative to predicted environmental changes (Enriquez-Urzelai et al., 2018, 2019b). Thus, species or populations living closer to their maximum thermal tolerance (e.g., southernmost populations of *R. temporaria*) might be especially vulnerable to climate change (Duarte et al., 2012; Gerick et al., 2014).

Furthermore, although the adults of *R. temporaria* show great adaptability or plasticity in terms of the onset of spawning period, the vulnerability of the larvae and adults in front of the increase of extreme phenomena in a scenario of climate change could be high. Montori et al. (2011) observe that mortality of amphibians increases due to more frequent sudden drops in temperature, which can affect both larvae and adults (Figure 9). If the advancement of reproduction continues in the coming years, the probability of post-spawning frost days will

increase, given the variability of the climate in the context of an increase in extreme phenomena. Reinforcing this hypothesis, Bison et al. (2021) observe the number of frost days during egg-development increased faster at high elevation. Then, early spawn could produce an added larval or spawn mortality due to increases of frost days (Montori et al. 2011). Enriquez-Urzelai (2019b) predicted extensive decreases in climatic suitability in Southern Europe, which harbors a significant fraction of the species' genetic diversity. Moreover, these authors suggest that climatic suitability of *R. temporaria* decreases at locations where water is scarce, or ponds reach temperatures $>40^{\circ}\text{C}$. This temperature is close to the critical thermal maxima of *R. temporaria* tadpoles (Enriquez-Urzelai et al., 2019b). In the shallow ponds in which *R. temporaria* commonly breeds, thermal conditions depend on degree of insolation and depth. Tadpoles suffer great thermal fluctuations of ponds, and thus extreme pond temperatures may set the limits of the distribution of pond-breeding amphibians. The reproduction ponds studied by Campeny (2001) in Santa Fe del Montseny show a maximum average annual temperature between 20.83 and 26.00°C , with maximums in summer above 32°C . In addition, these ponds are very shallow water with average depths oscillating from 8.19cm with SD of 4.54cm , to 15.32cm with SD of 8.19cm . In these abiotic conditions, the rising temperatures could increase the risk of larval mortality in the future.

Future distribution range contraction

The Montseny massif and the neighbouring Montnegre massif is the southernmost edge in East Iberia of ectothermic vertebrates adapted to temperate conditions (i.e. *Lacerta bilineata*, *Podarcis muralis*, *Vipera aspis* and *Zamenis longissimus*) that likely will be affected by the rise of temperatures and dryness. In this context the southwesternmost populations of Common Frog are even a more interesting species model because of the cold adaptation of the species.

Although our results provided evidence of range contraction in the Montseny, they failed to confidently predict the local extinction of the species. Amphibians are mostly low vagile and small vertebrates which rely on microclimatic conditions (Smith & Green, 2005; Hoffman et al., 2021) far from the scope of the climatic niche analysis. Range contraction is frequently predicted by climatic niche modelling in analysis of the consequences of global warming in cold-adapted species (Pauli et al., 2012; Ernakovich et al., 2014). In the Montseny massif, most of the reproductive ponds are placed in the east side, more temperate and humid, whereas the species experiences the harshest conditions in the southwestern slopes exposed to more Mediterranean climate. In this area, only four reproductive sites are known and the estimated number of reproductive females is dramatically small and undoubtedly, they are the most endangered and could disappear during the next decades.

Common frogs exhibit a large ecological plasticity, living marshes at the sea level from high altitude lakes in the Pyrenees (Kuzmin et al., 2009). In the Montseny massif they are associated to temporal pools in most cases in open areas in the margins of the riparian forest (F. Amat, unpublished results). The rise of the temperatures increases the risk of pond desiccation leading to the failure of the reproduction because most of them depend on irrigation from neighbouring streams to maintain long hydroperiod. Early reproduction, as our results indicated, may compensate for the shortening of the pond hydroperiod. However, even then, it cannot outweigh extreme spring dryness that predictably could be each time more frequent in the Mediterranean region (Quintana-Seguí et al., 2016). This phenomenon also could play a negative role in the preservation of the riparian forest that provides humid refugia for the activity of adults after reproduction.

Air temperatures fluctuate more than water temperatures (Feder and Hofmann 1999). Then, terrestrial stages are more likely to encounter more extreme temperatures than aquatic larvae. In contrast, they can use behavioural thermoregulation. This may not only allow individuals to escape unwanted temperatures (Kearney & Porter, 2009), but also may weaken directional selection on thermal traits, through a process known as the 'Bogert effect' (Huey et al. 2003; Buckley et al. 2015). Oppositely, in water, the potential of behavioural thermoregulation to buffer heat or cold waves may be more limited.

In amphibians, metamorphic and juvenile stages can thermoregulate better than larval stages. Although most forecasts of the consequences of global warming for biodiversity conservation ignore how thermal tolerance varies between life stages, the viability of the weakest link could restrict the future distribution of a species (Briscoe et al. 2012; Pincebourde and Casas 2015). Enriquez-Urzelai et al. (2020b) demonstrate that larval acclimation to high temperatures increases larval heat tolerance, but may reduce cold tolerance in immediately subsequent stages. If sudden drops in temperature are more frequent due to an advance in the reproduction date, this can endanger the survival of some tadpole pond populations.

