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Population responses to observed climate variability across multiple taxa

2 Abstract

3 A major challenge in ecology is to understand how populations are affected by increased climate variability. Here, we assessed the effects of observed climate variability on different taxonomic groups 4 5 (amphibians, insects, mammals, herbaceous plants and reptiles) by estimating the extent to which 6 interannual variation in the annual population growth rates (CV_{λ}) and the absolute value of the long-term 7 population growth rate ($|\log \lambda|$) were associated with short-term climate variability. We used empirical 8 data (≥ 20 consecutive years of annual abundances) from 59 wild populations in the Northern 9 Hemisphere, and quantified variabilities in population growth rates and climate conditions (temperature 10 and precipitation in active and inactive seasons) calculated over a four-year sliding time window. We 11 observed a positive relationship between the variability of growth rate (CV_{λ}) and the variability of 12 temperature in the active season across taxa. Moreover, $|\log \lambda|$ was positively associated with the 13 variability of precipitation in the inactive season. Otherwise, the direction of the relationships between 14 population dynamics and climate variability (if any) depended on the season and taxonomic group in 15 question. Both CV_{λ} and $|\log \lambda|$ correlated negatively with species' lifespan, indicating general differences 16 in population dynamics between short-lived and long-lived species that were not related to climate 17 variability. Our results suggest that although temporal variation in population growth rates and the 18 magnitude of long-term population growth rates are partially associated with short-term interannual 19 climate variability, demographic responses to climate fluctuations might still be population-specific 20 rather than taxon-specific, and driven by other factors than the observed climate variability.

Keywords: climate variability, demography, lifespan, long-term time series, population dynamics,
 population growth rate, taxonomic group, timescale

23 Introduction

24 Global climate change is likely to lead to concomitant changes in climate means, variability, and extremes, resulting in more variable and unpredictable environments for animal and plant populations. 25 The consequences of changes in climate means for ecological and evolutionary processes have been 26 27 extensively studied during the past few decades, with the general conclusion being that shifts in mean 28 temperature and precipitation have the ability to alter population fluctuations (reviewed in Walther et al. 29 2002, Parmesan and Yohe 2003, Oliver and Morecroft 2014). More recently, climate variability (e.g., 30 Lawson et al. 2015, Vázquez et al. 2015) and extremes (e.g., Palmer et al. 2017, van de Pol et al. 2017) 31 have received increasing attention as important factors that can mediate the effects of shifts in climate 32 means (Vasseur et al. 2014, Lawson et al. 2015). Over the last three decades, variability in regional year-33 to-year temperature has changed substantially worldwide. For example, in the Northern Hemisphere, 34 especially in North America and Europe, variability in temperature increased notably in the 1980s and 1990s (Huntingford et al. 2013) and extreme temperature events are expected to be even more frequent 35 36 in the future (IPCC 2014). Moreover, precipitation variability, including precipitation extremes, is 37 predicted to increase in the warmer future climate (IPCC 2014, Pendergrass et al. 2017). Such interannual climate variability has the potential to translate into fluctuations in the abundances of wild populations 38 39 through changes in individuals' vital rates, such as survival, growth, and fecundity (e.g., van de Pol et al. 40 2010, Genovart et al. 2013, Jenouvrier et al. 2015). This link between climate variability and population 41 fluctuations is based on the fact that, for many species, population growth rates are sensitive to shifts not 42 only in the means of vital rates, but also in their variance (Doak et al. 2005, Morris et al. 2008, Vázquez 43 et al. 2015). A major aim in ecology is thus to determine how climate variability can affect populations 44 (Lawson et al. 2015).

45 One way of measuring population fitness is with the long-term population growth rate, which is a 46 function of annual finite rates of increase (Lewontin and Cohen 1969). Environmental variability is often assumed to decrease the long-term population growth rate (Lewontin and Cohen 1969, Tuljapurkar 47 48 1982), thus being harmful for populations. However, previous theoretical and empirical studies have 49 shown that an adverse effect of climate variability on the population growth rate is not a foregone 50 conclusion (Drake 2005, Doak et al. 2005, Koons et al. 2009, Vázquez et al. 2015). Specifically, climate 51 variability can either increase or decrease the long-term population growth rate depending on a species' 52 life history and the vital rates affected (Boyce et al. 2006, Lawson et al. 2015, Colchero et al. 2019), as 53 well as on the mean climatic conditions encountered by the population (Bozinovic et al. 2011, García-54 Carreras and Reuman 2013). As an example, lifespan is generally expected to be a good predictor of the 55 sensitivity of species to climate variability across diverse taxa, with short-lived species showing greater responses to variations in vital rates than long-lived species are (Morris et al. 2008, Koons et al. 2009, 56 Dalgleish et al. 2010). 57

