

DR. MATTIA FALASCHI (Orcid ID : 0000-0002-4511-4816)

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Continental-scale determinants of population trends in European amphibians and reptiles

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Mattia Falaschi¹, Raoul Manenti¹, Wilfried Thuiller², Gentile Francesco Ficetola^{1,2}

¹ Department of Environmental Science and Policy, Università degli Studi di Milano, Via Celoria 2, 20133 Milan, Italy

² Univ. Grenoble Alpes, Univ. Savoie Mont Blanc, CNRS, LECA, Laboratoire d'Écologie Alpine, F-38000 Grenoble, France

Correspondence: Mattia Falaschi, Università degli Studi di Milano, Dipartimento di Scienze Politiche e Ambientali, Via Celoria 2, 20133 Milan, Italy.

Email: matt_fala@hotmail.it

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Abstract

The continuous decline of biodiversity is determined by the complex and joint effects of multiple environmental drivers. Still, a large part of past global change studies reporting and explaining biodiversity trends have focused on a single driver. Therefore, we are often unable to attribute biodiversity changes to different drivers, since a multi-variable design is required to disentangle joint effects and interactions. In this work, we used a meta-regression within a Bayesian framework to analyze 843 time-series of population abundance from seventeen European amphibian and reptile species over the last 45 years. We investigated the relative effects of climate change, alien species, habitat availability, and habitat change in driving trends of population abundance over time, and evaluated how the importance of these factors differs across species. A large number of populations (54%) declined, but differences between species were strong, with some species showing positive trends. Populations declined more often in areas with a high number of alien species, and in areas where climate change has caused loss of suitability. Habitat features showed small variation over the last 25 years, with an average loss of suitable habitat of 0.1% / year per population. Still, a strong interaction between habitat availability and the richness of alien species indicated that the negative impact of alien species was particularly strong for populations living in landscapes with less suitable habitat. Furthermore, when excluding the two commonest species, habitat loss was the main correlate of negative population trends for the remaining species. By analyzing trends for multiple species across a broad spatial scale, we identify alien species, climate change, and habitat changes as the major drivers of European amphibian and reptile decline.

KEYWORDS

Alien species, climate change, demography, land-cover change, meta-analysis, population trends, species distribution models

INTRODUCTION

Biodiversity is declining at an unprecedented rate (Butchart et al., 2005; IPBES, 2018). Understanding the main causes of these changes is a major endeavor for the scientific community, should we want to anticipate and mitigate future impacts. Climate change, land-use change, spread of alien species, atmospheric CO₂ increase, anthropogenic nitrogen deposition, and spread of disease are all drivers known to strongly influence the structure and distribution of biodiversity (Bateman et al., 2016; Gallardo, Clavero, Sánchez, & Vilà, 2016; Tracewski et al., 2016). These drivers do not affect biodiversity independently, rather they act in synergistic or antagonistic ways. For instance, in a global study comprising multiple taxa, Mantyka-Pringle, Martin, & Rhodes (2012) found that the negative effects of habitat loss and fragmentation on species abundance and diversity were magnified in areas where average rainfall has decreased in the past. Multi-variable studies, taking into account more than one driver of global change, are thus essential to disentangle the relative importance of different threats (Didham, Tylianakis, Gemmill, Rand, & Ewers, 2007). Nevertheless, a large part of past global change studies focused on one single driver, perhaps because it is difficult to retrieve standardized data across broad spatial extents, or because integrating multiple factors can result in overly complex models. In the last years, attention is growing toward the importance of disentangling the effects of multiple drivers (e.g. Campbell Grant et al., 2016; Northrup, Rivers, Yang, & Betts, 2019), because knowing the relative impact of different

drivers on the different biodiversity facets is essential to identify conservation priorities and management strategies (Brook, Sodhi, & Bradshaw, 2008).

Global change drivers impact populations in multiple ways and can, for instance, impact morphology, breeding success, survival, and abundance (Ficetola et al., 2016; Ficetola & Maiorano, 2016; Menzel et al., 2006; Saino et al., 2011). Trends of population abundance are connected to extinction risk and are commonly used to evaluate the conservation status of species, thus population trends are one of the key demographic parameters to assess the effects of global change drivers on biodiversity (Flesch, Rosen, & Holm, 2017; IUCN, 2012). However, studies on population abundance are generally local, thus limiting the possibility of drawing broad-scale, generalizable inference. Quantitative analyses of the results of multiple studies (meta-regressions) can alleviate this issue, as they allow to summarize information from a broad range of sources. Meta-regressions showed excellent performance in the analysis of multiple demographic time series and helped to obtain general inference on patterns of global change (Bonardi et al., 2011; Gurevitch, Koricheva, Nakagawa, & Stewart, 2018; Hadfield & Nakagawa, 2010).

Amphibians and reptiles are two vertebrate groups particularly threatened by global changes (Böhm et al., 2013; Hoffmann et al., 2010). Amphibian populations are declining at a greater pace than the other vertebrates, and their decline is determined by the combined effects of multiple threats, notably land-use change, climate change, and alien species (Hof, Araújo, Jetz, & Rahbek, 2011; Stuart et al., 2008). While the global reptile assessment has not been completed yet, land-use change, climate change, and alien species are listed as major threats also for reptiles (Todd, Willson, & Gibbons, 2010). Furthermore, climate change is expected to have a particularly strong impact on ectothermic vertebrates, because it can affect essential life-history processes that depend on the characteristics of the environment (Buckley, Hurlbert, & Jetz, 2012; Flesch et al., 2017). Finally, the response of local

populations to global drivers vary across taxa and geographic areas. It is thus important to assess whether different species show heterogeneous responses, in order to understand the generality of patterns of change (Muths et al., 2017).

In this study, we used meta-regression to quantify the relative importance of different global change drivers on population trends of European amphibians and reptiles (Figure 1). In particular, we tested four hypotheses:

- i) *Population trends are determined by changes in climatic suitability.* Climatic suitability is a measure of how much the climate of an area is suitable for a particular species (Araújo, Alagador, Cabeza, Nogués-Bravo, & Thuiller, 2011). Suitability can provide a better measure of the impact of climate change compared to climatic velocity since it accounts for the geographic position of a population. For instance, in a situation of poleward shift of the geographic range of a species, populations nearest to the pole can gain suitability, while the farthest ones often lose suitable space (Parmesan et al., 1999). We thus predict that a decrease in climatic suitability negatively affects population trends and vice versa;
- ii) *Population trends are negatively influenced by alien species.* Alien species exert multiple impacts on native biodiversity (Gallardo et al., 2016). Negative impacts increase with the abundance and richness of alien species (Vilà et al., 2010), thus we predict a negative relationship between the richness of alien species and population trends;
- iii) *Population trends are determined by habitat availability.* The amount of available habitat in the landscape is a key parameter influencing species distribution and population dynamics (Flesch, 2017; Seibold et al., 2017). For example, a low amount of suitable habitat leads to reduced carrying capacity and vital rates, and to a decrease in the amount of source populations that could provide migrants from

the surrounding landscape (Hodgson, Thomas, Wintle, & Moilanen, 2009). Because these processes can affect the long-term dynamics of populations and their probability of persistence, we predict a positive relationship between the amount of suitable habitat and population trends;

- iv) *Population trends are determined by changes in habitat availability.* Land-use has undergone heavy changes in the last decades, with the conversion of natural vegetation to urban or agricultural land-use in some areas and forest gain in others (Hansen et al., 2013). Habitat loss is considered the main cause of decline for the vast majority of vertebrates, hence we predict a negative relationship between the decrease in habitat availability and population trends (Hoffmann et al., 2010).