Probably, wider thermal fluctuations at high elevations favour more tolerant but less plastic phenotypes, thus reducing the risk of encountering stressful temperatures during unpredictable extreme events (Enriquez-Urzelai et al. 2020b). This wider thermal fluctuation also occurs in Montseny Massif population due your location in Mediterranean climate, but we can't conclude if the Montseny population presents more adaptability or plasticity, and how other authors suggest, if this adaptability has a genetic basis (Phillimore et al. 2010). Future studies should address this problem in populations that survive in the southernmost limit of its wide distribution.

Conclusions

The reproductive period of *Rana temporaria* in Sta. Fe del Montseny occurs between early February until the second half of March. Between 2009 to 2022 the average of advanced onset reproduction is 26 days/decade. From 1997 to 2021 the maximal temperature has been raised 0.404°C/decade. The previous week to onset spawn influences the date of onset breeding period. Pluviometry, relative humidity and atmospheric pressure not determine the onset of spawning. The days prior to the start of reproduction, the minimal temperature stabilised and showed less variance than the previous weeks. Our results confirm one highly and significant relation with the DOY of spawn and DOY of the last frozen days

Models based on scenarios ssp128 and ssp 585 considerably reduced the probability of species occurrence comparing the predictions achieved between 2040 and 2100. Our results highlighted the isolation between the populations in the southernmost edge, and between them and the Pyrenean ones. In the Montseny massif, the future predicted ranges in 2040 were similar than the currently occupied by the species, but occurrence probability drops and rejected an altitudinal shift towards the highest top mountains. The worst scenario, high level of emissions in 2100, predicts the species occurrence with low probability and only in the eastern side of the massif, suggesting the failure of its persistence in Montseny.

Wider thermal fluctuations occurs in Montseny Massif population due to your location in Mediterranean climate, but we can't conclude if the Montseny population presents more adaptability or plasticity, and how other authors suggest, if this adaptability have a genetic basis (Phillimore et al. 2010). Future studies should address this problem in populations that survive in the southernmost limit of its wide distribution.

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Figure 1

Geographic range of *Rana temporaria* in the Palearctic and in northeaster Iberia, and location of the Montseny Massif (black circle and red square).

A: Map of global distribution of Common Frog. B: Map of the Montseny massif. Green line: Administrative limit of Natural Park of Montseny. Red Line: Administrative limit of Natural Park and Biosphere Reserve of Montseny.

