

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

3

4 **Running title:** Continental determinants of population trends

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17 **Abstract**

18

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

39

40 **KEYWORDS**

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

## 43 INTRODUCTION

44 Biodiversity is declining at an unprecedented rate (Butchart et al., 2005; IPBES, 2018).  
45 Understanding the main causes of these changes is a major endeavor for the scientific  
46 community, should we want to anticipate and mitigate future impacts. Climate change, land-  
47 use change, spread of alien species, atmospheric CO<sub>2</sub> increase, anthropogenic nitrogen  
48 deposition, and spread of disease are all drivers known to strongly influence the structure and  
49 distribution of biodiversity (Bateman et al., 2016; Gallardo, Clavero, Sánchez, & Vilà, 2016;  
50 Tracewski et al., 2016). These drivers do not affect biodiversity independently, rather they act  
51 in synergistic or antagonistic ways. For instance, in a global study comprising multiple taxa,  
52 Mantyka-Pringle, Martin, & Rhodes (2012) found that the negative effects of habitat loss and  
53 fragmentation on species abundance and diversity were magnified in areas where average  
54 rainfall has decreased in the past. Multi-variable studies, taking into account more than one  
55 driver of global change, are thus essential to disentangle the relative importance of different  
56 threats (Didham, Tylianakis, Gemmill, Rand, & Ewers, 2007). Nevertheless, a large part of  
57 past global change studies focused on one single driver, perhaps because it is difficult to  
58 retrieve standardized data across broad spatial extents, or because integrating multiple factors  
59 can result in overly complex models. In the last years, attention is growing toward the  
60 importance of disentangling the effects of multiple drivers (e.g. Campbell Grant et al., 2016;  
61 Northrup, Rivers, Yang, & Betts, 2019), because knowing the relative impact of different  
62 drivers on the different biodiversity facets is essential to identify conservation priorities and  
63 management strategies (Brook, Sodhi, & Bradshaw, 2008).

64 Global change drivers impact populations in multiple ways and can, for instance,  
65 impact morphology, breeding success, survival, and abundance (Ficetola et al., 2016; Ficetola  
66 & Maiorano, 2016; Menzel et al., 2006; Saino et al., 2011). Trends of population abundance  
67 are connected to extinction risk and are commonly used to evaluate the conservation status of

68 species, thus population trends are one of the key demographic parameters to assess the  
69 effects of global change drivers on biodiversity (Flesch, Rosen, & Holm, 2017; IUCN, 2012).  
70 However, studies on population abundance are generally local, thus limiting the possibility of  
71 drawing broad-scale, generalizable inference. Quantitative analyses of the results of multiple  
72 studies (meta-regressions) can alleviate this issue, as they allow to summarize information  
73 from a broad range of sources. Meta-regressions showed excellent performance in the analysis  
74 of multiple demographic time series and helped to obtain general inference on patterns of  
75 global change (Bonardi et al., 2011; Gurevitch, Koricheva, Nakagawa, & Stewart, 2018;  
76 Hadfield & Nakagawa, 2010).

77 Amphibians and reptiles are two vertebrate groups particularly threatened by global  
78 changes (Böhm et al., 2013; Hoffmann et al., 2010). Amphibian populations are declining at a  
79 greater pace than the other vertebrates, and their decline is determined by the combined  
80 effects of multiple threats, notably land-use change, climate change, and alien species (Hof,  
81 Araújo, Jetz, & Rahbek, 2011; Stuart et al., 2008). While the global reptile assessment has not  
82 been completed yet, land-use change, climate change, and alien species are listed as major  
83 threats also for reptiles (Todd, Willson, & Gibbons, 2010). Furthermore, climate change is  
84 expected to have a particularly strong impact on ectothermic vertebrates, because it can affect  
85 essential life-history processes that depend on the characteristics of the environment  
86 (Buckley, Hurlbert, & Jetz, 2012; Flesch et al., 2017). Finally, the response of local  
87 populations to global drivers vary across taxa and geographic areas. It is thus important to  
88 assess whether different species show heterogeneous responses, in order to understand the  
89 generality of patterns of change (Muths et al., 2017).

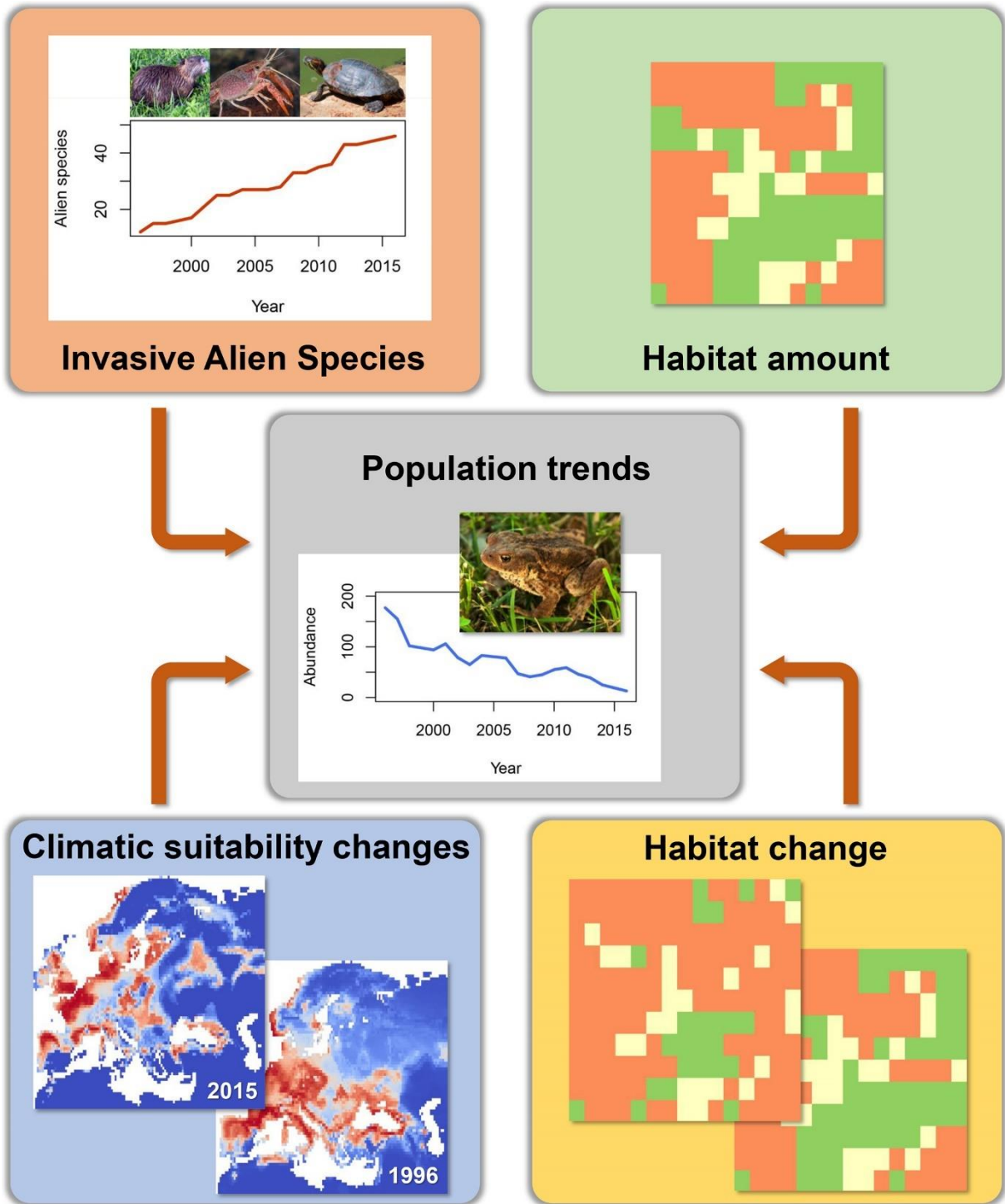
90 In this study, we used meta-regression to quantify the relative importance of different  
91 global change drivers on population trends of European amphibians and reptiles (Figure 1). In  
92 particular, we tested four hypotheses:

