RESEARCH ARTICLE

Connectivity among thermal habitats buffers the effects of warm climate on life-history traits and population dynamics

Félix Pellerin[1,2] | Elvire Bestion[3] | Laurane Winandy[1,3] | Lucie Di Gesu[1] | Murielle Richard[3] | Robin Aguilée[1] | Julien Cote[1]

[1]Laboratoire Évolution and Diversité Biologique (EDB), UMR5174, CNRS, IRD, Université Toulouse III Paul Sabatier, Toulouse, France

[2]Institute of Marine Ecosystem and Fishery Science (IMF), Center of Earth System Research and Sustainability (CEN), University of Hamburg, Hamburg, Germany

[3]Station d'Écologie Théorique et Expérimentale (SETE), UAR2029, CNRS, Moulis, France

Correspondence
Félix Pellerin
Email: felix.pellerin23@gmail.com

Abstract

1. Contemporary climate change affects population dynamics, but its influence varies with landscape structure. It is still unclear whether landscape fragmentation buffers or amplifies the effects of climate on population size and the age and body size of individuals composing these populations.

2. This study aims to investigate the impacts of warm climates on lizard life-history traits and population dynamics in habitats that vary in their connectivity.

3. We monitored common lizard *Zootoca vivipara* populations for 3 years in an experimental system in which both climatic conditions and connectivity among habitats were simultaneously manipulated. We considered two climatic treatments (i.e. present-day climate and warm climate [+1.4°C than present-day climate]) and two connectivity treatments (i.e. a connected treatment in which individuals could move from one climate to the other and an isolated treatment in which movement between climates was not possible). We monitored survival, reproduction, growth, dispersal, age and body size of each individual in the system as well as population density through time.

4. We found that the influence of warm climates on life-history traits and population dynamics depended on connectivity among thermal habitats. Populations in warm climates were (i) composed of younger individuals only when isolated; (ii) larger in population size only in connected habitats and (iii) composed of larger age-specific individuals independently of the landscape configuration. The connectivity among habitats altered population responses to climate warming likely through asymmetries in the flow and phenotype of dispersers between thermal habitats.

5. Our results demonstrate that landscape fragmentation can drastically change the dynamics and persistence of populations facing climate change.

KEYWORDS
climate change, dispersal, experiments, habitat fragmentation, lizard

1 | INTRODUCTION

Contemporary climate change is a major threat to biodiversity (Urban, 2015). Climate warming can result in local population extirpation (Sinervo et al., 2010) and changes in spatial distribution (i.e. range shift; Chen et al., 2011), phenotypic composition (Charmantier et al., 2008) and population dynamics (Whitfield et al., 2007). Climate-dependent population dynamics encompass changes in population size, age and body size structure (Daufresne et al., 2009; Whitfield et al., 2007). These alterations in population dynamics result from changes in life-history traits, namely survival, growth, reproduction and dispersal, depending on size or age. In fish populations, climate change positively affects somatic growth rate and survival of small individuals, while negatively affecting the survival and reproduction of bigger individuals and the population size structure (Fryxell et al., 2020; Vindenes et al., 2014). These changes in population dynamics could subsequently impact community functioning, through age- and size-dependent species interactions (Kalinkat et al., 2013), and are therefore central to predicting biodiversity in response to climate change.

However, climate impacts are often studied independently of other contemporary environmental changes simultaneously acting on population dynamics. In particular, landscape fragmentation is another major anthropogenic threat that interacts with climate change (Brook et al., 2008; Oliver et al., 2015; Opdam & Wascher, 2004). Landscape fragmentation splits suitable habitats into a number of small, isolated patches (Fahrig, 2003). Thus, landscape fragmentation alters population dynamics by reducing habitat patch size, increasing impacts of demographic and environmental stochasticity and limiting dispersal among habitats. Dispersal is a cornerstone of population dynamics via the direct effects of emigration and immigration rates on population density (Burgess & Marshall, 2011) or via particular life-history and phenotypic traits borne by dispersers (i.e. dispersal syndromes; Bowler & Benton, 2005; Clobert et al., 2009). For instance, in common lizards, dispersing females reproduce earlier but suffer earlier senescence than philopatric females (Cotto et al., 2015). Landscape fragmentation may modulate population dynamics by (i) limiting the number of emigrants and/or immigrants (Fahrig, 2003), (ii) modifying dispersal syndromes (Boudjemadi et al., 1999) and (iii) decreasing the survival rate through increased dispersal costs (Bonte et al., 2012; Fahrig, 2003).

Climate change and landscape fragmentation may interact in multiple ways to drive population dynamics (e.g. Gérard et al., 2021). For example, at the local scale, detrimental impacts of warming on reproduction and survival rates may be prevented by individual movements into cooler habitats. At the regional scale, landscapes have habitats with various microclimates (Milling et al., 2018) differently impacted by climate warming (Ashcroft et al., 2009). The least impacted habitats may serve as climatic refuges (Pearson, 2006), protecting individuals from extreme conditions (Scheffers et al., 2014; Suggitt et al., 2018) and acting as source populations for rescuing nearly extinct populations. Fragmentation may prevent individuals from accessing such refuges, thus strengthening the climate impacts on threatened populations.

Moreover, habitat fragmentation may also modulate the influence of dispersal on local adaptation. In the case of random dispersal (i.e. a random fraction of the population disperses, independently of individuals' phenotype and environmental conditions), fragmentation may prevent the incoming flow of immigrants with non-adapted phenotypes that dilute the adaptation to warmer conditions and may, therefore, promote the adaptation to different microclimates and thus population persistence. In contrast, when dispersal is adaptive (i.e. individuals bias their movements along local gradients in fitness; Armsworth & Roughgarden, 2005), fragmentation may reduce the incoming flow of adapted phenotypes, thereby slowing down adaptation and reducing population persistence.

Here, we experimentally investigated the impacts of warm climates on lizard life-history traits and population dynamics in habitats that vary in their connectivity. We monitored common lizard *Zootoca vivipara* populations for 3 years in an experimental system, simultaneously manipulating the climatic conditions and connectivity among habitats. Previous studies showed that warm climates influence common lizard population dynamics, with positive effects on reproductive onset and success and on juvenile body growth (Bestion, Teyssier, et al., 2015; Chamaillé-Jammes et al., 2006; Le Galliard et al., 2010; Rutschmann, Miles, Clobert, & Richard, 2016), which are offset by a higher mortality later in life. This accelerated pace of life is predicted to decrease population growth rate and lead to population extirpation (Bestion, Teyssier, et al., 2015). However, connectivity between habitats may influence these climate impacts on population dynamics. Massot et al. (2008) suggested that a reduction in habitat connectivity may exacerbate the risk of population extinction under climate change. However, Cotto et al. (2015) showed that dispersing females have a faster pace of life than philopatric females. This dispersal syndrome could either reinforce or soften the accelerating effects of warm climates on the pace of life depending on the asymmetry of movements between microclimates. We, therefore, studied whether habitat connectivity works together with warmer conditions to reinforce climate impacts on population dynamics, or whether dispersal dampens these detrimental effects by rescuing populations (e.g. through the use of refuge areas) that have a low growth rate.

2 | MATERIALS AND METHODS

2.1 | Experiments

Starting in 2015, we performed a 3-year-long experiment on the common lizard *Zootoca vivipara* using the Metatron, an experimental system comprising 48 interconnected semi-natural mesocosms (100 m² each; Legrand et al., 2012; Figure 1b) connected by 19-m-long corridors which allowed us to simultaneously manipulate temperature (with the help of automatic shutters) and connectivity (by opening or closing the doors which separate the mesocosm from the corridor, see details in Figure 1 and Appendix A, ethics permit number APAFIS#19523-201902281559649 v3).

