Contrasting effects of temperature and precipitation change on amphibian phenology, abundance and performance

Gentile Francesco Ficetola[1,2*], Luigi Maiorano[3]

1) Université Grenoble Alpes, Laboratoire d'Ecologie Alpine (LECA), F-38000 Grenoble, France
2) Centre National de la Recherche Scientifique (CNRS), LECA, F-38000 Grenoble, France
3) Dipartimento di Biologia e Biotecnologie "Charles Darwin" Università di Roma "La Sapienza". viale dell'Università 32 00185 Roma Italy
* Corresponding author. francesco.ficetola@gmail.com

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Abstract Climate change is determining a generalized phenological advancement, and amphibians are among the taxa showing the strongest phenological responsiveness to warming temperatures. Amphibians are strongly influenced by climate change, but we do not have a clear picture of how climate influences important parameters of amphibian populations, such as abundance, survival, breeding success and morphology. Furthermore, the relative impact of temperature and precipitation change remains underappreciated. We used Bayesian meta-analysis and meta-regression to quantify the impact of temperature and precipitation change on amphibian phenology, abundance, individual features and performance. We obtained effect sizes from studies performed in five continents. Temperature increase was the major driver of phenological advancement, while the impact of precipitation on phenology was weak. Conversely, population dynamics was mostly determined by precipitation: negative trends were associated with drying regimes. The impact of precipitation on abundance was particularly strong in tropical areas, while the importance of temperature was feeble. Both temperature and precipitation influenced parameters representing breeding performance, morphology, developmental rate and survival, but the response was highly heterogeneous among species. For instance, warming temperature increased body size in some species, and decreased size in others. Similarly, rainy periods increased survival of some species and reduced the survival of others. Our study showed contrasting impacts of temperature and precipitation changes on amphibian populations. Both climatic parameters strongly influenced amphibian performance, but temperature was the major determinant of the phenological changes, while precipitation had the major role on population dynamics, with alarming declines associated to drying trends.

Keywords: amphibian decline, breeding success, climatic oscillation, geographical bias, population dynamics

Introduction

Studies on the physical basis of climate change provide a clear picture of climatic modifications that have occurred during the last century, and allow to develop detailed scenarios on the potential changes for the next future (Intergovernmental Panel on Climate Change 2013). Such information has boosted research on how biodiversity has responded to climatic modifications in the past, and how may be affected in the future (Bellard et al. 2012; Maiorano et al. 2013). Range shifts toward higher latitudes or altitudes and phenological advancements are, as expected, among the most commonly observed effects, and are often considered as “fingerprints” of the impact of climate change on biodiversity (Walther et al. 2002; Parmesan and Yohe 2003; Root et al. 2003). Range shifts occur because species can modify their distribution to track their bioclimatic niche. For instance, Korean butterflies have shifted their ranges northward 1.6 km per year during the last 60 years, and the velocity of range shifts matched well the northward shift of isotherms of about 1.5 km per year (Kwon et al. 2014). Similarly, phenological changes have been detected on a variety of taxa across the globe. For example, European birds now lay their eggs about 6 days earlier than 30 years ago, with an advancement of about two days per degree of global warming (Dunn and Moller 2014).

However, species response to climate change may be more complex than just poleward shifts of ranges or phenological advancements. First, climate change determines a complex pattern, with a global temperature increase but also non-uniform modification of precipitation regimes (Intergovernmental Panel on Climate Change 2013). While precipitation modifications will certainly influence most species, the impact of this facet of climate change on biodiversity is not always predictable, and disentangling the relative importance of temperature and precipitation changes may be difficult. Second, climatic conditions may have multiple effects, beside the simple phenological shifts. Assessing the consequences of climatic change on individual performance and population dynamics may be extremely complex (Merilä and Hendry 2014), and consequently such responses are less widely understood than the impact on phenology and distribution (Dunn and Moller 2014). Still population dynamics is generally more relevant than simple phenological parameters to evaluate which species will suffer the strongest impact. Finally, responses to climatic changes are often heterogeneous among species and study sites (While and Uller 2014; Ge et al. 2015), lowering the possibility of drawing general conclusions.