- 93 i) *Population trends are determined by changes in climatic suitability.* Climatic  
94 suitability is a measure of how much the climate of an area is suitable for a  
95 particular species (Araújo, Alagador, Cabeza, Nogués-Bravo, & Thuiller, 2011).  
96 Suitability can provide a better measure of the impact of climate change compared  
97 to climatic velocity since it accounts for the geographic position of a population.  
98 For instance, in a situation of poleward shift of the geographic range of a species,  
99 populations nearest to the pole can gain suitability, while the farthest ones often  
100 lose suitable space (Parmesan et al., 1999). We thus predict that a decrease in  
101 climatic suitability negatively affects population trends and vice versa;
- 102 ii) *Population trends are negatively influenced by alien species.* Alien species exert  
103 multiple impacts on native biodiversity (Gallardo et al., 2016). Negative impacts  
104 increase with the abundance and richness of alien species (Vilà et al., 2010), thus  
105 we predict a negative relationship between the richness of alien species and  
106 population trends;
- 107 iii) *Population trends are determined by habitat availability.* The amount of available  
108 habitat in the landscape is a key parameter influencing species distribution and  
109 population dynamics (Flesch, 2017; Seibold et al., 2017). For example, a low  
110 amount of suitable habitat leads to reduced carrying capacity and vital rates, and to  
111 a decrease in the amount of source populations that could provide migrants from  
112 the surrounding landscape (Hodgson, Thomas, Wintle, & Moilanen, 2009).  
113 Because these processes can affect the long-term dynamics of populations and  
114 their probability of persistence, we predict a positive relationship between the  
115 amount of suitable habitat and population trends;
- 116 iv) *Population trends are determined by changes in habitat availability.* Land-use has  
117 undergone heavy changes in the last decades, with the conversion of natural

118           vegetation to urban or agricultural land-use in some areas and forest gain in others  
119           (Hansen et al., 2013). Habitat loss is considered the main cause of decline for the  
120           vast majority of vertebrates, hence we predict a negative relationship between the  
121           decrease in habitat availability and population trends (Hoffmann et al., 2010).

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

126



127

128

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



131 **MATERIALS AND METHODS**

132

133 **Abundance data**

134 The study area included Europe plus Anatolia, with eastern limit in the Ural Mountains and  
135 the Caucasus. We performed a literature search in February 2017. Published data on  
136 abundance for reptile and amphibian species were collected by searching in the ISI Web of  
137 Science for keywords “demography”, “population”, and “decline”, associated with “reptile”,  
138 and “amphibian” keywords. We reviewed the text and selected data of populations with at  
139 least 4 years of sampling. Shorter time series were discarded to ensure more relevant  
140 estimates of temporal trends. We also analyzed the data associated to the Houlahan, Findlay,  
141 Schmidt, Meyer, & Kuzmin (2000) paper on amphibian population trends, and retrieved all  
142 the time series from the study area, for which enough information was available to reconstruct  
143 the population locality. We also added two unpublished population times series for which we  
144 directly collected data for the period 2010-2016 (Manenti R., unpublished data). We obtained  
145 a total of 16 studies, comprising time-series for 843 populations of 17 different species (see  
146 Supporting Information Table S1 for a complete list of references).

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

154

155 **Climatic suitability changes**

156 We used species distribution models (SDM) to assess changes in climatic suitability through  
157 time for each population. To build SDM, species presence was derived from the European  
158 Herpetological Atlas (Sillero et al., 2014), at a resolution of 0.5°. All the frogs of the  
159 hybridogenic complex *Pelophylax* spp. were modeled as a single taxon; the distribution range  
160 of the grass snake *Natrix natrix* extends outside the boundaries of the European  
161 Herpetological Atlas, thus presences for this species were integrated with points obtained  
162 from the global biodiversity information facility (<https://www.gbif.org/>); The distribution  
163 records of newts (*Triturus cristatus* and *Lissotriton vulgaris*) were taken from Wielstra et al.,  
164 (2018) and Wielstra, Sillero, Vörös, & Arntzen (2014).

165 SDM were calibrated on the climatic conditions in the last 51 years (averaged from 1966 to  
166 2016), obtained from an updated version of the Climatic Research Unit dataset (Harris, Jones,  
167 Osborn, & Lister, 2014) (CRU TS v. 4.01), which reports monthly values of precipitation and  
168 temperature for the time-period 1901-2016. We used four climatic variables: mean annual  
169 temperature, total annual precipitation, annual temperature standard deviation, annual  
170 precipitation coefficient of variation. Minimum annual temperature and maximum annual  
171 temperature, and minimum / maximum temperature during breeding seasons, are additional  
172 variables important for tolerance and activity of ectotherms but are strongly correlated to  
173 mean temperature and standard deviation (Appendix S1). We thus also re-ran the SDMs using  
174 min/max values instead of mean and standard deviation of temperature and for subsequent  
175 analyses we used models with higher performance values (see results). Models were built  
176 within the biomod2 R package (Thuiller, Georges, Engler, & Breiner, 2016), running an  
177 ensemble of the following models: boosted regression trees, generalized additive models,  
178 classification tree analysis, multivariate adaptive regression splines, and random forests. For  
179 each species, we selected 3,000 pseudo-absence points within a radius of 1,000 km from the  
180 species distribution range. To get a meaningful evaluation of the models and to avoid over-

181 fitting, models were repeated five times to perform cross-validation, and for each run we  
182 used a random sample of 67% of the initial occurrence data to calibrate the models and the  
183 remaining 33% for evaluation. Models performance was assessed using the True Skill  
184 Statistic (TSS) and the Area Under the receiver operating characteristic Curve (AUC) (Liu,  
185 White, & Newell, 2011). Finally, we obtained an ensemble model through a weighted sum of  
186 the probability of occurrence, proportional to the cross-validated TSS.

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

196

### 197 **Alien species**

198 The richness of alien species was obtained from the Global Alien Species First Record  
199 Database (Seebens et al., 2017), which reports the first year of detection of alien species at the  
200 regional level resolution. At this scale, alien species richness can be a good proxy to measure  
201 negative effects on native biodiversity, because the number of impacts is higher in areas with  
202 more alien species (Latombe et al., 2017; Vilà et al., 2010). For each population, we extracted  
203 the total number of alien species starting from 1901 to the last year of sampling by summing  
204 the total number of vertebrates and crustaceans, as these taxa are known to have a major  
205 impact on amphibians and reptiles (Ficetola et al., 2011; Kats & Ferrer, 2003). The database

206 reports the occurrences of alien species at the regional level, but the considered regions had a  
207 coarser resolution than the localities used for our analyses. Therefore, the number of alien  
208 species obtained using this approach probably overestimates the actual number of alien  
209 species at a given locality. Nevertheless, the Global Alien Species First Record Database has  
210 the advantage that the alien species records are temporally explicit, thus allowing analyses of  
211 temporal processes. Furthermore, the number of alien species is strongly related to economic  
212 and political factors of territories, thus we expect a strong correlation between regional-level  
213 and local abundance of alien species (Pysek et al., 2010). For each time series, the total  
214 number of alien species from the year 1901 to the last year of the time series was considered  
215 as independent variable to measure the effect of alien species.

