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RESEARCH ARTICLE

Influence of landscape connectivity on newt's response to a warmer climate

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Abstract

Context Climate change and habitat fragmentation exert considerable pressures on biodiversity. The spatial distribution of microclimatic refuges in the landscape can influence species responses to warming climates.

Objectives Using a semi-natural experiment, we investigated the potential synergetic effects of climate warming and habitat connectivity on a single amphibian species.

Methods We monitored populations of the palmate newt, *Lissotriton helveticus*, under two climate treatments, a warmer climate (+ ~ 2 °C) or a present-day climate, in mesocosms either isolated or connected to the other climatic conditions. We assessed the abundance and phenotype (snout-vent length, body condition and skin coloration: darkness and redness) of juvenile and adult newts, and the dispersal propensity of juveniles.

Results Over the 4 years of climatic manipulation, populations tended to increase more in the present-day than in the warmer climate. Warmer climates decreased the abundance of adult newts and altered the phenotypic composition of populations with darker and less red newts. However, connectivity between the two climates cancelled out the effect of a warmer climate on abundance and reversed the effects on phenotype composition. We further found that juvenile newts from the present-day climate treatment tended to emigrate more from warmer conditions during our laboratory dispersal assay and that population isolation disrupted a common covariation between emigration propensity and body size, leg length and skin darkness.

Conclusions Our results point to a synergetic effect of climate warming and fragmentation on the demography of newt populations and emigration decisions of juveniles, suggesting that microclimate refuges and their accessibility play a key role in buffering the

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impacts of climate warming, with potential implications for amphibian diversity at a regional scale.

Keywords Amphibian · Global warming · Dispersal syndrome · Habitat fragmentation · Microclimate

Introduction

Global warming is one of the largest human-induced disturbances of natural ecosystems affecting biodiversity worldwide (Díaz et al. 2019) and could lead to the extinction of 5 to 37% of all species (Urban 2015). Direct evidence of warming-induced population extinction is scarce (Román-Palacios and Wiens 2020) because organisms may respond to climate change through phenotypic plasticity, selection or relocation (McGaughran et al. 2021). Climate change is indeed already changing the phenotypic composition and life history traits of populations (Merilä and Hendry 2014), with phenological shifts occurring in many species (Parmesan and Yohe 2003) and an accelerated pace of life in ectotherm species (Bestion et al. 2015b; Burraco et al. 2020), for example. These changes can alter population dynamics and increase the risk of population extinction, but they can also facilitate species persistence under new conditions (Pellerin et al. 2022). Phenotypic plasticity and genetic selection can result in behavioral, physiological and/or morphological adaptations to prevent extinction (Huey et al. 2012). A notable and widespread example of phenotypic plasticity is thermal acclimation, which allows species to extend their tolerance to higher temperatures (Seebacher et al. 2014).

Species can also shift their geographic range through dispersal towards suitable climatic conditions at higher latitudes and/or elevations (Lenoir and Svenning 2015). Highly mobile organisms, such as birds and butterflies, can travel long distances to locate suitable climatic conditions, while other taxa, such as amphibians and reptiles, are more limited in their movement. These less mobile species need much more time to disperse to distant cooler habitats (Sillero 2021), and may instead use locally variable habitats (i.e., microclimate refugia, Suggitt et al. 2018). The survival of these organisms could therefore be more dependent on successful short-distance movements across climatically heterogeneous environments. Heterogeneous landscapes can offer a high variety of microclimates (Milling et al. 2018), some of which are similar to conditions at higher latitude or elevation, and these conditions can buffer the consequences of extreme temperatures (i.e., extirpation, Scheffers et al. 2013; Suggitt et al. 2018). Dispersal therefore plays a central role in species' ability to locate habitats that meet their thermal requirements at regional or local scales (Bestion et al. 2015a). Yet dispersal among microclimates may vary by phenotype, and particularly by thermal requirements. Individuals with lower thermal requirements might disperse towards cooler microhabitats, while more thermally tolerant individuals tend to remain in or search for warmer environments (Bestion et al. 2015a; Pellerin et al. 2019). So-called adaptive dispersal syndrome (Clobert et al. 2009) can lead to climate-induced shifts in phenotypic distributions, with consequences for population persistence.

Climate-driven dispersal is structured by the spatial distribution of microclimate habitats, which are becoming increasingly fragmented due to human activities (Opdam and Wascher 2004). By reducing landscape connectivity, fragmentation may impede individual movements from temporarily or permanently local detrimental conditions to refuge areas, and may force some species to move longer distances. We therefore expect climate warming and habitat fragmentation to act synergistically to modify population responses to climate change (Opdam and Wascher 2004). However, empirical evidence of this phenomenon is scarce (Urban et al. 2014), necessitating new experimental approaches to test for the combined effects of habitat fragmentation and spatial variability in climate on dispersal.

As ectotherms, amphibians are particularly sensitive to climate change because their body temperature, and hence their physiological functions, strongly depend on environmental temperatures (Urban 2015). Moreover, the limited dispersal abilities of many amphibians restrict their options to relocate to optimal climates at regional scales, making them even more threatened by climate change (Urban et al. 2014). Yet thermal acclimation through phenotypic plasticity can potentially reduce the impact of climate change. Previous studies show that newts' locomotor activity, heat tolerance and metabolism rate can be acclimated to higher temperatures (Gvoždík et al. 2007; Winterová and Gvoždík 2021). At a morphological level, changing body size has emerged in many organisms as a response to climate warming but remains underexplored in amphibians (Li et al. 2013). Melanin-based coloration plays an important role in thermoregulation in many animals, with individuals of varying darkness presenting different levels of sensitivity to climate change: while dark skin may provide protection against UV-radiation, it can also increase the risk of overheating (Roulin 2014). In amphibians, skin coloration also results from carotenoid pigments (Mochida et al. 2013), which are acquired through diet and are associated with improved individual fitness and may prevent pro-oxidative effects of enhanced UV (Ogilvy and Preziosi 2012; Mochida et al. 2013). However, predicting the impact of climate change in accordance with color traits depends mostly on the adaptive function of the coloration and how it covaries with physiology and behavior in the studied species (Roulin 2014). For example, darkness is positively correlated to boldness, exploration and dispersal in some species (Mafli et al. 2011; Mateos-Gonzalez and Senar 2012; Roulin 2014; Saino et al. 2014) and would be expected to influence their responses to climate change, particularly in fragmented landscapes.