We used data on long-term population abundance of reptiles and amphibians to evaluate the support of these hypotheses and also investigated possible interactions among drivers. Furthermore, we appraised whether the response of populations to these drivers was heterogeneous across taxa.

MATERIALS AND METHODS

Abundance data

The study area included Europe plus Anatolia, with eastern limit in the Ural Mountains and the Caucasus. We performed a literature search in February 2017. Published data on abundance for reptile and amphibian species were collected by searching in the ISI Web of Science for keywords “demography”, “population”, and “decline”, associated with “reptile”, and “amphibian” keywords. We reviewed the text and selected data of populations with at least 4 years of sampling. Shorter time series were discarded to ensure more relevant estimates of temporal trends. We also analyzed the data associated to the Houlahan, Findlay, Schmidt, Meyer, & Kuzmin (2000) paper on amphibian population trends, and retrieved all

the time series from the study area, for which enough information was available to reconstruct the population locality. We also added two unpublished population times series for which we directly collected data for the period 2010-2016 (Manenti R., unpublished data). We obtained a total of 16 studies, comprising time-series for 843 populations of 17 different species (see Supporting Information Table S1 for a complete list of references).

From these time series, we derived population trends by calculating, for each population, the Pearson's correlation (r) between years of sampling and log-transformed population abundance. We then used Fisher's Z to calculate the effect size of temporal trends and the associated variance for each population (Ficetola & Maiorano, 2016). To identify the drivers of population trends, we then assessed the relationships between population trends (effect sizes) and four drivers: (i) climatic suitability changes, (ii) alien species richness, (iii) habitat availability, (iv) changes in habitat availability.

Climatic suitability changes

We used species distribution models (SDM) to assess changes in climatic suitability through time for each population. To build SDM, species presence was derived from the European Herpetological Atlas (Sillero et al., 2014), at a resolution of 0.5° . All the frogs of the hybridogenic complex *Pelophylax* spp. were modeled as a single taxon; the distribution range of the grass snake *Natrix natrix* extends outside the boundaries of the European Herpetological Atlas, thus presences for this species were integrated with points obtained from the global biodiversity information facility (<https://www.gbif.org/>); The distribution records of newts (*Triturus cristatus* and *Lissotriton vulgaris*) were taken from Wielstra et al., (2018) and Wielstra, Sillero, Vörös, & Arntzen (2014).

SDM were calibrated on the climatic conditions in the last 51 years (averaged from 1966 to 2016), obtained from an updated version of the Climatic Research Unit dataset (Harris, Jones, Osborn, & Lister, 2014) (CRU TS v. 4.01), which reports monthly values of precipitation and temperature for the time-period 1901-2016. We used four climatic variables: mean annual temperature, total annual precipitation, annual temperature standard deviation, annual precipitation coefficient of variation. Minimum annual temperature and maximum annual temperature, and minimum / maximum temperature during breeding seasons, are additional variables important for tolerance and activity of ectotherms but are strongly correlated to mean temperature and standard deviation (Appendix S1). We thus also re-ran the SDMs using min/max values instead of mean and standard deviation of temperature and for subsequent analyses we used models with higher performance values (see results). Models were built within the biomod2 R package (Thuiller, Georges, Engler, & Breiner, 2016), running an ensemble of the following models: boosted regression trees, generalized additive models, classification tree analysis, multivariate adaptive regression splines, and random forests. For each species, we selected 3,000 pseudo-absence points within a radius of 1,000 km from the species distribution range. To get a meaningful evaluation of the models and to avoid overfitting, models were repeated five times to perform cross-validation, and for each run we used a random sample of 67% of the initial occurrence data to calibrate the models and the remaining 33% for evaluation. Models performance was assessed using the True Skill Statistic (TSS) and the Area Under the receiver operating characteristic Curve (AUC) (Liu, White, & Newell, 2011). Finally, we obtained an ensemble model through a weighted sum of the probability of occurrence, proportional to the cross-validated TSS.

Subsequently, to assess changes in climatic suitability through time, the overall bioclimatic SDM for each species (calibrated for 1966-2016) was projected on the climatic conditions for the years for which information on population abundance was available. This allowed obtaining time series of climatic suitability for each population. Specifically, we calculated the trend of SDM suitability for each population by calculating the correlation between years of sampling and climatic suitability. Correlation coefficients were then transformed to Fisher's Z to obtain comparable measures of effect size. The trend of climatic suitability was considered as independent variable to measure the effect of changes of climatic suitability.

Alien species

The richness of alien species was obtained from the Global Alien Species First Record Database (Seebens et al., 2017), which reports the first year of detection of alien species at the regional level resolution. At this scale, alien species richness can be a good proxy to measure negative effects on native biodiversity, because the number of impacts is higher in areas with more alien species (Latombe et al., 2017; Vilà et al., 2010). For each population, we extracted the total number of alien species starting from 1901 to the last year of sampling by summing the total number of vertebrates and crustaceans, as these taxa are known to have a major impact on amphibians and reptiles (Ficetola et al., 2011; Kats & Ferrer, 2003). The database reports the occurrences of alien species at the regional level, but the considered regions had a coarser resolution than the localities used for our analyses. Therefore, the number of alien species obtained using this approach probably overestimates the actual number of alien species at a given locality. Nevertheless, the Global Alien Species First Record Database has the advantage that the alien species records are temporally explicit, thus allowing analyses of temporal processes. Furthermore, the number of alien species is strongly related to economic

and political factors of territories, thus we expect a strong correlation between regional-level and local abundance of alien species (Pysek et al., 2010). For each time series, the total number of alien species from the year 1901 to the last year of the time series was considered as independent variable to measure the effect of alien species.

Habitat availability and habitat changes

For each species, we identified a list of suitable land-cover classes in order to calculate the extent of suitable habitat (ESH) by integrating the habitat preferences obtained from the IUCN Red List with land-use information (see Table S2 for details; Rondinini et al., 2011). Land-use information was obtained from the time series of the European Space Agency Climate Change Initiative Land Cover project (<https://www.esa-landcover-cci.org/>). This map is available from 1992 and does not cover the whole 1972-2016 period. Hence, analyses which considered land use variables were limited to populations sampled in the period 1992-2016 ($N = 705$ populations). Previous analyses showed that ESH maps, built on the basis of the occurrence of suitable land-use classes, allow a good representation of the actual habitat that can be exploited by species, and provide useful information to estimate species trends (Ficetola, Rondinini, Bonardi, Baisero, & Padoa-schioppa, 2015; Rondinini et al., 2011; Tracewski et al., 2016). We used ESH to calculate the habitat availability at the beginning of the study period, and the trend of suitable habitat during the study period. Habitat variables were calculated within the 9×9 km cell surrounding each population; we selected this resolution because about 90% of amphibian species have a maximum dispersal ability of ~4.5 km (Smith & Green, 2005), and because it matched well the accuracy of population localities in our dataset.