We created two climatic treatments, a present-day and a warm climate, by automatically closing the shutters at ambient temperature thresholds of either 28 or 38°C (Bestion, Teyssier, et al., 2015). Given that mesocosms are intrinsically warmer than outside, present-day climates matched thermal conditions near the Metatron (meteorological station of Saint-Girons Antichan; Bestion, Teyssier, et al., 2015). As our treatments depended on outdoor climatic conditions, the generated climate regimes follow day-to-day fluctuations in a coordinated manner so that daily fluctuation and seasonality are efficiently reproduced. The climate manipulations were active and efficient during the summer daytime, and the difference between treatments varied with the weather (Figure 1c). Consequently, the warm climate treatment was on average 1.4 and 2.6°C warmer (mean and maximal summer daily temperatures) than the present-day climate treatment and the summer temperature slightly differed among years (Figure 1c).
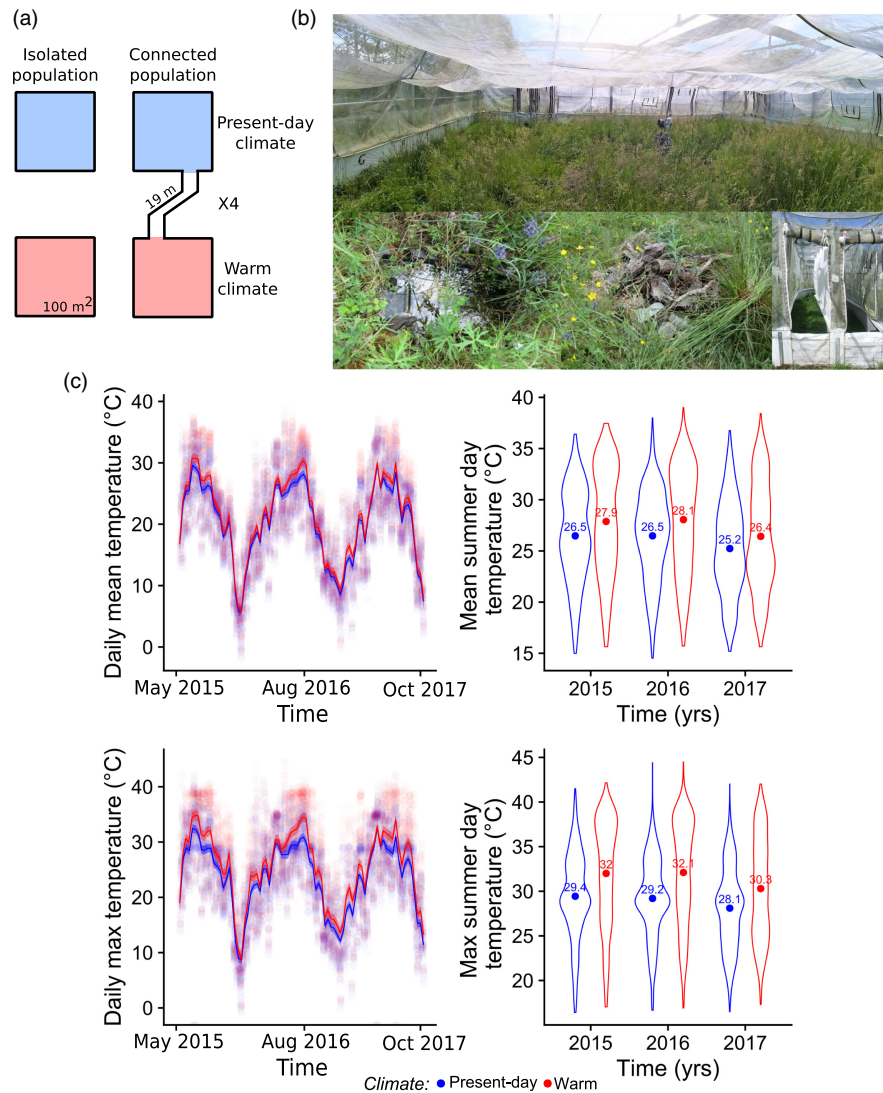

FIGURE 1 (a) Scheme of the experimental design. (b) View of the inside of a mesocosm of the metatron. On the top picture, a broad view of the mesocosm with dense vegetation and the temperature, hygrometry and illuminance recording station in the middle of the mesocosm. Each mesocosm also contains two water ponds (bottom left) and four microhabitats made of rocks and wood logs (bottom middle). The entrance of the corridors connecting mesocosms is also represented (bottom right). Photography by L. Winandy and E. Bestion. (c) Average (top) and maximum (bottom) temperature during the day (from 10 am to 6 pm) through time (left) and averaged over the summer period (21 June to 21 September, right) under present-day climate (blue) and warm climate (red) for the 3 years of the experiment. On the left panel, the dots represent the average (top) and maximum (bottom) day temperature for the different enclosures through time, and the curves represent the mean ± SE for each treatments. On the right panel the violin plots represent the distribution of average (top) and maximum (bottom) day temperatures along the summer period for each experimental year and each climatic treatment. Mean ± SE, and mean values are also represented. Note that the left panel is only representing mean and maximum daily temperature from May 2015 to October 2017 because temperature measures from October 2017 to May 2018 were missing due to a technical failure in saving the recorded temperatures. However the shutters were still active during this period even if temperatures never went above 28°C and so it did not influence the climate treatments.

The warm climate treatment matched the scenario SSP5-8.5 for 2041–2060 and SSP2-4.5, SSP3-7.0 and SSP5-8.5 for 2081–2100 (Masson-Delmotte et al., 2021).

Of the 48 mesocosms constituting the Metatron, we used 16 to create eight pairs of mesocosms that combined a present-day climate mesocosm and a warm climate mesocosm with two connectivity treatments, either opening or closing the connecting corridors (Figure 1a). For four pairs, lizards could move between climate treatments (connected treatment), while movement was prevented for the four remaining pairs (isolated treatment). In the connected treatments, corridors were opened from early March to mid-October each year, except in 2017 when corridors opened in late March, spanning the entire period of lizard activity.

2.2 | Population initialization

In 2015, 240 adults and 306 juveniles were released into 16 mesocosms. The individuals were descendants of lizards captured in the Cevennes, France, in 2010 and 2013, maintained in the Metatron (Ariège, France) for several experiments (Bestion et al., 2017, 2019; Bestion, Teyssier, et al., 2015) and intermixed regularly before the present experiment to prevent high levels of inbreeding. Each mesocosm was initially populated in early July 2015 with adult females, males and juveniles, with a later addition of four adults (two males, two females) in September 2015. The population size after this initialization period was 10 females, 5 males and 19 ± 1 juveniles, matching densities observed in natural populations. The individuals added in September were not considered in the analyses for the first year. At population initialization only, we split clutches among different mesocosms, and the different treatments to enhance genetic diversity within populations and released juveniles without their mother to prevent kin competition. All the lizards present in the system, individually tagged at birth by toe clipping (see Section 2.7, ethics permit number APAFIS#15897-2018070615164391 v3), were, therefore, of known age. We measured their body size (snout-vent length) at release and ensured that there were no differences in age structure and body size between treatments (p-values > 0.63 for the effects of climate, connectivity treatments and their interaction).

2.3 | Population monitoring

In May, from 2016 to 2018, before the females started laying eggs, we closed the corridors to recapture all the individuals and brought them to the laboratory. They were identified, measured for body size and mass and maintained in individual terraria ($18 \times 35 \times 22$ cm for adult females and gravid 1-year-old females and $15.5 \times 25 \times 15$ cm for males and non-gravid 1-year-old females). Terraria contained a 3-cm sterilized litter layer, a petri dish with water, a piece of absorbent paper, a cardboard and a plastic tube as a shelter. A light bulb (25 W) and an ultraviolet lamp (Zoomed Reptisun 5.0 UVB

36 W) provided heat for thermoregulation and light for 6 h per day (from 9:00 to 12:00 and from 14:00 to 17:00). Lizards were lightly sprayed with water three times a day (in the morning, at mid-day and in the evening) and offered two crickets *Acheta domestica* daily. Females laid eggs in their terrarium and the juveniles were isolated from their mother directly after parturition. They were marked by toe-clipping, measured for snout-vent length (nearest mm), weighed with an electronic scale (Thermofisher, 0.01 g) and a tail tip of 0.3 cm was collected for paternity analysis (ethics permit number APAFIS#19523-201902281559649 v3).