Climate change is expected to have a particularly strong impact on ectothermic vertebrates (Buckley et al. 2012). Temperature directly influences the activity patterns of ectotherms, with climate being a proximate driver for phenology/daily activity. Furthermore, impacts of climate change on population dynamics are expected to be particularly strong, because the metabolism of ectotherms is closely linked to environmental temperatures, and physiological performance strongly influences fitness components (Kearney and Porter 2009). For example, amphibians are among the taxa for which early breeding in response to warming has been first detected (Beebee 1995), and meta-analyses suggested that they are one of the taxa showing the strongest phenological advancement in response to global warming, with an average breeding advancement of 6.1 days per decade (While and Uller 2014), versus the average 2.8 days per decade measured across other taxa (Parmesan 2007). Less attention has been devoted to the consequences of changes in precipitation and water availability. A strong impact is expected at least in amphibians, because most species rely on humid environments, require water for reproduction, and are particularly active only during wet periods. Especially in the tropics, several amphibian declines and extinctions have been attributed to climate change (Pounds et al. 1997; Pounds et al. 1999; Laurance 2008; Menéndez-Guerrero and Graham 2013). Even stronger declines are expected to occur in the future, particularly according to extreme climate change scenarios, because of their small ecological niche and limited dispersal ability (e.g. Araujo et al. 2006; Courtois et al. 2015). However, in absence of quantitative summaries across multiple studies, it is difficult to identify general patterns in the response of amphibian populations, or to assess the key climatic drivers of abundance changes.

In this study, we used meta-analysis and meta-regression to assess the impact of climatic variation on amphibians across the globe. Usually, studies with observational data can only target a limited number of species within specific regions, but responses in some species or areas may be idiosyncratic, thus making uncertain the generality of conclusions of individual studies. The meta-analytic framework enables us to combine the results of multiple, heterogeneous sources, to obtain general trends and patterns (Arnqvist and Wooster 1995), allowing to draw more general and reliable conclusions about the impact of climate change, in comparison to individual and local studies (Parmesan et al. 2013). During the last years, many studies have investigated temporal trends in phenology, abundance and performance of amphibians, and have assessed whether climatic factors may play a role (see Li et al. 2013; Urban et al. 2014 for non-meta-analytic reviews). The data from these researches constitute an excellent basis to draw quantitative syntheses, and allow a detailed and objective description of the impact of climate change. A recent meta-analysis has clearly shown that amphibian populations consistently anticipate their breeding periods, and that such change is strongly determined by trends of global warming, particularly at the high latitudes (While and Uller 2014). However, such analysis did not consider the potential role of precipitation change on amphibian populations, and focused on phenology only. The aim of our study was to provide a more complete quantitative view of the consequences of climate change on amphibian populations, by using meta-analyses to evaluate impacts on three major population parameters: phenology, abundance and average individual features (breeding performance, development rate, morphology and survival). Furthermore, we assessed the relative importance of temperature and precipitation, by testing whether they have different impact on the population parameters considered.

Methods

Data selection

In May 2014, we conducted a search in the ISI Web of Science using the following search terms: TOPIC: (climate change) AND TOPIC: (amphibian* or frog* or toad* or salamander* or treefrog* or newt* or cecilian* or gymnophion*), which returned nearly 800 results. We also checked all the papers citing an early, seminal study showing impact of climate change on amphibian phenology (Beebee 1995), the papers reviewed in previous meta-analyses and reviews (Parmesan 2007; Li et al. 2013; While and Uller 2014), and the references cited in the identified studies (> 1000 individual papers). We individually checked all these papers, and identified all empirical studies analysing trends in amphibian populations, covering a time span of at least four years and reporting effect sizes representing: a) relationships between phenology and climatic parameters representing temperature or precipitation; b) relationships between population abundance or trends and climatic parameters; c) relationships between measures of individual performance / features and climate. Our main criterion for inclusion was that the studies must have reported summary statistics that could be converted into an effect size. If no effect size values were available but scatter plots or data with raw values were present, we extracted information from tables and plots (using tpsDIG2; Rohlf 2005) and calculated Pearson’s correlations. If the same data series was analysed in multiple papers, we only considered the paper analysing the longest time series or the most recent one (if all papers considered the full time series of data).