Habitat availability at the beginning of the period. We extracted the percentage cover of ESH in the first year of monitoring within the 9×9 km cell surrounding each population. We considered cover at the beginning of time series since we aimed at testing whether initial habitat amount can affect subsequent abundance changes within that landscape. We also repeated analyses using ESH at the end of the period and obtained very consistent results.

Habitat changes. To assess the impact of the change of ESH on population trends, we calculated the ESH within the 9×9 km cell surrounding each population in each year of monitoring, obtaining a time series of ESH. Hence, we calculated the Fisher's Z of the correlation between years of sampling and ESH, and considered this value as the trend of ESH (hereafter habitat change).

Statistical analyses

We used meta-regression to identify the most influential drivers of population trends (Gurevitch et al., 2018). Global change drivers were related to population trends through Bayesian generalized linear mixed models, using the effect size of population trends (Fisher's Z) as the dependent variable. First of all, the overall trend averaged across all the populations was assessed by performing a model of the mean (i.e. a meta-regression model including the intercept and without independent variables) (Kéry, 2010). We also ran a separate model of the mean for each species, in order to assess the average species trend. Then, four separate meta-regressions were run to assess the single-variable relationships between population trends at each locality and: (i) trend of climatic suitability, (ii) richness of alien species, (iii) habitat availability at the beginning of the period, (iv) trend of habitat availability (Figure 1). Independent variables used, and time period considered for each single-variable model are described in Table S3. Finally, we performed a multi-variable model including all four independent variables, for the period 1992-2016. We also tested pairwise interactions between

the four variables and, in the final model, we considered only interactions with 95% credible intervals (CIs) not overlapping zero. The biological rationale of tested interactions is listed in Table S4. Our multi-variable meta-regression included data from all the species, in order to evaluate the overall pattern. Subsequently, to assess if the effects were consistent across species, we re-run the meta-regression separately for the two commonest species (the common toad *Bufo bufo* and the common frog *Rana temporaria*) and then considering all the species except common toad and common frog.

Before the analysis, we tested the collinearity among the global change drivers and found no strong correlations ($|r| < 0.4$, Table S5). In meta-regressions we included as random effects: the study source of the data; species, family, order, and class, fitted as nested random intercepts, to consider the phylogeny; the id of the 0.5° cell, to take into account the non-independence of nearby populations (i.e. populations within the same cell). Furthermore, for models including alien species, we included region identity as an additional random effect because alien species data are derived from a regional-level database (Seebens et al., 2017). To take into account different variances of Fisher's Z among studies, we weighted the records by using the "mev" argument in the MCMCglmm function, considering $1 / \text{variance of } Z$ as weight (following Hadfield & Nakagawa, 2010). All models were run for 2,000,000 iterations, with 1,000,000 burn-in and a thinning of 250. The number of alien species was log-transformed and all variables were scaled (mean = 0, SD = 1) before analyses to allow comparison of their estimated effects. Finally, we used respectively Moran's I and Pagel's lambda, to assess whether the residuals of meta-regressions showed spatial or phylogenetic correlation. To test the phylogenetic signal, we used a phylogeny tree including all the 17 species, derived from the phylogenetic tree of the European tetrapods (Roquet, Lavergne, & Thuiller, 2014).

All analyses were performed in the R environment (R Core Team, 2017), using the packages `compute.es` (del Re, 2013) to compute population trends effect sizes and variance, `raster` (Hijmans, 2016) and `rgeos` (Bivand & Rundel, 2017) to process maps, `biomod2` (Thuiller et al., 2016) to create SDMs, `MCMCglmm` (Hadfield, 2010) to perform Bayesian generalized linear mixed models, `EcoGenetics` (Roser, Ferreyra, Saidman, & Vilaridi, 2017) to test spatial autocorrelation, and `caper` (Orme et al., 2018) to test phylogenetic autocorrelation.

RESULTS

Overall, we obtained 843 time-series for 17 species, covering 11 European countries across the period 1972-2016 (Figure S1; Appendix S2). 705 time-series were included in the period for which land cover information was available (after 1992, Appendix S3).

General trend

Out of the 843 populations, 458 (54%) showed negative population trends, 383 (45%) positive trends and two remained stable ($|r| < 0.01$). The averaged population trend (effect size), obtained from the models of the mean of the different species, was negative for ten species and positive for seven species (Figure 2). 95% CIs of the estimates of population trends did not overlap zero in seven out of 17 species (41%), however, there were strong differences of trends across populations (Figure 2). The population trend averaged across the populations of all species, was negative but credible intervals overlapped zero (mean = -0.084; 95% CI = -0.284 / 0.152).

Single-variable relationships

Climatic suitability changes. All bioclimatic models showed very good or excellent performance (Figure S2). The models built with mean annual temperature and annual temperature standard deviation showed higher TSS and AUC values than models including minimum and maximum annual temperature (Table S6) and were hence used to calculate climatic suitability.

Climatic suitability increased through time for 309 populations, decreased for 520 populations, and remained stable for 14 populations. For the period 1972-2016, the average change of climatic suitability/year was -0.15% (SD = 2.4%). The relationship between climatic suitability and population trends was positive, indicating more positive trends in populations experiencing improvement of suitability. Nevertheless, 95% CIs slightly overlapped zero (effect size = 0.046; 95% CI = -0.021 / 0.107). The pattern was similar when we limited analyses to the period 1992-2016, even though the effect size of the relationship between climatic suitability and population trends was slightly weaker (effect size = 0.038).

Alien species. The average number of alien species per region was 45 (SD = 24), and population trends declined in regions with more alien species. For the period 1972-2016, the 95% CIs of this relationship slightly overlapped zero, while 90% CIs did not (effect size = -0.061; 95% CI = -0.125 / 0.004; 90% CI = -0.112 / -0.008). When we limited analyses to 1992-2016, the effect size was significantly lower than zero (effect size = -0.093, 95% CI = -0.166 / -0.022).

Habitat availability. Average cover of suitable habitat was 29% (SD = 20%), and population trends were more positive in landscapes with high habitat availability (effect size = 0.069; 95% CI = 0.002 / 0.130; Table S7a).

Habitat change. Cover of suitable habitat increased for 33 populations, decreased for 396 populations, and remained stable for 276 populations ($|r| < 0.01$); the average absolute value of habitat change across all the populations was 0.17% / year (SD = 0.39%). The single-variable relationship between habitat change and population trends was weak, with CIs broadly overlapping zero (Table S7a).