These captures allowed (i) monitoring population size, mean age and body size of individuals that composed the populations through time, (ii) measuring clutch sizes (i.e. number of viable offspring), yearly survival probability, body growth (i.e. the difference in snout-vent length from 1 year compared with the previous one) and (iii) in connected treatments, the dispersal status of each individual every experimental year. Dispersers (respectively, residents) are defined as individuals recaptured after 1 year in a different (respectively, the same) mesocosm than the previous year. The dispersal probability observed in this experiment was similar to the one of a previous experiment (Legrand et al., 2012) with similar experimental conditions and in which movements were recorded daily, meaning that our 1-year movement monitoring provided a good indication of individual dispersal status. Nevertheless, seasonal back-and-forth movements might have occurred, as it has been previously estimated that 47% of individuals who moved at least once moved a second time in a course of a year (Legrand et al., 2012).

In early July, all males, females and their clutch were released into the Metatron into their population of origin. We released adult and juvenile individuals back into the mesocosm where they or their mothers were captured. To avoid stress-induced dispersal, we closed the corridors for 7 days after release and opened them later. Over the course of the experiment, two populations went extinct in 2016 (one of each climate treatment in the isolated treatment) and one in 2017 (from present-day climate in the isolated treatment). Extinctions were likely due to demographic fluctuations, as extinctions occurred only in isolated populations where population rescue from neighbouring populations was not possible. In 2016, the two extinct populations were reinitialized with the same density, age and sex structure and phenotypic composition as in 2015 using lizards from stock mesocosms that were not subject of any previous climatic experiment. In 2017, the extinct population was not reinitialized.

2.4 | Statistical analyses

2.4.1 | General statistical procedure

We analysed the additive and interactive effects of climate and habitat connectivity first on life-history traits, then on individuals' mean age and body size and finally on population size. We further investigated the influence of climate in each connectivity condition, by separately running the models for each connectivity treatment. All

the models are summarized in Tables S1 and S2. All continuous variables were centered and scaled in all analyses.

We used generalized/linear mixed models with random intercepts to account for the non-independency of the data points. We proceeded in two steps. First, we built full models with all fixed variables and random effects, and the random structure of each model was selected by AIC (Zuur et al., 2009). Second, we built models with the selected random effect(s) and with all possible combinations of fixed effects, including one without any fixed effects (i.e. null model), and ranked them by AIC. We obtained conditional estimates, standard errors, z-values, relative importance (RI), and p-values of all variables that featured in those models that had a delta AIC of less than 2 from the best model using a model averaging procedure (Burnham et al., 2011). Models containing all variables present in the averaged best models were run to calculate the conditional (R^2_c, effect of the fixed and random effects) and marginal (R^2_m, effect of the fixed effect) R^2 (Nakagawa et al., 2017). When the best model structure was that without random effect, the adjusted R^2 was calculated, except for models with zero-inflated distribution, where the pseudo-R^2 was calculated.

We provided both RI and p-value and chose to discuss the influence of variables when their RI, p-value and visual pattern on the figures were consistent (i.e. high RI, low p-value and clear visual pattern), without fixing absolute thresholds. Accordingly, when a treatment was retained in the best average model with low RI and high p-value, its effect was interpreted as weak.

All analyses were performed using R version 4.0.5 (R Core Team, 2021) and necessitate LME4 (Bates et al., 2015), GLMMADMB (Skaug et al., n.d.; Fournier et al., 2012), PERFORMANCE (Lüdecke et al., 2021), MuMIn (Barton, 2020), DHARMA (Hartig, 2021) and EMMEANS (Lenth, 2021) R packages.

2.4.2 | Life-history traits

All individuals older than 1 year were considered adults and analysed together, while younger individuals (hereafter named juveniles) were analysed separately. We analysed the clutch size, yearly survival probability and body growth rate (Table S1). The clutch sizes were analysed separately for each sex because (i) the reproductive strategy of each sex may differ with respect to the experimental treatments and (ii) to avoid testing for four-way interactions (i.e. climate×connectivity×time×sex). The clutch sizes of males were obtained via paternity analyses, and the results are presented in Appendix B. We used generalized mixed models with a binomial distribution for survival (n = 997 for juveniles and n = 639 for adults), with zero-inflated Poisson distribution for the clutch size (n = 141 for female juveniles, n = 179 for female adults, n = 130 for male juveniles and n = 156 for male adults) and linear mixed models for body growth (n = 278 for juveniles and n = 334 for adults). All models included climate treatments, connectivity treatments, number of year since population initialization (hereafter reffered to as 'time') as a continuous variable and their three-way interaction. The models

for the clutch size of juveniles did not converge with the three-way interaction due to a low number of reproductive juveniles and so this interaction was removed.

Models further included covariates known to influence life-history traits: body size (e.g. Cotto et al., 2015) for all analyses, sex (e.g. Bestion, Teyssier, et al., 2015) for survival and body growth analyses and birth date (e.g. Bestion, Teyssier, et al., 2015) in Julian days in the analyses on juveniles. Random intercepts included mesocosm identity, individual identity for analyses on adults and family identity for the analyses on juveniles as siblings were not independent.

In the connected treatment, juvenile and adult dispersal statuses (i.e. disperser or resident, n = 116 for juveniles and n = 113 for adults) were analysed (Table S1). The models included climate treatments, time, their interaction, body size and the interaction between body size and climate treatments, as body size strongly influences dispersal decisions, costs and benefits (Cote et al., 2007). Random structure only included mesocosm identity because models did not converge when individual identity was included, due to the low number of dispersers. Note that the mesocosm identity of an individual could change from 1 year to the other if the given individual dispersed.

2.4.3 | Mean age, body size and population size

We used generalized mixed models with Poisson distribution to analyse population size (n = 47) and mean age of individuals composing the populations (n = 617), and linear mixed models for individuals' mean body size (n = 617). For all models, the fixed effects were climate treatment, connectivity treatment, time and their three-way interaction. The fixed time effect estimates the temporal pattern of population dynamics, rather than controlling for temporal autocorrelation in our data. Nevertheless, we checked for potential temporal autocorrelation in the residuals of the final models (i.e. Durbin–Watson test and ACF plot). All tests revealed no autocorrelation in the residuals. All the data at time 0 (i.e. before climate treatment) were excluded from the analyses and when a population was reinitialized after extinction, time was set at 0. Models for population size also included mesocosm identity as a random intercept to take into account the repeated model structure (Table S2).

For individuals' mean age and body size (Table S2), the models were run at the individual level and included mesocosm and individual identities as random intercepts to account for the non-independency of individuals of the same population and the multiple occurrences of individuals over time. We also included sex and population density as fixed effects to control for the indirect effects of the treatments on age and body size structure through their effects on sex ratio and density. The age of the individuals was also included in the body size analysis to disentangle the direct effect of climate on body size from its indirect effect through age structure changes. The same model without age was additionally run (Table S7).

2.5 | Ethics statement

The Station d'Ecologie Théorique et Expérimentale has a national agreement for use of animals in the laboratory (number B09583), and our experiments are made in accordance with French ethics regulations (Ethics permits number APAFIS#15897-2018070615164391 v3 for toe clipping and APAFIS#19523-201902281559649 v3 for other experimental procedures, including the maintenance of lizards in the Metatron). The lizards were initially captured in the wild under licence numbers 2010-189-16 DREAL and 2013-274-0002.

3 | RESULTS

3.1 | Life-history traits

Climatic conditions differently influenced the reproduction of 1-year-old female juveniles in connected and isolated populations (Figure 2a, Table S3). Female juveniles had more offspring in warmer conditions than in present-day climates in isolated populations only (Figure 2a, Table S3, Table 1). In contrast, the reproduction of adult females and males was weakly influenced by climatic conditions and connectivity (Figure 2b for females, Figure S1 for males, Table S4), as climate treatments seldom appeared in averaged best models and had a very low estimate or a low RI (Figure 2b, Figure S1, Table 1, Tables S3 and S4).

