The upward elevational shifts of pond breeding amphibians following climate warming

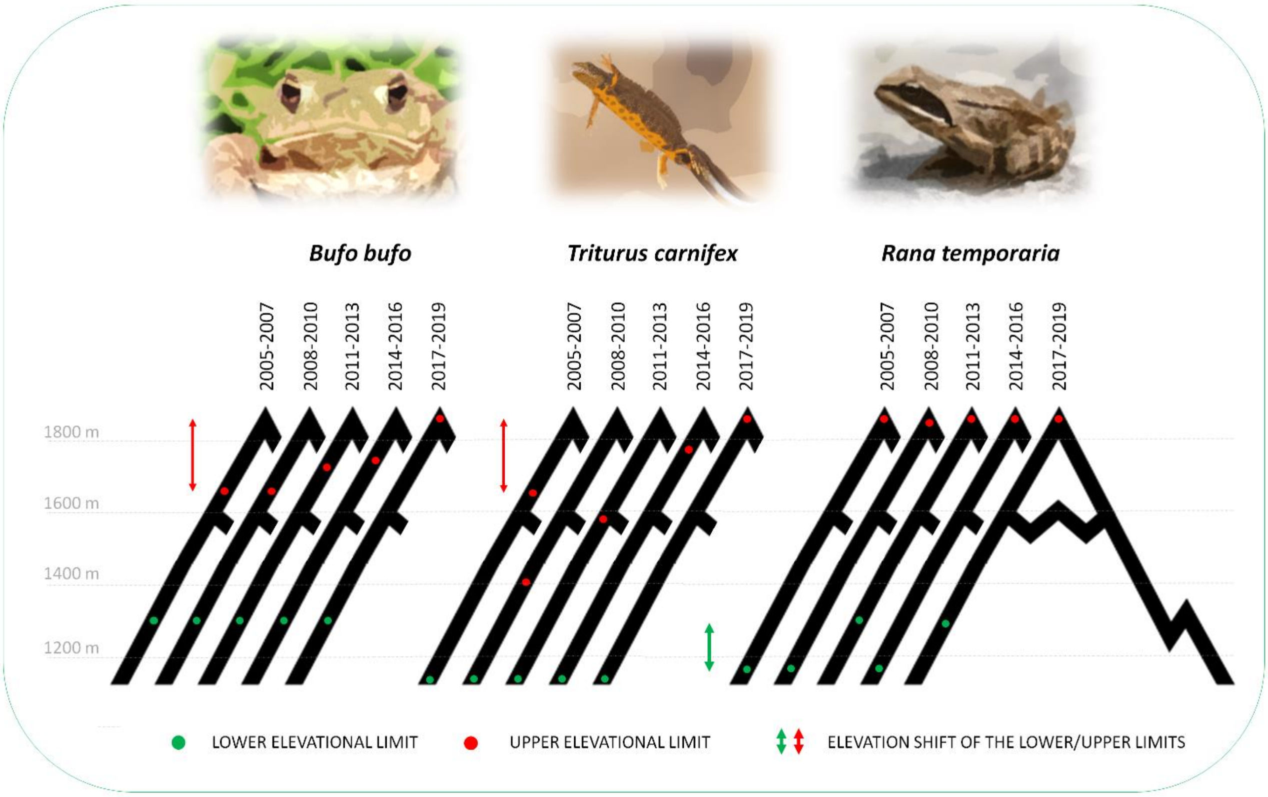
Abstract. Whilst poorly dispersing taxa such as amphibians may have limited scope to track recent and rapid climate change by means of large range shifts, they may follow their climate envelope with short elevational shifts in mountain areas. Such elevational shifts are poorly documented by empirical data for amphibians. In this study, we analysed a 15-year data series on the distribution of three amphibian species (*Bufo bufo*, *Triturus carnifex* and *Rana temporaria*) inhabiting a mountain pond network in the southern Italian Alps, where temperatures have increased significantly over the last decades. By using multi-season occupancy models, we estimated the occupancy trend of each species over the study period and tested the occurrence of an actual elevational shift after accounting for the probability of false absence. The upper elevational limit of the two eurythermal species (*B. bufo* and *T. carnifex*) underwent a significant and progressive upward shift of ca. 200 m. Our results provide evidence of the ability of amphibians to perform rapid elevational shifts, great enough to track predicted rates of climate warming. Preserving and improving habitat connectivity between lowlands and highlands could safeguard the opportunity for such elevational migrations, but mountain aquatic habitats must be preserved in order to provide a safe refuge for amphibians escaping climate warming.

Keywords. Dispersal, mountain refugia, connectivity, amphibian conservation, long-term study.

Highlights

- Whether amphibian distribution can track climate warming with the necessary rapidity is uncertain.
- Prior studies have shown weak or no evidence of latitudinal and elevational range shifts
- Amphibians’ capacity to perform upward elevational shifts during a period of climate warming is demonstrated.
- Lowland-highland connectivity and mountain breeding sites should be preserved or recovered in order for such range shifts to continue being possible.

Graphic abstract



Graphic abstract caption. Long-term data on the elevational distribution of amphibians provide evidence that eurythermal species (*B. bufo* and *T. carnifex*) can perform rapid upward elevational shifts, great enough to track predicted rates of climate warming.