216

### 217 **Habitat availability and habitat changes**

218 For each species, we identified a list of suitable land-cover classes in order to calculate the  
219 extent of suitable habitat (ESH) by integrating the habitat preferences obtained from the  
220 IUCN Red List with land-use information (see Table S2 for details; Rondinini et al., 2011).  
221 Land-use information was obtained from the time series of the European Space Agency  
222 Climate Change Initiative Land Cover project (<https://www.esa-landcover-cci.org/>). This map  
223 is available from 1992 and does not cover the whole 1972-2016 period. Hence, analyses  
224 which considered land use variables were limited to populations sampled in the period 1992-  
225 2016 ( $N = 705$  populations). Previous analyses showed that ESH maps, built on the basis of  
226 the occurrence of suitable land-use classes, allow a good representation of the actual habitat  
227 that can be exploited by species, and provide useful information to estimate species trends  
228 (Ficetola, Rondinini, Bonardi, Baisero, & Padoa-schioppa, 2015; Rondinini et al., 2011;  
229 Tracewski et al., 2016). We used ESH to calculate the habitat availability at the beginning of  
230 the study period, and the trend of suitable habitat during the study period. Habitat variables

231 were calculated within the  $9 \times 9$  km cell surrounding each population; we selected this  
232 resolution because about 90% of amphibian species have a maximum dispersal ability of ~4.5  
233 km (Smith & Green, 2005), and because it matched well the accuracy of population localities  
234 in our dataset.

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

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

245

## 246 **Statistical analyses**

247 We used meta-regression to identify the most influential drivers of population trends  
248 (Gurevitch et al., 2018). Global change drivers were related to population trends through  
249 Bayesian generalized linear mixed models, using the effect size of population trends (Fisher's  
250  $Z$ ) as the dependent variable. First of all, the overall trend averaged across all the populations  
251 was assessed by performing a model of the mean (i.e. a meta-regression model including the  
252 intercept and without independent variables) (Kéry, 2010). We also ran a separate model of  
253 the mean for each species, in order to assess the average species trend. Then, four separate  
254 meta-regressions were run to assess the single-variable relationships between population  
255 trends at each locality and: (i) trend of climatic suitability, (ii) richness of alien species, (iii)

256 habitat availability at the beginning of the period, (iv) trend of habitat availability (Figure 1).  
257 Independent variables used, and time period considered for each single-variable model are  
258 described in Table S3. Finally, we performed a multi-variable model including all four  
259 independent variables, for the period 1992-2016. We also tested pairwise interactions between  
260 the four variables and, in the final model, we considered only interactions with 95% credible  
261 intervals (CIs) not overlapping zero. The biological rationale of tested interactions is listed in  
262 Table S4. Our multi-variable meta-regression included data from all the species, in order to  
263 evaluate the overall pattern. Subsequently, to assess if the effects were consistent across  
264 species, we re-run the meta-regression separately for the two commonest species (the  
265 common toad *Bufo bufo* and the common frog *Rana temporaria*) and then considering all the  
266 species except common toad and common frog.

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

281 correlation. To test the phylogenetic signal, we used a phylogeny tree including all the 17  
282 species, derived from the phylogenetic tree of the European tetrapods (Roquet, Lavergne, &  
283 Thuiller, 2014).

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

290

## 291 **RESULTS**

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

295

### 296 **General trend**

297 Out of the 843 populations, 458 (54%) showed negative population trends, 383 (45%)  
298 positive trends and two remained stable ( $|r| < 0.01$ ). The averaged population trend (effect  
299 size), obtained from the models of the mean of the different species, was negative for ten  
300 species and positive for seven species (Figure 2). 95% CIs of the estimates of population  
301 trends did not overlap zero in seven out of 17 species (41%), however, there were strong  
302 differences of trends across populations (Figure 2). The population trend averaged across the  
303 populations of all species, was negative but credible intervals overlapped zero (mean = -  
304 0.084; 95% CI = -0.284 / 0.152).

305

## 306 **Single-variable relationships**

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

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

320

321 *Alien species.* The average number of alien species per region was 45 (SD = 24), and  
322 population trends declined in regions with more alien species. For the period 1972-2016, the  
323 95% CIs of this relationship slightly overlapped zero, while 90% CIs did not (effect size = -  
324 0.061; 95% CI = -0.125 / 0.004; 90% CI = -0.112 / -0.008). When we limited analyses to  
325 1992-2016, the effect size was significantly lower than zero (effect size = -0.093, 95% CI = -  
326 0.166 / -0.022).

327

328 *Habitat availability.* Average cover of suitable habitat was 29% (SD = 20%), and population  
329 trends were more positive in landscapes with high habitat availability (effect size = 0.069;  
330 95% CI = 0.002 / 0.130; Table S7a).



331

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

337

### 338 **Multi-variable analysis**

339 Out of the six possible paired interactions among the four candidate drivers, only the  
340 interaction between the richness of alien species and the initial habitat availability showed  
341 95% CIs not overlapping zero and was included in the meta-regression analysis including all  
342 the predictors and all the populations (full model; N = 705 populations). The effect sizes of  
343 predictors were nearly identical between the models and without the interaction (Table S7b,  
344 S7c).

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

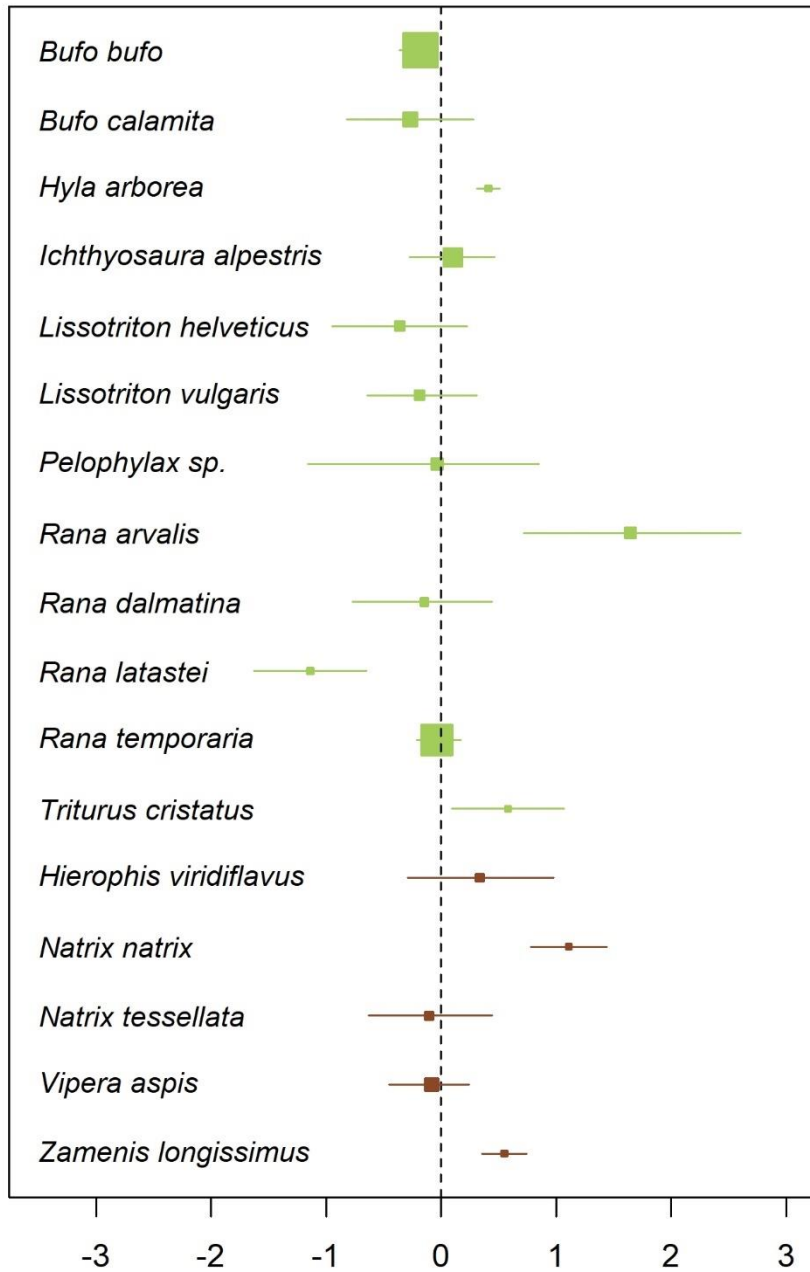
355 autocorrelation (Moran's  $I = 0.001$ ; 95% CIs =  $-0.009 - 0.010$ ; Pagel's Lambda = 0; 95% CIs  
356 =  $0 - 0.503$ ).