The body growth rate of juveniles separately varied with climatic conditions, habitat connectivity and time, despite a very weak three-way interaction between climate, connectivity and time in the best average model (Figure S2a, Table S3). Separate analyses per connectivity treatment showed a positive influence of warm climates, the difference between present-day and warm climates increasing over time in isolated habitats and a weaker influence in connected habitats (Figure S2a, Table S5). Moreover, juveniles grew more in connected habitats than in isolated habitats (Figure S2a, Table S3). Both climate and connectivity treatments appeared in the best averaged model of adult growth rate, even though their influences on adult growth rate were weak (Figure S2b, Table S3).

Finally, warm climates had no effect on juvenile survival probability, while juvenile survival probability increased across time in the connected treatment but decreased over time in the isolated treatment (Figure 2c, Table S3). Separate analyses per connectivity treatment showed a weak positive effect, increasing over time, of warm climates on juvenile survival in isolated populations only (Table 1). Climatic conditions influenced adult survival differently in isolated and connected populations and differently over time (Figure 2d, Table S3). In isolated populations, warmer conditions decreased adult survival probability and this effect vanished over time (Figure 2d, Table 1). The same effect was observed in connected populations in the first year, but adult survival probability in present-day conditions then dropped, resulting in higher adult survival in warmer conditions later on (Figure 2d, Table 1). Habitat connectivity also had a negative effect on adult survival probability that was more pronounced later in the experiment (Table S3).
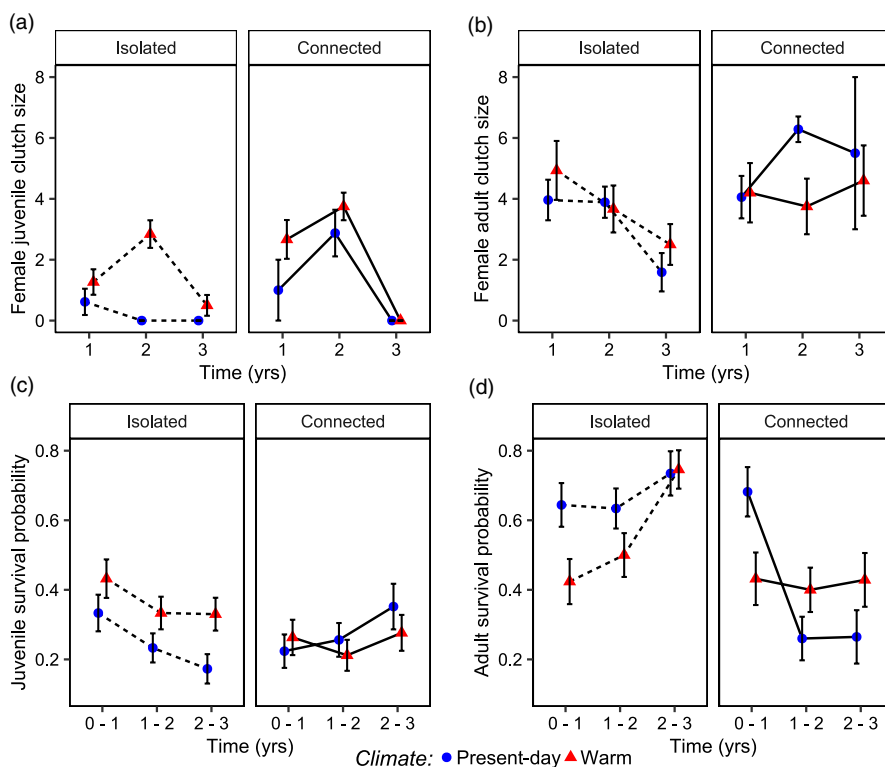

FIGURE 2 Female juvenile clutch size (a), female adult clutch size (b), juvenile survival probability (c), adult survival probability (d), through time in isolated (dashed lines) and connected (solid lines) habitats under present-day (blue circles) and warm climate (red triangles). Mean ± SE are represented.

TABLE 1 Effects of climatic conditions on clutch size of juveniles ($n = 85$, pseudo-$R^2 = 0.349$ and $n = 56$, pseudo-$R^2 = 0.100$) and adults ($n = 120$, pseudo-$R^2 = 0.104$ and $n = 59$, pseudo-$R^2 = 0.080$) and survival probability of juveniles ($n = 548$, $R^2_c = 0.416$, $R^2_m = 0.105$ and $n = 449$, $R^2_c = 0.235$, $R^2_m = 0.004$) and adults ($n = 365$, $R^2_c = 0.254$, $R^2_m = 0.049$ and $n = 274$, adjusted-$R^2 = 0.074$) in isolated and connected populations. Estimates for climate and sex are given for warm climate and males respectively

	Isolated populations					Connected populations				
	Estimate	SE	z-value	RI	p-value	Estimate	SE	z value	RI	p-value
Clutch size of female juveniles										
Intercept	−2.19	0.53	−4.13	1	<0.001	1.24	0.24	5.084	1	<0.001
Time						−0.37	0.21	1.716	0.4	0.086
Climate	1.89	0.41	4.62	1	<0.001					
Birth date						−0.19	0.12	1.509	0.3	0.131
Body size	1.61	0.24	6.8	1	<0.001	0.22	0.14	1.569	0.53	0.117
Random effect										
Clutch size of female adults										
Intercept	1.63	0.06	24.90	1	<0.001	1.72	0.07	26.03	1	<0.001
Time	−0.10	0.06	1.76	0.72	0.079					
Climate	0.11	0.10	1.11	0.28	0.267					
Body size	0.16	0.06	2.77	1	0.006	0.16	0.08	2.16	1	0.031
Random effect										
Survival probability of juveniles										
Intercept	−1.60	0.56	2.88	1	0.004	−1.31	0.20	6.46	1	<0.001
Time	−0.38	0.24	1.56	0.73	0.118	0.08	0.15	0.56	0.16	0.574
Climate	0.92	0.76	1.21	0.57	0.200	0.06	0.29	0.22	0.14	0.83
Birth date	−0.18	0.14	1.28	0.28	0.009					
Body size	0.41	0.16	2.61	1	0.227	−0.03	0.14	0.23	0.14	0.821
Sex						0.15	0.24	0.61	0.17	0.541
Time×Climate	0.48	0.25	1.90	0	0.057					
Random effect	+(1|Mesocosm ID)+(1|Family ID)					(1|Family ID)				
Suvivalprobability of adults										
Intercept	−0.05	0.45	0.12	1	0.908	−0.71	0.23	−3.12	1	0.002
Time	−0.33	0.22	1.48	0.64	0.140	−0.85	0.21	−4.05	1	<0.001
Climate	−0.26	0.67	0.38	0.64	0.701	0.14	0.26	0.55	1	0.582
Sex	0.57	0.24	2.33	1	0.020	0.58	0.27	2.17	1	0.030
Time×Climate	0.69	0.28	2.49	0.64	0.013	0.79	0.27	2.96	1	0.003
Random effect	+(1|Mesocosm ID)									

3.2 | Dispersal

In connected populations, adult individuals were more likely to disperse from present-day than from warm climates (Figures S3b and S4b, Table 2). However, this effect varied with their body size. Adults leaving present-day climate habitats were smaller than those staying and conversely in warm climate habitats (Figure S5b, Table 2). In contrast, there was no significant effect of the climatic conditions on the dispersal rate and phenotype of juvenile dispersers (Figures S3–S5, Table 2).

3.3 | Mean traits and population size

Climatic conditions influenced the mean age of individuals composing populations differently in isolated and connected habitats

(Figure 3a, Table S6, Table 3). Separate analyses showed that populations in warmer conditions are made up of younger individuals compared with present-day climates in isolated populations only (Figure 3a, Table 3). Individual's mean age decreased over time in connected populations independently of climates (Figure 3a, Table S6, Table 3).