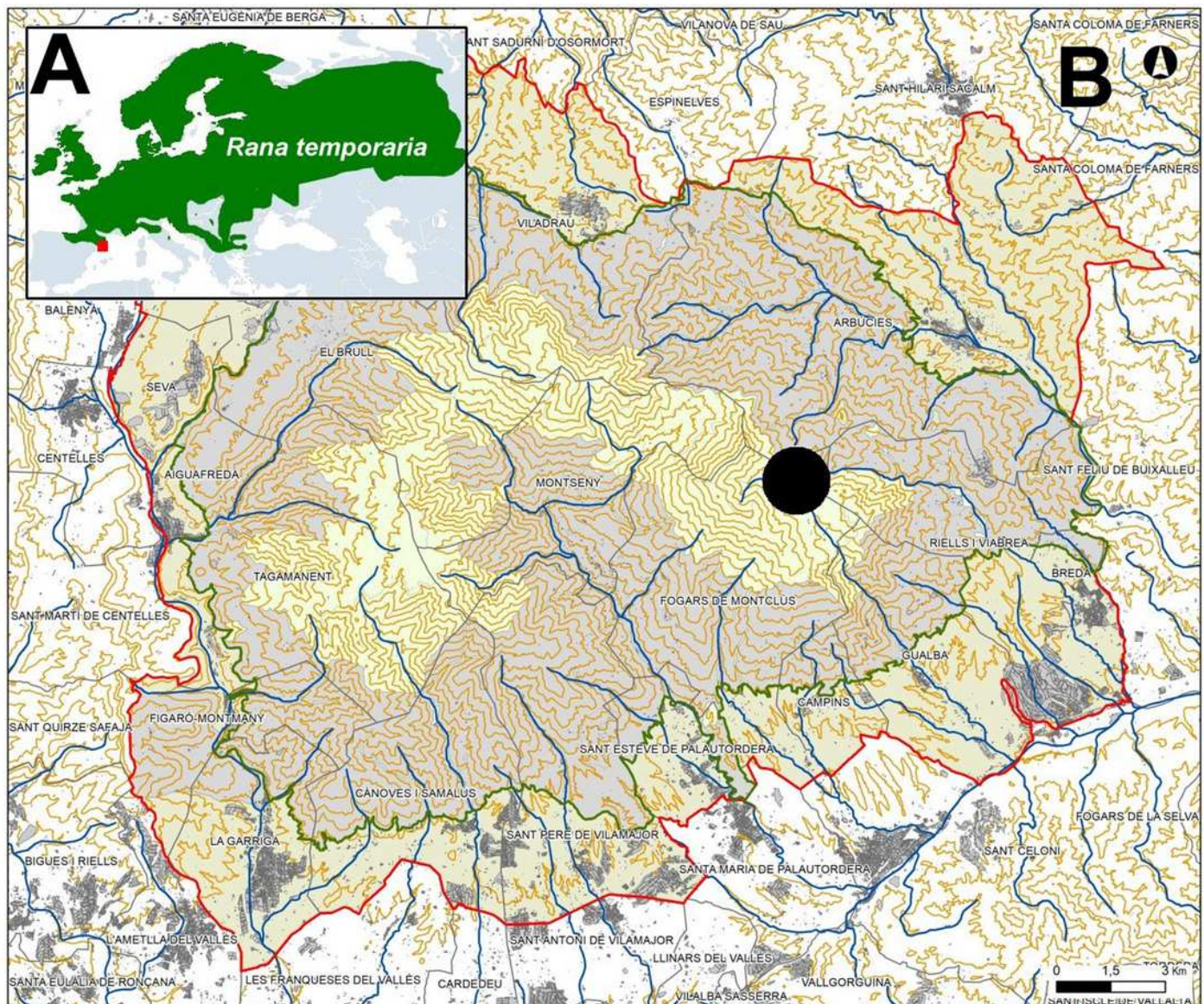


Figure 2

Linear regression between the day of onset reproduction from January, 1 (DOY) of *Rana temporaria* in the study site and the year, for the period 2009-2022.

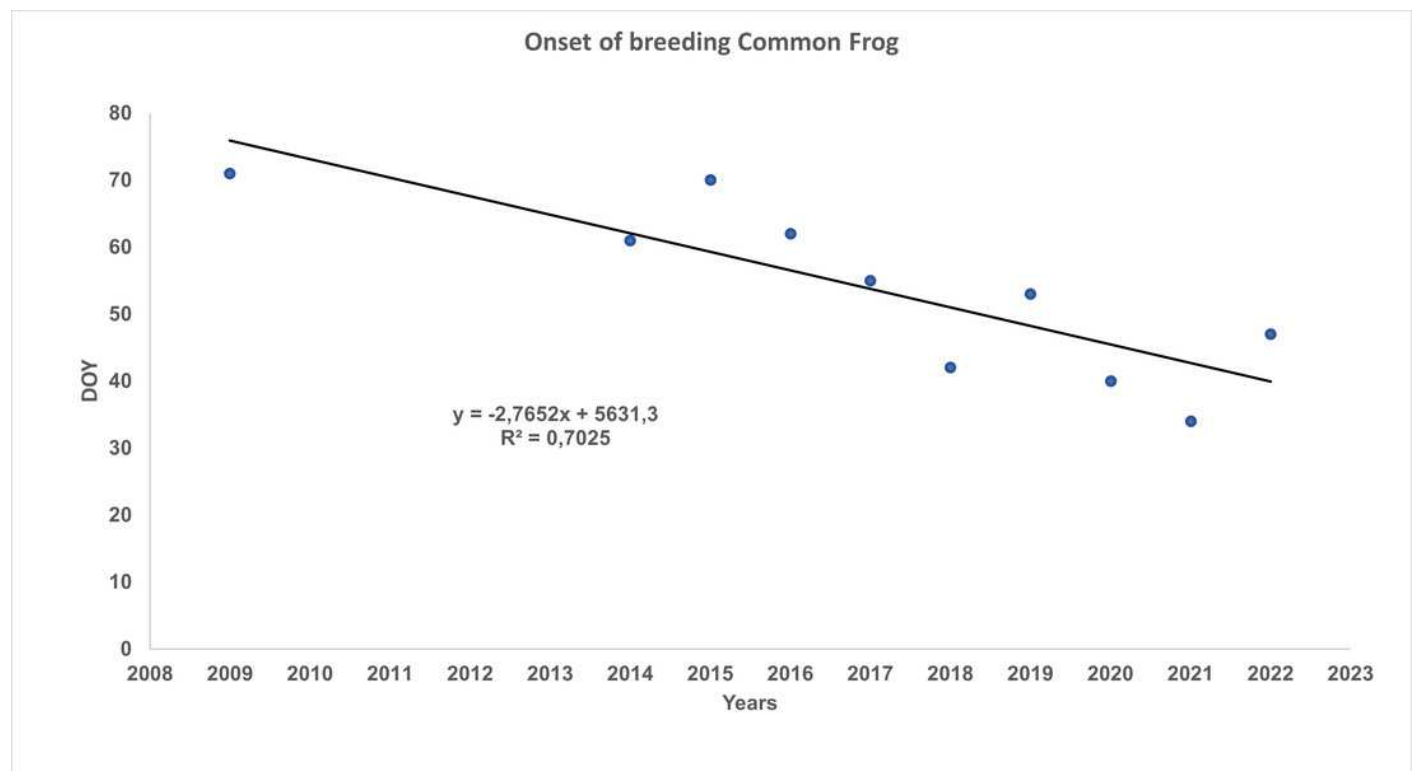


Figure 3

Evolution of maximal and minimal temperatures, rain (Pluviometry) and number of frozen days along the previous four weeks to onset breeding period, during the overall study period.