Multi-variable analysis

Out of the six possible paired interactions among the four candidate drivers, only the interaction between the richness of alien species and the initial habitat availability showed 95% CIs not overlapping zero and was included in the meta-regression analysis including all the predictors and all the populations (full model; N = 705 populations). The effect sizes of predictors were nearly identical between the models and without the interaction (Table S7b, S7c).

The full model confirmed that population trends were negatively related to the richness of alien species (Figures 3 and 4b). There was a positive relationship between the trend of climatic suitability and population trends (Figure 4a) and, even though the 95% CIs slightly overlapped zero, the 90% CIs did not (Figure 3; Table S7c). Population trends were positively related to habitat availability and to the habitat trend (Figure 4c and 4d), but credible intervals overlapped zero for both variables (Figure 3). Furthermore, there was a strong interaction between habitat availability and richness of alien species, showing that the negative impact of alien species was particularly strong in landscapes with a low amount of suitable habitat (Figure 5). Values of random intercepts for the multiple regression model are listed in Table S8. The residuals of the model showed no significant spatial or phylogenetic

autocorrelation (Moran's $I = 0.001$; 95% CIs = $-0.009 - 0.010$; Pagel's Lambda = 0 ; 95% CIs = $0 - 0.503$).

Robustness to interspecific variation

When we repeated meta-regression including only common toad populations, results were generally consistent with the full analysis. Common toad population trends were more negative in sites with more alien species, were positively related to the trend of climatic suitability and were more positive in landscapes with higher habitat availability, even though 95% intervals were broader than in the analysis including all the species. Conversely, trends were unrelated to habitat change and to the interaction between habitat availability and richness of alien species (Figure 6a). Common frog populations showed a different pattern compared to the full analysis, as population trends only showed a weak positive relationship with habitat change (Figure 6b).

Results remained partially consistent when we repeated analyses excluding the two most common species (the common toad and the common frog), even though credible intervals were much broader than in the full analysis. Population trends were positively related to climatic suitability trend and negatively related to alien species. While the effect size of habitat availability was close to zero, this analysis confirmed the interaction between habitat availability and richness of alien species (Figure 6c). Moreover, in this analysis we observed a strong positive effect of habitat changes, indicating that population trends were more positive in landscapes where the extent of suitable habitat increased through time (Figure 6c).

DISCUSSION

Our study provides one of the first broad-scale and long-term assessments of the impact of multiple global change drivers on population trends of amphibians and reptiles. Despite amphibians and reptiles having a major functional role in ecosystems, these vertebrates remain underrepresented in population trend analyses, and they only account for a tiny part of studies even in global databases of species abundance (Dornelas et al., 2018; Santini, Isaac, & Ficetola, 2018). Our work summarized the trends of multiple European amphibian and reptile populations through 45 years and showed that climate change, alien species, habitat availability, and habitat change have complex impacts on their dynamics, even though their importance differed among taxa (Figures 3 and 6).

Population trends of amphibians and reptiles were jointly determined by multiple drivers. In the multi-variable analysis, alien species showed the largest effect, followed by climate change and habitat availability (Figure 3), indicating that they might be among the most influential drivers of population trends for many amphibians and reptiles. Alien species have a major impact on the European native fauna (Vilà et al., 2010); unfortunately, the number of alien species is quickly growing in all the continents, stressing the urgency of prevention and mitigation actions in order to limit the intensification of impacts in the future (Seebens et al., 2017; Vilà et al., 2010). Nevertheless, the effect of alien species differed across taxa, as they showed a negative effect on the common toad and on other amphibians and reptiles, while were unrelated to the trends of common frogs (Figure 6). Other studies on population trends detected heterogeneous responses to broad-scale environmental stressors (Campbell Grant et al., 2016; Flesch et al., 2017; Muths et al., 2017). For instance, Muths et al. (2017) analyzed the demographic response of amphibian populations to climate and observed that the magnitude and direction of the response were highly heterogeneous across taxa and even within species. This confirms the importance of studies including species with

various ecological tolerances, in order to disentangle the heterogeneous effects of global changes on natural populations.

Global change scenarios suggest that climate change will have a growing impact on biodiversity (Intergovernmental Panel on Climate Change, 2015). However, the impact of climate change can be heterogeneous among species and even among populations within a given species. For instance, in the northern hemisphere, climatic warming can determine the extinction of populations in southern portions of species ranges, while can have positive effects on northern populations (Parmesan et al., 1999). To assess the impact of climate change it is thus important to develop appropriate measures of how climatic variation influences populations in different areas of the species' range. Climatic suitability can provide information on the actual effect of climatic variation on populations because it considers the differences that can occur across distant geographic areas. Therefore, in our analyses we considered climatic suitability instead of raw temperature/precipitation change. Despite 95% CIs slightly overlapping zero, the effects of suitability changes were consistent with our predictions (Figures 3, 4 and 6) with negative changes in climatic suitability corresponding to negative population trends. Studies relating the trends of amphibians and reptiles to climate change obtained mixed results. For instance, Ficetola and Maiorano (2016) found that changes in precipitation can have a significant impact on amphibian trends, but did not detect a clear effect of changes in temperature. Conversely, when using climatic suitability, we found a consistent pattern across species (Figures 3 and 6). Changes in climatic suitability are often used to explore potential impacts of future climate change on biodiversity (Araújo et al., 2011; Thuiller et al., 2011), while fewer studies have used this approach to understand the impact of changes occurring in the past (e.g. Bateman et al., 2016; Fouquet, Ficetola, Haigh, & Gemmill, 2010). Our analysis suggests that suitability can provide a measure of the impact of climate change more comparable across species. The moderate effect of suitability change

on population trends can also be related to the ability of populations to adapt in response to climate change (Seebacher, White, & Franklin, 2015). The integration of ongoing adaptive changes is a challenge for global change research and could allow to better understand the responses of populations and to make better predictions (Hoffman & Sgró, 2011).

While the effects of alien species and climate were generally consistent across taxa, the effects of habitat availability and habitat change were more complex. Even though habitat loss is described as the factor threatening the largest number of amphibians and reptiles (Stuart et al., 2008), relationships between changes in habitat availability and population trends were only detected in a subset of analyses. Population trends were more positive in landscapes with more habitat (Table S7a), but the effects of habitat availability were weak when taking into account also other factors and potential interactions (Figure 3; Table S7b).