The mean body size of individuals depended mainly on climatic conditions and less on the interaction with time and connectivity (Figure 3b, Table S6). The interactions between climate and connectivity and between time and connectivity were retained in the best model, but with weak influence (Table S6). Individuals were bigger in warm compared with present-day climates in both connectivity conditions, but this effect increased over time in connected populations (Figure 3b, Table 3). Without individuals' age in the model, a marginal three-way interaction between climate, connectivity and

TABLE 2 Effects of climatic conditions and body size on emigration probability of juveniles ($n = 116$, $R^2_c = 0.287$, $R^2_m = 0.145$) and adults ($n = 113$, adjusted-$R^2 = 0.224$). Estimates for climate and sex are given for warm climate and males respectively

|	Juveniles					Adults				
	Estimate	SE	z-value	RI	p-value	Estimate	SE	z-value	RI	p-value
Emigration probability										
Intercept	−1.27	0.55	2.29	1	0.022	−1.54	0.50	3.07	1	0.002
Time	−0.17	0.32	0.54	0.25	0.588	−0.15	0.33	0.47	0.5	0.640
Climate	−0.72	0.78	0.91	0.18	0.361	−1.43	0.62	2.27	1	0.024
Body size	−0.40	0.32	1.21	0.62	0.226	−0.67	0.44	1.50	1	0.133
Sex	0.78	0.51	1.53	0.48	0.126	1.25	0.61	2.03	0.8	0.042
Time × Body size	0.56	0.32	1.71	0.18	0.088	−0.65	0.33	1.93	0.5	0.053
Climate × Body size						1.82	0.64	2.83	1	0.005
Random effect	+(1|Mesocosm ID)									
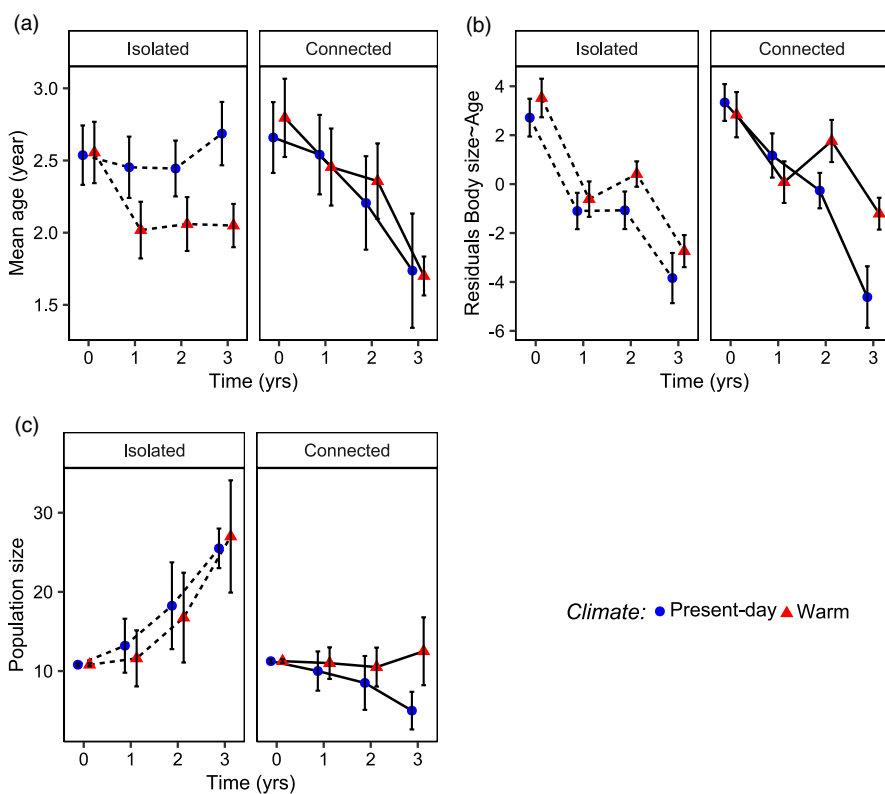
FIGURE 3 Age (a), residuals of the linear model body size ~ age (b) and population size (c) through time in isolated (dashed lines) and connected (solid lines) habitats under present-day (blue circles) and warm climates (red triangles). Mean ± SE are represented.

time appeared in the best models (Figure S6, Table S7). The climatic effect persisted in connected populations, with an increasing effect over time, while there was an overall decrease in body size with time in isolated populations (Figure S6, Table S7).

Finally, population size depended on habitat connectivity, time and their interaction, as well as on the climate and the interactions between time and climate (Figure 3c, Table S6). Habitat isolation and warmer conditions both had a positive influence over time on population size (Figure 3c, Table 3, Table S6). However, separate analyses for each connectivity treatment showed that the positive effect of warming was restricted to connected habitats (Figure 3c, Table 3).

4 | DISCUSSION

Our 3-year-long experiment showed that warm climates led to a faster pace of life, with increased growth, earlier reproductive onset and reduced survival of older individuals in isolated populations and as a consequence to a shift in the population structure towards younger and bigger individuals with no effect on population size. However, the consequences of warm climates were considerably altered by landscape connectivity. Indeed, we found that populations that were connected displayed no differences in age structure between climates while the density of present-day populations became lower than the density of warm populations. These differences

TABLE 3 Effect of climatic conditions on individuals' age ($n = 391$, $R^2_c = 0.285$, $R^2_m = 0.040$ and $n = 226$, $R^2_c = 0.241$, $R^2_m = 0.030$), body size ($n = 391$, $R^2_c = 0.825$, $R^2_m = 0.529$ and $n = 226$, $R^2_c = 0.861$, $R^2_m = 0.546$) and population size ($n = 23$, $R^2_c = 0.856$, $R^2_m = 0.044$ and $n = 24$, $R^2_c = 0.580$, $R^2_m = 0.334$), in isolated and connected populations. Estimates for climate and sex are given for warm climate and males respectively

	Isolated populations					Connected populations				
	Estimate	SE	z-value	RI	p-value	Estimate	SE	z value	RI	p-value
Age										
Intercept	0.82	0.07	12.31	1	<0.001	0.67	0.07	9.57	1	<0.001
Time	0.11	0.05	2.25	1	0.025	−0.11	0.05	2.02	0.84	0.043
Climate	−0.23	0.09	2.67	1	0.008					
Density	−0.08	0.05	1.63	0.67	0.102	−0.04	0.05	0.67	0.18	0.502
Sex	0.06	0.09	0.74	0.21	0.460	0.11	0.11	1.05	0.25	0.293
Random effect	+(1|Ind ID)					+(1|Ind ID)				
Body size										
Intercept	0.10	0.07	1.35	1	0.177	0.23	0.14	1.70	1	0.089
Time	−0.04	0.04	0.96	0.36	0.335	−0.18	0.07	2.52	0.7	0.012
Climate	0.23	0.09	2.48	1	0.013	0.17	0.17	0.98	0.7	0.329
Age	0.72	0.04	17.12	1	<0.001	0.67	0.05	14.02	1	<0.001
Density	−0.10	0.04	2.81	1	0.005	−0.04	0.05	0.78	0.22	0.437
Sex	−0.63	0.09	6.97	1	<0.001	−0.74	0.10	7.16	1	<0.001
Time×Climate						0.22	0.09	2.59	0.7	0.010
Random effect	+(1|Ind ID)					(1|Mesocosm ID)+(1|Ind ID)				
Population size										
Intercept	2.47	0.24	10.51	1	<0.001	2.06	0.18	10.80	1	<0.001
Time	0.16	0.05	3.05	1	0.002	−0.27	0.11	2.35	0.42	0.019
Climate						0.41	0.22	1.75	0.72	0.081
Time×Climate						0.33	0.14	2.20	0.42	0.028
Random effect	+(1|Mesocosm ID)					+(1|Mesocosm ID)				

may be due to asymmetrical dispersal between warm and present-day climates, with respect to dispersal rate and the phenotype of dispersers.

The accelerated pace of life in warm and isolated populations is highly consistent with the patterns previously observed after a single year (Bestion, Teyssier, et al., 2015) and were maintained over 3 years in the present study. Warm climate likely increased juvenile growth rate through a faster metabolism (Gillooly et al., 2001) and the onset and outcomes of reproduction in juveniles through a larger body size, a trigger of reproduction in this species (Cotto et al., 2015). However, the positive effect of warm climates on juvenile reproductive outcome was still detected when controlling for individuals' body size, suggesting that body growth rate was not the only driver of enhanced juvenile reproduction in warm climates. This effect might have consequences on survival later in life, as shown in natural populations where investment in first reproduction is associated with decreased survival with age (Cotto et al., 2015; Massot et al., 2011). Lower adult survival in warmer climates is likely related to restriction of activity during warm hours of the day, more than a direct effect of overheating, as the microclimatic variation within a mesocosm provides for potential hiding spots during heatwaves

(Bestion, Teyssier, et al., 2015). Warmer temperatures could therefore favour individuals with a faster pace of life (Brans & De Meester, 2018), increasing development rate, promoting reproductive success and reducing life span. This shift in life-history traits led to populations composed of younger individuals in warm climates.