Here, we experimentally assessed the interaction between warmer climate and landscape connectivity on the abundance, phenotypic distribution and movement strategy of the palmate newt (*Lissotriton helveticus*). We monitored populations of palmate newts inhabiting 24 semi-natural mesocosms undergoing either a warmer (+ ~ 2 °C) or a present-day climatic treatment across multiple years. Two mesocosms, one for each set of climatic conditions, were paired and either isolated or connected with corridors. We assessed the impact of these conditions on juvenile and adult population abundance and phenotypic traits. We predicted newt abundance would be lower in warm and isolated populations, where newts could not evade the warming temperatures. We also measured morphological traits (body size, body condition), coloration (darkness and redness) and dispersal propensity and their covariation with temperature and phenotype. We predicted phenotypic differences between newts experiencing different climatic conditions, particularly in isolated populations, where the lack of connectivity prevents them from evading warming temperatures. More specifically, we predicted a reduction in body size and body condition at warmer temperatures, as has been shown in previous studies (Reading 2007). We expected that thermal stress would decrease the red coloration, while the expected effects on skin melanism were less clear since darkness of color can have either positive (UV protection) or negative (overheating risk) effects on thermoregulation.

Finally, we measured the emigration propensity of juvenile newts at two temperatures in a laboratory setting and its covariation with phenotypic traits (i.e., dispersal syndrome). We expected newts coming from present-day climate populations to emigrate more from warmer temperatures than newts that were exposed initially to warmer conditions (i.e., from warmer climates), suggesting that newts coming from warmer climates would be acclimated to warmer temperatures. While emigrants are expected to have greater body and leg length and to be darker (e.g., Winandy et al. 2019), we expected challenging environmental conditions experienced in warm and/or isolated populations to disrupt dispersal syndrome (e.g., Cote et al. 2017, 2022), possibly inciting all individuals to emigrate regardless of phenotype (Legrand et al. 2015).

Material and methods

Model species

The palmate newt (*Lissotriton helveticus*) is a small salamandridae (i.e., tailed amphibian) occurring in a wide range of habitats in Europe, from wooded to more open areas such as meadows, field edges and gardens. The palmate newt has an aquatic larval stage before undergoing metamorphosis into terrestrial juveniles. Juveniles usually stay on land for 2 to 3 years before reaching sexual maturity and returning to the water to breed. Adult newts have strictly aquatic reproduction and remain in the water during the mating period which lasts several months. As home ranges of newts are quite small ($< 50{,}000$ m^2 (Verell 1987)), aquatic breeding sites must be close to the terrestrial habitat (Joly and Miaud 1989). Breeding sites range from small puddles to larger ponds or even lakes and are usually stagnant, permanent or filled with water for at least 3 months covering the period of reproduction and larval development. On land, newts are usually found sheltering under logs or stones or in small burrows.

Study site and experimental design

The study took place in the Station d'Ecologie Théorique et Expérimentale in Moulis (France). The Station has a national agreement for use of animals in the laboratory (number B09583), and our experiments were conducted in accordance with French ethics regulations (Ethics permit number APAFIS#30486-2021031815341692v4). The newts were caught in the Metatron under license number 09-2016-02. At the end of the experiment, they were released exactly where they were caught, following recommendations of the permit.

For this study, we used populations of palmate newts naturally occurring in the Metatron, which is a system of 48 semi-natural and interconnected mesocosms in which climatic conditions can be manipulated (Legrand et al. 2012). Mesocosms are large (10×10 m), delimited by tarpaulins buried 30 cm into the ground, and fully enclosed with a net allowing the isolation of each enclosure. This system prevents both the escape of the study species and predation from birds and snakes present outside of the Metatron. Each mesocosm acts as a mini-ecosystem of a wet meadow with dense natural vegetation, two permanent pools ($30\times50\times15$ cm), shelters (logs and rocks) and large invertebrate communities. They therefore offer all the ecological features required for the different life stages of palmate newts. Temperature, light intensity and hygrometry in each enclosure are monitored every 30 min and can be manipulated using motor-driven shutters and a sprinkler system. In addition, mesocosms can be connected by 19 m-long corridors allowing species to move between mesocosms. Newts usually exhibit strong breeding site fidelity, with individuals frequently returning to their natal site (Joly and Miaud 1989) and thus movements between mesocosms and breeding patches could be considered as dispersal (Clobert et al. 2009). While breeding adult newts usually disperse between twenty to a few hundred meters (Cayuela et al. 2018; Denoël et al. 2018), natal dispersal distances are unknown and likely higher as juvenile newts wander on land for several years (Pittman et al. 2014). While the corridor length in the mesocosms does not allow for distinguishing dispersal from migration movements, the harsh conditions in corridors (i.e., a narrow width devoid of shelter and/or puddles) make the crossing challenging for newts and ensures that movements between mesocosm are not routine foraging movements (Fronhofer et al. 2018).