Data analysis

Climate, phenology and abundance

For analyses of phenology and population abundance, we considered the relationship between these two population parameters and two climatic variables 1) temperature; 2) precipitation / water availability. Three studies reported data on drought frequency (e.g. Stewart 1995; Hossack et al. 2013; Mac Nally et al. 2013). In these cases, we assumed that a negative relationship between drought and abundance indicates positive relationship with precipitation, and vice-versa. We did not analyse the relationship between breeding date and year (i.e. we did not test whether amphibians changed their breeding period) as previous meta-analyses have already demonstrated a strong trend toward early breeding at the global scale (Parmesan 2007; While and Uller 2014). For abundance analyses, we considered studies on all life stages (egg masses, adults…), and methods for abundance estimates (counts, mark-recapture…).

For most studies, we obtained the Pearson's correlation coefficient r, and calculated the effect size (Z) and variance (Z-var) using Fisher's transformation. If studies did not report correlation coefficients, the reported statistics (t, F, z, R^2, means and standard deviations) were used to estimate r (Rosenthal 1994; Wilson and Lipsey 2000; Nakagawa et al. 2007). If only significance and sample size were available, we extracted effect size following Cooper et al. (2009) using the compute.es package in R.

We used a 'meta-regression' approach, which allows testing the effects of multiple predictors in a single meta-analytical model (Hadfield and Nakagawa 2010; While and Uller

2014). We performed mixed-effect meta-analyses and meta-regressions using MCMC generalized linear mixed models (MCMCglmm; Hadfield 2010). In MCMCglmm, we used a non-informative inverse Wishart prior for the random effects [$V = 0.002$, $nu = 1$; Gelman and Hill (2007)] and the vector of variances of Z was included into MCMCglmm using the *mev* argument (see supplemental material in Hadfield and Nakagawa 2010). All models were run for 1 250 000 iterations, with 250 000 iterations removed as a burn-in and a sampling interval of 1000. For each model, we ran three MCMC chains; for all models the Gelman-Rubin statistics were approximately 1, indicating convergence (Kéry 2010). We used the posterior distributions from the first of the three chains to calculate the results (While and Uller 2014).

First, in order to assess whether phenology and abundance variation are most strongly influenced by temperature or precipitation variables, we used meta-regression to test if the absolute value of effect size was significantly different between studies considering temperature and precipitation-related variables (MCMC *P*-values). Subsequently we ran distinct meta-analyses, by considering separately studies relating population parameters to temperature and precipitation. To estimate the mean effect size across studies, we first ran the meta-analysis without fixed effects but including species and study identity as random factors. Subsequently, we included three parameters as fixed effects in the model: 1) absolute value of the latitude (studies come from both the Northern and the Southern hemisphere), as stronger effects of climate change have been proposed for species living at high latitudes; 2) the range of variation in temperature and 3) in precipitation at each site, calculated as the range (maximum – minimum) during the study period covered by each time series, on the basis of the CRU 3.22 climate grids (Harris et al. 2014; seeWhile and Uller 2014 for a similar approach). The CRU 3.22 climate grids reports monthly values of temperature and precipitation for the period 1901-2013 (resolution: 0.5°), on the basis of data from meteorological stations over the globe (Harris et al. 2014). Range of variation (i.e., maximum-minimum) was included as populations experiencing greater variation of a climatic parameter may be more responsive to it (While and Uller 2014). Temperature variation was used as independent variable for models analysing responsiveness to temperature, and precipitation variation was the independent variable for models analysing responsiveness to precipitation. We used Egger regression and funnel plots to evaluate the occurrence of publication bias in the analysed datasets, and we used the file drawer analysis to calculate the number of studies required to reduce the overall effect size to non-significant values (Rosenberg 2005).