58 So far, many studies have explored the effect of climatic variation on populations by theoretically 59 perturbing vital rates and assuming that all vital rates experience similar proportional changes (e.g., 60 Morris et al. 2008, Dalgleish et al. 2010, Jonzén et al. 2010, van de Pol et al. 2010, but see e.g., Palmer 61 et al. 2017). However, such theoretical perturbations may not reflect the actual changes in vital rates. 62 Instead, a more direct way to assess the consequences of ongoing climate change for wildlife is to 63 examine the actual responses of wild populations to climate variability. Here, we used data of population 64 abundances (≥20 consecutive years) from 11 countries to investigate the effect of short-term interannual 65 climate variability on different taxonomic groups (amphibians, insects, mammals, herbaceous plants, reptiles) based on 59 wild populations belonging to 54 species. We limited the study to terrestrial, non-66 67 migratory species in the Northern Hemisphere (Western Europe and North America), where the timing

68 of climate seasonality for populations is mostly synchronized. We sought to determine which taxonomic 69 groups (if any) were particularly sensitive to the observed climatic variability. We characterized the interannual variability in annual population growth rate as coefficient of variation (CV), and interannual 70 71 climate variability using average temperature and precipitation in the fall-winter and spring-summer 72 seasons (the inactive and active seasons, respectively). Although we do not expect that these two climate 73 variables would be equally important to all taxonomic groups, we consider them biologically meaningful 74 for the terrestrial species included here (e.g., Post and Stenseth 1999, Deguines et al. 2017, Mills et al. 75 2017). All variability was quantified within a four-year moving time window. More specifically, we 76 focused on the relationships between i) climate variability and the temporal variation in the observed 77 annual population growth rates (CV_{λ}), as well as ii) climate variability and the absolute value of the longterm population growth rate ($|\log \lambda|$). The use of $|\log \lambda|$ enabled us to assess the magnitude of population 78 79 responses to environmental variability regardless of direction because both negative and positive 80 responses are possible (Lawson et al. 2015). As environmental fluctuations can lead to population 81 fluctuations (Tuljapurkar 1982), we predicted that we would find a positive relationship between climate variability and CV_{λ} (i.e. we predicted to find an environmental signal in population dynamics). However, 82 because the species included in this comparative study represent diverse life histories, we hypothesized 83 that the effects of the climate variables considered would vary among taxonomic groups and lifespans. 84 85 Particularly, we predicted that $|\log \lambda|$ would be higher for short-lived species, which have been reported to be more sensitive to environmental variability than longer-lived species (Morris et al. 2008). As a 86 consequence, the populations of short-lived species would either decline or increase at a higher rate than 87 88 those of longer-lived species relative to climate variability.

89 Methods

90 Population and climatic data collection

91 Time series on population abundances (either annual population densities or population counts) were 92 extracted from two global databases, the NERC Imperial College Global Population Dynamics Database (GPDD; NERC Centre for Population Biology, 2010) and the Living Planet Index (LPI; Collen et al., 93 94 2009), based on two main criteria. First, demographic data came from non-migratory, terrestrial species 95 located in the Northern Hemisphere (see Fig. 1) and consisted of at least 20 consecutive years (selected 96 data were updated when possible using recently published sources; a list of all data sources can be found 97 in Appendix S1, Table S1.1 in Supporting Information). By restricting our analysis to such long-term 98 time series, we hoped to have sufficient information to assess relationships between population dynamics 99 and climate variables (Teller et al. 2016). Second, only wild, unmanaged populations were considered 100 (e.g., harvest data were removed; see Appendix S1 for further details about criteria). Moreover, we 101 included a subset of weed data from the Broadbalk experiment (Moss et al. 2004) which consisted of the 102 annual frequencies of 19 weed species monitored for 21 years between 1991 and 2014 (3 years of data 103 were missing when the plots were fallowed; see Appendix S1 for details). To find more studies, we also 104 conducted a literature search in July 2018 in the Web of Science using the following search term 105 combinations: (population) AND (demograph*) AND (abundance OR density OR population size OR 106 number) AND (time series OR monitoring) AND (long-term). This search produced 615 matches, of which eleven studies met our selection criteria. Overall, a total of 59 population time series were 107 108 analyzed; these represented 54 species with different life histories, including 4 amphibian, 6 insect, 20 109 mammal, 22 herbaceous plant, and 7 reptile populations from 28 locations across Europe and North 110 America. The mean length of the studies was 26.2 ± 8.4 years, with the study periods ranging from 1939 111 to 2016. Estimates of species' lifespans were obtained from PanTHERIA (Jones et al. 2009), AnAge (http://genomics.senescence.info/species/), Animal Diversity Web (ADW (http://animaldiversity.org/), 112 113 Ecoflora (http://ecoflora.org.uk/), and peer-reviewed literature.