In this study, we used 24 mesocosms in which we applied the climatic treatment for 4 years (2013–2017) and the connectivity treatments for 2 years (2015–2017). The climatic treatment was created with shutters that automatically closed above certain temperature thresholds: 28 °C for the present-day climate and 38 °C for the warm climate. Mesocosms were intrinsically warmer than outside because of the greenhouse effect associated with the nets. The present-day climate treatment created temperatures similar to the mean temperature outside of the Metatron (Bestion et al. 2015a). Since climatic treatments depended on outdoor climatic conditions, they were efficient only during daytime in summer (from mid-June to October), with variation within and between days. This resulted in a 1–2 °C difference in mean summer daily temperatures between the present-day and warm climates from June 2013 to July 2017 ($\chi^2_1=77.12$, $P<0.001$, the mean ± SE are 26.49 ± 0.10 °C and 27.76 ± 0.11 °C for present-day and warm climate treatments respectively). There was also a 2–3 °C difference of the summer maximum temperature ($\chi^2_1=135.62$, $P<0.001$, the mean ± SE are 29.43 ± 0.13 °C and 31.88 ± 0.20 °C for present-day and warm climate treatments respectively). 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). While most global warming studies focus on the effects of a strict increase in mean temperatures, an increase in the magnitude of daily temperature fluctuation (i.e., difference between the maximum and the minimum day temperature) is also predicted (Thompson et al. 2013). Accordingly, in our study, there was also an effect of treatments on the difference between the maximum and the minimum temperature during summer ($\chi^2_1=124.96$, $P<0.001$, the mean ± SE are 15.39 ± 0.15 °C and 17.94 ± 0.20 °C for present-day and warm climate treatment respectively). During the climate treatment, all mesocosm were watered with soft water every day in the evening to avoid a drying effect of the treatment.

We used 12 pairs of present-day and warm climate mesocosms that were either connected by opening the corridor between them (i.e., for connected treatment) or not to simulate habitat fragmentation (i.e., isolated treatment). The six pairs of each connectivity treatment were randomly distributed across the system.

Population monitoring in the Metatron

After the construction of the Metatron in 2009, all mesocosms remained open for an entire year and, between 2010 and 2012, for 2–3 weeks a year to allow colonization by local species (e.g., plants, insects, amphibians, mollusks) present on the site. The palmate newts within habitats around the Metatron rapidly colonized and established themselves inside the mesocosms. In 2012, the 24 mesocosms were closed for a long-term experiment on common lizards (see Bestion et al. 2015b; Pellerin et al. 2022) and migration to and from the mesocosms was thus impossible. The climatic treatment began in 2013 while the connectivity treatment began in 2015. Newt abundance in each mesocosm was estimated annually beginning in 2013 with a standardized sampling effort. Our climate treatments were only applied in the summer (from the end of June to the beginning of October) and during the warmest times of the day, while our sampling took place in the early mornings in June, prior to climate treatments. Consequently, we assumed our probability of detection did not differ across climate treatments. Between 2013 and 2016, the sampling consisted of two observers searching for newts in the vegetation during 10 min on the four sides of each mesocosm, where newts were localized due to the presence of moss providing moist conditions.

In June 2017, we estimated newt abundance with a more thorough sampling. To estimate juvenile newt abundance, we did three sessions (on different days) of standardized sampling early in the morning, when there was still morning dew and juvenile newts were more active. Each capture session was conducted by the same two people searching for newts for 10 min in each mesocosm. After each session, all newts captured were brought back to the lab. As described above, the climate treatment was not applied during early June and dawn was coolest and wettest part of the day, thus we assumed that there was no difference in detection probability between treatments during sampling. Yet the large size of the mesocosm and the dense vegetation cover likely prevented detection and capture of all juvenile newts. Therefore, the number of captured juveniles in this study represents an estimate of abundance that is comparable between treatments due to equal sampling effort.

With respect to adult newts, we ran two capture sessions on different days by dipnetting for 5 min in each of the two pools available to newts in each mesocosm. In June, most adults inhabit water for reproduction purposes. Given the small size of the pools (30×50×15 cm), we were confident of capturing all adults present in the water at that time. Therefore, we feel that our abundance estimates are likely to match the actual number of adults in each mesocosm.

Housing conditions and phenotype assessment

From the sampling above, we kept 67 randomly selected juvenile newts from 16 mesocosms in the lab: 31 newts were from seven mesocosms in warm climate (n = 15 in isolated and n = 16 in connected treatments); 36 newts were from nine mesocosms in present-day climate (n = 18 in isolated and n = 18 in connected treatments). The remaining juveniles were released back to the mesocosms after a maximum of 3 days spent in the lab. The 67 juveniles were identified using dorsal and ventral pictures (see below) and housed in individual terraria (25×15.5×15 cm) filled with natural moss, an egg carton as a shelter, and a small pool (3 cm diameter 1 cm depth). Newts were fed five micro-crickets (2–3 mm, *Acheta domestica*) daily. A natural neon light provided light from 9am to 7pm and the temperature of the room was set at 18 °C, which is in the range of preferential temperatures for European newts (Balogová & Gvoždík 2015; Gvoždík 2015). All terraria were sprayed with water twice a day to maintain a high humidity level. Juvenile newts were housed in common environmental conditions for 2 weeks prior the dispersal test (see below) to reduce the effect of stressful new condition on their emigration rate.

We also randomly selected 86 adult newts: 32 from nine mesocosms with the warm climate (n = 6 in isolated and n = 26 in connected treatments); 54 from 10 mesocosms with the present-day climate (n = 28 in isolated and n = 26 in connected treatments). Adult newts were kept in the lab to measure morphological traits for several days before being released back in the mesocosms. Newts were housed in aquaria (35 cm L×18 cm l×20 cm water deep) with a maximum of four individuals from the same mesocosm per aquarium. We provided a shelter and an egg laying substrate (strips of filter paper) and fed individuals 50 mg of thawed *Chironomus* larvae per newt daily to create optimal conditions for palmate newts during aquatic reproduction.