1. Introduction

Climate warming is forcing wildlife to escape or develop eco-evolutionary adaptations to new, unfavourable conditions. Many taxa are moving poleward and to higher elevations, looking for cooler conditions (Walther et al., 2002; Chen et al., 2011). Preserving and opening ecological corridors enabling species to track their climatic envelopes is one of the most challenging conservation priorities of our epoch, in particular for the conservation of many species with low dispersal capacity (Krosby et al., 2010; Butikofer et al., 2020). When considering terrestrial vertebrates, these corridors may be of particular importance for amphibians, due not only to their limited capability for dispersal but also as their distribution - based on biogeographic evidence - tracks their climatic requirements, e.g., during the postglacial climatic amelioration many amphibians recolonized the continents from warm refugia (Zeisset and Beebee 2008; Gutiérrez-Rodríguez et al., 2017; Dufresnes et al., 2020). Range shifts are also predicted by many models of the future distribution of amphibians under various climate change scenarios (e.g., Girardello et al., 2010; D’Amen et al., 2011; Mokhatla et al, 2015; Duan et al., 2016). However, because of their limited active dispersal capacity (usually in the range of <1 km-10 km/year; D’Amen et al., 2011), amphibians may have limited scope to track recent and rapid climate change by dispersal (Henle et al., 2008), in particular when polewards movements are considered. With a decline of ca. -1 °C for every 150 km poleward and considering current habitat fragmentation (Krosby et al., 2010), most amphibians would need much better dispersal abilities in order to track environmental changes and evidence of poleward migrations among amphibians is lacking (Hickling et al. 2006; Li et al., 2013; Enriquez-Urzelai et al., 2019). However, the altitudinal gradient of air temperature is much steeper (ca. -1 °C for every 100 m upward) and, in mountainous areas, very different climatic conditions can be found over short distances, which would be theoretically compatible with amphibian dispersal capacity. Elevational shifts may therefore represent a very important adaptive strategy for amphibians.

Whether amphibians are able to perform such altitudinal shifts is still uncertain and field evidence is still scarce (see Martínez ‐ Solano et al., 2003; Bustamante et al., 2005; Corn, 2005; Blaustein et al., 2010; Li et al., 2013; Moskwik 2014; Enriquez-Urzelai et al., 2019). In addition, it is unclear if observed or estimated elevational shifts are sufficiently rapid for amphibians to track their climatic envelopes under the predicted climatic scenarios (Enriquez-Urzelai et al., 2019). Overall, our understanding of the timing and dynamics of amphibian elevational shifts is still insufficient. Research based on continued, long-term time series is needed to reliably document how amphibian distributions change, but such data are rarely available for many species and regions.

In the present study, we analysed a 15-year long (2005-2019) data series on the distribution of three amphibian species breeding in a mountain area in the southern Italian Alps, searching for an altitudinal shift in their occurrence. The study area is the Area of Herpetological Relevance ‐ ARE ITA064LOM024 Monte Guglielmo (southern Italian Alps, Brescia; SHI, 2019; Fig. 1), which has experienced a sharp increase in temperatures over the last decades (ca. +1.5 ˚C in the last 40 years; Fig. 2a).

The main study hypothesis is that amphibians should respond to long-term climatic trends by shifting their elevational distribution. To test our hypothesis we considered the predictions that under warmer climatic conditions, i) eurythermal, low-elevation species (i.e., common toad *Bufo bufo* L. 1758 and Italian crested newt *Triturus carnifex* L. 1758) should be able to colonize breeding sites at higher elevations and ii) cold stenothermic, mountain-top species (i.e., common frog *Rana temporaria* L. 1758) should abandon part of their low-elevation breeding sites.

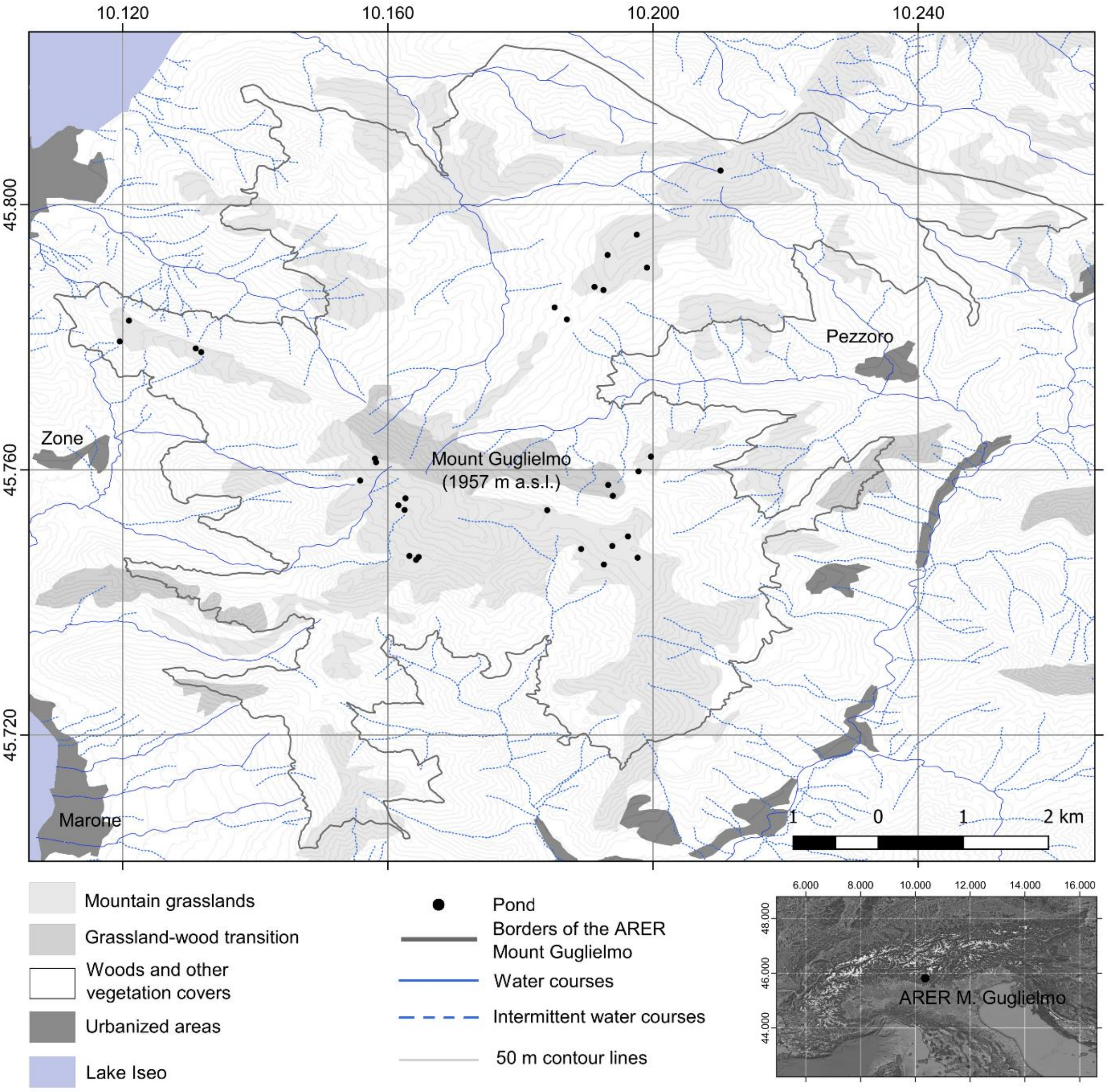


Fig.1 The network of mountain ponds in the ARE Mount Guglielmo and its position in the Italian Alps.