Line: Average. Black Bars: Standard deviation.

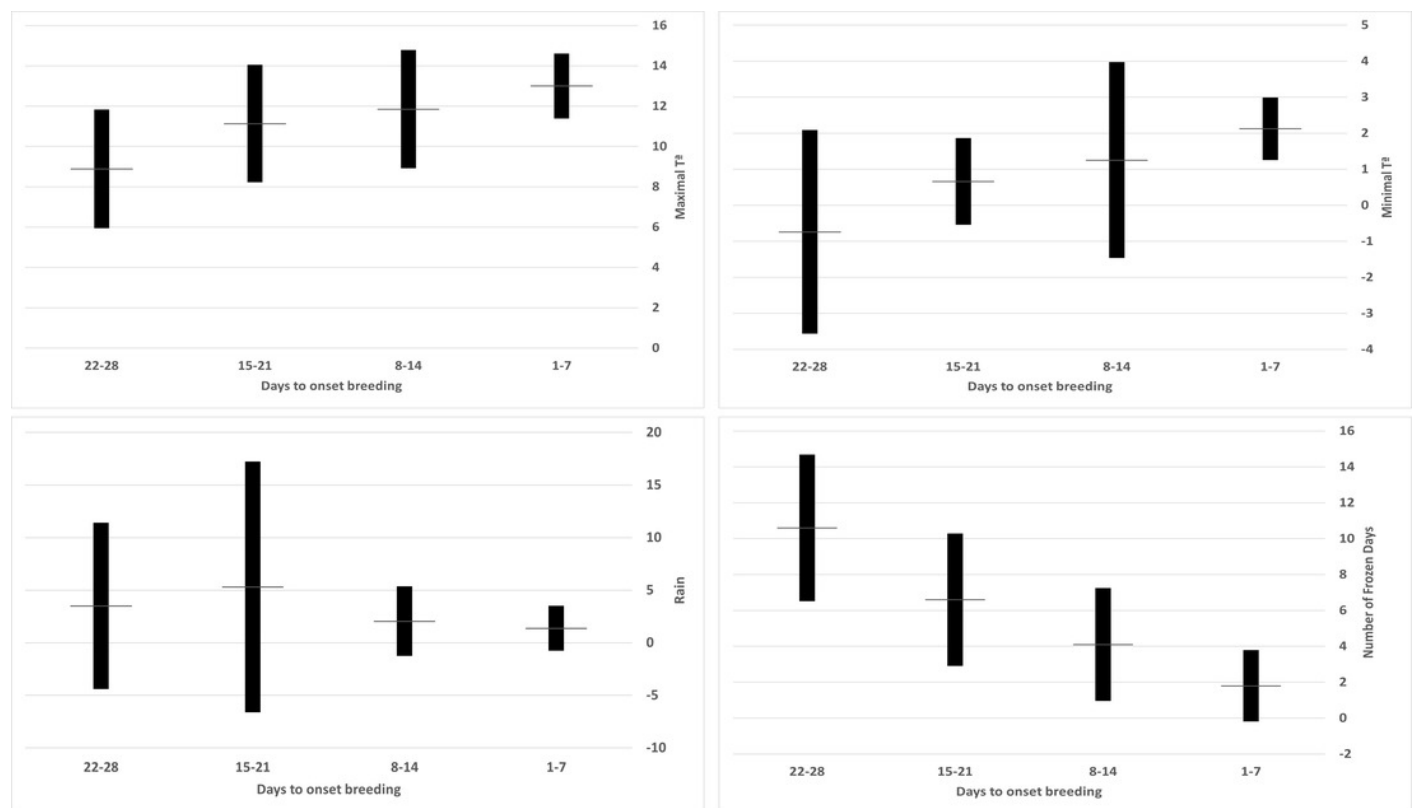


Figure 4

Evolution of minimal temperature four weeks before the onset of breeding period (top) and the interannual variance (bottom) in the 28 days previous to onset of breeding period.