Morphological traits

We measured snout-vent length and total length of newts using a ruler (measurement to the mm) and weighed (to 0.001 g) the selected newts (n = 67 juveniles and n = 86 adults) on the day of their capture. The body mass of newts highly depends on their degree of hydration, so we made sure to weigh fully hydrated newts. Adult newts in their aquatic phase, are obviously fully hydrated. For the juveniles, just after capture, they were maintained in boxes filled with soaked paper towels, ensuring their proper hydration. We calculated the body condition of newts using the mass/snout-vent length residuals. We took ventral and dorsal photographs to assess skin coloration of the 67 juveniles. However, due to a technical issue we were only able to photograph 27 adult newts [warm climate: 12 newts from 7 mesocosms (2 in isolated and 10 in connected treatments), present-day climate: 15 newts from 7 mesocosms (9 in isolated and 6 in connected treatments)]. For photographs, each newt was carefully positioned on a computer scanner (Canon CadoscanLide110) lined with high density foam to avoid injuries. Photographs were taken at a resolution of 400 dpi and analyzed using ImageJ software. We delimited a zone for the dorsal (from the top of the neck to the posterior legs) and ventral areas (from the throat to the posterior legs). The photographs were transformed in shades of grey and then in black and white according to a fixed grey threshold of 60 chosen to maximize variance in darkness among individuals. A mean grey value and a percentage of black pixels in each zone were computed. We further extracted HSL values (Hue Saturation Lightness). Hue, often referred to as ‘color’ (i.e., the difference between green, red or blue), corresponds to the angular position on a color circle where 0° corresponds to red. Saturation refers to the intensity of a hue, from grey tone (scored as 0) to pure and vivid color (scored as 1). Lightness is the luminance (a photometric measure of the luminous intensity per unit area of light travelling in a given direction) ranging from dark (scored as 0) to light (scored as 1). On the ventral images we also measured hindlimb length (to the nearest mm) of juvenile newts, as leg length is a locomotor trait potentially linked to emigration propensity (Denoël et al. 2018; Winandy et al. 2019).

Using the FactoMinR package (Lê et al. 2008), adult and juvenile darkness was scored with Principal Component Analyses (PCA) on the mean grey, the percentage of black pixels, and the lightness values of both dorsal and ventral photographs (mean and variance scaled). In adults, the PC1 axis explained 52.6% of variance, had an eigenvalue of 3.16, and was positively correlated to dorsal and ventral lightness and mean grey, and negatively correlated to the percentage of black pixels (Table S1). In juveniles, the PC1 axis explained 57.3% of variance, had an eigenvalue of 3.43, and was positively correlated to dorsal and ventral lightness and mean grey, and negatively correlated to the percentage of black (Table S1). To obtain a darkness score ranging from pale to dark, we multiplied scores by − 1.

We scored the red coloration of juvenile newts with PCA using the dorsal and ventral hue and saturation values (variance and mean scaled). The PC1 axis explained 54.4% of variance, had an eigenvalue of 2.17, and was positively correlated to dorsal and ventral hue, and negatively correlated to ventral and dorsal saturation (Table S1). To obtain a redness score (Fig. 1), from grey tone yellow to pure red, we multiplied scores by − 1. We did not measure redness in adult newts as they have a beige-brown coloration.

Emigration propensity

Emigration propensity was assessed only in juvenile newts two weeks after their capture, allowing a period of acclimation to common garden conditions in the laboratory. We used eight experimental systems placed in a greenhouse with controlled temperature and natural light for this experiment. Each system was made of two 130 L plastic containers 78 × 56 × 43 cm) connected by a circuitous plastic pipe (diameter: 10 cm, total length: 4.4 m). The departure container was filled with soil litter, with several terrestrial shelters and a pool (25 cm diameter, filled with water and natural moss). The corridor (plastic pipe) was directly connected to the departure container and filled with a thin layer of moist soil. To go from the departure to the arrival containers, juvenile newts had to enter the plastic pipe (i.e., the corridor) and fall into the arrival container which was filled with natural moss. Once in

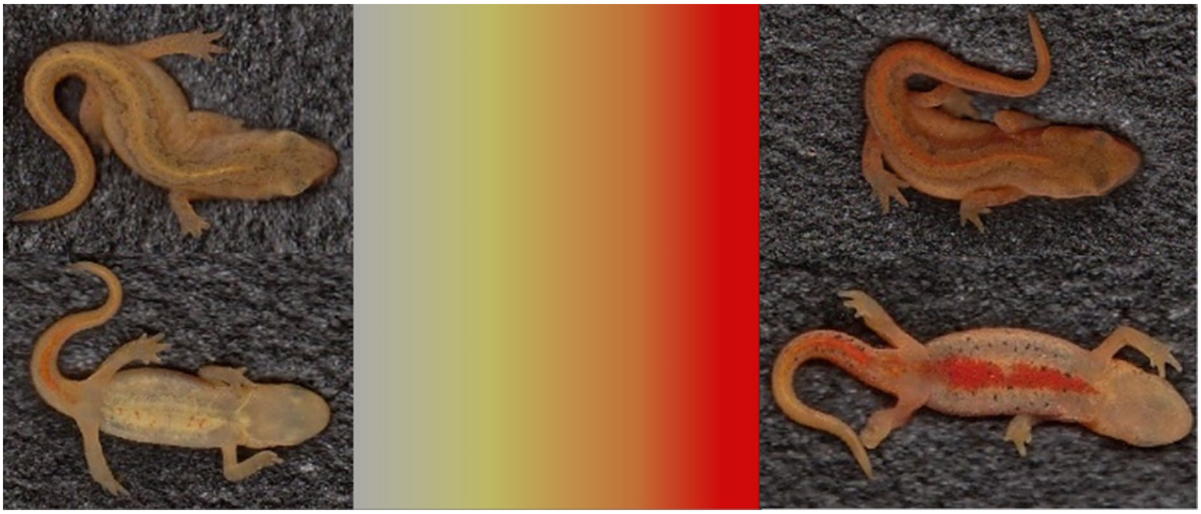

Fig. 1 Coloration of juvenile newts. Redness scores scale from high hue and low saturation (grey-tone yellow coloration) to low hue and high saturation (pure red), photography by L. Winandy

the arrival container, newts could not re-enter the corridor. This system has been used in previous studies to assess palmate newt's emigration decisions (Fronhofer et al. 2018; Cote et al. 2022). Here we measured the emigration probability of each individual at two different temperature regimes: a warm temperature (with a daytime temperature of 30.7 ± 0.27 °C and a nighttime temperature of 24.6 ± 0.07 °C), and a cooler temperature (with a daytime temperature of 22.83 ± 0.18 °C and a nighttime temperature of 20.6 ± 0.3 °C). These temperatures corresponded to local natural temperatures at this time of the year (i.e., in July).