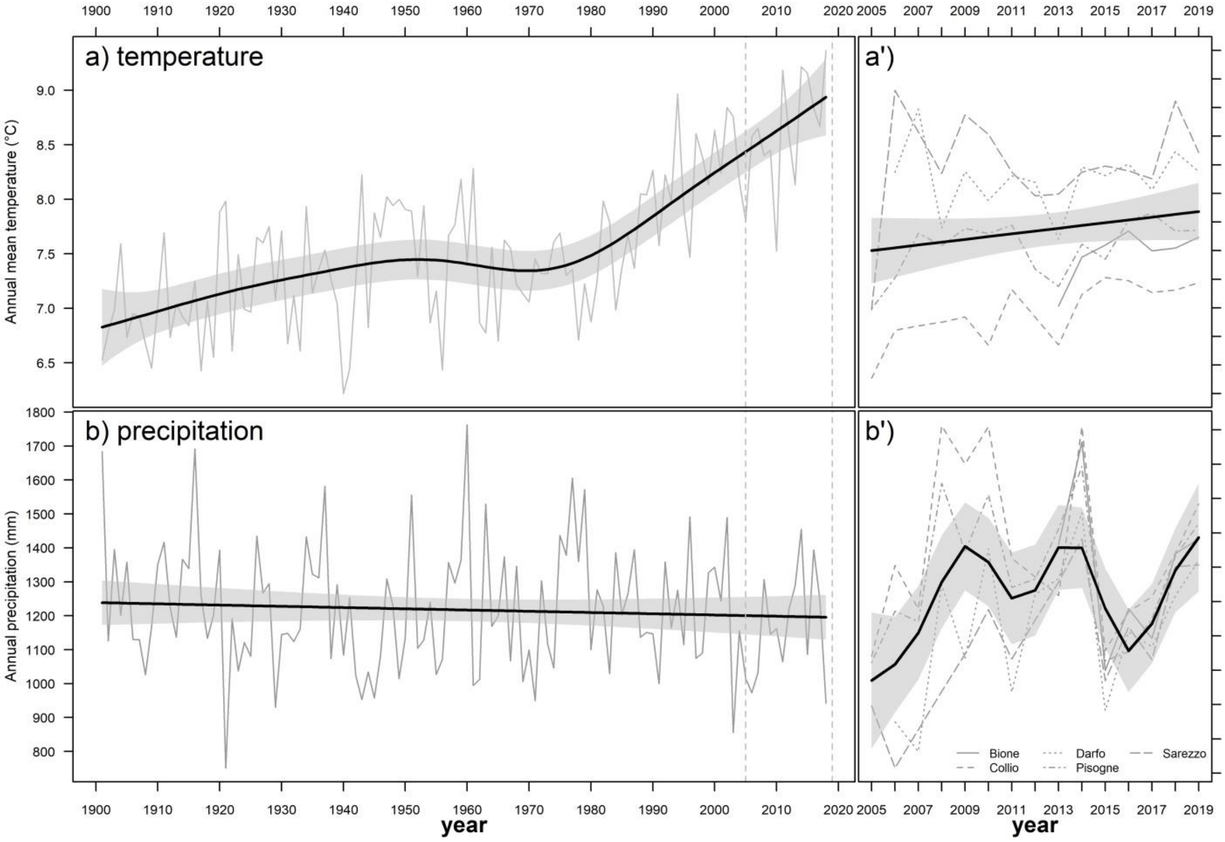


Fig. 2 Panel a) and b) represent annual temperatures and cumulative precipitations (interpolated data) from 1900 to 2018 in the 0.5° latitude/longitude grid cell containing the study area (latitude N of the cell centre: 45.75; longitude E of the cell centre: 10.25; Harris et al., 2014). The vertical dashed lines highlight the 15-years period corresponding to this study; panels a') and b'): represent annual temperatures and cumulative precipitations from 2005 to 2019 measured at the available meteorological stations within 15 km of the peak of Mount Guglielmo (Bione: 45.669839N, 10.342187E, 911 m a.s.l.; Collio: 45.808881N, 10.349489E, 1069 m a.s.l.; Darfo: 45.898024N, 10.256399E, 222 m a.s.l.; Pisogne: 45.808490N, 10.145796E, 842 m a.s.l.; Sarezzo: 45.667952N, 10.192056E, 290 m a.s.l.). In all panels, the thick lines, and associated shaded areas, represent the temporal trend (mean and 95% confidence intervals of the mean) of the climatic variables obtained by a generalized additive model, with "year" as the independent variable (Wood 2011).

2. Methods

2.1. Study area

The ARE Monte Guglielmo is an isolated massif of the southern Alps (group of the Garda mountains; Fig. 1) which is situated between Valtrompia and the large, prealpine Lake Iseo, and which surrounds the eponymous peak Mount Guglielmo (Lat. N: 45˚45'44"; Long. E: 10˚09'40"; 1957 m a.s.l.). This massif consists of an imposing calcareous ridge extending in a NW–SE direction surrounded by some minor reliefs. Mount Guglielmo is dominated by woodlands and grasslands and has a typical alpine climate. Local temperatures increased about 1 °C over the study period (Fig. 2 a'), while precipitation levels fluctuated widely (Fig. 2 b'). The temperature increase is more apparent when looking at the variation in the mean annual temperatures of the region surrounding the study area over the last decades (Fig. 2 a; Harris et al., 2014). In contrast, even on a broader scale, there was no clear trend in annual precipitation (Fig. 2 b; Harris et al., 2014).