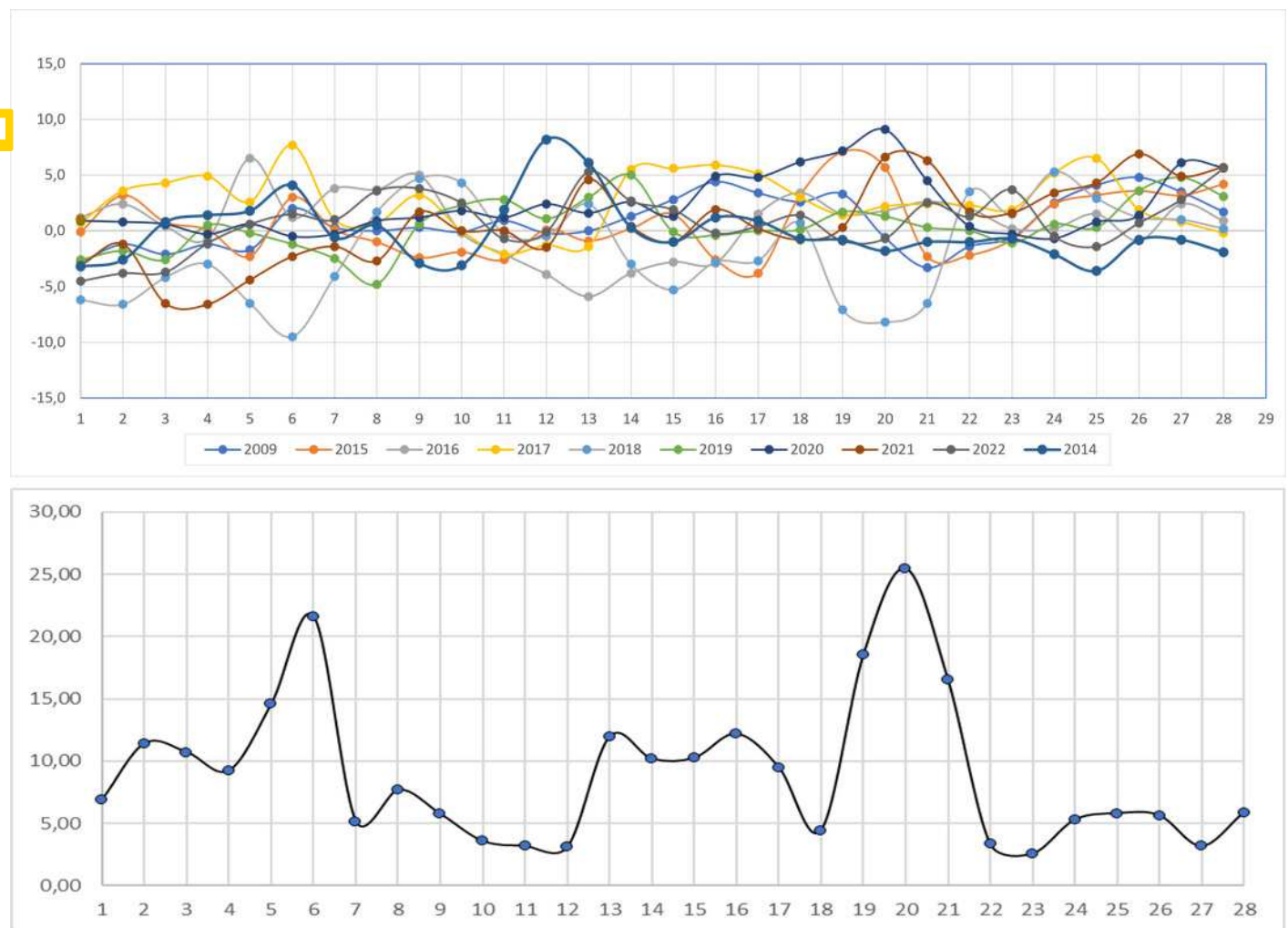


Figure 5

Relationship between the last day of year with air temperature below 0°C (FDOY1) previous to onset spawn and the DOY of onset egg-spawning of the Common Frog *Rana temporaria* (Left), and between the last day of year with three consecutive days with a

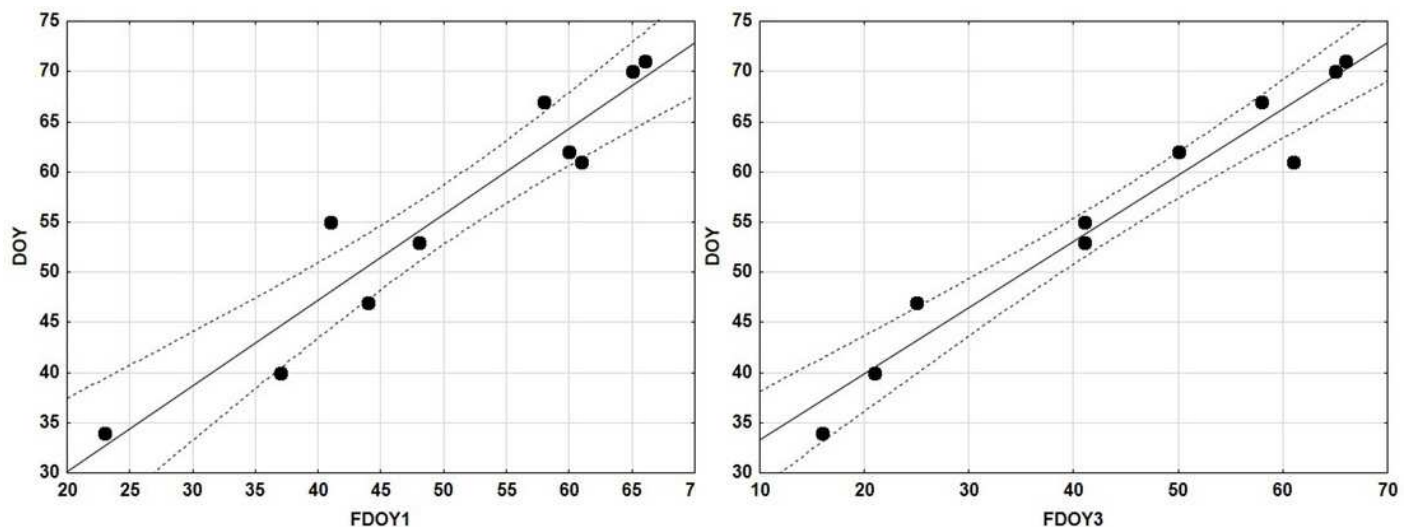


Figure 6



Factorial Analysis plot of two first factors (See table 2)