Changes in mean population age were not associated with decreased mean body size, yet a smaller body size has been advocated to be the third universal ecological response to climate change in both correlative and theoretical studies (Daufresne et al., 2009; Gardner et al., 2011; Sheridan & Bickford, 2011). Our results are not consistent with this general pattern or with the temperature-size rule (see Appendix C), rather we even found a positive effect of warm climate on body size when controlling for age. This pattern seems to be general among studies on common lizards as long-term monitoring of their natural populations revealed a positive effect of climate change on body size (Chamaillé-Jammes et al., 2006), while a similar effect was seen in tropical lizards *Tropidurus torquatus* (Piantoni et al., 2019), suggesting that the positive response of body size to climate warming could be widespread among lizards. One potential explanation for this discrepancy might come from the diet generalism of the common lizard (Avery, 1966): predators with a diverse diet

could compensate for their increased metabolic rate under climate change by shifting their diet towards bigger prey, therefore continuing to grow after maturity (Sheridan & Bickford, 2011).

We did not observe any influence of climate-dependent life-history traits on the population size of isolated populations. At large spatial scales, the effect of climate change on ectotherm density is predicted to depend on the geographic location, with populations at higher latitudes benefiting from warmer climates whereas those at lower latitudes should decrease in density (Deutsch et al., 2008; Tewksbury et al., 2008). In our study, the positive effect of warm climates on reproductive success of young individuals was offset by its negative effect on adult survival and therefore no change in population size was observed. Using data extracted from two 1-year-long warming experiments, Bestion, Teyssier, et al. (2015) predicted population extirpations at the southern margin due to climate change in 20 years, because of the higher sensitivity of population growth rate to adult survival than to the fecundity of 1-year-old individuals. We did not observe the expected population decline in our 3-year-long experiment. The effect of climatic conditions on adult survival rate even vanished in the last year of experiment, possibly due to the adaptation of adult lizards to warm climates or because of the cooler climate in the last year (Figure 1b). Nevertheless, a recent study on natural lizard populations of *Tropidurus torquatus* reported that climate warming may favour population growth by promoting the growth of juveniles and earlier reproduction, while having no influence on an individual's life span (Piantoni et al., 2019). Accordingly, it has been shown that maternal effects may reduce the cost of warm climates on life span, while still promoting higher juvenile growth (Hao et al., 2021). Longer experiments are still needed to disentangle the short-term effect of warmer conditions on population dynamics and life-history traits from its long-term effect.

The impacts of climatic conditions on life-history traits and population dynamics further vary with the connectivity among habitats. When individuals had access to a cooler microclimate, the effect of warm climates on population age structure was offset. In connected habitats, the positive effects of warm climates on juvenile growth rate, reproductive outputs and survival were weaker compared with isolated populations, while the negative effect of warm climate on adult survival that we observed in isolated habitats was reversed in connected habitats. In continuous landscapes, individuals can access warm and cool microclimates more easily, and thus avoid temporary extreme climate events (e.g. heatwaves; Scheffers et al., 2014; Suggitt et al., 2018) and may take advantage of warmer environments without incurring the costs. Intra-annual movements between microclimates may buffer the effect of warm climates on population dynamics. In our study, we recorded individual position once a year. Nevertheless, temporary movements (e.g. seasonal movements) were possible and might have allowed individuals in warm climates to take temporary refuge in cooler habitats.

Dispersal movements (i.e. more definitive movements) could however influence population dynamics through (i) emigration and immigration rates (Burgess & Marshall, 2011) and (ii) the characteristics of dispersers (Clobert et al., 2009). We showed that both

processes occurred and could explain our results. First, we observed a strongly biased dispersal in adults from present-day climate populations to warm climate populations. The flow of individuals influenced population dynamics by cancelling the difference in the mean age of individuals between the two climates and by reducing population size in present-day climates. Indeed, this biased dispersal was more pronounced in adults than in juveniles and could have both decreased the population size and the mean age in connected populations of present-day climates. We could have expected adults to disperse more from warm climates given the lower survival. However, 1.4°C warmer conditions may appear attractive and beneficial for an ectotherm species, while the costs of living there (i.e. physiological exhaustion, heatwave) may not be easy to predict for a candidate disperser. Second, we found that movements were non-random regarding phenotypic traits and could have reduced the difference in body size between climatic conditions. Adult immigrants from warm climates were larger than their resident counterparts, whereas the opposite was true in present-day climates. Several hypotheses may explain this climate-dependent dispersal syndrome. Because metabolism and energy needs depend on the interplay between temperature and body size (Speakman, 2005), warmer conditions may impose additional costs for larger individuals, through enhanced energetic expenditure, stronger competition and rare resources, while being beneficial for the growth of smaller individuals, in turn driving dispersal decisions. Alternatively, body size may be related to thermal type; ectotherm species may display a hot-cold continuum in phenotypic thermal adaptations (i.e. thermal types, Goulet et al., 2017) which may be part of phenotypic and pace-of-life syndromes ranging from *r*- to *K*-types, including body size and potentially linked to matching habitat choice (Bestion, Clobert, & Cote, 2015). Although further experiments are needed to uncover the mechanisms underpinning these dispersal syndromes, our results show that the connectivity among microhabitats altered the impact of warm climates on population dynamics.

Increasing efforts have recently been made to improve our understanding of climate impacts on natural populations and to better predict their future dynamics, but few studies have investigated the combined effect of different drivers of global change on biodiversity (Brook et al., 2008; Comte et al., 2016; Hof et al., 2011; Jetz et al., 2007; Opdam & Wascher, 2004; Warren et al., 2001). Here, we demonstrated the complex interacting effect of climate change and habitat fragmentation on the population dynamics of common lizards. While climate change is not spatially homogeneous (Ashcroft et al., 2009), maintenance of connectivity could buffer the impact of warm climates on population dynamics by allowing access to refuge areas (Scheffers et al., 2014; Suggitt et al., 2018). However, we showed that these movements between microclimates could be costly in terms of density for populations less impacted by climate warming. Accounting for the central role of demography in local adaptation and range shift (i.e. eco-evolutionary dynamics, Pelletier et al., 2009), landscape structure may shape population and species responses to climate change (Rutschmann, Miles, Le Galliard, et al., 2016). Integrative studies

taking into account climate change and landscape structure on population dynamics and its link to adaptation are therefore needed to improve our understanding of anthropogenic impacts on biodiversity.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All the data and R scripts used in the present manuscript are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.p5hqbzksf (Pellerin et al., 2022).

ORCID

Félix Pellerin https://orcid.org/0000-0002-7062-4957
Elvire Bestion https://orcid.org/0000-0001-5622-7907
Laurane Winandy https://orcid.org/0000-0001-6255-2503
Murielle Richard https://orcid.org/0000-0003-2135-8194
Robin Aguilée https://orcid.org/0000-0002-3388-9921
Julien Cote https://orcid.org/0000-0002-4453-5969

REFERENCES

Armsworth, P. R., & Roughgarden, J. E. (2005). The impact of directed versus random movement on population dynamics and biodiversity patterns. *The American Naturalist*, *165*(4), 449–465. https://doi.org/10.1086/428595

Ashcroft, M. B., Chisholm, L. A., & French, K. O. (2009). Climate change at the landscape scale: Predicting fine-grained spatial heterogeneity in warming and potential refugia for vegetation. *Global Change Biology*, *15*(3), 656–667. https://doi.org/10.1111/j.1365-2486.2008.01762.x

Avery, R. A. (1966). Food and feeding habits of the common lizard (*Lacerta vivipara*) in the west of England. *Journal of Zoology*, *149*(2), 115–121.