Land cover in the region is shaped by alpine transhumance, an ancestral farming practice where herds are brought to high elevation pastures during the Summer months. As Mount Guglielmo is a calcareous karstic massif, surface water is largely absent at its higher altitudes. Water supply for cattle was traditionally obtained by digging watering ponds, representing virtually the only surface aquatic habitat in high altitude pasturelands. The study area hosts a network of 30 of these ponds which are situated within a 700 m elevational range (Fig. 1). The mean altitude of the ponds is 1535 m a.s.l. (range: 1166-1863 m a.s.l.), mean surface area is 706 m^2 (range: 140-3400 m^2), and mean depth is 0.81 m (range: 0.2-2.0 m; values based on the maximum seasonal depths measured in May-July 2006). These ponds represent the most important reproductive habitat for most of the amphibians inhabiting the study area, in particular for the common toad, the Italian crested newt and the common frog (Tiberti 2015). The former two species are both eurythermal, with similar thermal requirements (Lanza et al., 2009), and with an upper elevational limit falling within the elevation range of the study area. The common frog is a cold stenothermal species, which has been present up to the highest ponds from the beginning of the study period and with its local lower elevational limit falling below the elevation range of the study area (<1000 m a.s.l.; Tiberti 2015). Two other amphibian species (yellow-bellied toad *Bombina variegata* L. 1758 and fire salamander *Salamandra salamandra* L. 1758) are also present in the study area and are occasionally found in the ponds but, because of their very low occurrence (less than 5 observations; Tiberti 2015), they were not included in the present study.

2.2. Field surveys

Overall, 861 site surveys (1-5 per pond per year) were performed over 15 years (2005–2019) during a long - term monitoring campaign of the local herpetofauna. Surveys were performed between April and September (156 surveys in April, 520 in May, 109 in June, 49 in July, 6 in August, 21 in September), but mainly during the local reproductive season (April - June). During this period, before the annual transfer of cattle to the mountain pastures (alpine transhumance), pond water is usually clear enough to easily observe all amphibian species. The presence/absence of each amphibian species was determined by Visual Encounter Survey (VES) (Crump and Scott 1994), walking around the entire perimeter of each pond. VES was used for observing the adult individuals of all target species, as well as common frog and common toad eggs (which are laid in large masses/cords) and their tadpoles (which aggregate in the littoral area). Because newt eggs are wrapped in aquatic vegetation and their larvae are mostly pelagic they cannot be easily observed and were not considered during the VESs. All occurrence data have been uploaded on *ornitho.it* (a web platform for the collection of georeferenced ecological data in Italy) and are therefore available for institutional purposes, given the authors' authorization.

2.3. Data analysis

Given the study purposes, i.e., detecting an elevational shift in the site occupancy for the three monitored species, as well as the available data, two complementary analyses were performed (Tingley and Beissinger 2009). Firstly, the occupancy of the monitored sites during the study period (15 years) was modelled using dynamic (or multi-season) occupancy models (Royle and Kéry 2007). Such models use information about the observed site occupancy during the study period to model the occupancy probability of each site in each primary-period (e.g., year, season; hereafter, PP) by combining the estimations of the initial occupancy probability (ψ_0), the probabilities of colonization (γ) and extinction (ε) between two subsequent PPs, and accounting for detection probability (p). The four parameters of the model (ψ_0, γ, ε, p) can be independently related to spatial and temporal covariates.

To avoid discarding sites or sampling years, for sites which were only visited once per year during part of the monitoring period, the whole monitoring period (15 years) was divided into five three-year PPs. Consequently, we assumed occupancy to be constant within each PP, which is consistent with the general site-fidelity development of the study species (Schlupp and Podloucky 1994; Laurila and Aho 1997; Mori et al., 2017; Denoël et al., 2018) and may compensate for short-term occupancy fluctuations (Cheng et al., 2019). Thus, for each PP, three standard surveys were assumed (one for each year), assigning to the observed occupancy state of each site at each survey the value 1 if the species was detected at least once during the visits performed that year (which numbered between 1 and 5), and zero otherwise. The number of surveys for each site in each year (effort) was added to the models as a covariate to account for its possible effect on the detection probability. For each species, different models were fitted, taking into consideration potential effects of covariates on detection, colonization, and survival probabilities. A model selection procedure was then applied (see below).

With regard to detectability (p), three alternative models were compared: p ~ constant, p ~ effort and p ~ time (i.e., PP). Colonization and survival probabilities were modelled according to four hypotheses: i) γ, ε ~ constant; ii) γ, ε ~ time; iii) γ, ε ~ elevation; iv) ε ~ constant and γ ~ neighbours site occupancy. For this last model, the occupancy state of a site was allowed to be influenced by the occupancy state of the neighbouring sites, weighted by their relative proximity (Brooks et al., 2019). This spatially explicit model used a negative exponential function of site-to-site distance to model γ (see Brooks et al., 2019 for details). Thus, twelve models were obtained for each species, all having the initial occupancy state (ψ_0) kept constant. A Bayesian framework with flat priors was chosen to fit all the models, using JAGS 4.3.0 (http://mcmc-jags.sourceforge.net/). Three independent chains were run, with 12,000 iterations each. The first 2,000 values were discarded, and thinning was set to 5 in order to break within-chain autocorrelation (Kéry, 2010). Convergence was checked via visual inspection of results and using Gelman and Rubic diagnostic (Gelman and Rubin 1992; Brooks and Gelman 1998). Model selection was based on leave-one-out information criterion (LOOIC) (Vehtari et al., 2017). We calculated the mean LOOIC and its standard error (SE) for each model. Two models were ranked differently if their mean ± 1 SE LOOIC intervals did not overlap, the preferred model being the one with the lower LOOIC. When two or more models ranked equivalently, the simplest was chosen (Occam's razor). From the best models, the following additional parameters were derived: the equilibrium occupancy probability $\psi_{eq} = \gamma/(\gamma + \varepsilon)$, i.e., the occupancy probability at the equilibrium between colonization and extinction (Royle and Kéry 2007) and the finite-sample occupancy (ψ_t^{fs}) for each sub-period t, i.e., the proportion of occupied sites at time t. While ψ_t estimates the population average occupancy (for infinite sites), ψ_t^{fs} applies to the sampled sites only (Royle and Kéry 2007).