114 For each study location, we extracted monthly gridded values of two key climate variables - temperature 115 (degrees Celsius) and precipitation (mm/month) - at a $0.5^{\circ} \times 0.5^{\circ}$ spatial resolution from the Climatic Research Unit's time-series datasets (CRU TS; Harris, Jones, Osborn, & Lister, 2014). Both of these 116 117 climate variables have been found to affect population dynamics of most of the taxonomic groups 118 considered here (Post and Stenseth 1999, Deguines et al. 2017, Mills et al. 2017) and therefore, we chose 119 to use the same climate variables for all taxa. From these climate data, we derived values for the six-120 month average of temperature and precipitation for the periods April-September and October-March. In 121 the Northern Hemisphere, these two periods correspond to the active growing season (spring-summer) 122 and the non-active season (fall-winter), respectively, with each period reflecting different environmental 123 conditions. Although less-studied than climatic conditions during the active growing season, changes in 124 winter climatic conditions can also influence the survival, overwintering success, and performance of 125 individuals during the following growing season, which can ultimately affect the population growth rate 126 and its variability (Roland and Matter 2013, Williams et al. 2015).

127

128 Estimating demographic and climate variability

129 For each time series, we calculated the observed annual population growth rate (λ) from year t to year t+1 as N_{t+1}/N_t , where N denotes population abundance. For the weeds, annual observations were missing 130 131 for three distinct years in each time series and therefore, we adjusted the growth-rate estimates by the 132 length of the census interval (Morris & Doak, 2002, p. 68). We used the coefficient of variation (CV) as our measure of temporal variability in annual population growth rates and in the variability of 133 precipitation to compare the relative amounts of variation across populations and variables that have 134 135 different means. For the temporal variability of temperature, an interval scale variable, standard deviation was used as a metric of variability. The interannual SD of temperature (SD_{Temp}) and the interannual CV 136

137 of precipitation (CV_{Prec}) were estimated separately for both active and inactive seasons after detrending 138 the data for each population to remove variation attributable to a long-term linear trend. The climate 139 variables were also scaled by population to ease comparison among populations experiencing different 140 climatic conditions. Moreover, to describe population dynamics in a variable environment and population 141 responses to climate variability, we calculated the long-term population growth rate (log λ) as the 142 arithmetic mean of the logged annual population growth rates (Morris and Doak 2002) and considered 143 the absolute values of log λ . That is, we focused on change in population size regardless of its direction. 144 Examining $\log \lambda$ per se across multiple species is not informative for our purpose because the direction 145 of the relationship between climate variability and log λ varies within species depending on both the 146 shape of the population response curve and the mean climatic conditions encountered (Lawson et al. 147 2015). For example, temperature variability enhances the population growth rate of the fruit fly 148 Drosophila melanogaster at a low mean temperature, but decreases it at high mean temperature 149 (Bozinovic et al. 2016). Consequently, if populations in different taxonomic groups in the present dataset 150 happened to represent contrasting environmental conditions, negative and positive responses could 151 cancel each other out, resulting in no overall response when assessed based on log λ , while this can be avoided using $|\log \lambda|$. 152

153 We then examined the effects of climatic variability on the variation in the annual population growth 154 rates (CV_{λ}) and the absolute value of the long-term population growth rate ($|\log \lambda|$) within a four-year 155 period (Pearson's correlation coefficient between the two variables: r=0.33). The four-year time window 156 was chosen because a short timescale may better reflect temporal climate variability that is relevant to 157 populations (when high local variations are more pronounced, e.g., extreme events; van de Pol et al., 158 2017). In the present study, the four-year time window enables multiple observations per population, 159 capturing periods of lower and higher climatic variation during the study period (≥ 20 years) at each 160 location. For a sliding time window of four years, the starting year was moved forward one year at a time to estimate CV_{λ} , SD_{Temp} , and CV_{Prec} . The coefficient of variation was corrected for bias in small sample size as following: $(1 + \frac{1}{4n}) * CV$, where n refers to the number of records from the time period considered (e.g., n=4 for the CVs of climatic conditions estimated over the period of four years; Sokal & Rohlf, 1995). In those few cases where an annual estimate of λ was missing (weed time series), the climate variables were adjusted to a five-year time period.