Several factors can explain the limited effects of habitat variables. First, a significant interaction between habitat availability and the richness of alien species indicates that the impact these two variables can be context dependent, complicating the detection of their effects. Second, we assessed habitat change on the basis of broad-scale land cover maps, which do not provide measures of the specific resources and conditions needed by different species. Obtaining accurate measures of habitats is particularly complex for small vertebrates, which often exploit specific microhabitats (Ficetola, Lunghi, et al., 2018; Mendenhall, Sekercioglu, Oviedo Brenes, Ehrlich, & Daily, 2011). For instance, agricultural mechanization can determine loss of suitable micro-habitats (e.g. hedgerows, ditches) even in areas with a stable amount of agricultural lands, thus impacting species that can exploit semi-natural landscapes. Third, average rates of habitat change were extremely low during the study period (average: ~0.1% / year). Such a limited variation is characteristic of broad areas of Europe (Figure S3) but reduces the possibility to detect relationships and can explain the weak effect of this driver. Furthermore, population declines often do not occur immediately

after environmental pressures (Dullinger et al., 2013), thus we might experience the legacy of present anthropogenic pressures in the next decades. Nevertheless, habitat change showed a clear effect when we removed the commonest species (common toad and common frogs) from our dataset, with more positive population trends in landscapes where the amount of suitable habitat increased through time. Common toad and common frog are widespread, generalist species that can exploit a very wide range of habitats (Table S2), therefore it may be more difficult detecting their response to habitat change, compared to habitat specialists. This further stresses the need of monitoring a wide range of species in order to obtain generalizable information of the effects of global changes on biodiversity loss and highlights the importance of comparing the responses of both widespread and specialized species.

Habitat availability showed a strong interaction with the richness of alien species, as the negative impact of alien species was particularly strong in landscapes with less habitat availability (Figure 5). The importance of interactions among different drivers is increasingly recognized by global change studies, as interactive effects can both magnify and mitigate the impact of stressors (Blaustein & Kiesecker, 2002; Mantyka-Pringle et al., 2012). Alien species show complex relationship with the availability of natural habitats, which can strongly modify their impact. For instance, invasive species can be more abundant in human-modified landscapes, thus native populations living in landscape with a less natural habitat can suffer a stronger impact by invasives (Blaustein & Kiesecker, 2002; Didham et al., 2007; Quinn, Schooler, & Van Klinken, 2011). The complex interactions between alien species and habitat availability further stress the importance of conservation actions targeting multiple threats and also considering synergies among drivers of decline in order to mitigate biodiversity loss (Brook et al., 2008; Didham et al., 2007).

Despite the broad temporal and geographic extent, our analyses have some limitations. Most of the data are from amphibian populations, and one species (the common toad, *Bufo bufo*) accounted for more than half of populations (Table S9). This occurs because the common toad is one of the most abundant amphibians in Europe and is regularly monitored by many citizen science programs. Common amphibians have a major role in ecosystem functioning and nutrient transfer (Beard, Eschtruth, Vogt, Vogt, & Scatena, 2003; Kyek, Kaufmann, & Lindner, 2017). Several studies have shown negative trends in toad populations (e.g. Bonardi et al., 2011; Petrovan & Schmidt, 2016) and understanding the factors underlying a common species decline is extremely important to maintain ecosystem functioning (Gaston & Fuller, 2008). Alien species and climate change showed a similar effect across most of the taxa: despite broader credible intervals, effect sizes pointed in the same direction even if we removed the most common species (Figure 6c), suggesting that uneven sample size across species did not bias our conclusions. In our dataset we collected fewer data regarding reptiles than amphibians. This is a recurrent pattern in the herpetological literature and hampered separate analyses of these taxa. Estimating the abundance of reptiles is usually harder compared to amphibians, because reptiles often have low detection probability, and estimating their abundance requires effort-demanding survey methods (e.g. capture mark recapture instead of repeated counts) (Ficetola, Romano, Salvidio, & Sindaco, 2018). Increasing the monitoring efforts toward reptile populations is urgently required to better assess the drivers of the decline of this group and guide future conservation efforts. Finally, our analyses were limited both in space and in time by the availability of population and land-cover data. Continuous series of land-cover data are only available since 1992, thus preventing us from assessing the effects of habitat availability during previous periods, when the velocity of habitat change in Europe was probably stronger than in recent years (Falcucci, Maiorano, & Boitani, 2007). Furthermore, the majority of our data came from just two

European countries, potentially limiting the spatial representativeness of our dataset (Figure S1). Despite not spanning the whole Europe, analyzed localities provide good coverage of the features occurring through Europe for habitat availability and changes (Figure S4), richness of alien species (Figure S5), and climatic features (with the exception of coldest climates; Figure S6). Overall, the frequency of declining populations in our dataset was similar to previous broad-scale estimates of trends of herps in Europe (e.g. Houlahan et al., (2000); 53% negative and 43% positive trends). This suggests that our analyses can provide an accurate picture of patterns occurring throughout most of Europe.

Population trends of European reptiles and amphibians are driven by the combined effects of alien species, climate change, habitat features, and habitat changes, with complex joint and interactive effects among factors. Even though we identified general patterns in the response to some environmental drivers, when retrieving broad-scale patterns it is important to consider that the same factors can act differently among taxonomic groups (Campbell Grant et al., 2016; Muths et al., 2017). For instance, habitat change showed a contrasting effect across species and its crucial role was only evident for a subset of them. Understanding the impact of global change drivers is the first step for management. This requires drawing general syntheses of the combined effects of multiple drivers but also considering how responses can be different across species.

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REFERENCES

- Araújo, M. B., Alagador, D., Cabeza, M., Nogués-Bravo, D., & Thuiller, W. (2011). Climate change threatens European conservation areas. *Ecology Letters*, *14*(5), 484–492. <https://doi.org/10.1111/j.1461-0248.2011.01610.x>
- Bateman, B. L., Pidgeon, A. M., Radeloff, V. C., Vanderwal, J., Thogmartin, W. E., Vavrus, S. J., & Heglund, P. J. (2016). The pace of past climate change vs. potential bird distributions and land use in the United States. *Global Change Biology*, *22*(3), 1130–1144. <https://doi.org/10.1111/gcb.13154>
- Beard, K. H., Eschtruth, A. K., Vogt, K. A., Vogt, D. J., & Scatena, F. N. (2003). The effects of the frog *Eleutherodactylus coqui* on invertebrates and ecosystem processes at two scales in the Luquillo Experimental Forest, Puerto Rico. *Journal of Tropical Ecology*, *19*(6), 607–617. <https://doi.org/10.1017/S0266467403006011>
- Bivand, R. S., & Rundel, C. (2017). rgeos: Interface to Geometry Engine - Open Source ('GEOS'). *R Package Version 0.3-26*. <https://CRAN.R-Project.Org/Package=rgeos>.
- Blaustein, A. R., & Kiesecker, J. M. (2002). Complexity in conservation: lessons from the global decline of amphibian populations. *Ecology Letters*, *5*(4), 597–608.
- Böhm, M., Collen, B., Baillie, J. E. M., Bowles, P., Chanson, J., Cox, N., ... Zug, G. (2013). The conservation status of the world's reptiles. *Biological Conservation*, *157*, 372–385. <https://doi.org/10.1016/j.biocon.2012.07.015>
- Bonardi, A., Manenti, R., Corbetta, A., Ferri, V., Fiacchini, D., Giovine, G., ... Ficetola, G. F. (2011). Usefulness of volunteer data to measure the large scale decline of “common” toad populations. *Biological Conservation*, *144*(9), 2328–2334. <https://doi.org/10.1016/j.biocon.2011.06.011>
- Brook, B. W., Sodhi, N. S., & Bradshaw, C. J. A. (2008). Synergies among extinction drivers under global change. *Trends in Ecology and Evolution*, *23*(8), 453–460.