Climate variation and individual features / performance

In this case, it was not possible to perform a formal meta-analysis, because different studies used very heterogeneous measures of individual features and performance (survival, body condition index, body size, length of larval stage, breeding performance). Furthermore, it was difficult to find a-priori expectations on the relationships between climatic variation and performance. For instance, it might be tempting to hypothesize that warm winters improve performance, for instance by reducing cold-caused mortality (McCaffery and Maxell 2010), but also the inverse may be envisaged, as warm conditions increase metabolism and therefore the energetic demand (McCaffery and Maxell 2010). Therefore, for this analysis we first reviewed the literature gathered following the above described criteria, evaluated the proportion of studies showing significant relationships, and used a χ^2 test to compare the observed frequency of significant relationships to the null expectation of 5% tests expected to be significant. Reading and Clarke (Reading and Clarke 1995, 1999; Reading 2003, 2007, 2010) published multiple analyses over the same population along multiple years (Appendix S1), thus we tested whether our conclusions are robust to the exclusion of these studies. As we already mentioned for the analyses on climate phenology and abundance, if multiple papers over the same population analysed similar traits in different periods, we selected the time series covering the longest temporal span. In some cases, the same study reported multiple analyses considering similar pairs of variables (e.g. body condition index vs. summer temperature, winter temperature and annual temperature; hereafter named "very similar relationships"; Appendix S1). As we did not perform a true meta-analysis, in absence of strong a-priori expectations we considered all the measures reported by studies. The results of our analyses remained identical if we randomly omitted such very similar relationships.

Subsequently, we tested whether there are differences in outcome among studies considering precipitation and temperature as predictor, or among studies considering different measures of performance. First, we performed a meta-regression as described above, considering the absolute value of effect size as dependent variable. The measure of performance and the climatic parameter were the fixed predictors, while study and species identity were the random variables. Second, we ran a generalized mixed model with binomial error, considering whether a study is significant or not as dependent variable, and using the same fixed and random effects of the meta-regression. The mixed model was run using lme4 in R. Also in this case, we report the results of the analysis considering all the very similar relationships, but results remain identical if the very similar relationships are randomly omitted.

Results

Overall, we obtained 140 effect sizes from 43 different papers relating amphibian phenology, abundance or performance to climatic parameters (Appendix S1). Studies represented 49 different species or species complexes of anurans and urodeles. One study did not consider specific taxa, but analysed the decline and extinction over 14 frog species (Laurance 2008).

Eighty-one effect sizes described variation in phenology, 29 represented variation in abundance, and 30 represented variation for various performance parameters.

Studies showed strong geographical bias. Phenology studies come only from Europe (mostly UK), North America and Japan (Supplementary online material, Fig. 1). Tropical and sub-tropical areas were better represented in abundance analyses, with some analyses from the Neotropics and Australia. Performance studies were mostly from Europe (particularly UK) and N America, with one notable exception from Africa (Fig. 1). The average length of time series (±SD) was 27.9±15.9 years for phenology, 28.3± 2.7 years for abundance and 20.7±12.3 years for performance studies.

Phenological changes

Sixty-six studies out of 81 considered relationships between phenology and variables representing temperature, while the remaining considered precipitation-related variables. There were significant differences in the magnitude of effect sizes between analyses considering precipitation and temperature as predictors (P_{MCMC}=0.006). Specifically, effect sizes were significantly smaller than zero for phenology/temperature relationships (mean Z=-0.626, 95% CI = -0.781/-0.496) but not for phenology/precipitation relationships (mean Z=-0.200, 95% CI = -0.494/0.054). Therefore, variation in phenology was strongly linked to variation in temperature, while the overall relationship with precipitation was weak (Fig. 2 a-c). Even though sample size was smaller for the relationships phenology / precipitation, the absolute value of the effect size of temperature was >3 times larger than the effect size of precipitation.