Secondly, the local shift in the elevation limit of each species was quantified comparing the altitudinal range in the first (2005-2007) and last (2017-2019) PP respectively (Cheng et al., 2019). The probability of false absence (P_{fa}) (Moritz et al., 2008; Tingley and Beissinger, 2009) was used to assess if the observed shift could be due to a systematic lack of detection. P_{fa} was computed from the p value estimated by the best dynamic occupancy model, and represented the probability that a species actually occurred in at least one out of the m sites responsible for the measured shift, but that it was not detected, according to the formula (Tingley and Beissinger 2009):

$$P_{fa} = \prod_{j}^{m} \prod_{i}^{n} (1 - p_{ij})$$

where p_{ij} is the specific detection probability at site i during the jth visit, m is the number of sites where the species was not detected, and n the number of surveys for each site. $P_{fa} < 0.05$ suggests a true shift. Although P_{fa} has been considered a conservative approach in assessing an elevation shift (Tingley et al., 2012), to be more cautious, rather than computing p_{ij} separately for sites and visits, we reported the maximum P_{fa} value obtained from the available sample of the posterior distribution of p, i.e., the P_{fa} corresponding to the minimum posterior estimation of p.

Data preparation, model settings, call to JAGS, convergence diagnostic, and posterior elaborations were done in R 3.5.2 (R Core Team 2018) using the packages: R2jags (Su and Yajima 2015); loo (Vehtari et al., 2019), and coda (Plummer et al., 2006). Raw data from this study areavailable via the Figshare Repository (doi: 10.6084/m9.figshare.13273223).

3. Results

The 30-ponds system showed a species-specific change in observed occupancy over the study period. The common frog was observed in 27 ponds out of 30 (90%), both at the beginning (2005-2007) and at the end (2017-2019) of the study, with a constant maximum elevation (1863 m a.s.l.) and an upshift of the minimum observed elevation (from 1181 to 1309 m a.s.l.). In contrast, the common toad and the Italian crested newt both expanded their observed distribution; from 5 to 16 sites, and from 6 to 18 respectively. Furthermore, whilst their lower limit remained constant (1304 m for toads, and 1146 m for newts), the upper limit was elevated from 1664 to 1863 m in the common toad, and from 1652 to 1863 m in the Italian crested newt.

Of the twelve dynamic occupancy models built for each species, only those including neighbouring sites that were also occupied (m14, m24, m34) achieved tangibly inferior results than the others (Table 1), with LOOIC values well outside one SE from the mean value of the best model for the common toad and Italian crested newt and marginally overlapping for the common frog. All other models showed very similar LOOIC, suggesting that the contribution made by the hypothesized covariates as a means of influencing detection (effort, season) or occupancy dynamic (season, elevation) was minimal. Consequently, in the absence of any variable playing a pivotal role, the estimates of the dynamic occupancy model parameters were based on the least complex model i.e., the model in which all parameters were kept constant (m11; Table 1). Nonetheless, in the online Appendix 1, we reported also the coefficient estimates for the m22 model (Table A1) which, despite performing similarly or worse than m11, can shed light on the effects of elevation on extinction and colonization probabilities.

The initial occupancy ψ_0 was higher in the common frog than in the common toad or the Italian crested newt (Table 2). Colonization probability γ was also higher in the common frog than in the other species (Table 2). The extinction probability ε was similarly low in all the study species (Table 2), being lower than colonization probability in all cases. The common frog showed higher levels of detectability p (Table 2). Elevation positively affected only colonization probability of common frog, while it did not influence both extinction and colonization probabilities of the other two species (Table A1; Figure A1).

Considering the occupancy variation throughout the five PPs, the common frog showed a constant ψ, matching the equilibrium occupancy ψ_{eq}, and a slightly oscillating finite sample occupancy ψ^{fs}, with all values being above 0.8 (Fig. 3, top panel). Thus, there was a widespread occurrence of the common frog population in the study area, which appeared to be at equilibrium. In contrast, the common toad and the Italian crested newt were both characterized by an increasing ψ and ψ^{fs}, which only began to reach the lower part of the ψ_{eq} range in the last two periods (Fig. 3, top panel). Overall, occupancy changed from ≈ 0.2 (*B. bufo*: mean = 0.189; C.I.95% = 0.078 - 0.336; *T. carnifex*: mean = 0.224; C.I.95% = 0.096 - 0.390) to ≈ 0.6 (*B. bufo*: mean = 0.549; C.I.95% = 0.375 - 0.708; *T. carnifex*: mean = 0.556; C.I.95% = 0.388 - 0.715). This occupancy increase was also accompanied by a significant (probability of false absence $P_{fa} < 0.0001$) and progressive upward shift of the upper altitudinal limit in both species (Fig. 3, bottom panel) with a final shift being of around 200 m. A significant upward shift (128 m; $P_{fa} < 0.05$) was also detected for the common frog, but this only affected the lower altitudinal limit, and it did not display any progressive trend (Fig. 3, top panel).

Table 1. Structure and corresponding LOOIC values for the 27 dynamic occupancy models (9 models × 3 species) for observed occupancy over the five time periods for each of the three species. See methods for the definition of the structure of the competing models. LOOIC values are means ± SE. The minimum values (best models) for each species are shown in bold.