<https://doi.org/10.1016/j.tree.2008.03.011>

Buckley, L. B., Hurlbert, A. H., & Jetz, W. (2012). Broad-scale ecological implications of ectothermy and endothermy in changing environments. *Global Ecology and*

Biogeography, 21(9), 873–885. <https://doi.org/10.1111/j.1466-8238.2011.00737.x>

Butchart, S. H. M., Stattersfield, a J., Baillie, J., Bennun, L. a, Stuart, S. N., Akçakaya, H. R.,

... Mace, G. M. (2005). Using Red List Indices to measure progress towards the 2010

target and beyond. *Philosophical Transactions of the Royal Society B: Biological*

Sciences, 360(1454), 255–268. <https://doi.org/10.1098/rstb.2004.1583>

Campbell Grant, E. H., Miller, D. A. W., Schmidt, B. R., Adams, M. J., Amburgey, S. M.,

Chambert, T., ... Muths, E. (2016). Quantitative evidence for the effects of multiple

drivers on continental-scale amphibian declines. *Scientific Reports*, 6, 25625.

<https://doi.org/10.1038/srep25625>

del Re, A. C. (2013). compute.es: Compute Effect Sizes. *R Package Version 0.2-2*. URL

<Http://Cran.r-Project.Org/Web/Packages/Compute.Es>.

Didham, R. K., Tylianakis, J. M., Gemmell, N. J., Rand, T. A., & Ewers, R. M. (2007).

Interactive effects of habitat modification and species invasion on native species decline.

Trends in Ecology and Evolution, 22(9), 489–496.

<https://doi.org/10.1016/j.tree.2007.07.001>

Dornelas, M., Antão, L. H., Moyes, F., Bates, A. E., Magurran, A. E., Adam, D., ... Zettler,

M. L. (2018). BioTIME: A database of biodiversity time series for the Anthropocene.

Global Ecology and Biogeography, 27(7), 760–786.

<https://doi.org/https://doi.org/10.1111/geb.12729>

Dullinger, S., Essl, F., Rabitsch, W., Erb, K.-H., Gingrich, S., Haberl, H., ... Hulme, P. E.

(2013). Europe's other debt crisis caused by the long legacy of future extinctions.

Proceedings of the National Academy of Sciences, 110(18), 7342–7347.

<https://doi.org/10.1073/pnas.1216303110>

Falcucci, A., Maiorano, L., & Boitani, L. (2007). Changes in land-use/land-cover patterns in Italy and their implications for biodiversity conservation. *Landscape Ecology*, 22(4), 617–631. <https://doi.org/10.1007/s10980-006-9056-4>

Ficetola, G. F., Colleoni, E., Renaud, J., Scali, S., Padoa-Schioppa, E., & Thuiller, W. (2016). Morphological variation in salamanders and their potential response to climate change. *Global Change Biology*, 22(6), 2013–2024. <https://doi.org/10.1111/gcb.13255>

Ficetola, G. F., Lunghi, E., Canedoli, C., Padoa-Schioppa, E., Pennati, R., & Manenti, R. (2018). Differences between microhabitat and broad-scale patterns of niche evolution in terrestrial salamanders. *Scientific Reports*, 8, 10575. <https://doi.org/10.1038/s41598-018-28796-x>

Ficetola, G. F., & Maiorano, L. (2016). Contrasting effects of temperature and precipitation change on amphibian phenology, abundance and performance. *Oecologia*, 181(3), 683–693. <https://doi.org/10.1007/s00442-016-3610-9>

Ficetola, G. F., Romano, A., Salvidio, S., & Sindaco, R. (2018). Optimizing monitoring schemes to detect trends in abundance over broad scales. *Animal Conservation*, 21(3), 221–231. <https://doi.org/10.1111/acv.12356>

Ficetola, G. F., Rondinini, C., Bonardi, A., Baisero, D., & Padoa-schioppa, E. (2015). Habitat availability for amphibians and extinction threat: a global analysis. *Diversity and Distributions*, 21(3), 302–311. <https://doi.org/10.1111/ddi.12296>

Ficetola, G. F., Siesa, M. E., Manenti, R., Bottoni, L., De Bernardi, F., & Padoa-Schioppa, E. (2011). Early assessment of the impact of alien species: differential consequences of an invasive crayfish on adult and larval amphibians. *Diversity and Distributions*, 17(6), 1141–1151. <https://doi.org/10.1111/j.1472-4642.2011.00797.x>

Flesch, A. D. (2017). Influence of local and landscape factors on distributional dynamics: A

species-centred, fitness-based approach. *Proceedings of the Royal Society B: Biological Sciences*, 284(1858). <https://doi.org/10.1098/rspb.2017.1001>

Flesch, A. D., Rosen, P. C., & Holm, P. (2017). Long-term changes in abundances of Sonoran Desert lizards reveal complex responses to climatic variation. *Global Change Biology*, 23(12), 5492–5508. <https://doi.org/10.1111/gcb.13813>

Fouquet, A., Ficetola, G. F., Haigh, A., & Gemmell, N. (2010). Using ecological niche modelling to infer past, present and future environmental suitability for *Leiopelma hochstetteri*, an endangered New Zealand native frog. *Biological Conservation*, 143(6), 1375–1384. <https://doi.org/10.1016/j.biocon.2010.03.012>

Gallardo, B., Clavero, M., Sánchez, M. I., & Vilà, M. (2016). Global ecological impacts of invasive species in aquatic ecosystems. *Global Change Biology*, 22(1), 151–163. <https://doi.org/10.1111/gcb.13004>

Gaston, K. J., & Fuller, R. A. (2008). Commonness, population depletion and conservation biology. *Trends in Ecology and Evolution*, 23(1), 14–19. <https://doi.org/10.1016/j.tree.2007.11.001>

Gurevitch, J., Koricheva, J., Nakagawa, S., & Stewart, G. (2018). Meta-analysis and the science of research synthesis. *Nature*, 555(7695), 175–182. <https://doi.org/10.1038/nature25753>

Hadfield, J. D. (2010). MCMC Methods for Multi-Response Generalized Linear Mixed Models: The MCMCglmm R Package. *Journal of Statistical Software*, 33(2), 1–22. <https://doi.org/10.18637/jss.v033.i02>

Hadfield, J. D., & Nakagawa, S. (2010). General quantitative genetic methods for comparative biology: Phylogenies, taxonomies and multi-trait models for continuous and categorical characters. *Journal of Evolutionary Biology*, 23(3), 494–508. <https://doi.org/10.1111/j.1420-9101.2009.01915.x>

Hansen, M. C., Potapov, P. V, Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., ...