Funnel plots and eggers regression did not suggest evidence of publication bias for analyses relating phenology to temperature or precipitation (Fig. S1a-b; temperature: b=-1.11, 95% CI = -2.22/0.04; precipitation: b=-1.33, 95% CI = -3.79/1.06). According to the file drawer analysis, >7000 non-published studies averaging null results would be required to reduce the effect size of the relationship between temperature and phenology to values not significantly different from zero.

The relationship between phenology and temperature was particularly strong at the highest latitudes and in study sites experiencing a stronger temperature range (Table 1a). Conversely, the strength of the relationship between phenology and precipitation was unrelated to latitude or precipitation range (Table 1b).

Changes in abundance

Twenty-three studies out of 29 analysed the relationships between abundance and variables representing precipitation pattern, while the remaining considered variables representing temperature. Across these studies, we detected significant differences in the absolute value of effect size between analyses considering precipitation and temperature as potential predictors (P_{MCMC} = 0.002). Specifically, effect sizes were significantly larger than zero for abundance/precipitation relationships (mean Z=0.590, 95% CI = 0.123/1.039), with larger populations in wetter years, but not for abundance/temperature relationships (mean Z=-0.044, 95% CI = -0.346/0.276). Therefore, variation in abundance was strongly related to variation in precipitation, while was unrelated to variation in temperature (Fig. 2 b-d). Even though the number of effect sizes was limited for the relationships abundance / temperature, the absolute value of the effect size of precipitation was 13 times larger than the effect size of temperature.

Eggers regression did not show evidence of publication bias for analyses relating abundance to temperature or precipitation (temperature: b=2.11, CI = -0.53/4.42;

precipitation: b=1.20, CI = -0.65/3.68; Fig. S1c). Funnel plots suggested some publication bias for analyses relating precipitation and abundance, as the strongest, positive effect sizes were slightly associated with the smallest sample size (Fig. S1d). However, the file drawer analysis showed that 272 studies averaging null results would be required to make it the effect size of the abundance/precipitation analysis not significantly different from zero. Furthermore, when we repeated analyses excluding studies with N<7 (Fig S2d), results confirmed the positive relationships between abundance and precipitation (mean Z = 0.439, 95% CI = 0.090 / 0.779), supporting the outcome of the model considering all the studies.

We then explored potential factors affecting the strength of relationships between variation in abundance and climate. The relationship between abundance and precipitation was particularly strong at low latitudes, while was unrelated to precipitation range (Table 1d). Conversely, the strength of the relationship between abundance and temperature was unrelated to latitude or temperature range (Table 1c).

Impact of climate on individual features and performance

From 11 papers measuring relationships between climatic variation and performance or individual features, we obtained 30 measures of effect size. Different papers considered very heterogeneous parameters, representing survival, morphology (body condition index and body size), development rate of larvae, and breeding success; parameters representing morphology and survival were the most frequent (Fig. 1, Appendix 1). 20/30 tested relationships were significant at the 5% alpha-level, a proportion significantly higher than expected by chance (χ^2_1= 24.0, P < 0.0001). The number of unpublished, non-significant studies required to make the proportion of significant studies not significantly higher than expected by chance would be 83. Results remain consistent if the 12 effect sizes reported by

Reading and Clarke (Reading and Clarke 1999; Reading 2003, 2007, 2010) on *Bufo bufo* are removed (12/18 relationships are significant, χ^2_1= 14.4, $P = 0.0001$). Overall, relationships were highly heterogeneous among studies. For instance, warm winter temperature decreased survival of crested newts in UK (Griffiths et al. 2010), while increased the survival of boreal toads in Colorado (Scherer et al. 2008). Analogously, years with warm climate were correlated with increased body size in the water frogs *Pelophylax lessonae* and *P. ridibundus*, while in the same years their hybridogenetic hybrid *P. esculentus* showed a decline in body size (Tryjanowski et al. 2006).