357

### 358 **Robustness to interspecific variation**

359 When we repeated meta-regression including only common toad populations, results were  
360 generally consistent with the full analysis. Common toad population trends were more  
361 negative in sites with more alien species, were positively related to the trend of climatic  
362 suitability and were more positive in landscapes with higher habitat availability, even though  
363 95% intervals were broader than in the analysis including all the species. Conversely, trends  
364 were unrelated to habitat change and to the interaction between habitat availability and  
365 richness of alien species (Figure 6a). Common frog populations showed a different pattern  
366 compared to the full analysis, as population trends only showed a weak positive relationship  
367 with habitat change (Figure 6b).

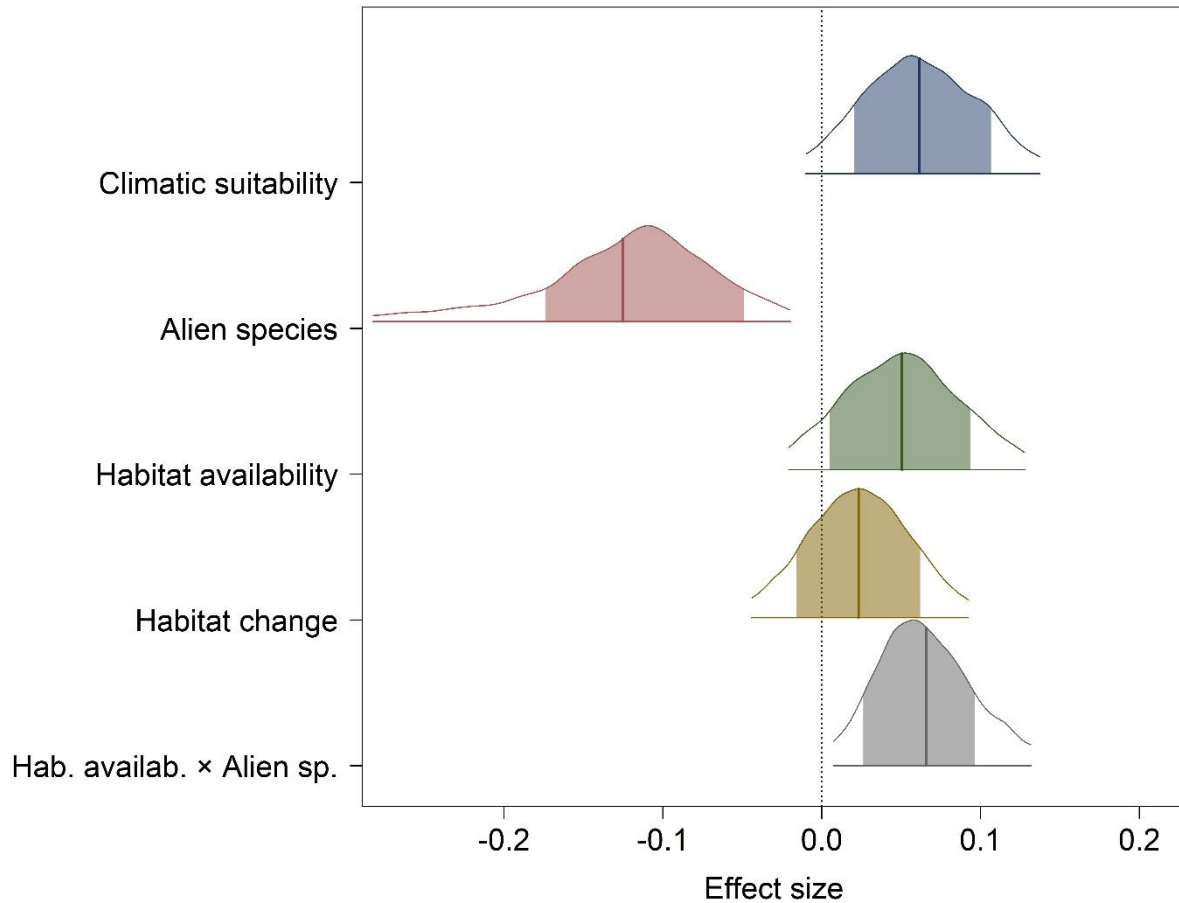
368 Results remained partially consistent when we repeated analyses excluding the two  
369 most common species (the common toad and the common frog), even though credible  
370 intervals were much broader than in the full analysis. Population trends were positively  
371 related to climatic suitability trend and negatively related to alien species. While the effect  
372 size of habitat availability was close to zero, this analysis confirmed the interaction between  
373 habitat availability and richness of alien species (Figure 6c). Moreover, in this analysis we  
374 observed a strong positive effect of habitat changes, indicating that population trends were  
375 more positive in landscapes where the extent of suitable habitat increased through time (Figure  
376 6c).



377

378

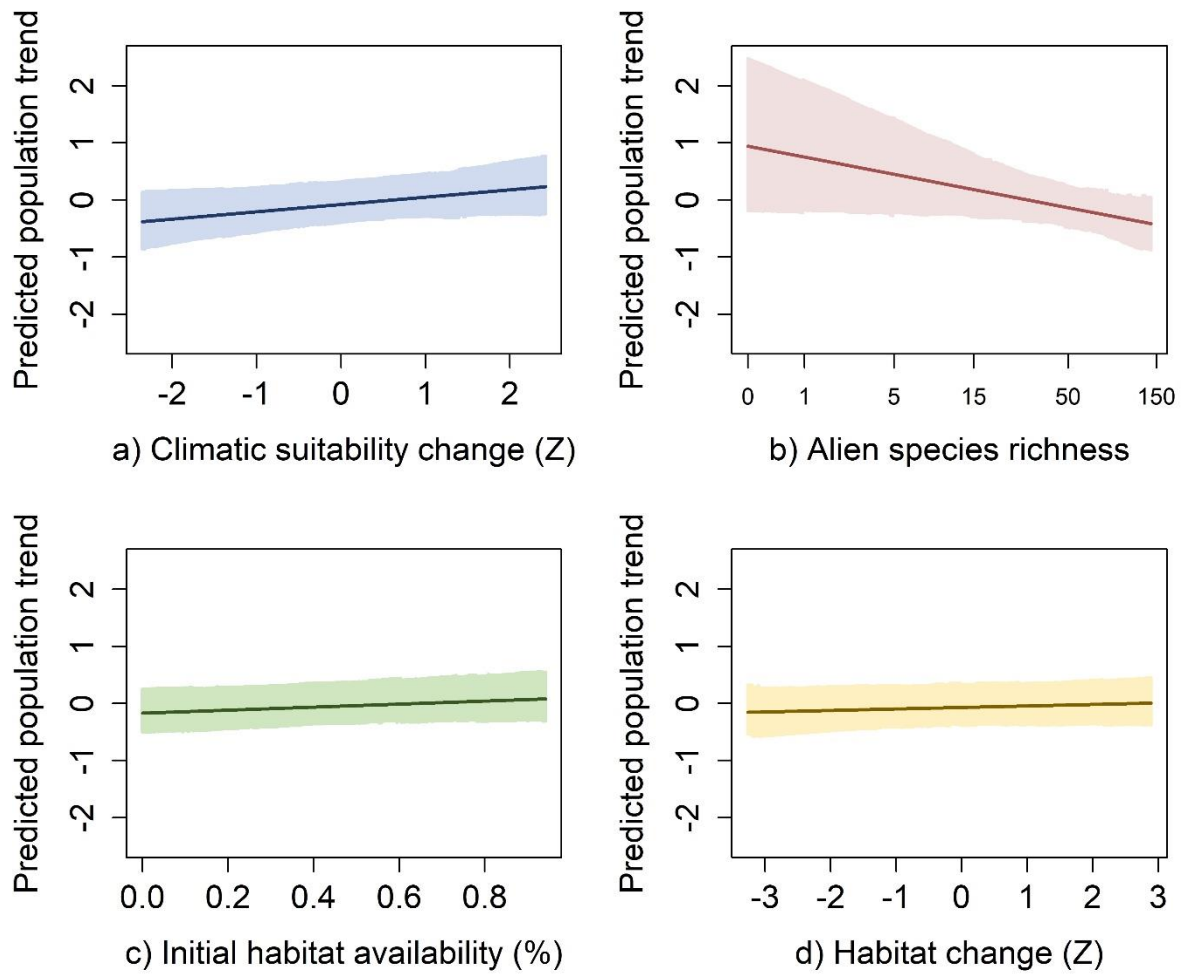
379 **FIGURE 2** Average population trend of species, with 95% credible intervals. Point size is  
 380 proportional to the number of populations considered in this study. Amphibians are shown in  
 381 green, reptiles in brown.