Assays were run on small groups (4–5 newts per system) to prevent high density in departure populations. We carried out two temporal replicates of eight experimental groups each. Juvenile newts from each climatic treatment and mesocosm were homogenously distributed between the temporal replicates. Half of the newts were tested first at the cooler temperature and the other half were tested first at the warmer temperature. Replicates were done several days apart, and the moss and water pools were changed to limit the risk of scent remaining inside the system. 10 days after the first assays, we repeated the assay under the other temperature treatment. For each assay, groups of newts were released in the departure tank in the late afternoon for a 24-h acclimation period to the system and thermal conditions. Food (micro-crickets) was available ad libitum in the departure tank. During the acclimation period, the dispersal pipes were closed to prevent any stress-induced movement from the departure tank. We then opened the pipes for one night as juvenile newts usually move from dusk to dawn. The next morning, we closed all dispersal pipes, captured residents and emigrants (i.e., newts found in departure and arrival tanks, respectively) and identified individuals using the ventral and dorsal photographs. No newts were found inside the dispersal pipes.

Statistical analysis

Abundance

Firstly, we ran a generalized linear mixed model (GLMM) using a poisson family (with a log link function) to assess the effect of climatic treatments (warm vs. present-day) on the evolution of newt abundance across years (from 2013 to 2017). The mesocosm identity (Mesocosm_ID) was included as a random intercept. Since the connectivity treatment only began in summer 2015, we checked that there was no prior effect of this treatment on newt abundance using a a generalized linear model (GLM), using a quasipoisson family to correct for overdispersion, and testing the effect of connectivity treatment (isolated vs.

connected) and its interaction with climatic treatment on newt abundance every year from 2013 to 2015.

Secondly, we analyzed abundance in 2017, in which sampling was more extensive than previous sampling and took place after 2 years of connectivity treatment. We ran a GLM using a quasipoisson family for adult and juvenile abundance, testing the effect of the climate treatments, the connectivity treatment, and their interaction as fixed effects. Since mesocosms were not seeded with the same number of individuals prior to the start of the experiment, we added the abundance of newts in 2013 as a covariate. For juvenile abundance, we also added the adult abundance as a covariate to prevent multiple testing issues as juvenile and adult abundances should be positively correlated.

Phenotype

We ran linear mixed models (LMM) for morphological traits [body size (i.e., snout-vent length), body condition (i.e., mass/size residuals) and darkness for adults and juveniles plus leg length (using leg length/body size residuals) and red coloration for juveniles]. All models included the climate treatments, the connectivity treatment, and their interaction as fixed effects. The mesocosm identity (Mesocosm_ID) was included as a random intercept. For adult body size and body condition, the sex and its interaction with treatments were included. Redness and darkness were positively correlated ($F_{1,65} = 18.91$; $P < 0.001$), so for both variables we used the residuals of the regression models (residuals of redness on darkness for the redness variable and darkness/redness residuals for the darkness variable) to obtain an independent analysis of color parameters. For coloration traits, we also added body size (i.e., snout-vent length) as a covariate in the models.

Emigration probability

We used a generalized linear mixed model (GLMM) with a binomial error distribution and a logit link function for the emigration status of juveniles (i.e., 0 = resident, 1 = emigrant), with climate, connectivity, and temperature treatments during the emigration assay and all interactions between these factors as fixed effects. Individual identity (Newt_ID), experimental group (Group_ID) and the mesocosm identity (Mesocosm_ID) were added as random intercepts. The order of passage (warm or cooler temperature first) as well as the temporal replicate (i.e., first or second block of eight experimental groups) did not affect the emigration rate ($\chi^2_1 = 0.355$, $P = 0.552$; $\chi^2_1 = 0.624$, $P = 0.43$, respectively) and were therefore removed from the model to avoid over parameterization.

Dispersal syndromes

We performed a multivariate analysis of variance (MANOVA) to assess the effects of treatments and emigration status on newt phenotypes. The dependent variables were body size, leg length (using leg length/body size residuals), darkness (using darkness/redness residuals), and redness (using redness/darkness residuals). These variables were centered and scaled. Fixed effects included climate treatment, connectivity treatment, and their interactions with the emigration status. In a second step, we ran univariate analysis on the four traits separately.

General procedure

Analyses were performed in R 3.5.1 (www.r-project.org). We checked model assumptions by visually screening the residuals for normality and homoscedasticity. Body size for adult newts and body condition for juvenile newts were log-transformed to achieve normality. We used lme4 (Bates et al. 2008) and sjstats (Lüdecke and Lüdecke 2019) packages for all models and estimated the significance of factors with Wald χ^2 and likelihood ratio tests. We used a backward selection procedure (with a priori level of significance of 0.05) to remove non-significant interactions and covariates, while keeping the main factors of interest (i.e. the climatic and connectivity treatments) in the models. After the model selection, we used the performance package (Lüdecke et al. 2021) to calculate adjusted R^2 for GLMs and conditional R^2 (R^2_c, effect of the fixed and random effects) and marginal R^2 (R^2_m, effect of the fixed effect) for LMMs and GLMMs. For mixed models, when the variance of a random effect was equal to 0 (i.e., $R^2_c = NA$), the random variable of concern was removed from the model and the adjusted R^2 was calculated if there were no more random variables included in the model. When we found a significant interaction between climate and connectivity treatments, we investigated the influence of climate in each connectivity treatment by separately running the models for each connectivity treatment.

Results

Abundance

During the 4 years of study, we found no effect on abundance from the climate treatment ($\chi^2_1 = 0.201$, $P = 0.65$). However, we found a strong effect for the specific year ($\chi^2_4 = 330.331$, $P < 0.001$), showing an increase of newt abundance over time and a marginal interaction between year and climate treatment ($\chi^2_4 = 8.834$, $P = 0.065$), with newt abundance increasing slightly more in the present-day climate than in the warm climate (Fig. 2A). The conditional and marginal R^2 of the model were $R^2_c = 0.889$ and $R^2_m = 0.36$, respectively, and the variance of the mesocosm identity was 1.532 ± 1.238SD. Before 2017, there was no effect of connectivity treatment or any interaction with climate treatment on newt abundance ($P > 0.2$ for all years from 2013 to 2015, see Table S2 for details).