Barton, K. (2020). *MuMIn: Multi-model inference*. https://cran.r-project.org/package=MuMIn

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Bestion, E., Clobert, J., & Cote, J. (2015). Dispersal response to climate change: Scaling down to intraspecific variation. *Ecology Letters*, *18*(11), 1226–1233. https://doi.org/10.1111/ele.12502

Bestion, E., Jacob, S., Zinger, L., Di Gesu, L., Richard, M., White, J., & Cote, J. (2017). Climate warming reduces gut microbiota diversity in a vertebrate ectotherm. *Nature Ecology & Evolution*, *1*, 161. https://doi.org/10.1038/s41559-017-0161

Bestion, E., Soriano-Redondo, A., Cucherousset, J., Jacob, S., White, J., Zinger, L., Fourtune, L., Di Gesu, L., Teyssier, A., & Cote, J. (2019). Altered trophic interactions in warming climates: Consequences for predator diet breadth and fitness. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1914), 20192227. https://doi.org/10.1098/rspb.2019.2227

Bestion, E., Teyssier, A., Richard, M., Clobert, J., & Cote, J. (2015). Live fast, die young: Experimental evidence of population extinction risk due to climate change. *PLoS Biology*, *13*(10), e1002281.

Bonte, D., Van Dyck, H., Bullock, J. M., Coulon, A., Delgado, M., Gibbs, M., Lehouck, V., Matthysen, E., Mustin, K., Saastamoinen, M., Schtickzelle, N., Stevens, V. M., Vandewoestijne, S., Baguette, M., Barton, K., Benton, T. G., Chaput-Bardy, A., Clobert, J., Dytham, C., … Travis, J. M. J. (2012). Costs of dispersal. *Biological Reviews*, *87*(2), 290–312.

Boudjemadi, K., Lecomte, J., & Clobert, J. (1999). Influence of connectivity on demography and dispersal in two contrasting habitats: An experimental approach. *Journal of Animal Ecology*, *68*(6), 1207–1224. https://doi.org/10.1046/j.1365-2656.1999.00363.x

Bowler, D. E., & Benton, T. G. (2005). Causes and consequences of animal dispersal strategies: Relating individual behaviour to spatial dynamics. *Biological Reviews*, *80*(2), 205–225. https://doi.org/10.1017/S1464793104006645

Brans, K. I., & De Meester, L. (2018). City life on fast lanes: Urbanization induces an evolutionary shift towards a faster life style in the water flea daphnia. *Functional Ecology*, *32*(June), 2225–2240. https://doi.org/10.1111/1365-2435.13184

Brook, B. W., Sodhi, N. S., & Bradshaw, C. J. A. (2008). Synergies among extinction drivers under global change. *Trends in Ecology & Evolution*, *23*(8), 453–460. https://doi.org/10.1016/j.tree.2008.03.011

Burgess, S. C., & Marshall, D. J. (2011). Are numbers enough? Colonizer phenotype and abundance interact to affect population dynamics. *Journal of Animal Ecology*, *80*(3), 681–687. https://doi.org/10.1111/j.1365-2656.2010.01802.x

Burnham, K. P., Anderson, D. R., & Huyvaert, K. P. (2011). AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons. *Behavioral Ecology and Sociobiology*, *65*(1), 23–35. https://doi.org/10.1007/s00265-010-1029-6

Chamaillé-Jammes, S., Massot, M., Aragon, P., & Clobert, J. (2006). Global warming and positive fitness response in mountain populations of common lizards Lacerta vivipara. *Global Change Biology*, *12*(2), 392–402.

Charmantier, A., McCleery, R. H., Cole, L. R., Perrins, C., Kruuk, L. E. B., & Sheldon, B. C. (2008). Adaptive phenotypic plasticity in response

to climate change in a wild bird population. *Science (New York, N.Y.)*, *320*(5877), 800–803.

Chen, I.-C., Hill, J. K., Ohlemueller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science (New York, N.Y.)*, *333*(6045), 1024–1026. https://doi.org/10.1126/science.1206432

Clobert, J., Galliard, L., Cote, J., Meylan, S., & Massot, M. (2009). Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecology Letters*, *12*(3), 197–209. https://doi.org/10.1111/j.1461-0248.2008.01267.x

Comte, L., Hugueny, B., & Grenouillet, G. (2016). Climate interacts with anthropogenic drivers to determine extirpation dynamics. *Ecography*, *39*(10), 1008–1016. https://doi.org/10.1111/ecog.01871

Cote, J., Clobert, J., & Fitze, P. S. (2007). Mother–offspring competition promotes colonization success. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(23), 9703–9708.

Cotto, O., Massot, M., Ronce, O., & Clobert, J. (2015). Dispersal as a source of variation in age-specific reproductive strategies in a wild population of lizards. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1820), 20151741. https://doi.org/10.1098/rspb.2015.1741

Daufresne, M., Lengfellner, K., & Sommer, U. (2009). Global warming benefits the small in aquatic ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(31), 12788–12793. https://doi.org/10.1073/pnas.0902080106

Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghalambor, C. K., Haak, D. C., & Martin, P. R. (2008). Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(18), 6668–6672.

Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, *34*(1), 487–515. https://doi.org/10.1146/annurev.ecolsys.34.011802.132419

Fournier, D. A., Skaug, H. J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M. N., Nielsen, A., & Sibert, J. (2012). AD model builder: Using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optimization Methods and Software*, *27*, 233–249.

Fryxell, D. C., Hoover, A. N., Alvarez, D. A., Arnesen, F. J., Benavente, J. N., Moffett, E. R., Kinnison, M. T., Simon, K. S., & Palkovacs, E. P. (2020). Recent warming reduces the reproductive advantage of large size and contributes to evolutionary downsizing in nature: Warming leads to evolutionary downsizing. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1928), 20200608. https://doi.org/10.1098/rspb.2020.0608rspb20200608

Gardner, J. L., Peters, A., Kearney, M. R., Joseph, L., & Heinsohn, R. (2011). Declining body size: A third universal response to warming? *Trends in Ecology and Evolution*, *26*(6), 285–291. https://doi.org/10.1016/j.tree.2011.03.005

Gérard, M., Marshall, L., Martinet, B., & Michez, D. (2021). Impact of landscape fragmentation and climate change on body size variation of bumblebees during the last century. *Ecography*, *44*(2), 255–264.

Gillooly, J. F., Brown, J. H., West, G. B., Savage, V. M., & Charnov, E. L. (2001). Effects of size and temperature on metabolic rate. *Science (New York, N.Y.)*, *293*(5538), 2248–2251.

Goulet, C. T., Thompson, M. B., Michelangeli, M., Wong, B. B. M., & Chapple, D. G. (2017). Thermal physiology: A new dimension of the pace-of-life syndrome. *Journal of Animal Ecology*, *86*(5), 1269–1280. https://doi.org/10.1111/1365-2656.12718

Hao, X., Zou, T., Han, X., Zhang, F., & Du, W. (2021). Grow fast but don't die young: Maternal effects mediate life-history trade-offs of lizards under climate warming. *Journal of Animal Ecology*, *90*(6), 1550–1559.

Hartig, F. (2021). *DHARMa: Residual diagnostics for hierarchical (multi-level/mixed) regression models.* https://cran.r-project.org/package=DHARMa

Hof, C., Araújo, M. B., Jetz, W., & Rahbek, C. (2011). Additive threats from pathogens, climate and land-use change for global amphibian diversity. *Nature*, *480*(7378), 516–519.

Jetz, W., Wilcove, D. S., & Dobson, A. P. (2007). Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biology*, *5*(6), 1211–1219. https://doi.org/10.1371/journal.pbio.0050157

Kalinkat, G., Schneider, F. D., Digel, C., Guill, C., Rall, B. C., & Brose, U. (2013). Body masses, functional responses and predator-prey stability. *Ecology Letters*, *16*(9), 1126–1134. https://doi.org/10.1111/ele.12147

Le Galliard, J. F., Marquis, O., & Massot, M. (2010). Cohort variation, climate effects and population dynamics in a short-lived lizard. *Journal of Animal Ecology*, *79*(6), 1296–1307. https://doi.org/10.1111/j.1365-2656.2010.01732.x

Legrand, D., Guillaume, O., Baguette, M., Cote, J., Trochet, A., Calvez, O., Zajitschek, S., Zajitschek, F., Lecomte, J., Bénard, Q., Le Galliard, J.-F., & Clobert, J. (2012). The Metatron: An experimental system to study dispersal and metaecosystems for terrestrial organisms. *Nature Methods*, *9*(8), 828–833.