Townshend, J. R. (2013). High-Resolution Global Maps of 21st-Century Forest Cover Change. *Science*, 342(6160), 850–853. <https://doi.org/10.1126/science.1244693>

Harris, I., Jones, P. D., Osborn, T. J., & Lister, D. H. (2014). Updated high-resolution grids of monthly climatic observations - the CRU TS3.10 Dataset. *International Journal of Climatology*, 34(3), 623–642. <https://doi.org/10.1002/joc.3711>

Hijmans, R. J. (2016). Raster: Geographic Data Analysis and modeling. *R Package Version 2.5-8*. <https://CRAN.R-Project.Org/Package=raster>.

Hodgson, J. A., Thomas, C. D., Wintle, B. A., & Moilanen, A. (2009). Climate change, connectivity and conservation decision making: Back to basics. *Journal of Applied Ecology*, 46(5), 964–969. <https://doi.org/10.1111/j.1365-2664.2009.01695.x>

Hof, C., Araújo, M. B., Jetz, W., & Rahbek, C. (2011). Additive threats from pathogens, climate and land-use change for global amphibian diversity. *Nature*, 480(7378), 516–519. <https://doi.org/10.1038/nature10650>

Hoffman, A. A., & Sgró, C. M. (2011). Climate change and evolutionary adaptation. *Nature*, 470(7335), 479–485. <https://doi.org/10.1038/nature09670>

Hoffmann, M., Hilton-Taylor, C., Angulo, A., Böhm, M., Brooks, T. M., Butchart, S. H. M., ... Stuart, S. N. (2010). The impact of conservation on the status of the world's vertebrates. *Science*, 330(6010), 1503–1509. <https://doi.org/10.1126/science.1194442>

Houlahan, J. E., Findlay, C. S., Schmidt, B. R., Meyer, A. H., & Kuzmin, S. L. (2000). Quantitative evidence for global amphibian population declines. *Nature*, 404(6779), 752–755. <https://doi.org/https://doi.org/10.1038/35008052>

Intergovernmental Panel on Climate Change. (2015). *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. IPCC, Switzerland.

IPBES. (2018). IPBES-6 Plenary. Retrieved November 2, 2018, from

<https://www.ipbes.net/event/ipbes-6-plenary>

IUCN. (2012). *IUCN Red List Categories and Criteria: Version 3.1. Second edition*. Gland, Switzerland and Cambridge, UK.

Kats, L. B., & Ferrer, R. P. (2003). Alien predators and amphibian declines: Review of two decades of science and the transition to conservation. *Diversity and Distributions*, 9(2), 99–110. <https://doi.org/10.1046/j.1472-4642.2003.00013.x>

Kéry, M. (2010). *Introduction to WinBUGS for ecologists: A Bayesian approach to regression, ANOVA, mixed models and related analyses. 1st Edition*.

Kyck, M., Kaufmann, P. H., & Lindner, R. (2017). Differing long term trends for two common amphibian species (*Bufo bufo* and *Rana temporaria*) in alpine landscapes of Salzburg, Austria. *PLoS ONE*, 12(11), 1–17.

<https://doi.org/10.1371/journal.pone.0187148>

Latombe, G., Pyšek, P., Jeschke, J. M., Blackburn, T. M., Bacher, S., Capinha, C., ...

McGeoch, M. A. (2017). A vision for global monitoring of biological invasions.

Biological Conservation, 213, 295–308. <https://doi.org/10.1016/j.biocon.2016.06.013>

Liu, C., White, M., & Newell, G. (2011). Measuring and comparing the accuracy of species distribution models with presence-absence data. *Ecography*, 34(2), 232–243.

<https://doi.org/10.1111/j.1600-0587.2010.06354.x>

Mantyka-Pringle, C. S., Martin, T. G., & Rhodes, J. R. (2012). Interactions between climate and habitat loss effects on biodiversity: A systematic review and meta-analysis. *Global Change Biology*, 18(4), 1239–1252. <https://doi.org/10.1111/j.1365-2486.2011.02593.x>

Mendenhall, C. D., Sekercioglu, C. H., Oviedo Brenes, F., Ehrlich, P. R., & Daily, G. C.

(2011). Predictive model for sustaining biodiversity in tropical countryside. *Proceedings of the National Academy of Sciences*, 108(39), 16313–16316.

<https://doi.org/10.1073/pnas.1111687108>

Menzel, A., Sparks, T. H., Estrella, N., Koch, E., Aaasa, A., Ahas, R., ... Zust, A. (2006).

European phenological response to climate change matches the warming pattern. *Global Change Biology*, *12*(10), 1969–1976. <https://doi.org/10.1111/j.1365-2486.2006.01193.x>

Muths, E., Chambert, T., Schmidt, B. R., Miller, D. A. W., Hossack, B. R., Joly, P., ... Grant,

E. H. C. (2017). Heterogeneous responses of temperate-zone amphibian populations to climate change complicates conservation planning. *Scientific Reports*, *7*, 17102.

<https://doi.org/10.1038/s41598-017-17105-7>

Northrup, J. M., Rivers, J. W., Yang, Z., & Betts, M. G. (2019). Synergistic effects of climate

and land-use change influence broad-scale avian population declines. *Global Change Biology*, *25*(5), 1561–1575. <https://doi.org/10.1111/gcb.14571>

Orme, D., Freckleton, R., Thomas, G., Petzoldt, T., Fritz, S., Isaac, N., & Pearse, W. (2018).

caper: Comparative Analyses of Phylogenetics and Evolution in R. *R Package Version 1.0.1*. Retrieved from <https://cran.r-project.org/package=caper>

Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J. K., Thomas, C. D., Descimon, H., ...

Warren, M. (1999). Poleward shifts in geographic ranges of butterfly species associated with regional warming. *Nature*, *399*(6736), 579–583.

<https://doi.org/https://doi.org/10.1038/21181>

Petrovan, S. O., & Schmidt, B. R. (2016). Volunteer conservation action data reveals large-

scale and long-term negative population trends of a widespread amphibian, the common toad (*Bufo bufo*). *PLoS ONE*, *11*(10), e0161943.

<https://doi.org/10.1371/journal.pone.0161943>

Pysek, P., Jarosik, V., Hulme, P. E., Kuhn, I., Wild, J., Arianoutsou, M., ... Winter, M.