166

167 Statistical analysis

To explore whether climate variability explained a significant proportion of variation in CV_{λ} (sqrt-168 169 transformed) or $|\log \lambda|$ (sqrt-transformed), we fitted linear mixed-effects models by including several 170 covariates to control for environmental conditions and spatial heterogeneity. For both analyses and for 171 each season (active and inactive), our full model included CV_{Prec}, SD_{Temp}, taxonomic group (amphibians, 172 insects, mammals, herbaceous plants, reptiles), species' lifespan (a continuous variable), mean 173 temperature and mean precipitation (in the active or inactive season), latitude, and longitude as fixed 174 effects. Moreover, two-way interactions between the climate variabilities and taxonomic group, and between the climate variabilities and lifespan were also specified (see the full models in Table 1 and 175 176 Appendix S2). Population ID was included in all models as a random effect. In all statistical analyses, 177 the continuous explanatory variables (covariates) were rescaled: they were centralized and standardized 178 to ease model interpretation. Multicollinearity was checked for all climatic variables calculated in the 179 active and inactive seasons and for the variables of each full model using the coefficient of correlation 180 and variance inflation factors (Zuur et al. 2009). We also visually tested for spatial autocorrelation in the 181 residuals of the linear mixed models (Zuur et al. 2009) and found none. All models included a first-order 182 autoregressive correlation structure to account for temporal pseudoreplication (see details for model 183 selection in Appendix S2, Fig. S2.1).

184 For each analysis, model selection was performed based on the Akaike's Information Criterion adjusted 185 for small sample size (AICc; Burnham & Anderson, 2002). As a general approach, we started model selection from the full model (see Table S2.1) by testing for all two-way interaction terms, and then used 186 187 the most-parsimonious model to test for the main effects. If multiple models were equivalent (i.e., $\Delta AICc$ < 2), we chose the simplest model based on the principle of parsimony (Table 1; see the full model 188 selection in tables S2.2-S2.5, Appendix S2). To describe the proportion of variance explained by the 189 fixed factors, we calculated marginal R^2 values from the final simplified models which best inferred our 190 191 results (Nakagawa and Schielzeth 2013, Nakagawa et al. 2017). Models were fitted with the nlme 192 package (Bates et al. 2015, Pinheiro et al. 2017) in R 3.6.0 (R Core Team 2019).

193

194 **Results**

195 *Climate variability and CV_{\lambda}*

In both active and inactive seasons, species' lifespan was negatively associated with CV_{λ} , indicating 196 197 higher temporal variability in annual population growth rates for short-lived species than for long-lived 198 species (Tables 1 and 2; Fig. 2a - note that in Fig. 2a, the high values of CV_{λ} when lifespan = 30 represent 199 a single population of Eastern box turtles). Longitude was a significant covariate in both models (Table 200 2). During the active season, SD_{Temp} correlated positively with CV_{λ} across taxa (Table 2; Fig. 2b), 201 suggesting that the annual population growth rate fluctuated slightly more under variable than under stable climatic conditions. Moreover, the relationship between CV_{Prec} and CV_{λ} differed between taxa as 202 indicated by a significant interaction between CV_{Prec} and taxonomic group in the active season (Table 2). 203 CV_{λ} tended to increase with increasing CV_{Prec} for herbaceous plants, while it decreased for amphibians; 204 insects and mammals were less responsive to CV_{Prec} (Fig. 2c). During the inactive season, the relationship 205 206 between SD_{Temp} and CV_{λ} differed between taxa, with the CV_{λ} of herbaceous plants showing a positive response (Table 2, Fig. 3). Additionally, CV_{λ} did increase slightly with increasing mean precipitation in the inactive season (Table 2).

209

210 *Climate variability and |\log \lambda|*

The absolute value of the long-term population growth rate, $|\log \lambda|$, declined with increasing lifespan and with increasing longitude (Table 3). In the active season, the relationship between CV_{Prec} and $|\log \lambda|$ differed between taxa, with particularly insects exhibiting a positive association and mammals a negative association between these two variables (Table 3, Fig. 4). In the inactive season, CV_{Prec} was marginally and positively associated with $|\log \lambda|$ across taxa (Table 3). Moreover, $|\log \lambda|$ tended to differ among taxonomic groups, being lower on average for mammals and herbaceous plants than for insects (Table 3).

218

219 Discussion

220 For the five taxonomic groups considered (amphibians, insects, mammals, herbaceous plants, reptiles) 221 from the Northern Hemisphere, we found some support for our first hypothesis that climate variability 222 translates into temporal variation in the annual population growth rates (CV_{λ}). We detected a positive 223 relationship between CV_{λ} and SD_{Temp} across taxa in the active season. Moreover, for herbaceous plants, 224 CV_{λ} increased with the increasing variability of precipitation and temperature in the active and inactive 225 seasons, respectively. Our second hypothesis of a positive relationship between climate variability and 226 the absolute value of the long-term population growth rate ($|\log \lambda|$) particularly for short-lived species 227 was not supported; we observed no interaction between the climate variability and lifespan regarding log 228 λ . Overall, our results suggest that different taxonomic groups were weakly affected by the observed 229 climate variability during the study period.