Lenth, R. V. (2021). *Emmeans: Estimated marginal means, aka least-squares means.* https://cran.r-project.org/package=emmeans

Lüdecke, D., Ben-Shachar, M. S., Patil, I., Waggoner, P., & Makowski, D. (2021). Assessment, testing and comparison of statistical models using R. *Journal of Open Source Software*, *6*(59), 3112. https://doi.org/10.31234/osf.io/vtq8f

Masson-Delmotte, V., Zhai, P., Pirani, A., Connors, S. L., Péan, C., Berger, S., Caud, N., Chen, Y., Goldfarb, L., Gomis, M. I., Huang, M., Leitzell, K., Lonnoy, E., Matthews, J. B. R., Maycock, T. K., Waterfield, T., Yelekçi, O., Yu, R., & Zhou, B. (2021). IPCC, 2021: Climate change 2021: The physical science basis. In *Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change.* Cambridge University Press. https://doi.org/10.1260/095830507781076194

Massot, M., Clobert, J., & Ferriere, R. (2008). Climate warming, dispersal inhibition and extinction risk. *Global Change Biology*, *14*(3), 461–469.

Massot, M., Clobert, J., Montes-Poloni, L., Haussy, C., Cubo, J., & Meylan, S. (2011). An integrative study of ageing in a wild population of common lizards. *Functional Ecology*, *25*(4), 848–858. https://doi.org/10.1111/j.1365-2435.2011.01837.x

Milling, C. R., Rachlow, J. L., Olsoy, P. J., Chappell, M. A., Johnson, T. R., Forbey, J. S., Shipley, L. A., & Thornton, D. H. (2018). Habitat structure modifies microclimate: An approach for mapping fine-scale thermal refuge. *Methods in Ecology and Evolution*, *9*(6), 1648–1657. https://doi.org/10.1111/2041-210X.13008

Nakagawa, S., Johnson, P. C. D., & Schielzeth, H. (2017). The coefficient of determination R^2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *Journal of the Royal Society Interface*, *14*(134), 20170213.

Oliver, T. H., Marshall, H. H., Morecroft, M. D., Brereton, T., Prudhomme, C., & Huntingford, C. (2015). Interacting effects of climate change and habitat fragmentation on drought-sensitive butterflies. *Nature Climate Change*, *5*(10), 941–945.

Opdam, P., & Wascher, D. (2004). Climate change meets habitat fragmentation: Linking landscape and biogeographical scale levels in research and conservation. *Biological Conservation*, *117*(3), 285–297. https://doi.org/10.1016/j.biocon.2003.12.008

Pearson, R. G. (2006). Climate change and the migration capacity of species. *Trends in Ecology & Evolution*, *21*(3), 111–113. https://doi.org/10.1016/j.tree.2005.11.022

Pellerin, F., Bestion, E., Winandy, L., Di Gesu, L., Richard, M., Aguilée, R., & Cote, J. (2022). Data from: Connectivity among thermal habitats buffers the effects of warm climate on life-history traits and population dynamics. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.p5hqbzksf

Pelletier, F., Garant, D., & Hendry, A. P. (2009). Eco-evolutionary dynamics. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1523), 1483–1489. https://doi.org/10.1098/rstb.2009.0027

Piantoni, C., Navas, C. A., & Ibargüengoytía, N. R. (2019). A real tale of Godzilla: Impact of climate warming on the growth of a lizard. *Biological Journal of the Linnean Society*, *126*(4), 768–782. https://doi.org/10.1093/biolinnean/bly216

R Core Team. (2021). *R: A language and environment for statistical computing*. https://www.r-project.org/

Rutschmann, A., Miles, D. B., Clobert, J., & Richard, M. (2016). Warmer temperatures attenuate the classic offspring number and reproductive investment trade-off in the common lizard, *Zootoca vivipara*. *Biology Letters*, *12*(6), 20160101. https://doi.org/10.1098/rsbl.2016.0101

Rutschmann, A., Miles, D. B., Le Galliard, J. F., Richard, M., Moulherat, S., Sinervo, B., & Clobert, J. (2016). Climate and habitat interact to shape the thermal reaction norms of breeding phenology across lizard populations. *Journal of Animal Ecology*, *85*(2), 457–466. https://doi.org/10.1111/1365-2656.12473

Scheffers, B. R., Edwards, D. P., Diesmos, A., Williams, S. E., & Evans, T. A. (2014). Microhabitats reduce animal's exposure to climate extremes. *Global Change Biology*, *20*(2), 495–503. https://doi.org/10.1111/gcb.12439

Sheridan, J. A., & Bickford, D. (2011). Shrinking body size as an ecological response to climate change. *Nature Climate Change*, *1*(8), 401–406. https://doi.org/10.1038/nclimate1259

Sinervo, B., Mendez-De-La-Cruz, F., Miles, D. B., Heulin, B., Bastiaans, E., Villagrán-Santa Cruz, M., Lara-Resendiz, R., Martìnez-Méndez, N., Calderón-Espinosa, M. L., Meza-Lázaro, R. N., Gadsden, H., Avila, L. J., Morando, M., De la Riva, I. J., Sepulveda, P. V., Rocha, C. F. D., Ibargüengoytía, N., Puntriano, C. A., Massot, M., … Sites, J. W., Jr. (2010). Erosion of lizard diversity by climate change and altered thermal niches. *Science (New York, N.Y.)*, *328*(5980), 894–899.

Skaug, H., Fournier, D., Bolker, B., Magnusson, A., & Nielsen, A. (n.d.). *Generalized linear mixed models using "AD Model Builder"*.

Speakman, J. R. (2005). Body size, energy metabolism and lifespan. *Journal of Experimental Biology*, *208*(9), 1717–1730. https://doi.org/10.1242/jeb.01556

Suggitt, A. J., Wilson, R. J., Isaac, N. J. B., Beale, C. M., Auffret, A. G., August, T., Bennie, J. J., Crick, H. Q. P., Duffield, S., Fox, R., Hopkins, J. J., Macgregor, N. A., Morecroft, M. D., Walker, K. J., & Maclean, I. M. D. (2018). Extinction risk from climate change is reduced by microclimatic buffering. *Nature Climate Change*, *8*(8), 713–717. https://doi.org/10.1038/s41558-018-0231-9

Tewksbury, J. J., Huey, R. B., & Deutsch, C. A. (2008). Animals the scale of prediction. *Science (New York, N.Y.)*, *320*, 1296–1297.

Urban, M. C. (2015). Accelerating extinction risk from climate change. *Science (New York, N.Y.)*, *348*(6234), 571–573. https://doi.org/10.1126/science.aaa4984

Vindenes, Y., Edeline, E., Ohlberger, J., Langangen, Ø., Winfield, I. J., Stenseth, N. C., & Vøllestad, L. A. (2014). Effects of climate change on trait-based dynamics of a top predator in freshwater ecosystems. *The American Naturalist*, *183*(2), 243–256. https://doi.org/10.1086/674610

Warren, M. S., Hill, J. K., Thomas, J. A., Asher, J., Fox, R., Huntley, B., Roy, D. B., Telfer, M. G., Jeffcoate, S., Harding, P., Jeffcoate, G., Willis, S. G., Greatorex-Davies, J. N., Moss, D., & Thomas, C. D. (2001). Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature*, *414*, 65–69. https://doi.org/10.1038/35102054

Whitfield, S. M., Bell, K. E., Philippi, T., Sasa, M., Bolanos, F., Chaves, G., Savage, J. M., & Donnelly, M. A. (2007). Amphibian and reptile declines over 35 years at La Selva, Costa Rica. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(20), 8352–8356. https://doi.org/10.1073/pnas.0611256104

Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. Springer Science & Business Media.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.