In 2017, over all mesocosms, we captured 187 juvenile newts and 118 adults (52 males and 66 females, see Table S3 for details on the number of newts captured in each mesocosm). We captured 80% of adults in the water during the first session and 13% during the second session. Only 7% of adults were captured on land during the 3 sessions of juvenile sampling (i.e. $n = 8$; 4 newts in each climate treatment), confirming that finding adult newts on land was rare at this time of the year. We found an interaction between the effects of climate and connectivity treatments on the abundance of adult newts (Table 1). In isolated populations, newt abundance was much lower in the warm climate treatment than in the present-day treatment (Fig. 2B; $\chi^2_1 = 7.182$, $P = 0.007$), while there was no difference in the connected populations (Fig. 2B; $\chi^2_1 = 0.13$, $P = 0.718$). We found no effect of treatment on juvenile abundance, but there was a positive relationship between juvenile and adult abundance (Table 1). The abundance of adult newts in 2013 and 2017 were positively correlated, but the abundance of adults in 2013 and juvenile abundance in 2017 were not related (Table 1).

Phenotypic differences

The climate and connectivity treatments alone or in interaction did not influence body size, leg length or body condition of adult or juvenile newts (Table S4). Adult newts were significantly darker in warm than

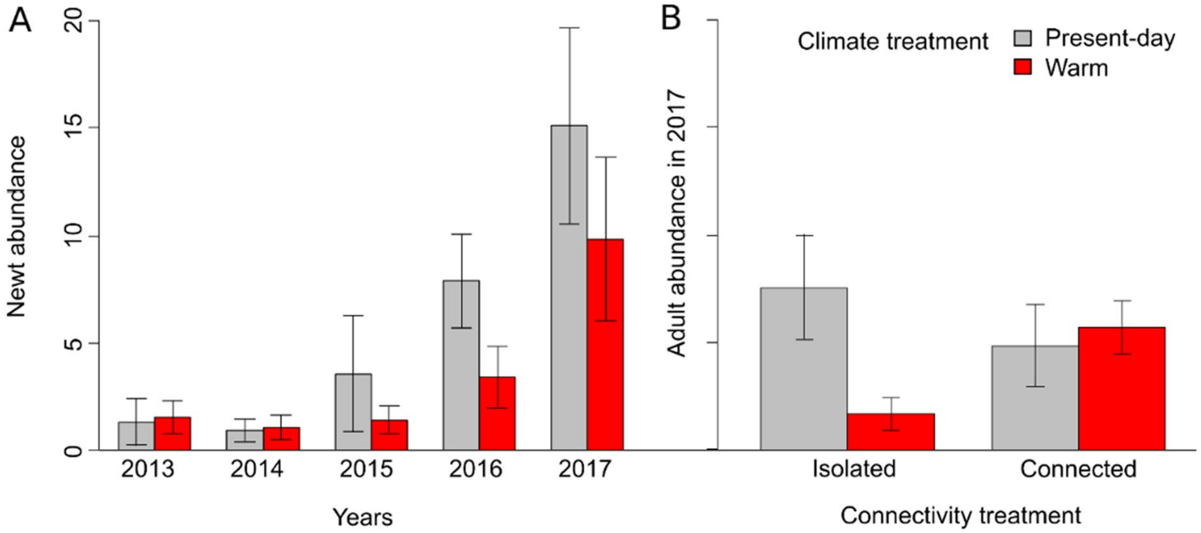

Fig. 2 Effect of climate treatments (mean ± SE) on newt abundance across years (**A**), and of climate and connectivity treatments on adult newt abundance in 2017 (**B**)

Table 1 Results of GLM (after backward selection procedure) testing the effect of climate treatment, connectivity treatment, and their interaction on the abundance of adult ($R^2_{adj}=0.903$) and juvenile newts ($R^2_{adj}=0.227$) in 2017

Newt stage	Factors	Estimates	χ^2_1	CI (95%)	P
Adults	Climate	4.4527	0.948	(1.721, 10.719)	0.330
	Connectivity	3.093	1.382	(0.238, 8.397)	0.190
	Climate*Connectivity	– 6.667	4.262	(– 13.377, – 0.385)	0.039
	Abundance in 2013	1.092	7.629	(0.04, 0.24)	0.006
Juveniles	Climate	– 0.657	0.815	(– 12.823, 9.129)	0.367
	Connectivity	– 0.834	1.839	(– 20.371, 4.624)	0.175
	Adult abundance	0.156	7.279	(0.114, 0.173)	0.007
	Abundance in 2013	0.063	0.574	(– 0.10, 0.25)	0.449

Estimates for climate and connectivity are given for the present-day climate and the connected population, respectively

in present-day climates (Table 2, Fig. 3A), while connectivity treatments had no effect (Table 2). There was an interaction between climate and connectivity treatments on juvenile darkness (Table 2, Fig. 3B): in connected populations, newts were darker in the present-day climate than in the warm climate ($\chi^2_1=4.564$, $P=0.033$). However this was not the case for isolated populations ($\chi^2_1=0.740$, $P=0.39$). There was an interaction between climate and connectivity treatments on juveniles' redness (Table 2, Fig. 3C): in isolated populations, newts were redder in the present-day climate than in the warm climate ($F_{1,31}=6.462$, $P=0.016$), while in connected populations newts tended to be redder in the warm climate than in the present-day climate ($F_{1,32}=2.764$, $P=0.106$). Body size had no effect on coloration traits in adults or in juveniles ($P>0.1$ in all models) and was therefore removed during model selection.

Emigration probability and dispersal syndromes

While connectivity treatments had no effect on emigration probability and dispersal syndromes, we found a marginal interaction between climate and assay temperature treatments (Table 3, Fig. 4), showing that newts coming from the present-day climates tended to emigrate more often in warm conditions than in cooler conditions, but that the difference was not significant ($\chi^2_1=2.300$, $P=0.129$). Newts coming from the warm climate emigrated similarly in warm and cooler conditions ($\chi^2_1=0.512$, $P=0.474$).