382

383

384 **FIGURE 3** Density plots of the posterior distribution for the relationships between trends of  
 385 705 populations of amphibians and reptiles and the candidate drivers (from top to bottom:  
 386 trend of climatic suitability, richness of alien species, initial habitat availability, habitat  
 387 change through time, interaction between initial habitat availability and richness of alien  
 388 species). Thick vertical lines represent the average effect size, outer lines represent the 95%  
 389 credible interval, inner colors represent the 75% credible interval. The y-axis indicates the  
 390 frequency of posterior distributions and it is consistent for the five plots.

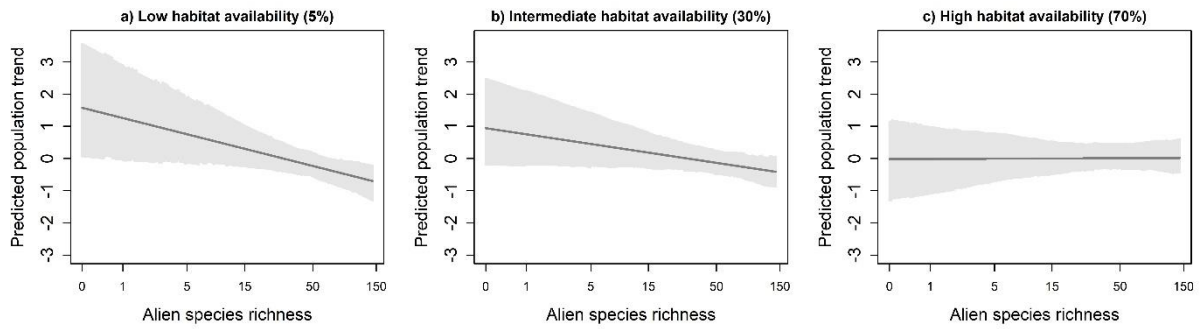


391

392

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

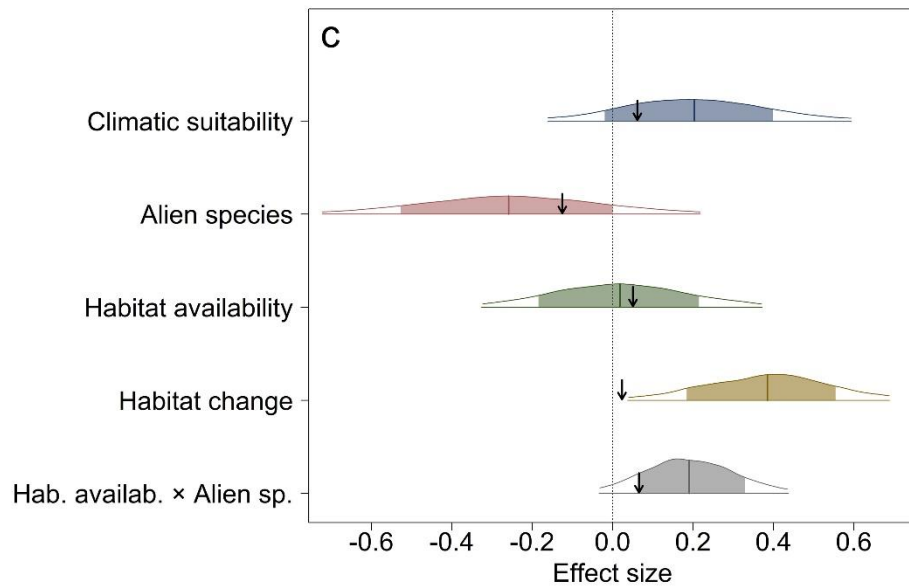
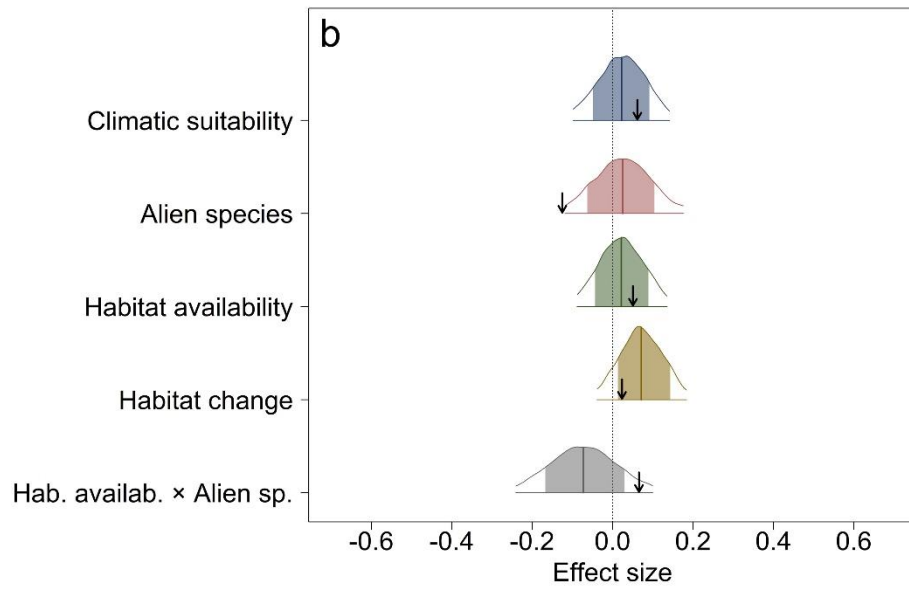
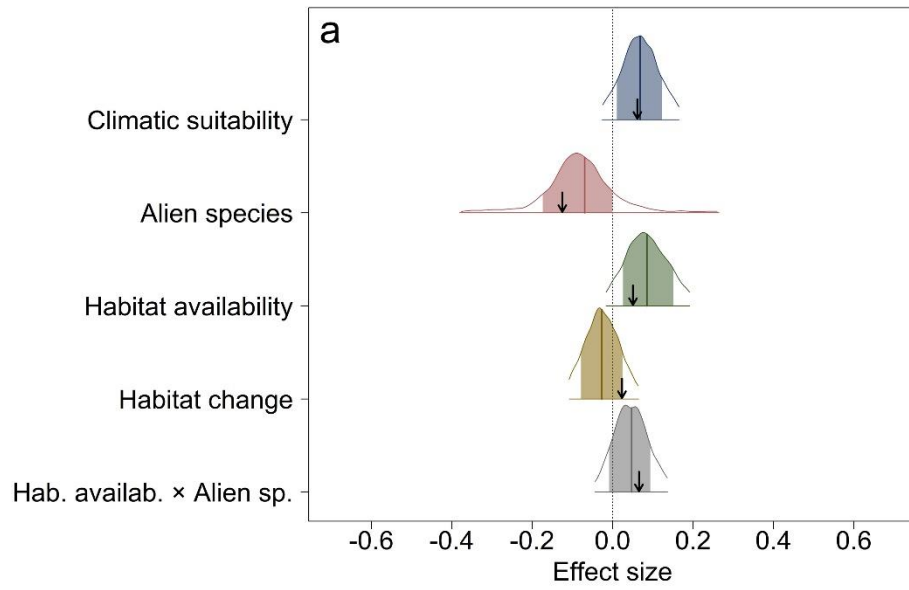
396



397

398

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



405

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

415



416 **DISCUSSION**

417

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

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

441 taxa and even within species. This confirms the importance of studies including species with  
442 various ecological tolerances, in order to disentangle the heterogeneous effects of global  
443 changes on natural populations.