The absolute value of effect size was not different between analyses focusing on precipitation variables and analyses focusing on temperature variables ($P_{\mathrm{MCMC}} = 0.68$) nor between analyses considering different performance parameters (all $P_{\mathrm{MCMC}} > 0.25$). Furthermore, the frequency of significant results was consistent among studies considering precipitation and temperature (mixed model: $\chi^2_1 = 1.2$, $P = 0.28$) and among studies measuring different parameters ($\chi^2_3 = 3.1$, $P = 0.37$) (Fig. 3).

Discussion

How do climate change affects amphibian populations? Advancement of breeding activity in response to global warming is perhaps the best documented fingerprint of climate change on amphibian populations (Beebee 1995; While and Uller 2014), but early breeding is not the only consequence of climate change, and perhaps not the most alarming one. Our meta-analysis, covering >50 species over five continents, showed contrasting impacts of temperature and precipitation changes on amphibian populations. Both temperature and precipitation change strongly influenced amphibians, but temperature was the major determinant of the phenological changes, while precipitation had the major role on population dynamics, with smaller populations in dry years.

Temperature vs. precipitation change

Climate change has long been hypothesized as a cause of global amphibian decline, but evidence remained elusive for more than one decade (Beebee and Griffiths 2005; Corn 2005; Rohr et al. 2008). Our study provides quantitative evidence on the multiple impacts of climate change, and of the relative importance of variation for two key parameters: temperature and precipitation.

Climatic variation significantly influenced multiple parameters of individual performance, and temperature and precipitation apparently showed comparable importance. For instance, dry periods were associated with lower adult survival in the frog *Hemisus marmoratus* and low breeding success in the toad *Bufo calamita* (Banks et al. 1994; Grafe et al. 2004), while warm periods reduced body condition index in the toad *B. bufo* and decreased survival in the newt *Triturus cristatus* (Reading 2007; Griffiths et al. 2010) (Appendix S1).

However, precipitation and temperature showed different impacts on phenology and population dynamics. On the one hand, our analysis confirmed that temperature is the main driver of phenological advancement. Amphibians use multiple cues to start breeding activities, and for many species the onset of reproduction occurs during rainy periods and / or when temperature rises above a given threshold (Timm et al. 2007). Nevertheless, our analysis indicates that temperature is the dominant driver. Despite some species showing early breeding during rainy years, in most cases the relationship between precipitation and phenology was weak, and the overall effect size was not significantly different from zero

(Fig. 2). Actually, most of species showing relationships between precipitation and phenology were from one single study (Todd et al. 2011). Nevertheless, conclusions on the relative importance of precipitation and temperature might be influenced by geographic and taxonomic bias, and interactions between these two parameters are possible. For instance, populations in humid and cold areas may be more likely to adjust their phenology in response to temperature thresholds, whereas populations in warm and dry areas may depend more on precipitation.

Conversely, precipitation slowed the strongest effect on population size. In almost all the cases, population declines were associated to dry periods. Water availability is clearly a major driver of fitness for amphibians, as it increases survival of larvae and enhances breeding success in species requiring waterbodies for reproduction (Banks et al. 1994). Furthermore, most species have limited desiccation tolerance, thus high environment humidity and wet periods are needed for the activity of adults (Zug et al. 2001; Ficetola et al. 2012). Links between amphibian decline and global warming are less clear, and the effect sizes of temperature/abundance relationships were generally small (Appendix S1).