The multivariate analysis revealed a significant interaction between emigration status and connectivity treatment (Table 4, Fig. 5). Compared to residents in connected populations, emigrants were bigger (Fig. 5A), had longer legs (Fig. 5B), and were darker (Fig. 5C), while in isolated populations they had shorter legs (Fig. 5B) and were redder (Fig. 5D). The univariate analyses showed that this interaction was particularly significant for darkness and leg length (Table 4). Emigrants were darker than residents in connected populations ($F_{(1,65)}=4.39$, $P=0.04$, Fig. 5A) but not in isolated populations ($F_{(1,58)}=0.90$, $P=0.347$, Fig. 5A). Emigrants had slightly but non-significantly longer legs than residents in connected populations ($F_{(1,65)}=2.44$, $P=0.123$), Fig. 5B), while in isolated populations emigrants had slightly shorter legs than residents ($F_{(1,55)}=3.80$, $P=0.056$, Fig. 5B). The univariate analysis also revealed that emigrants tended to be redder than residents (mean ± SE 0.21 ± 0.14 and -0.44 ± 0.29, respectively, Table 4). Finally, the univariate analysis also revealed a marginal interaction between climate treatment and emigration status on leg length (Table 4). In the warm climate, residents tended to have longer legs than emigrants (mean ± SE 0.45 ± 0.010 and 0.42 ± 0.010, respectively, $F_{(1,56)}=3.21$, $P=0.079$), while residents and emigrants had similar leg length in the present-day climate (mean ± SE 0.40 ± 0.01 and 0.43 ± 0.01, respectively; $F_{(1,67)}=0.41$, $P=0.526$).

Discussion

Using experimental mesocosms to simulate natural habitats, we investigated whether population and phenotypic responses of palmate newts to a ~ 2 °C warmer climate depended on the connectivity

Table 2 Results of LMM (after backward selection procedure) testing the effect of climate treatment, connectivity treatment, and their interaction on the darkness of adults (n = 27, $R^2_c = 0.350$, $R^2_m = 0.206$) and on darkness and redness of juveniles (n = 67, $R^2_c = 0.238$, $R^2_m = 0.083$ and $R^2_{adj} = 0.12$)

Newt coloration	Factors	Estimates	SE	Test value	CI (95%)	P
Adult darkness	Climate	− 1.609	0.781	$\chi^2_1 = 4.247$	(− 3.07, -0.15)	0.039
	Connectivity	0.180	0.790	$\chi^2_1 = 0.052$	(− 1.3, 1.66)	0.820
	1| Mesocosm_ID	Variance = 0.512 ± 0.716SD				
Juvenile darkness	Climate	− 0.928	0.742	$\chi^2_1 = 0.0004$	(− 2.23, 0.36)	0.985
	Connectivity	− 1.31	0.782	$\chi^2_1 = 0.269$	(− 2.68, 0.05)	0.604
	Climate* Connectivity	1.847	1.042	$\chi^2_1 = 3.968$	(0.04, 3.71)	0.046
	1| Mesocosm_ID	Variance = 1.35 ± 1.16SD				
Juvenile redness	Climate	1.125	0.430	$F_{1,63} = 0.739$	(0.27, 1.98)	0.393
	Connectivity	1.445	0.442	$F_{1,63} = 3.105$	(0.56, 2.33)	0.083
	Climate*Connectivity	− 1.703	0.602	$F_{1,63} = 8.002$	(− 2.91, -0.50)	0.006
	1| Mesocosm_ID	Variance = 0[a]				

Estimates for climate and connectivity are given for the present-day climate and for the connected population, respectively

[a]Since the variance of the mesocosm identity (Mesocosm_ID) was equal to 0 it was removed from the final model

between warmer and cooler habitats. We found that warmer climates negatively influenced the abundance of newts, altered the phenotype composition of populations, and influenced the emigration propensity in juvenile newts. As predicted, connectivity between thermal habitats negated or reversed these main effects and added a distinct effect on dispersal syndromes. Our results highlight the importance of considering habitat connectivity and microclimates in predicting species responses to warming climates.

Population abundance and phenotypic composition

Newt abundance decreased over 4 years in mesocosms with warmer climates as has been demonstrated in previous studies where climate warming reduced newt survival and increased the risk of

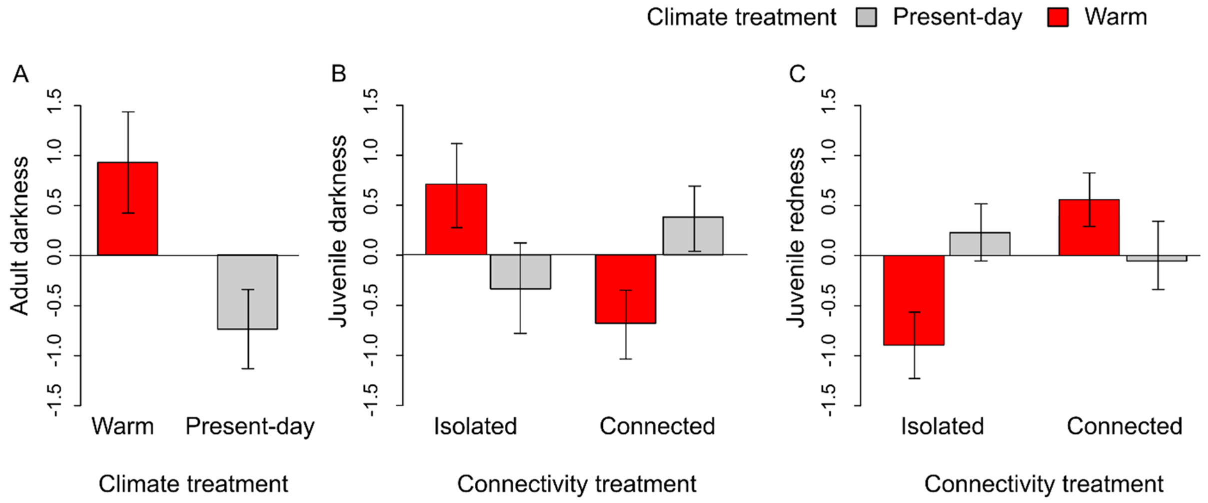

Fig. 3 Effect of treatments on newt coloration (mean ± SE): Effect of climate treatment (red bar for warm climate and grey bar for present-day climate) on adult newt darkness (**A**), and of climate and connectivity treatments on juvenile newt darkness (**B**) and on juvenile newt redness (**C**)