Model	model structure		LOOIC		
	Detection	Occupancy	*Bufo bufo*	*Rana temporaria*	*Triturus carnifex*
m11	p ~ constant	$\psi_0, \gamma, \varepsilon$ ~ constant	-23.96 ± 5.21	-2.76 ± 1.88	-20.18 ± 4.98
m12	p ~ constant	ψ_0 ~ constant γ, ε ~ elevation	-24.01 ± 5.24	-2.73 ± 1.94	-20.26 ± 4.98
m13	p ~ constant	ψ_0 ~ constant γ, ε ~ time	-23.61 ± 5.13	-2.74 ± 1.84	-19.54 ± 4.83
m14	p ~ constant	ψ_0, ε ~ constant γ ~ neighbours	-2.48 ± 0.58	-1.09 ± 0.35	-2.84 ± 0.52

m21	p ~ effort	$\psi_0, \gamma, \varepsilon$ ~ constant	**-24.14 ± 5.22**	**-2.85 ± 1.90**	-20.10 ± 4.93
m22	p ~ effort	ψ_0 ~ constant γ, ε ~ elevation	-24.09 ± 5.24	-2.61 ± 1.90	**-20.32 ± 4.95**
m23	p ~ effort	ψ_0 ~ constant γ, ε ~ time	-23.68 ± 5.10	-2.83 ± 1.86	-19.62 ± 4.82
m24	p ~ effort	ψ_0, ε ~ constant γ ~ neighbours	-2.40 ± 0.50	-1.06 ± 0.31	-2.83 ± 0.57
m31	p ~ time	$\psi_0, \gamma, \varepsilon$ ~ constant	-24.06 ± 5.25	-2.56 ± 1.85	-20.06 ± 4.91
m32	p ~ time	ψ_0 ~ constant γ, ε ~ elevation	-24.10 ± 5.29	-2.41 ± 1.85	-20.17 ± 4.93
m33	p ~ time	ψ_0 ~ constant γ, ε ~ time	-23.61 ± 5.14	-2.43 ± 1.67	-19.07 ± 4.66
m34	p ~ time	ψ_0, ε ~ constant γ ~ neighbours	-3.40 ± 0.66	-0.78 ± 0.22	-3.85 ± 0.77

Table 2. Parameter estimates from the best dynamic occupancy models for the three study species (m11; Table 1). ψ_0, γ, ε are: occupancy in the first primary period, colonization probability, and extinction probability respectively. p is the detection probability. For each parameter/species, mean (above) and 95% credible intervals (below, in parenthesis) are reported.

Model parameter	**Species**		
	Bufo bufo	*Rana temporaria*	*Triturus carnifex*
ψ_0	0.189 (0.078-0.336)	0.880 (0.744-0.971)	0.224 (0.096-0.390)
γ	0.165 (0.095-0.250)	0.612 (0.368-0.828)	0.200 (0.122-0.292)
ε	0.047 (0.002-0.143)	0.086 (0.039-0.147)	0.103 (0.016-0.225)
P	0.596 (0.511-0.676)	0.833 (0.794-0.868)	0.629 (0.543-0.709)

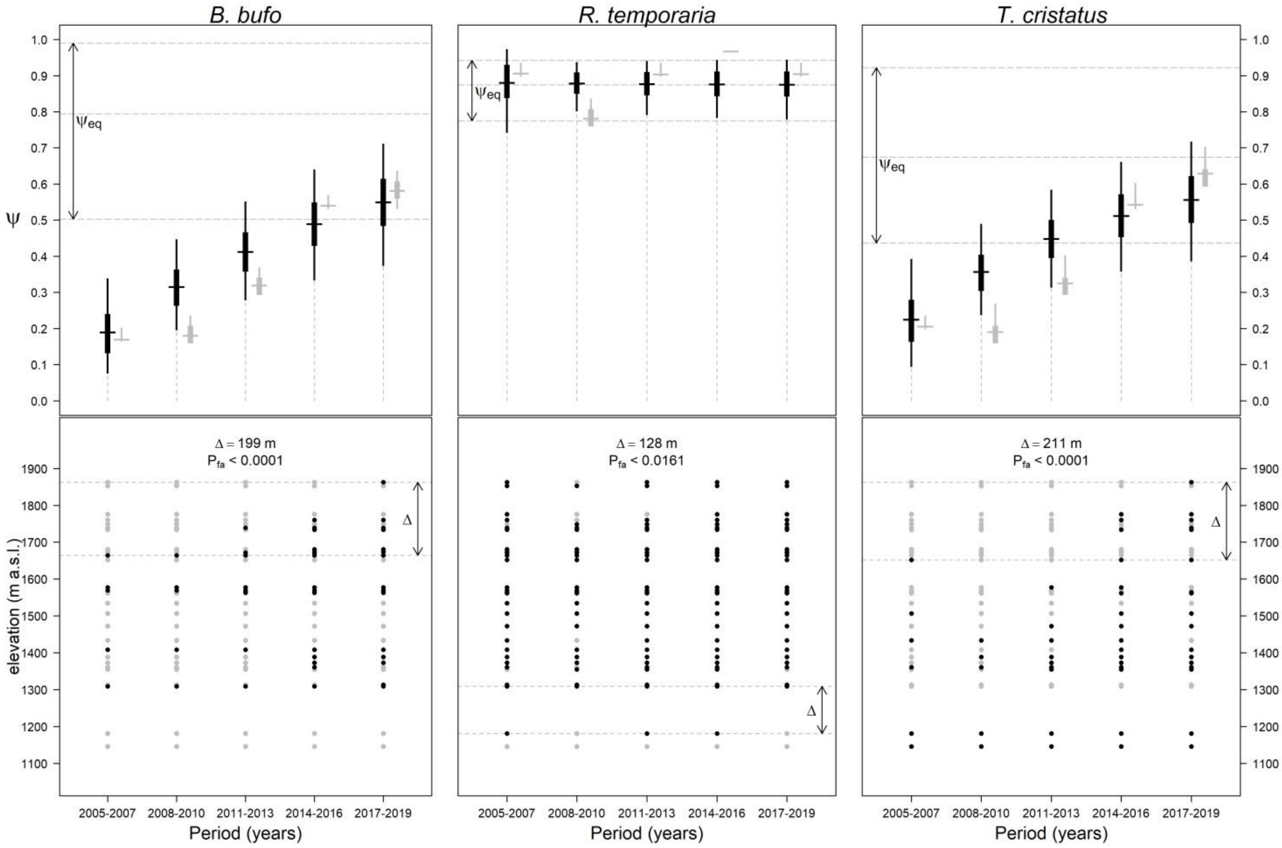


Figure 3. Occupancy and altitudinal shift of the three species during the 15 year study. *Top panel*. In black, estimated occupancy ψ value for each of the five three-year periods. Horizontal dash = mean ψ value. Thick vertical line = 50% credible interval. Thin vertical line = 95% credible interval. In grey, the corresponding values for the finite-sample occupancy (ψ^{fs}), with the same legend. The grey horizontal dashed lines are the mean value and the 95% credible intervals of the equilibrium occupancy (ψ_{eq}). *Bottom panel*. Altitudinal shift. Grey dots = observed unoccupied sites. Black dots = observed occupied sites. Δ = upward shift of the upper or lower species limit. P_{fa} = probability that the observed shift was due to detection issues (see methods for details).