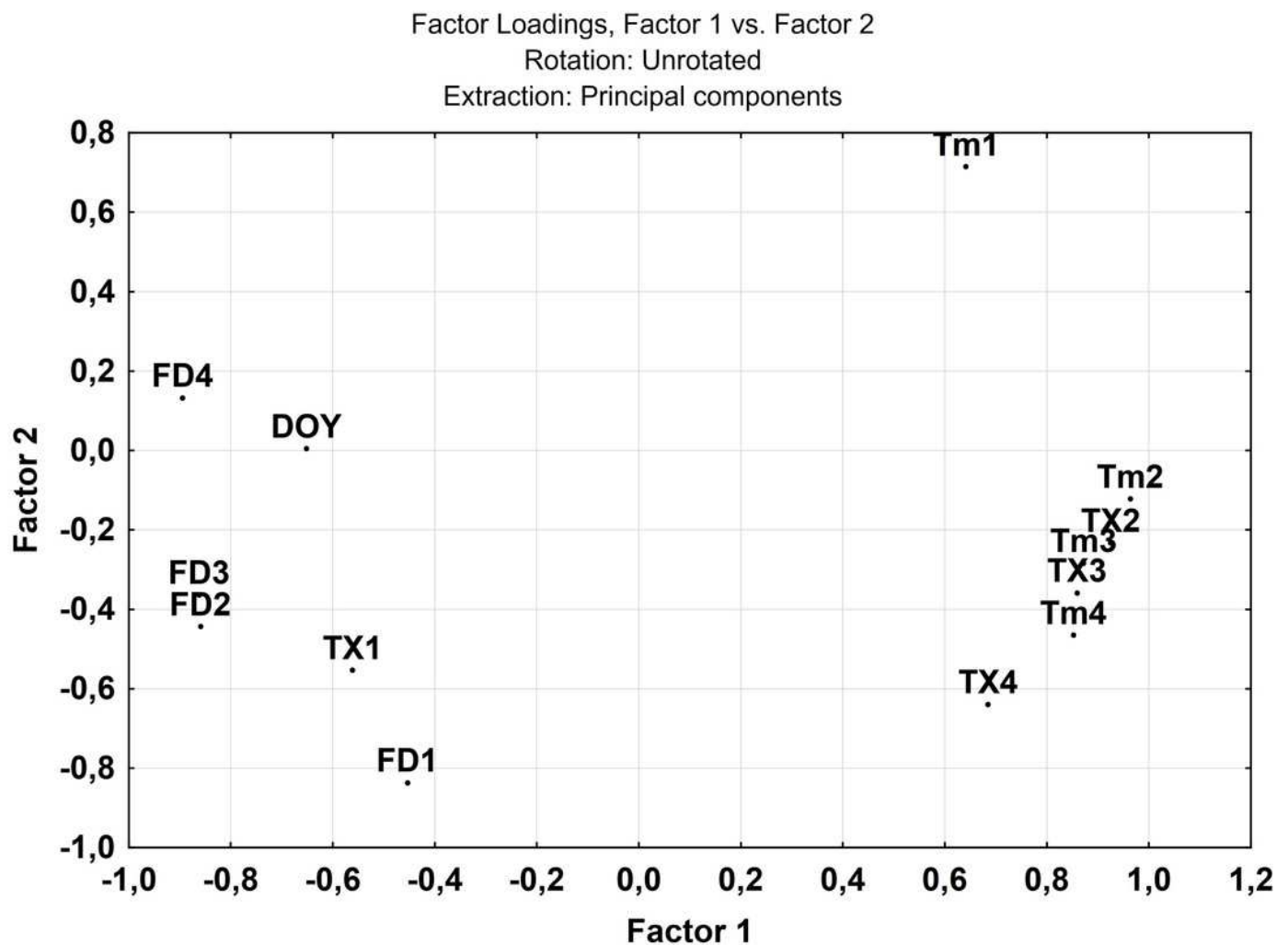


Figure 7

Habitat suitability and categorical predictability for *Rana temporaria* in northeastern Iberia during the periods 2021-2040 and 2081-2100 predicted by MaxEnt algorithm based on CNRM-CM6 1 under low (left) and high (right) emission scenarios. 