230 *Climate variability and* CV_{λ}

231 In the present study, inferences about the effect of climate variability on population fluctuations partially 232 depended on the season, with the active and inactive seasons yielding different outcomes. When the 233 effect of climate variability was assessed based on the active season, variation in temperature was weakly 234 positively associated with CV_{λ} . We also found that CV_{λ} for herbaceous plants slightly increased with 235 increasing CV_{Prec} in the active season. These findings were thus in line with our predictions. In the 236 inactive season, associations between climate variability and population fluctuations were less 237 prominent; a positive association between SD_{Temp} and CV_{λ} was detected only for plants. The discrepancy between the two seasons might be due to the greater importance of environmental conditions on 238 239 populations during the active season. Our results indicate that, particularly for herbaceous plant 240 populations, increasing climatic variability might increase their vulnerability to other sources of variation OR// to other biotic and abiotic factors // and to extinction by increasing their fluctuations (however, we 241 242 did not detect an effect on their $|\log \lambda|$). Contrary to our expectations, we also found a negative relationship between CV_{λ} and CV_{Prec} for amphibians. This result diverges from that reported previously 243 244 in a meta-analysis for amphibians in the Northern hemisphere, in which no significant relationship 245 between yearly rainfall and the magnitude of population fluctuations was observed (Marsh 2001). These different findings might be due to heterogeneous responses of individual populations. Climatic 246 247 conditions, including rainfall and drought conditions, are known to influence population dynamics in 248 many amphibian species, but populations responses to these main climate drivers can be highly 249 heterogeneous in direction and magnitude both among and within taxa (Cayuela et al. 2016, Muths et al. 250 2017). However, a correlative approach, as used in the present study, may also produce spurious relationships between explanatory variables and the data, particularly if the model is over-parameterized 251 252 (Knape and De Valpine 2011), or if some of the explanatory variables are strongly correlated (Zuur et al. 253 2010). Although over-parameterization and collinearity were not likely in our case, the observed negative

254 relationship between variation in precipitation and CV_{λ} for amphibians may still be spurious, and reflect 255 other, non-measured processes that correlate with these climate variables. Indeed, interannual variation 256 in population growth rates results from a complex assortment of causal interactions including both the 257 direct and indirect effects of non-climatic factors, such as habitat (e.g., fragmentation or heterogeneity) 258 and biotic factors (e.g., interspecific competition), which might correlate with climatic conditions (Adler et al. 2012, Mantyka-Pringle et al. 2012, Oliver and Morecroft 2014, Papanikolaou et al. 2017). As has 259 260 been reported in previous studies (García et al. 2008, Morris et al. 2008), we found that short-lived 261 species exhibited more variable growth rates than long-lived species. This higher variation in the annual 262 population growth rates of short-lived species was not, however, due to climatic variability, as we 263 observed no interactions between variation in temperature or precipitation and lifespan. The greater 264 degree of population fluctuation found in short-lived species (e.g., insects, small mammals) could be due 265 to other biotic factors, such as the abundance of predators, which may regulate prev population sizes 266 more directly than local weather conditions (e.g., Hanski et al. 2001).

267 Overall, the observed associations between climate variability and population variability were 268 statistically significant but weak, which is not surprising given the diversity of taxa that were included. Indeed, Knape & De Valpine (2011) reported that climate effects on animal populations are often difficult 269 270 to detect in time-series analyses even for large datasets which contain hundreds of time series. Moreover, 271 we acknowledge the fact that the present study covers a large spatial scale (the Northern Hemisphere), 272 which may even overestimate the magnitude of population responses to climate variability compared to studies conducted in single locations (Elmendorf et al. 2015). However, such a large spatial scale 273 274 considered should not affect the direction of population response (Elmendorf et al. 2015). As a 275 consequence, our findings on the effects of observed climate variability on different taxonomic groups 276 should be interpreted qualitatively rather than quantitatively.