444 Global change scenarios suggest that climate change will have a growing impact on  
445 biodiversity (Intergovernmental Panel on Climate Change, 2015). However, the impact of  
446 climate change can be heterogeneous among species and even among populations within a  
447 given species. For instance, in the northern hemisphere, climatic warming can determine the  
448 extinction of populations in southern portions of species ranges, while can have positive  
449 effects on northern populations (Parmesan et al., 1999). To assess the impact of climate  
450 change it is thus important to develop appropriate measures of how climatic variation  
451 influences populations in different areas of the species' range. Climatic suitability can provide  
452 information on the actual effect of climatic variation on populations because it considers the  
453 differences that can occur across distant geographic areas. Therefore, in our analyses we  
454 considered climatic suitability instead of raw temperature/precipitation change. Despite 95%  
455 CIs slightly overlapping zero, the effects of suitability changes were consistent with our  
456 predictions (Figures 3, 4 and 6) with negative changes in climatic suitability corresponding to  
457 negative population trends. Studies relating the trends of amphibians and reptiles to climate  
458 change obtained mixed results. For instance, Ficetola and Maiorano (2016) found that  
459 changes in precipitation can have a significant impact on amphibian trends, but did not detect  
460 a clear effect of changes in temperature. Conversely, when using climatic suitability, we  
461 found a consistent pattern across species (Figures 3 and 6). Changes in climatic suitability are  
462 often used to explore potential impacts of future climate change on biodiversity (Araújo et al.,  
463 2011; Thuiller et al., 2011), while fewer studies have used this approach to understand the  
464 impact of changes occurring in the past (e.g. Bateman et al., 2016; Fouquet, Ficetola, Haigh,  
465 & Gemmell, 2010). Our analysis suggests that suitability can provide a measure of the impact

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

471         While the effects of alien species and climate were generally consistent across taxa,  
472 the effects of habitat availability and habitat change were more complex. Even though habitat  
473 loss is described as the factor threatening the largest number of amphibians and reptiles  
474 (Stuart et al., 2008), relationships between changes in habitat availability and population  
475 trends were only detected in a subset of analyses. Population trends were more positive in  
476 landscapes with more habitat (Table S7a), but the effects of habitat availability were weak  
477 when taking into account also other factors and potential interactions (Figure 3; Table S7b).  
478 Several factors can explain the limited effects of habitat variables. First, a significant  
479 interaction between habitat availability and the richness of alien species indicates that the  
480 impact these two variables can be context dependent, complicating the detection of their  
481 effects. Second, we assessed habitat change on the basis of broad-scale land cover maps,  
482 which do not provide measures of the specific resources and conditions needed by different  
483 species. Obtaining accurate measures of habitats is particularly complex for small vertebrates,  
484 which often exploit specific microhabitats (Ficetola, Lunghi, et al., 2018; Mendenhall,  
485 Sekercioglu, Oviedo Brenes, Ehrlich, & Daily, 2011). For instance, agricultural  
486 mechanization can determine loss of suitable micro-habitats (e.g. hedgerows, ditches) even in  
487 areas with a stable amount of agricultural lands, thus impacting species that can exploit semi-  
488 natural landscapes. Third, average rates of habitat change were extremely low during the  
489 study period (average: ~0.1% / year). Such a limited variation is characteristic of broad areas  
490 of Europe (Figure S3) but reduces the possibility to detect relationships and can explain the

491 weak effect of this driver. Furthermore, population declines often do not occur immediately  
492 after environmental pressures (Dullinger et al., 2013), thus we might experience the legacy of  
493 present anthropogenic pressures in the next decades. Nevertheless, habitat change showed a  
494 clear effect when we removed the commonest species (common toad and common frogs)  
495 from our dataset, with more positive population trends in landscapes where the amount of  
496 suitable habitat increased through time. Common toad and common frog are widespread,  
497 generalist species that can exploit a very wide range of habitats (Table S2), therefore it may  
498 be more difficult detecting their response to habitat change, compared to habitat specialists.  
499 This further stresses the need of monitoring a wide range of species in order to obtain  
500 generalizable information of the effects of global changes on biodiversity loss and highlights  
501 the importance of comparing the responses of both widespread and specialized species.

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

515           Despite the broad temporal and geographic extent, our analyses have some limitations.  
516 Most of the data are from amphibian populations, and one species (the common toad, *Bufo*  
517 *bufo*) accounted for more than half of populations (Table S9). This occurs because the  
518 common toad is one of the most abundant amphibians in Europe and is regularly monitored  
519 by many citizen science programs. Common amphibians have a major role in ecosystem  
520 functioning and nutrient transfer (Beard, Eschtruth, Vogt, Vogt, & Scatena, 2003; Kyek,  
521 Kaufmann, & Lindner, 2017). Several studies have shown negative trends in toad populations  
522 (e.g. Bonardi et al., 2011; Petrovan & Schmidt, 2016) and understanding the factors  
523 underlying a common species decline is extremely important to maintain ecosystem  
524 functioning (Gaston & Fuller, 2008). Alien species and climate change showed a similar  
525 effect across most of the taxa: despite broader credible intervals, effect sizes pointed in the  
526 same direction even if we removed the most common species (Figure 6c), suggesting that  
527 uneven sample size across species did not bias our conclusions. In our dataset we collected  
528 fewer data regarding reptiles than amphibians. This is a recurrent pattern in the herpetological  
529 literature and hampered separate analyses of these taxa. Estimating the abundance of reptiles  
530 is usually harder compared to amphibians, because reptiles often have low detection  
531 probability, and estimating their abundance requires effort-demanding survey methods (e.g.  
532 capture mark recapture instead of repeated counts) (Ficetola, Romano, Salvidio, & Sindaco,  
533 2018). Increasing the monitoring efforts toward reptile populations is urgently required to  
534 better assess the drivers of the decline of this group and guide future conservation efforts.  
535 Finally, our analyses were limited both in space and in time by the availability of population  
536 and land-cover data. Continuous series of land-cover data are only available since 1992, thus  
537 preventing us from assessing the effects of habitat availability during previous periods, when  
538 the velocity of habitat change in Europe was probably stronger than in recent years (Falcucci,  
539 Maiorano, & Boitani, 2007). Furthermore, the majority of our data came from just two

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

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

558

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560

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567

568 **REFERENCES**

569

570 Araújo, M. B., Alagador, D., Cabeza, M., Nogués-Bravo, D., & Thuiller, W. (2011). Climate  
571 change threatens European conservation areas. *Ecology Letters*, *14*(5), 484–492.