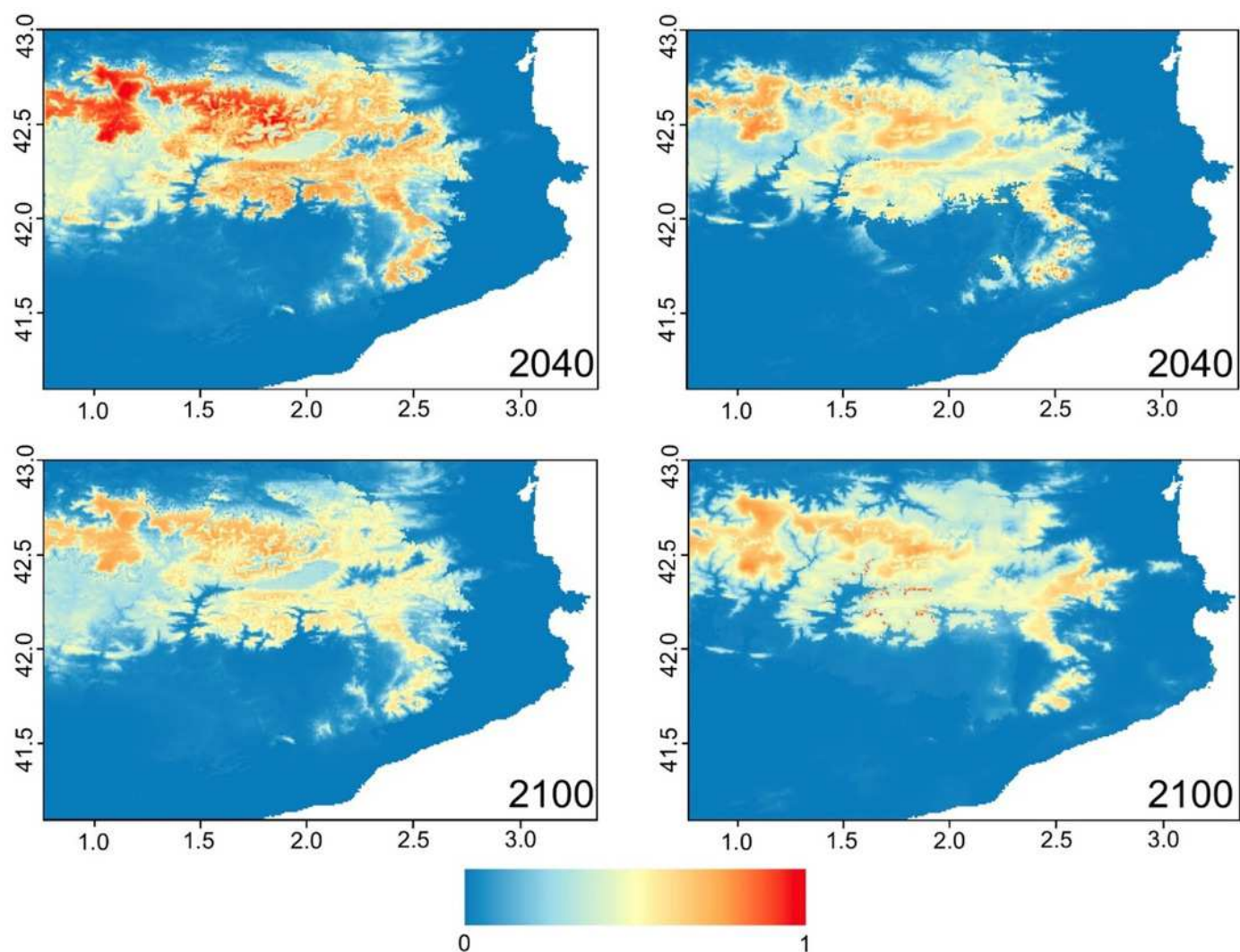


Figure 8

Diminishing of the *Rana temporaria* habitat suitability in the Montseny Natural Park predicted by the current scenario (blue dot) under the lowest emission scenario (in black) and the highest (in red). Points are the number of grids where the probabi