4. Discussion

In the framework of global change and climate warming, the ability to shift distribution ranges will be decisive for species' survival (Chen et al., 2011). Whilst poorly dispersing taxa, such as amphibians, may have a limited capacity for tracking rapid environmental changes, elevational shifts may enable amphibians to follow their climatic envelope within short distances in mountainous areas (Enriquez-Urzelai et al., 2019). Whether amphibians can perform such elevational shifts is an open question. Some previous studies have failed to detect any directional change in elevation of amphibians (e.g., Livo and Yeakley 1997) or have provided contrasting results (both upward and downward shifts in different amphibian species; Raxworthy et al., 2008; Moskwik, 2014). Existing evidence usually stems from studies that have either only compared two periods (i.e., historical vs. present distribution) without controlling for likely unpaired sampling efforts (Martínez–Solano et al., 2003; Bustamante et al., 2005), or that have been related to major landscape changes (Seimon et al., 2007; Moskwik, 2014), an element which may overcome the direct effects of climatic variables on amphibian physiological limits, e.g., Seimon et al. (2007) report an upward elevational shift to a pond system in the Andes which was previously covered by a glacier. A recent study from Enriquez-Urzelai et al. (2019), however, reports a significant average upwards elevational shift of 84 m in the distribution range of Iberian amphibians comparing the periods 1901-1990 and 2001-2015 and controlling for sampling efforts. However, it remains unclear if observed or estimated elevational shifts are quick enough in order for amphibians to track their climatic envelopes within future climatic scenarios.

Our results show carefully analysed evidence of how amphibian altitudinal distributions can change over a 15 year period of warming. We describe how the upper altitudinal limit of the common toad and the Italian crested newt gradually shifted by about 200 m upward in 15 years, up to the highest reproductive site represented in the study area (1863 m a.s.l.). In contrast, the observed elevational shift of the lower altitudinal limit of the common frog was weakly supported and may depend upon site-specific colonization/extinction rates and may also be related to other occupied sites at lower elevations and outside the study area. The elevation range of the study area included the upper limits of both the former species, but not the lower limit of the common frog (<1000 m a.s.l.; Tiberti 2015), which may have prevented us from clearly observing the common frog abandoning its lower sites of occurrence. In addition, it is likely that the observed elevational shifts of the common toad and the Italian crested newt were already in motion before the beginning of the study and were therefore greater than that which was observed, i.e., when compared to 2005 (study commencement), toads and newts were restricted to fewer and lower-elevation sites in 1990-1992 (Bennati 1992).

Our results confirm findings from a few previous observational studies (Martínez–Solano et al., 2003; Bustamante et al., 2005) and from the study by Enriquez-Urzelai et al. (2019). The latter study has already provided evidence that upwards movement is common among amphibians on a broad geographic scale (Iberian peninsula). To complement this, our study provides a description of the timing of such elevational shifts, relevant information which was previously lacking in scientific literature.

Observed colonization dynamics suggest that, when colonizable habitats are available, amphibian elevational shifts can be fast enough to track rapid elevational shifts of environmental conditions caused by climate warming, i.e., 200 m elevational shift in 15 years vs. +1.5 ˚C temperature increase in 40 years. Despite the observed uphill range expansions, we did not find evidence that colonization or extinction parameters were influenced by altitude, with colonizations occurring throughout much of the elevational ranges of both the expanding species (Fig. 3). Because neither species was present at the highest sites at the start of the surveys, the result of this excess of colonizations over local extinctions (Fig. 3) is an uphill expansion in both cases. This may indicate that the environmental conditions over the whole elevational range studied have generally improved for the common toad and the Italian crested newt, but without clearly affecting common frog distribution. This is most likely due to the fact that the common frog was already widespread in the study area at the beginning of the monitoring period.

Despite this general improvement in environmental conditions over the whole study area and despite the fact that during the study period both the common toad and the Italian crested newt expanded their range, the common toad never colonized the cluster of 8 ponds north-east of the peak of M. Guglielmo and just a few individuals were found in the north-westerly cluster of 4 ponds (Fig. 1). The same goes for the Italian crested newt, which never colonized the cluster of 6 ponds south-east of the peak of M. Guglielmo (Fig. 1). Since there are no apparent differences in the environmental conditions of the cluster of ponds (i.e., similar bedrock geology, pond morphometries and surrounding habitats), this may indicate the presence of barriers hindering colonization, or, more likely, it may indicate that the colonization process is still incomplete. In partial support of the latter hypothesis, the non-colonized pond clusters represent those which are furthest from the sites of occurrence of both the species during the first PP. Curiously, the models explicitly including the neighbouring site distance as predictor performed worse than all the other models. This may not exclude a more complex spatial effect, i.e., not generalizable, but related to particular barriers (which are not easily detectable) affecting only a particular cluster of sites. This would require targeted investigations.