Studies on individual performance could help to identify mechanisms relating population dynamics to temperature, but the response of individuals to temperature change was heterogeneous among studies. Some temperate species showed reduced body condition, size and survival after warm years. This might occur because in mild winter individuals continue to dissipate energy during hibernation or because of limited prey availability during warm summers, and in the long term this might determine declines (Reading 2007; Griffiths et al. 2010; Caruso et al. 2014; Benard 2015). However, opposite trends have been observed in some mountain species, with higher survival during the mild winters (Scherer et al. 2008). Even though global warming determines a consistent trend toward early breeding, it is difficult to predict how early breeding may impact population dynamics. On the one hand, early breeding can determine early maturity, and this might be beneficial (Alvarez and Nicieza 2002; Altwegg and Reyer 2003; but see Schmidt et al. 2012; Earl and Semlitsch 2013 for different conclusions). On the other hand, phenological advancements might be different among interacting species within communities, with potential demographic effects. For instance, it has been proposed that different phenological trends between birds and their prey may determine a mismatch between breeding and seasonal peaks of food supply. Phenological mismatch can reduce fitness and determine population declines (Both et al. 2006; Moller et al. 2008), but its overall importance remains controversial (Dunn and Moller 2014). We have a limited knowledge of the potential effects of phenological mismatches between amphibian breeding and their resources. Such mismatches might have a limited effect on generalist such as many anurans (Benard 2015), while consequences can be stronger for active predators, such as urodeles (Beebee 2002; Anderson et al. 2015; Reinhardt et al. 2015). However, more studies are required to understand the potential effects of phenological mismatches on amphibian populations.

Geographical patterns

Meta-analyses with global coverage provide some of the most reliable information on the impact of climate change (Parmesan et al. 2013). Although we tried to gather all the available information, geographical bias was evident. Out of 140 effect sizes considered, >20% were from the UK, even if just 0.1% of the currently described amphibians are native of this country. Conversely, data are nearly lacking in the areas hosting the highest amphibian diversity and the largest number of threatened amphibians (South America, Equatorial Africa and SE Asia; Stuart et al. 2008) (Fig. 1). Tropical amphibians have unique ecological and life history features. For instance, most of temperate amphibians have aquatic reproduction, while in the tropics more species have terrestrial reproduction or direct development (Gomez-Mestre et al. 2012). This can affect the impact of climatic parameters on populations, thus conclusions of studies performed in temperate regions may not be generalizable to the tropics. The scarcity of field data from megadiverse tropical areas is widely recognised as a major research issue (Ficetola 2015). Although increasing research effort is being made in some tropical areas, filling the knowledge gap will be particularly complex, as decades of field data would be required to obtain time series comparable to the ones from Europe and North America. Nevertheless, we were able to gather data partially covering at least some tropical areas, particularly in Australia, and these data are particularly important to understand impacts across different climates.

Which populations will be more affected by climate change? Studies based on species distribution models suggest complex patterns, with strong declines predicted to occur both in tropical, subtropical and cold regions (Araujo et al. 2006; Lawler et al. 2010; Hof et al. 2012). Analyses on phenology show that the amphibian response to climate change is spatially heterogeneous (Fig. 2). For temperature, climate change is strongest at high latitudes (Intergovernmental Panel on Climate Change 2013), and populations living there showed the strongest impact and the greatest responsiveness, as they advanced more their phenology in response to warming (e.g. Mazaris et al. 2013; While and Uller 2014). It has been proposed that the high responsiveness of northern populations might occur because, at the high latitudes, phenology is more limited by the abiotic environmental conditions, compared to the low latitudes (Mazaris et al. 2013), or because northern populations are adapted to warm temperatures, compared to the ones usually encountered in nature (Phillimore et al. 2010).

A strong impact of latitude on responsiveness was also observed for the relationship between abundance and precipitation (Fig. 2d), but in this case the trend was the opposite one: tropical populations showed the strongest responses. Within this dataset, precipitation strongly decreased from the tropical to the temperate sites (correlation between mean annual precipitation and the absolute value of latitude: $r = -0.8$, $P < 0.001$). In other words, populations living in humid, tropical climates seem to be the less tolerant to dry periods. Tropical amphibians have highly diverse life histories. For instance, many tropical species do not require large waterbodies for breeding, and may exploit very small resources (e.g. phytotelmata, the small waterbodies accumulated by terrestrial plants), may complete the reproduction outside water (Gomez-Mestre et al. 2012), and have longer activity periods. Individuals thus require constantly high humidity levels, to avoid desiccation. Climate change scenarios suggest that precipitation loss may be severe in some tropical areas (e.g. Northern Australia, Mesoamerica, the Amazon basin and Madagascar) (Intergovernmental Panel on Climate Change 2013) that currently host the highest amphibian diversity levels, but also harbour many species that do not require large waterbodies for breeding (Gomez-Mestre et al. 2012). This may be an additional threat to these areas, which already harbour some of the highest numbers of threatened species (Stuart et al. 2008).