277 *Climate variability and |\log \lambda|*

278 Theory predicts that climate variability can translate into changes in the long-term population growth rate (Tuljapurkar 1982), but that the direction of these changes is likely to vary across species, depending 279 280 on their life history, ecology, and demographic status (Boyce et al. 2006, Lawson et al. 2015, Vázquez 281 et al. 2015). For instance, empirical findings have indicated that short-lived species might be more 282 vulnerable to climate variability than long-lived species (Morris et al. 2008, Dalgleish et al. 2010), 283 whereas a previous theoretical study suggests that short-lived species with high reproductive output 284 might actually benefit from environmental variation (Koons et al. 2009). As observed in many 285 ectotherms, populations may also respond in a qualitatively different manner to environmental variability 286 depending on the mean environmental conditions encountered and the geographical location within the 287 species' range (Bozinovic et al. 2011, García-Carreras and Reuman 2013, Vasseur et al. 2014, Lawson 288 et al. 2015). Therefore, we used the absolute value of the long-term population growth rates to assess 289 population responses (regardless of their direction) to climate variability. We hypothesized that the 290 relationship between $|\log \lambda|$ and climate variability would be positive for the species that are most 291 responsive to climate variability, such as shorter-lived species. Despite the fact that temperature 292 variability in the active season was positively associated with temporal variation in annual population 293 growth rates across taxa, this variability did not translate into higher absolute values of the long-term 294 population growth rate, $|\log \lambda|$. In contrast to previous studies that have highlighted the essential role of 295 lifespan in population responses to environmental variability (Morris et al. 2008, Koons et al. 2009, 296 Dalgleish et al. 2010), we observed no such an effect (i.e. the interaction between climate variability and 297 lifespan was not significant). In other words, changes in the long-term growth rates of both short-lived 298 and long-lived species were similarly associated with realised climate variability considered. We only 299 found a negative relationship between $|\log \lambda|$ and lifespan, suggesting that the populations of short-lived species generally either declined or increased more rapidly than those of longer-lived species. However, we observed differences in $|\log \lambda|$ in relation to CV_{Prec} in the active season among some taxonomic groups. The positive relationship between CV_{Prec} and $|\log \lambda|$ of insects, a taxonomic group involving only short-lived species, suggests that their abundances changed more rapidly when interannual variability in precipitation was high. In the context of climate change, this result indicates that insects might be particularly sensitive to expected changes in climate variability.

306 Previous comparative studies across taxa are based on hypothetical climate variability and vital rate 307 perturbations (Dalgleish et al., 2010; Morris et al., 2008), while our study relies on true climate 308 variability, which can be smaller than hypothetical variability. Therefore, it is possible that no particular 309 taxonomic group was heavily affected by the observed climate variability during the past 77 years. This 310 view is also partially supported by a previous study by Palmer et al. (2017), which reported that the 311 responses of 238 British Lepidoptera and bird species to climate variability since 1968 were species-312 specific. From an evolutionary perspective, adaptation to climate variability via demographic buffering 313 or bet-hedging strategies (e.g., Morris and Doak 2004, Nevoux et al. 2010, but see Jongejans et al. 2010) 314 could be partially responsible for the lack of a significant correlation between climate variability and log 315 λ . Nevertheless, as we investigated the relationship between climate variability and population responses 316 at the four-year time scale only, we cannot rule out the possibility that a different timescale might have 317 revealed a different environmental signal in $|\log \lambda|$. For instance, changes in the intra-annual variation of 318 climate conditions may also affect population fluctuations and, consequently, population growth rates by 319 modifying the timing of weather conditions and therefore the seasonal abiotic and biotic environments 320 of a population (e.g., Shriver 2016, Papanikolaou et al. 2017). Similarly, the resolution of climate data 321 may also affect the conclusions of climate effects (Morrison et al. 2019). In the present study, the resolution of climate surface was rather coarse, but the same resolution has been used also previously for
multispecies studies (e.g., Knape and De Valpine 2011, Spooner et al. 2018).

In summary, the present study suggests that temporal fluctuations in population growth rates and the magnitude of long-term population growth rates are partially associated with short-term interannual climate variability, but that these associations may vary depending on the season and taxonomic groups considered. Species lifespan did not explain sensitivity to observed climate variability in our study. These findings thus indicate that populations might respond individualistically to climate fluctuations and that factors other than the observed climate variability (e.g., density dependence, biotic interactions, local microclimate) are probably more important to the dynamics of wild populations.

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- 463 **Data Accessibility**: Data supporting the results are available in the GPDD and LPI databases and
- 464 published sources (detailed in Table S1.1, Appendix S1).

Table 1. Model selection table for the temporal variability in the annual population growth rates (CV_{λ}) and the absolute value of the long-term population growth rate ($|\log \lambda|$) calculated across a four-year sliding time window. Linear mixed-effects models were fitted using a first-order autoregressive structure and Population ID was treated as a random effect. Climatic mean and variability variables in the active and inactive season were investigated separately. The best models ($\Delta AICc < 2$, in italics) and the full model (M_{Full}) are presented with corresponding df (number of parameters), AICc (Akaike's Information Criterion), and $\Delta AICc$. See Appendix S2, Tables S2.2-S2.5 for the full model selection.