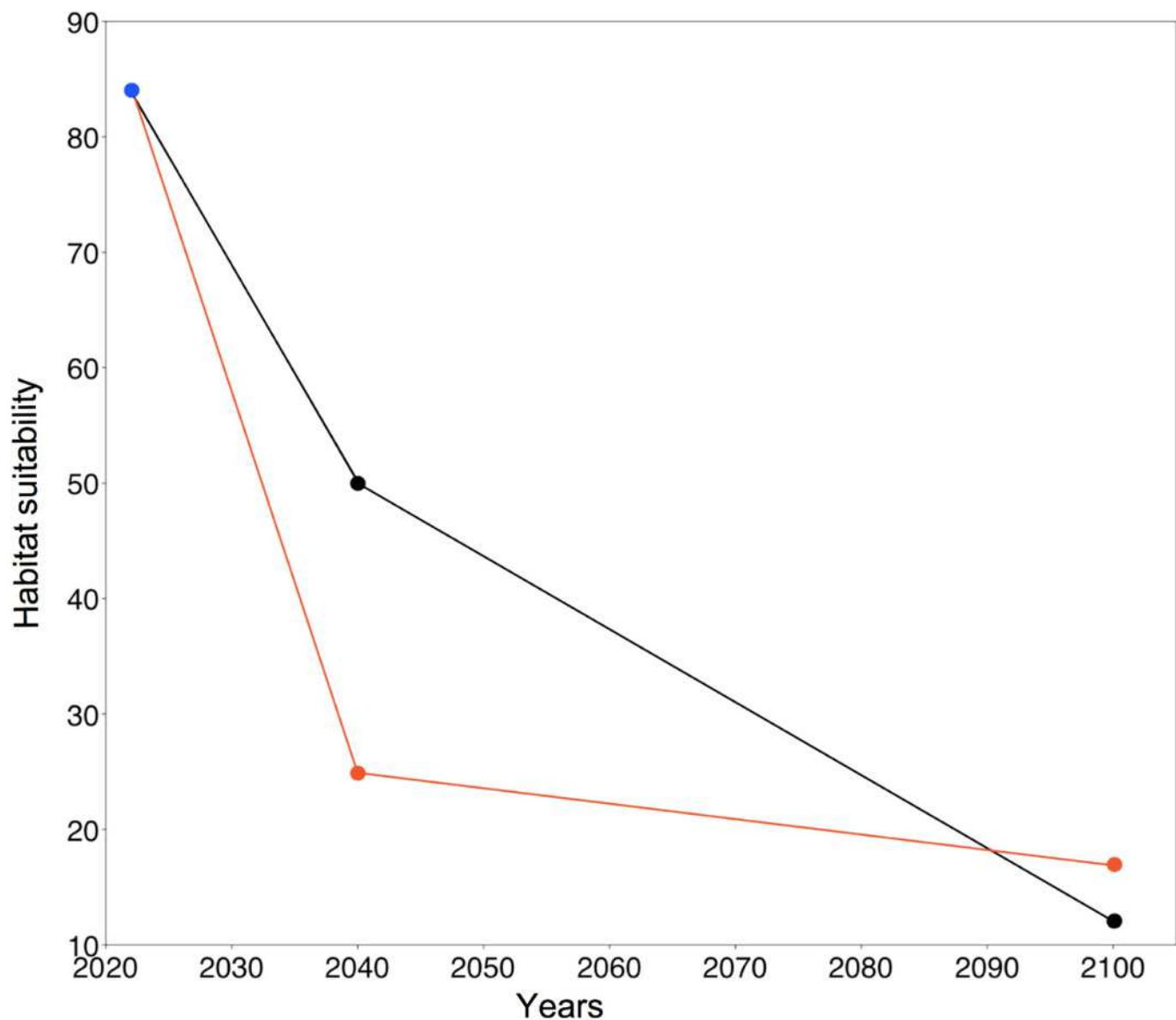


Figure 9

Adults of Common Frog dead crushed by ice by sudden temperature drop in Pyrenean Chain (Liat Valley. Pyrenean Chain. Val d'Aran. Lleida. Catalonia. Spain. 1900m a.s.l.). Photo credit: Albert Montori.



Figure 10

Kruskal-Wallis analyses results. 1st ,2nd ,3rd and 4th previous weeks to onset breeding period. Only significant variables are showed (*). Pluviometry (Rain), relative humidity, wind and Atmospheric pressure are not significant. T^a Av, Max and Min: Weakly

			Multiple Comparisons z' values between weeks						
Kruskal-Wallis test: H (3, N= 36)			Week	2		3		4	
				z	p	z	p	z	p
T ^a Av.	11.4164	0.0097*	1	0,9396	1,0000	2,2595	0,1431	3,1096	0,0112*
T ^a Max.	10.2592	0.0165*	1	0,8949	1,0000	2,0806	0,2248	2,9755	0,0176*
T ^a Min.	9.57457	0.0226*	1	1,2752	1,0000	2,1924	0,1701	2,9307	0,0203*
FD<0°C	8.97857	0.0296*	1	1,0850	1,0000	1,8569	0,3800	2,8300	0,0280*
IR	8.38596	0.0387*	1	1,7226	0,5097	2,0694	0,2311	2,7853	0,0321*

~~Figure 11~~

Table 2.- Factor coordinates of the variables, based on correlations and Eigenvalues of correlation matrix and related statistics. FD: Number of days with temperature below 0°C. 1, 2 3, and 4: weeks before onset breeding. TX: maximal temperature. Tm: mini

Variable	Factor 1	Factor 2
DOY	0,652040	0,004689
FD4	-0,874749	0,132583
FD3	-0,859343	-0,363795
FD2	0,843404	-0,443237
FD1	-0,453862	-0,836335
Tm1	0,640920	0,714930
Tm2	0,963254	-0,122021
Tm3	0,859055	-0,358827
TX3	0,859055	-0,358827
TX2	0,924646	-0,232611
TX4	0,684461	-0,639220
TX1	-0,561564	-0,553076
Tm4	0,851790	-0,464659
Eigenvalue	8.115321	2,765514
% total Variance	62.42555	21.27329
Cum. Eigenvalue	8.115321	10.88084
% Cum. Variance	62.42555	86.69873