572 <https://doi.org/10.1111/j.1461-0248.2011.01610.x>

573 Bateman, B. L., Pidgeon, A. M., Radeloff, V. C., Vanderwal, J., Thogmartin, W. E., Vavrus,

574 S. J., & Heglund, P. J. (2016). The pace of past climate change vs. potential bird

575 distributions and land use in the United States. *Global Change Biology*, *22*(3), 1130–

576 1144. <https://doi.org/10.1111/gcb.13154>

577 Beard, K. H., Eschtruth, A. K., Vogt, K. A., Vogt, D. J., & Scatena, F. N. (2003). The effects

578 of the frog *Eleutherodactylus coqui* on invertebrates and ecosystem processes at two

579 scales in the Luquillo Experimental Forest, Puerto Rico. *Journal of Tropical Ecology*,

580 *19*(6), 607–617. <https://doi.org/10.1017/S0266467403006011>

581 Bivand, R. S., & Rundel, C. (2017). rgeos: Interface to Geometry Engine - Open Source

582 ('GEOS'). *R Package Version 0.3-26*. <https://CRAN.R-Project.Org/Package=rgeos>.

583 Blaustein, A. R., & Kiesecker, J. M. (2002). Complexity in conservation: lessons from the

584 global decline of amphibian populations. *Ecology Letters*, *5*(4), 597–608.

585 Böhm, M., Collen, B., Baillie, J. E. M., Bowles, P., Chanson, J., Cox, N., ... Zug, G. (2013).

586 The conservation status of the world's reptiles. *Biological Conservation*, *157*, 372–385.

587 <https://doi.org/10.1016/j.biocon.2012.07.015>

588 Bonardi, A., Manenti, R., Corbetta, A., Ferri, V., Fiacchini, D., Giovine, G., ... Ficetola, G. F.

589 (2011). Usefulness of volunteer data to measure the large scale decline of “common”

590 toad populations. *Biological Conservation*, *144*(9), 2328–2334.

591 <https://doi.org/10.1016/j.biocon.2011.06.011>

592 Brook, B. W., Sodhi, N. S., & Bradshaw, C. J. A. (2008). Synergies among extinction drivers



593 under global change. *Trends in Ecology and Evolution*, 23(8), 453–460.  
594 <https://doi.org/10.1016/j.tree.2008.03.011>

595 Buckley, L. B., Hurlbert, A. H., & Jetz, W. (2012). Broad-scale ecological implications of  
596 ectothermy and endothermy in changing environments. *Global Ecology and*  
597 *Biogeography*, 21(9), 873–885. <https://doi.org/10.1111/j.1466-8238.2011.00737.x>

598 Butchart, S. H. M., Stattersfield, a J., Baillie, J., Bennun, L. a, Stuart, S. N., Akçakaya, H. R.,  
599 ... Mace, G. M. (2005). Using Red List Indices to measure progress towards the 2010  
600 target and beyond. *Philosophical Transactions of the Royal Society B: Biological*  
601 *Sciences*, 360(1454), 255–268. <https://doi.org/10.1098/rstb.2004.1583>

602 Campbell Grant, E. H., Miller, D. A. W., Schmidt, B. R., Adams, M. J., Amburgey, S. M.,  
603 Chambert, T., ... Muths, E. (2016). Quantitative evidence for the effects of multiple  
604 drivers on continental-scale amphibian declines. *Scientific Reports*, 6, 25625.  
605 <https://doi.org/10.1038/srep25625>

606 del Re, A. C. (2013). compute.es: Compute Effect Sizes. *R Package Version 0.2-2*. URL  
607 <Http://Cran.r-Project.Org/Web/Packages/Compute.Es>.

608 Didham, R. K., Tylianakis, J. M., Gemmill, N. J., Rand, T. A., & Ewers, R. M. (2007).  
609 Interactive effects of habitat modification and species invasion on native species decline.  
610 *Trends in Ecology and Evolution*, 22(9), 489–496.  
611 <https://doi.org/10.1016/j.tree.2007.07.001>

612 Dornelas, M., Antão, L. H., Moyes, F., Bates, A. E., Magurran, A. E., Adam, D., ... Zettler,  
613 M. L. (2018). BioTIME: A database of biodiversity time series for the Anthropocene.  
614 *Global Ecology and Biogeography*, 27(7), 760–786.  
615 <https://doi.org/https://doi.org/10.1111/geb.12729>

616 Dullinger, S., Essl, F., Rabitsch, W., Erb, K.-H., Gingrich, S., Haberl, H., ... Hulme, P. E.  
617 (2013). Europe's other debt crisis caused by the long legacy of future extinctions.

618 *Proceedings of the National Academy of Sciences*, 110(18), 7342–7347.  
619 <https://doi.org/10.1073/pnas.1216303110>

620 Falcucci, A., Maiorano, L., & Boitani, L. (2007). Changes in land-use/land-cover patterns in  
621 Italy and their implications for biodiversity conservation. *Landscape Ecology*, 22(4),  
622 617–631. <https://doi.org/10.1007/s10980-006-9056-4>

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

626 Ficetola, G. F., Lunghi, E., Canedoli, C., Padoa-Schioppa, E., Pennati, R., & Manenti, R.  
627 (2018). Differences between microhabitat and broad-scale patterns of niche evolution in  
628 terrestrial salamanders. *Scientific Reports*, 8, 10575. [https://doi.org/10.1038/s41598-018-](https://doi.org/10.1038/s41598-018-28796-x)  
629 [28796-x](https://doi.org/10.1038/s41598-018-28796-x)

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

633 Ficetola, G. F., Romano, A., Salvidio, S., & Sindaco, R. (2018). Optimizing monitoring  
634 schemes to detect trends in abundance over broad scales. *Animal Conservation*, 21(3),  
635 221–231. <https://doi.org/10.1111/acv.12356>

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

639 Ficetola, G. F., Siesa, M. E., Manenti, R., Bottoni, L., De Bernardi, F., & Padoa-Schioppa, E.  
640 (2011). Early assessment of the impact of alien species: differential consequences of an  
641 invasive crayfish on adult and larval amphibians. *Diversity and Distributions*, 17(6),  
642 1141–1151. <https://doi.org/10.1111/j.1472-4642.2011.00797.x>

643 Flesch, A. D. (2017). Influence of local and landscape factors on distributional dynamics: A  
644 species-centred, fitness-based approach. *Proceedings of the Royal Society B: Biological*  
645 *Sciences*, 284(1858). <https://doi.org/10.1098/rspb.2017.1001>

646 Flesch, A. D., Rosen, P. C., & Holm, P. (2017). Long-term changes in abundances of Sonoran  
647 Desert lizards reveal complex responses to climatic variation. *Global Change Biology*,  
648 23(12), 5492–5508. <https://doi.org/10.1111/gcb.13813>

649 Fouquet, A., Ficetola, G. F., Haigh, A., & Gemmell, N. (2010). Using ecological niche  
650 modelling to infer past, present and future environmental suitability for *Leiopelma*  
651 *hochstetteri*, an endangered New Zealand native frog. *Biological Conservation*, 143(6),  
652 1375–1384. <https://doi.org/10.1016/j.biocon.2010.03.012>

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

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

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

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

665 Hadfield, J. D., & Nakagawa, S. (2010). General quantitative genetic methods for  
666 comparative biology: Phylogenies, taxonomies and multi-trait models for continuous and  
667 categorical characters. *Journal of Evolutionary Biology*, 23(3), 494–508.

668 <https://doi.org/10.1111/j.1420-9101.2009.01915.x>

669 Hansen, M. C., Potapov, P. V, Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., ...  
670 Townshend, J. R. (2013). High-Resolution Global Maps of 21st-Century Forest Cover  
671 Change. *Science*, 342(6160), 850–853. <https://doi.org/10.1126/science.1244693>

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

675 Hijmans, R. J. (2016). Raster: Geographic Data Analysis and modeling. *R Package Version*  
676 *2.5-8*. <https://CRAN.R-Project.Org/Package=raster>.