NAM E	DF	AICc	ΔAICc	MODEL DESCRIPTION				
	CV_{λ} - active season							
M1	17	-187.34	0.00	$CV_{Prec} + SD_{Temp} + group + lifespan + longitude + latitude + CV_{Prec}:group$				
M2	16	-187.04	0.29	$CV_{Prec} + SD_{Temp} + group + lifespan + longitude + CV_{Prec}$:group				
М3	18	-185.35	1.99	$CV_{Prec} + SD_{Temp} + group + lifespan + longitude + latitude + mean_{Prec} + CV_{Prec} - group$				
M _{Full}	25	-179.53	7.81	CV _{Prec} + SD _{Temp} + group + lifespan + longitude + latitude + mean _{Temp} + mean _{Prec} + CV _{Prec} :group + SD _{Temp} :group + CV _{Prec} :lifespan + SD _{Temp} :lifespan				
	CV_{λ} - inactive season							
M1	17	-183.24	0.00	SD_{Temp} + group + lifespan + longitude + latitude + mean _{Prec} + SD_{Temp} :group				
М2	16	-182.89	0.35	$SD_{Temp} + group + lifespan + longitude + mean_{Prec} + SD_{Temp}$; group				
М3	18	-181.39	1.84	SD_{Temp} + group + lifespan + longitude + latitude + mean _{Prec} + CV_{Prec} + SD_{Temp} · group				
M _{Full}	25	-168.44	14.79	CV _{Prec} + SD _{Temp} + group + lifespan + longitude + latitude + mean _{Temp} + mean _{Prec} + CV _{Prec} :group + SD _{Temp} :group + CV _{Prec} :lifespan + SD _{Temp} :lifespan				
	$ \log \lambda $ - active season							
М1	17	-272.12	0	$CV_{Prec} + SD_{Temp} + group + lifespan + longitude + mean_{Temp} + CV_{Prec}$:group				
М2	18	-270.54	1.58	$CV_{Prec} + SD_{Temp} + group + lifespan + longitude + mean_{Temp} + mean_{Prec} + CV_{out}$ group				
М3	16	-270.42	1.70	CV_{Prec} + SD_{Temp} + group + lifespan + longitude + CV_{Prec} :group				
M4	16	-270.40	1.72	CV_{Prec} + group + lifespan + longitude + mean _{Temp} + CV_{Prec} :group				
М5	18	-270.14	1.98	$CV_{Prec} + SD_{Temp} + group + lifespan + longitude + latitude + mean_{Temp} + CV_{rec}$ group				
M _{Full}	25	-263.72	8.40	CV_{Prec} + SD_{Temp} + group + lifespan + longitude + latitude + mean _{Temp} + mean _{Prec} + CV_{Prec} :group + SD_{Temp} :group + CV_{Prec} :lifespan + SD_{Temp} :lifespan				
	$ \log \lambda $ - inactive season							
М1	11	-267.49	0	CV _{Prec} + group + lifespan + longitude				
M _{Full}	25	-255.30	12.19	CV _{Prec} + SD _{Temp} + group + lifespan + longitude + latitude + mean _{Temp} + mean _{Prec} + CV _{Prec} :group + SD _{Temp} :group + CV _{Prec} :lifespan + SD _{Temp} :lifespan				

472 <u>Abbreviations</u>: CV_{Prec}= precipitation coefficient of variation during a given season (scaled per population); SD_{Temp}= temperature

473 standard deviation during a given season (scaled per population); mean_{Prec}= mean precipitation during a given season (scaled

474 per population); mean_{Temp}= mean temperature during a given season (scaled per population); group= taxonomic groups
475 (amphibians, insects, mammals, herbaceous plants and reptiles).

Table 2. Results from the simplified mixed models that best explained the interannual variability in population growth rates (CV_{λ}) across taxa (n=59 populations from the Northern Hemisphere; Models M2 for the active and inactive seasons in Table 1). All continuous variables were scaled based on detrended data. The estimates, the 95% confidence intervals (95% CI) and marginal R^2 values (conditional R^2 in brackets) are presented.

	Estimat	95% CI	Intercep	Residu	R^2
	е		t	al	
	Active s	eason			
Fixed factors					
Intercept	0.55	[0.38, 0.72]			
Group _[Insecta]	0.04	[-0.20, 0.27]			
Group _[Mammalia]	-0.03	[-0.22, 0.16]			
Group _[Herb. plant]	-0.01	[-0.21, 0.18]			
Group _[Reptilia]	0.13	[-0.10, 0.36]			
Lifespan	-0.12	[-0.18, - 0.06]			
Longitude	-0.09	[-0.15, - 0.04]			
SD _{Temp}	0.02	[0.01, 0.04]			
CV _{Prec}	-0.06	[-0.12, 0.01]			
CV _{Prec} : Group _[Insecta]	0.06	[-0.02, 0.14]			
CV _{Prec} : Group _{(Mammalia})	0.05	[-0.01, 0.12]			
CV _{Prec} : Group _{[Herb.}	0.09	[0.02, 0.16]			
CV _{Prec} : Group _[Reptilia]	0.08	[0.003, 0.15]			
Random factors					
pop.ID			0.15	0.25	0.15 (0.37)
Fixed factors	Inactive	season			
Intercent	0.55	[0.38 0.72]			
Group	0.00	[-0.20,			
Group _[Insecta]	0.04	0.28]			
Group _[Mammalia]	-0.03	[-0.22, 0.16]			