We were unable to confirm the causal relationship between climatic trends in the last ca. 40 years (Fig. 2a) and the observed amphibian distribution shifts. The effects of climatic variability on amphibian ranges may become evident after an undetermined number of years, but a lack of both measured climatic data before 2005 and a longer time-series prevented us from attempting specific statistical tests such as time-series analyses. However, plausible alternative hypotheses explaining the observed elevational shift are not currently apparent to us. In particular, changes in land cover and management may alter amphibian distribution (Moskwik, 2014) but, even if some grassland-wood transition areas in previously grazed areas indicate a reduced grazing pressure (Fig. 1), the surroundings of the study ponds have not undergone any major changes in living memory and therefore remain an extensively exploited pasture. Thus, a causal relationship with recent climate warming seems a reasonable assumption. Nevertheless, even if we assume complete independence from climatic trends, the observed elevational shifts should be considered a sample of amphibian dispersal capacity in mountain areas hosting a network of suitable reproductive habitats.

The study system has helped in achieving such results, as it was particularly appropriate to test our predictions due to the simultaneous occurrence of two fortunate characteristics: i) the presence of many colonizable habitats evenly distributed along a 700 m wide elevational interval (i.e., high permeability of the study area to amphibian dispersal) encompassing the altitudinal limits of two out of three amphibian species inhabiting the area (Tiberti 2015), and ii) the fact that the study area and amphibians experienced a steep temperature increase over the last decades (Fig. 2a). However, it was our 15 year-long monitoring effort which provided the most important source of ecological information and conservation insights. Put together, the peculiarities of the study area and the availability of long-term monitoring data may explain the clarity of our results compared to those available in literature (Enriquez-Urzelai et al., 2019). We also took advantage of modern modelling techniques, which helped us to rigorously handle unbalanced monitoring efforts (e.g., among ponds and years), a common issue in field environmental data which, if not correctly addressed, may increase uncertainty in the interpretation of results. In addition, using modern statistical modelling techniques may also provide indications on how to optimize and allocate monitoring efforts. For example, in our case study, replicating many yearly surveys was not as important as maintaining the survey effort over a long term period, due to the fact that detectability was high for all the study species and was therefore barely influenced by the monitoring effort. In a context of limited resources and given the study objectives and the difficulties associated with the monitoring of remote mountain habitats, the maintenance of long-term monitoring programs should be prioritized over the completion of intensive monitoring campaigns. We do however acknowledge that the number of annual surveys should be adjusted depending on the detectability of the target species, in order to obtain good model estimates. The idea that long term data series are essential for studying the response of wild populations to climate change is probably the core idea of our research approach.

The common toad and the Italian crested newt are phylogenetically distant and possess different dispersal capacities (i.e., 1.6 km/year for common toad and 0.3 km/year for Italian crested newt; Sinsch 1988; Schabetsberger et al., 2004). This suggests that the ability to track climate warming through elevational shifts over short ecological periods may be independent from taxonomy and may be shared by a large variety of amphibians, including even species with low dispersal abilities. In this way, our results suggest that preserving and improving habitat connectivity between lowland and highland areas could conserve the opportunity for elevational shifts for many amphibian species. This may be a better strategy for providing poorly dispersing amphibians with better opportunities for adaptation to climate change than preserving and opening efficient latitudinal ecological corridors, although the latter does represent a basic strategy for the conservation of many terrestrial species (Littlefield et al., 2019).

The ecological connections between lowlands and mountains should be preserved through the removal of barriers preventing amphibian movements and through the prioritization of the protection and recovery of pristine lowland habitats close to mountain foothills. Ecological connectivity between lowlands and mountains may be naturally provided by rivers and their riparian habitats, but fluvial systems may be greatly degraded by a number of human activities (channelization, damming, pollution, etc.) and may require protection and habitat recovery (e.g., renaturalization of riverbanks) to secure their function as ecological corridors. Lentic and many other terrestrial lowland habitats can also be important for amphibians, but they may be isolated from mountains by distance and natural or constructed barriers, such as roads, railways, etc. Removing such barriers by, for example, creating safe passages would likely be a positive step for amphibian conservation. Nevertheless, elevational shifts do not represent a generalizable solution for amphibians escaping climate warming, because, unlike in our study area, colonizable higher elevation sites may be too few and far between or simply absent, which is the case in many arid massifs. Elevational shifts may funnel many species into an ecological trap if amphibians cannot find safe aquatic habitats for reproduction and larval development, with mountain-top species being particularly vulnerable (Early and Sax 2011; Forero-Medina et al., 2011; Cordier et al., 2019). Conservation strategies should therefore be adjusted based on the permeability of each particular mountain region to amphibian colonization. Worryingly, even where mountain aquatic habitats are available, they are often far from safe for amphibians. Water exploitation and abstraction (Channing et al., 2006; Yarnell et al., 2012), introduced fish for recreational angling (Bosch et al., 2019; Knapp et al., 2016), and emerging infectious diseases (Zampiglia et al., 2013) will probably hinder the movement of amphibians into the mountainous areas. Therefore, a conservation-minded management of mountain aquatic habitats including habitat recoveries (e.g., alien fish eradications; Knapp et al., 2016; Tiberti et al., 2019) is of pivotal importance for the long-term conservation of amphibians. In some cases, where natural colonizable habitats are absent, creating and restoring constructed mountain wetlands could provide amphibians with a chance of surviving climate warming; our case study represents a good example of where the disappearance of mountain ponds was avoided by periodic maintenance (e.g., removal of sediments and aquatic vegetation from watering ponds), which enabled native amphibians to continue to move from one pond to another (Tiberti 2018). Whichever the conservation strategy will be, amphibians moving upward are nevertheless expected to become more and more isolated and therefore vulnerable than was previously the case (Forero-Medina et al., 2011). In some urgent cases (e.g., endangered mountaintop populations/species) “assisted colonization” (*sensu* Hoegh-Guldberg et al., 2008) could be necessary for preventing extinction (D’amen et al., 2011).

Acknowledgements

We thank Dr. Marco Zatti (municipality of Zone) and the Comunità Montana Basso Sebino Bresciano for the logistic support in the research and conservation efforts in the ARE Monte Guglielmo. We also extend thanks to Fiorenzo and Paola for their help and company during many field surveys, Laura Bohin for the linguistic revision, and two anonymous reviewers for their constructive comments.

Supporting information

The following online appendix is available for this article online:
Appendix 1. Model m22: coefficient estimates.

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