Precipitation, temperature or more complex causes?

To draw quantitative conclusions through meta-analysis, we focused on studies evaluating simple relationships between population or individual-level features and climatic parameters, and we actually found evidence of such relationships. Nevertheless, the impact of climate change on amphibian populations may be more complex. For instance, climatic change might increase the impact of other threatening factors, such as pathogens, land-use change, UV radiation, pollution or invasive alien species, which in turn will impact populations (Blaustein and Kiesecker 2002; Pounds et al. 2006; Hof et al. 2012; Li et al. 2013). However, finding strong evidence for complex relationships is difficult. For example, Pounds et al. (2006)

proposed that warming temperatures at highland localities are increasing the suitability for the pathogen *Batrachochytrium dendrobatidis*, which in turn is determining amphibian declines and extinctions, but subsequent studies have challenged the actual relevance of warming on the spread of this pathogen (Lips et al. 2008; Rohr et al. 2008), and have suggested that the impact of climatic variability in susceptibility to diseases may be particularly complex and non-linear, with a strong effect of unpredictable temperature fluctuations (Raffel et al. 2013).

Our study revealed a new fingerprint of climate change on amphibians: while phenological changes are mostly linked to temperature changes, population dynamics are most strongly determined by the variation of precipitation. However, climate change is only one facet of the ongoing global changes, and multi-factorial studies, considering the potential effect of multiple factors on populations (e.g. climate, habitat changes, diseases, presence of invasive species…) are strongly needed to unravel the complex causes. Unfortunately, studies on amphibian conservation are increasingly focused on one single stressor (Ficetola 2015), and this will hamper our understanding of the complex consequences of global changes on amphibians. More than one decade ago, Balustain and Kieseker (2002) called for more studies analyzing the complexity of factors determining amphibian declines. This remains a major task for the research to do.

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Table 1. Meta-regression models analysing the responsiveness of amphibian breeding phenology / abundance to temperature / precipitation.

Fixed effects	Posterior mean	95% HPD CI[a]
a) Relationship between phenology and temperature		
Intercept	-0.578	-0.630 / -0.462
Latitude	-0.174	-0.296 / -0.044
Temperature range	0.135	0.036 / 0.258
b) Relationship between phenology and precipitation		
Intercept	-0.180	-0.452 / 0.093
Latitude	0.061	-0.311 / 0.440
Precipitation range	-0.228	-0.817 / 0.405
c) Relationship between abundance and temperature		
Intercept	0.226	-0.785 / 1.199
Latitude	0.060	-0.240 / 0.395
T(Reading and Clarke 1999)emperature range	0.609	-1.678 / 2.861
d) Relationship between abundance and precipitation		
Intercept	0.611	0.220 / 1.001
Latitude	-0.544	-1.095 / -0.098
Precipitation range	-0.202	-0.805 / 0.340

[a] 95% Bayesian highest posterior density credible intervals.

Figure captions.

Fig. 1 Global distribution of studies used for meta-analyses. Diamonds: studies analysing phenological changes; triangles: studies analysing changes in abundance; open dots: studies analysing variation in performance. Some points are superimposed due to geographical proximity.

Fig. 2 Forest plots showing the overall effect size and the moderators for a) relationship between phenology and temperature; b) relationship between abundance and temperature; c) relationship between phenology and precipitation; d) relationship between abundance and precipitation. The estimates of the intercepts ("overall") are the meta-analytical means (see main text). Estimates for the moderators are from Table 1. Temper. Range and Precip. Range are the range of variation in temperature and in precipitation at each site, calculated as max. - min. during the study period covered by each time series.

Fig. 3 Number of studies showing significant (dark bars) and non-significant (pale bars) relationships between climate and the parameters representing individual features and performance.