Group _[Herb. plant]	-0.01	[-0.21, 0.18]			
Group _[Reptilia]	0.13	[-0.10, 0.36]			
Lifespan	-0.12	[-0.18, - 0.06]			
Longitude	-0.09	[-0.15, - 0.04]			
Mean _{Prec}	0.02	[0.01, 0.04]			
SD _{Temp}	-0.03	[-0.08, 0.02]			
SD _{Temp} : Group _[Insecta]	0.01	[-0.05, 0.07]			
SD _{Temp} : Group _[Mammalia]	0.04	[-0.02, 0.09]			
SD _{Temp} : Group _{[Herb.}	0.07	[0.01, 0.12]			
SD _{Temp} : Group _(Reptilia)	0.02	[-0.04, 0.08]			
Random factors					
pop.ID			0.15	0.25	0.15 (0.36)

Table 3. Results from the simplified mixed models that best explained the variability in the absolute value of the long-term population growth rate ($|\log \lambda|$) across taxa (n=59 populations from the Northern Hemisphere). All continuous variables were scaled. The estimates, the 95% confidence intervals and marginal R^2 values (conditional R^2 in brackets) of model M3 for the active season and M1 for the inactive season (Table 1) are presented.

	Estimat	95% CI	Intercep	Residu	R^2
	е		t	al	
	Active se	ason			
Fixed factors					
Intercept	0.43	[0.32, 0.55]			
Group _[Insecta]	0.11	[-0.06, 0.27]			
Group _[Mammalia]	-0.09	[-0.22, 0.04]			
Group _[Herb. plant]	-0.06	[-0.20., 0.07]			
Group _[Reptilia]	0.01	[-0.15, 0.17]			
Lifespan	-0.07	[-0.1, -0.03]			
Longitude	-0.06	[-0.10, -0.02]			
CV _{Prec}	-0.01	[-0.06, 0.04]			
SD _{Temp}	0.01	[-0.001, 0.02]			
CV _{Prec} : Group _[Insecta]	0.05	[-0.02, 0.11]			
CV _{Prec} :	-0.02	[-0.08, 0.04]			
plantl	0.03	[-0.03, 0.09]			
CV _{Prec} : Group _[Reptilia]	0.02	[-0.04, 0.08]			
Random factors					
Pop.ID			0.11	0.21	0.13 (0.30)
	Inactive s	eason			
Fixed factors					
Intercept	0.43	[0.32, 0.55]			
Group _[Insecta]	0.11	[-0.06, 0.27]			
Group _[Mammalia]	-0.09	[-0.22, 0.04]			
Group _[Herb. plant]	-0.06	[-0.20, 0.07]			
Group _[Reptilia]	0.01	[-0.15, 0.17]			
Lifespan	-0.07	[-0.11, -0.03]			
Longitude	-0.06	[-0.10, -0.02]			
CV _{Prec}	0.01	[0.002, 0.03]			
Random factors					
Pop.ID			0.11	0.21	0.12 (0.29)

488 Figure 1. Locations of the 59 study populations included in the dataset. Note that each location may489 contain multiple populations.



Figure 2. Temporal variability in annual population growth rates (CV_{λ}) calculated across a four-year sliding time window for 59 populations from the Northern Hemisphere and plotted against (a) species' lifespan, (b) variation in temperature (SD_{Temp}) across taxa in the active season, and (c) variation in precipitation in the active season (CV_{Prec}) for each taxonomic group. The fitted lines with 95% confidence intervals are estimated from model M2, Table 1 $(CV_{\lambda}$ - active season).



Interannual CV_{Prec} in the active season (scaled)

Figure 3. Temporal variability in annual population growth rates (CV_{λ}) calculated across a four-year sliding time window for 59 populations from the Northern Hemisphere and plotted against variation in temperature (SD_{Temp}) in the inactive season for each taxonomic group considered. The fitted lines with 500 95% confidence intervals are from the mixed model M2, Table 1 (CV_{λ} - inactive season).



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Figure 4. Relationships between the absolute value of the long-term population growth rate ($|\log \lambda|$) and the variation in precipitation (CV_{Prec}) in the active season, for each taxonomic group considered (based on 59 populations from the Northern Hemisphere). Values are calculated across a four-year sliding time window, the fitted values (black) with 95% confidence intervals are from the linear mixed model M3, Table 1 ($|\log \lambda|$ - active season).



Interannual CV_{Prec} in the active season (scaled)