(2010). Disentangling the role of environmental and human pressures on biological invasions across Europe. *Proceedings of the National Academy of Sciences*, *107*(27),

12157–12162. <https://doi.org/10.1073/pnas.1002314107>

Quinn, L. D., Schooler, S. S., & Van Klinken, R. D. (2011). Effects of land use and environment on alien and native macrophytes: Lessons from a large-scale survey of Australian rivers. *Diversity and Distributions*, *17*(1), 132–143. <https://doi.org/10.1111/j.1472-4642.2010.00726.x>

R Core Team. (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Retrieved from <https://www.r-project.org/>

Rondinini, C., di Marco, M., Chiozza, F., Santulli, G., Baisero, D., Visconti, P., ... Boitani, L. (2011). Global habitat suitability models of terrestrial mammals. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1578), 2633–2641. <https://doi.org/10.1098/rstb.2011.0113>

Roquet, C., Lavergne, S., & Thuiller, W. (2014). One Tree to Link Them All: A Phylogenetic Dataset for the European Tetrapoda. *PLOS Currents Tree of Life*, *6*(Aug 8), 1–16. <https://doi.org/10.1371/currents.tol.5102670fff8aa5c918e78f5592790e48>

Roser, L. G., Ferreyra, L. I., Saidman, B. O., & Vilardi, J. C. (2017). EcoGenetics: An R package for the management and exploratory analysis of spatial data in landscape genetics. *Molecular Ecology Resources*, *17*(6), e241–e250. <https://doi.org/10.1111/1755-0998.12697>

Saino, N., Ambrosini, R., Rubolini, D., Von Hardenberg, J., Provenzale, A., Hüppop, K., ... Sokolov, L. (2011). Climate warming, ecological mismatch at arrival and population decline in migratory birds. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1707), 835–842. <https://doi.org/10.1098/rspb.2010.1778>

Santini, L., Isaac, N. J. B., & Ficetola, G. F. (2018). TetraDENSITY: A database of population density estimates in terrestrial vertebrates. *Global Ecology and*

Biogeography, 27(7), 787–791. <https://doi.org/10.1111/geb.12756>

Seebacher, F., White, C. R., & Franklin, C. E. (2015). Physiological plasticity increases resilience of ectothermic animals to climate change. *Nature Climate Change*, 5(1), 61–66. <https://doi.org/10.1038/nclimate2457>

Seebens, H., Blackburn, T. M., Dyer, E. E., Genovesi, P., Hulme, P. E., Jeschke, J. M., ... Essl, F. (2017). No saturation in the accumulation of alien species worldwide. *Nature Communications*, 8, 14435. <https://doi.org/10.1038/ncomms14435>

Seibold, S., Bässler, C., Brandl, R., Fahrig, L., Förster, B., Heurich, M., ... Müller, J. (2017). An experimental test of the habitat-amount hypothesis for saproxylic beetles in a forested region. *Ecology*, 98(6), 1613–1622. <https://doi.org/10.1002/ecy.1819>

Sillero, N., Campos, J., Bonardi, A., Corti, C., Creemers, R., Crochet, P. A., ... Vences, M. (2014). Updated distribution and biogeography of amphibians and reptiles of Europe. *Amphibia-Reptilia*, 35(1), 1–31. <https://doi.org/10.1163/15685381-00002935>

Smith, M. A., & Green, D. M. (2005). Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations? *Ecography*, 28(1), 110–128. <https://doi.org/10.1111/j.0906-7590.2005.04042.x>

Stuart, S. N., Hoffmann, M., Chanson, J. S., Cox, N. A., Berridge, R. J., & Young, B. E. (Eds.). (2008). *Threatened Amphibians of the World*. Barcelona, Spain; IUCN, Gland, Switzerland; Conservation International, Arlington, Virginia, USA.

Thuiller, W., Georges, D., Engler, R., & Breiner, F. (2016). biomod2: Ensemble Platform for Species Distribution Modeling. *R Package Version 3.3-7*. Retrieved from <https://cran.r-project.org/package=biomod2>

Thuiller, W., Lavergne, S., Roquet, C., Boulangeat, I., Lafourcade, B., & Araujo, M. B. (2011). Consequences of climate change on the tree of life in Europe. *Nature*, 470(7335), 531–534. <https://doi.org/10.1038/nature09705>

Todd, B., Willson, J., & Gibbons, J. (2010). The Global Status of Reptiles and Causes of Their Decline. In D. W. Sparling, G. Linder, C. A. Bishop, & S. Krest (Eds.), *Ecotoxicology of Amphibians and Reptiles, Second Edition* (pp. 47–67). CRC Press, Boca Raton, USA.

Tracewski, Ł., Butchart, S. H. M., Di Marco, M., Ficetola, G. F., Rondinini, C., Symes, A., ... Buchanan, G. M. (2016). Toward quantification of the impact of 21st-century deforestation on the extinction risk of terrestrial vertebrates. *Conservation Biology*, 30(5), 1070–1079. <https://doi.org/10.1111/cobi.12715>

Vilà, M., Basnou, C., Pyšek, P., Josefsson, M., Genovesi, P., Gollasch, S., ... Zagatti, P. (2010). How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. *Frontiers in Ecology and the Environment*, 8(3), 135–144. <https://doi.org/10.1890/080083>

Wielstra, B., Canestrelli, D., Cvijanović, M., Denoël, M., Fijarczyk, A., Jablonski, D., ... Babik, W. (2018). The distributions of the six species constituting the smooth newt species complex (*Lissotriton vulgaris* sensu lato and *L. montandoni*) – an addition to the New Atlas of Amphibians and Reptiles of Europe. *Amphibia-Reptilia*, 39(2), 252–259. <https://doi.org/10.1163/15685381-17000128>

Wielstra, B., Sillero, N., Vörös, J., & Arntzen, J. W. (2014). The distribution of the crested and marbled newt species (Amphibia: Salamandridae: Triturus) - an addition to the New Atlas of Amphibians and Reptiles of Europe. *Amphibia-Reptilia*, 35(3), 376–381. <https://doi.org/10.1163/15685381-00002960>

Figure captions:

FIGURE 1 General framework of the study. We assessed the relative importance of multiple global change drivers on population trends of European amphibians and reptiles.

FIGURE 2 Average population trend of species, with 95% credible intervals. Point size is proportional to the number of populations considered in this study. Amphibians are shown in green, reptiles in brown.

FIGURE 3 Density plots of the posterior distribution for the relationships between trends of 705 populations of amphibians and reptiles and the candidate drivers (from top to bottom: trend of climatic suitability, richness of alien species, initial habitat availability, habitat change through time, interaction between initial habitat availability and richness of alien species). Thick vertical lines represent the average effect size, outer lines represent the 95% credible interval, inner colors represent the 75% credible interval. The y-axis indicates the frequency of posterior distributions and it is consistent for the five plots.

FIGURE 4 Relationship between the four independent variables and population trends, as predicted by the full model. In each plot the dark line shows the predicted value of population trends (Fisher's Z) and the shaded area indicates the 95% credible interval.

FIGURE 5 Interaction between habitat availability and alien species. Plots show the relationship between the richness of alien species and the population trends predicted by the full model at different levels of habitat availability: a) habitat availability = 5%, b) habitat availability = 30%, c) habitat availability = 70%. In each plot the dark line shows the predicted value of population trends and the shaded area indicates the 95% credible interval.

FIGURE 6 Density plots of the posterior distribution for the relationships between population trends and the candidate drivers (from top to bottom: trend of climatic suitability, richness of alien species, initial habitat availability, habitat change through time, interaction between initial habitat availability and richness of alien species), considering a) common toad populations only, b) common frog populations only and c) all data except for common toad and common frog populations. Thick vertical lines represent the average effect size, outer lines represent the 95% credible interval, inner colors represent the 75% credible interval. Arrows represent the mean effect size of the analysis including all the species. The y-axis indicates the frequency of posterior distributions and it is consistent for all the plots.