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

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

683 Hoffman, A. A., & Sgró, C. M. (2011). Climate change and evolutionary adaptation. *Nature*,  
684 470(7335), 479–485. <https://doi.org/10.1038/nature09670>

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

688 Houlahan, J. E., Findlay, C. S., Schmidt, B. R., Meyer, A. H., & Kuzmin, S. L. (2000).  
689 Quantitative evidence for global amphibian population declines. *Nature*, 404(6779),  
690 752–755. <https://doi.org/https://doi.org/10.1038/35008052>

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

693           *the Intergovernmental Panel on Climate Change*. IPCC, Switzerland.

694 IPBES. (2018). IPBES-6 Plenary. Retrieved November 2, 2018, from  
695           <https://www.ipbes.net/event/ipbes-6-plenary>

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

698 Kats, L. B., & Ferrer, R. P. (2003). Alien predators and amphibian declines: Review of two  
699           decades of science and the transition to conservation. *Diversity and Distributions*, 9(2),  
700           99–110. <https://doi.org/10.1046/j.1472-4642.2003.00013.x>

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

703 Kyek, M., Kaufmann, P. H., & Lindner, R. (2017). Differing long term trends for two  
704           common amphibian species (*Bufo bufo* and *Rana temporaria*) in alpine landscapes of  
705           Salzburg, Austria. *PLoS ONE*, 12(11), 1–17.  
706           <https://doi.org/10.1371/journal.pone.0187148>

707 Latombe, G., Pyšek, P., Jeschke, J. M., Blackburn, T. M., Bacher, S., Capinha, C., ...  
708           McGeoch, M. A. (2017). A vision for global monitoring of biological invasions.  
709           *Biological Conservation*, 213, 295–308. <https://doi.org/10.1016/j.biocon.2016.06.013>

710 Liu, C., White, M., & Newell, G. (2011). Measuring and comparing the accuracy of species  
711           distribution models with presence-absence data. *Ecography*, 34(2), 232–243.  
712           <https://doi.org/10.1111/j.1600-0587.2010.06354.x>

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

716 Mendenhall, C. D., Sekercioglu, C. H., Oviedo Brenes, F., Ehrlich, P. R., & Daily, G. C.  
717           (2011). Predictive model for sustaining biodiversity in tropical countryside. *Proceedings*

718 *of the National Academy of Sciences*, 108(39), 16313–16316.  
719 <https://doi.org/10.1073/pnas.1111687108>

720 Menzel, A., Sparks, T. H., Estrella, N., Koch, E., Aasa, A., Ahas, R., ... Züst, A. (2006).  
721 European phenological response to climate change matches the warming pattern. *Global*  
722 *Change Biology*, 12(10), 1969–1976. <https://doi.org/10.1111/j.1365-2486.2006.01193.x>

723 Muths, E., Chambert, T., Schmidt, B. R., Miller, D. A. W., Hossack, B. R., Joly, P., ... Grant,  
724 E. H. C. (2017). Heterogeneous responses of temperate-zone amphibian populations to  
725 climate change complicates conservation planning. *Scientific Reports*, 7, 17102.  
726 <https://doi.org/10.1038/s41598-017-17105-7>

727 Northrup, J. M., Rivers, J. W., Yang, Z., & Betts, M. G. (2019). Synergistic effects of climate  
728 and land-use change influence broad-scale avian population declines. *Global Change*  
729 *Biology*, 25(5), 1561–1575. <https://doi.org/10.1111/gcb.14571>

730 Orme, D., Freckleton, R., Thomas, G., Petzoldt, T., Fritz, S., Isaac, N., & Pearse, W. (2018).  
731 caper: Comparative Analyses of Phylogenetics and Evolution in R. *R Package Version*  
732 *1.0.1*. Retrieved from <https://cran.r-project.org/package=caper>

733 Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J. K., Thomas, C. D., Descimon, H., ...  
734 Warren, M. (1999). Poleward shifts in geographic ranges of butterfly species associated  
735 with regional warming. *Nature*, 399(6736), 579–583.  
736 <https://doi.org/https://doi.org/10.1038/21181>

737 Petrovan, S. O., & Schmidt, B. R. (2016). Volunteer conservation action data reveals large-  
738 scale and long-term negative population trends of a widespread amphibian, the common  
739 toad (*Bufo bufo*). *PLoS ONE*, 11(10), e0161943.  
740 <https://doi.org/10.1371/journal.pone.0161943>

741 Pysek, P., Jarosik, V., Hulme, P. E., Kuhn, I., Wild, J., Arianoutsou, M., ... Winter, M.  
742 (2010). Disentangling the role of environmental and human pressures on biological

743           invasions across Europe. *Proceedings of the National Academy of Sciences*, 107(27),  
744           12157–12162. <https://doi.org/10.1073/pnas.1002314107>

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

749   R Core Team. (2017). R: A language and environment for statistical computing. *R*  
750           *Foundation for Statistical Computing, Vienna, Austria*. Retrieved from [https://www.r-](https://www.r-project.org/)  
751           [project.org/](https://www.r-project.org/)

752   Rondinini, C., di Marco, M., Chiozza, F., Santulli, G., Baisero, D., Visconti, P., ... Boitani, L.  
753           (2011). Global habitat suitability models of terrestrial mammals. *Philosophical*  
754           *Transactions of the Royal Society B: Biological Sciences*, 366(1578), 2633–2641.  
755           <https://doi.org/10.1098/rstb.2011.0113>

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

759   Roser, L. G., Ferreyra, L. I., Saidman, B. O., & Vilardi, J. C. (2017). EcoGenetics: An R  
760           package for the management and exploratory analysis of spatial data in landscape  
761           genetics. *Molecular Ecology Resources*, 17(6), e241–e250. [https://doi.org/10.1111/1755-](https://doi.org/10.1111/1755-0998.12697)  
762           [0998.12697](https://doi.org/10.1111/1755-0998.12697)

763   Saino, N., Ambrosini, R., Rubolini, D., Von Hardenberg, J., Provenzale, A., Hüppop, K., ...  
764           Sokolov, L. (2011). Climate warming, ecological mismatch at arrival and population  
765           decline in migratory birds. *Proceedings of the Royal Society B: Biological Sciences*,  
766           278(1707), 835–842. <https://doi.org/10.1098/rspb.2010.1778>

767   Santini, L., Isaac, N. J. B., & Ficetola, G. F. (2018). TetraDENSITY: A database of

768 population density estimates in terrestrial vertebrates. *Global Ecology and*  
769 *Biogeography*, 27(7), 787–791. <https://doi.org/10.1111/geb.12756>

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

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

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

779 Sillero, N., Campos, J., Bonardi, A., Corti, C., Creemers, R., Crochet, P. A., ... Vences, M.  
780 (2014). Updated distribution and biogeography of amphibians and reptiles of Europe.  
781 *Amphibia-Reptilia*, 35(1), 1–31. <https://doi.org/10.1163/15685381-00002935>

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

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

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

791 Thuiller, W., Lavergne, S., Roquet, C., Boulangeat, I., Lafourcade, B., & Araujo, M. B.  
792 (2011). Consequences of climate change on the tree of life in Europe. *Nature*, 470(7335),



793 531–534. <https://doi.org/10.1038/nature09705>

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

798 Tracewski, Ł., Butchart, S. H. M., Di Marco, M., Ficetola, G. F., Rondinini, C., Symes, A., ...  
799 Buchanan, G. M. (2016). Toward quantification of the impact of 21st-century  
800 deforestation on the extinction risk of terrestrial vertebrates. *Conservation Biology*,  
801 *30*(5), 1070–1079. <https://doi.org/10.1111/cobi.12715>

802 Vilà, M., Basnou, C., Pyšek, P., Josefsson, M., Genovesi, P., Gollasch, S., ... Zagatti, P.  
803 (2010). How well do we understand the impacts of alien species on ecosystem services?  
804 A pan-European, cross-taxa assessment. *Frontiers in Ecology and the Environment*, *8*(3),  
805 135–144. <https://doi.org/10.1890/080083>

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

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

815