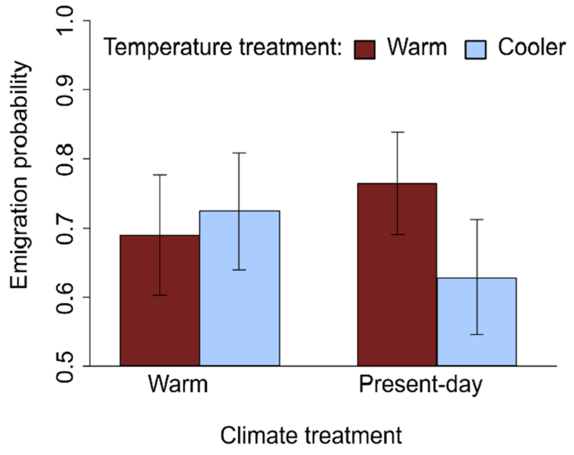

Fig. 4 Interactive effect of climate treatment and temperature treatment (i.e., applied during the emigration assay) on newt emigration probability (mean ± SE)

population extinction (Li et al. 2013; Weinbach et al. 2018). The change in newt abundance differed by life-stage, as only adult abundance was reduced in warmer climates. However, our results must be interpreted cautiously as our initial abundance estimates were based on natural colonization of newts rather than establishing standardized population sizes across all mesocosms. Nonetheless this initial abundance was not different across the two climate treatments and our results provide evidence suggesting a negative impact of warm climate on population growing over time. Warmer climates could have impacted adults more than juveniles because adults may not be able to compensate for the energy expenditures induced by warmer conditions. Indeed, unlike juveniles, adult newts may spend part of the summer in the aquatic habitat to avoid hot and dry conditions in the terrestrial habitat (Denoël 2006). However, such habitat shifts might include a cost in depletion of caloric reserves as the metabolic rate of newts is higher in water than on land (Kristín and Gvoždík 2014). Adults may therefore enter hibernation with a lower body condition, in turn impacting their survival. Alternatively, warm climates could provoke an ageing effect that could impact adult survival as observed in other ectotherms (reviewed in Burraco et al. 2020).

Previous studies have reported deleterious effects of hot summers on juvenile newt abundance, due mostly to desiccation of breeding sites. Desiccation of breeding sites drastically reduced larval amphibian survival, which had a direct impact on the abundance of post-metamorphic juveniles (Cayuela et al. 2016; Weinbach et al. 2018). In our study, we added water to mesocosms daily, so the aquatic habitats did not dry out even in the warm climate, which could explain the absence of any effect of a warm climate on juvenile abundance. In some species, early life stages are also less impacted by warmer climates (Bestion et al. 2015b) because accelerated energy acquisition in warmer climates are useful for growth. While warmer temperature can accelerate larval development and the timing of metamorphic emergence in amphibians (Gvoždík 2022), it can also result in a smaller size at metamorphosis, which can reduce post metamorphic survival (Urban et al. 2014). At early life stages, amphibians can also show greater thermal

Table 3 Results of GLMM (after backward selection procedure) testing the effect climate treatment, connectivity treatment, temperature treatment, and their interaction on the emigration probability of juvenile newts (n = 67, $R^2_c = 0.990$, $R^2_m = 0.013$)

Response	Factors	Estimates	SE	χ^2_1	CI (95%)	P
Emigration probability	Climate	− 0.2	1.681	0.014	(− 3.5, 3.1)	0.991
	Connectivity	− 0.018	1.679	0.0001	(− 3.31, 3.27)	0.905
	Temperature	− 1.298	1.003	1.675	(− 3.26, 0.67)	0.196
	Climate*Temperature	− 6.342	3.456	3.368	(− 13.11, 0.43)	0.066
	1| newt_ID	Variance = 311.3 ± 17.64SD				
	1| Group_ID	Variance = 0[a]				
	1| Mesocosm_ID	Variance = 0[a]				

Estimates for climate, connectivity and temperature are given for the present-day climate, for the connected population, and for cooler temperatures, respectively

[a] Since the variance of the experimental group (Group_ID) and the mesocosm identity (Mesocosm_ID) were equal to 0, these were removed from the final model

Table 4 Results of the multivariate analysis (MANOVA) and univariate analysis (ANOVAs) testing the effect of emigration status and its interaction with the climate and the connectivity treatment on newt traits

	Emigration status		Emigration status*Connectivity		Emigration status*Climate		Emigration status*Connectivity*Climate	
	F-test	P	F-test	P	F-test	P	F-test	P
Manova								
All traits	$F_{(4,119)}=1.72$	0.149	$F_{(4,119)}=3.63$	**0.008**	$F_{(4,119)}=1.62$	0.175	$F_{(4,119)}=0.44$	0.780
Anovas								
Body size	$F_{(1,119)}=2.32$	0.130	$F_{(1,119)}=0.52$	0.473	$F_{(1,119)}=0.24$	0.624	$F_{(1,119)}=0.07$	0.797
Leg length	$F_{(1,119)}=0.10$	0.747	$F_{(1,119)}=6.62$	**0.011**	$F_{(1,119)}=3.74$	0.055	$F_{(1,119)}=1.05$	0.308
Darkness	$F_{(1,119)}=0.40$	0.529	$F_{(1,119)}=5.68$	**0.019**	$F_{(1,119)}=0.21$	0.651	$F_{(1,119)}=0.52$	0.472
Redness	$F_{(1,119)}=3.64$	0.059	$F_{(1,119)}=2.35$	0.128	$F_{(1,119)}=1.83$	0.179	$F_{(1,119)}=0.27$	0.604

Significant and marginal effects are respectively highlighted in bold and underlined

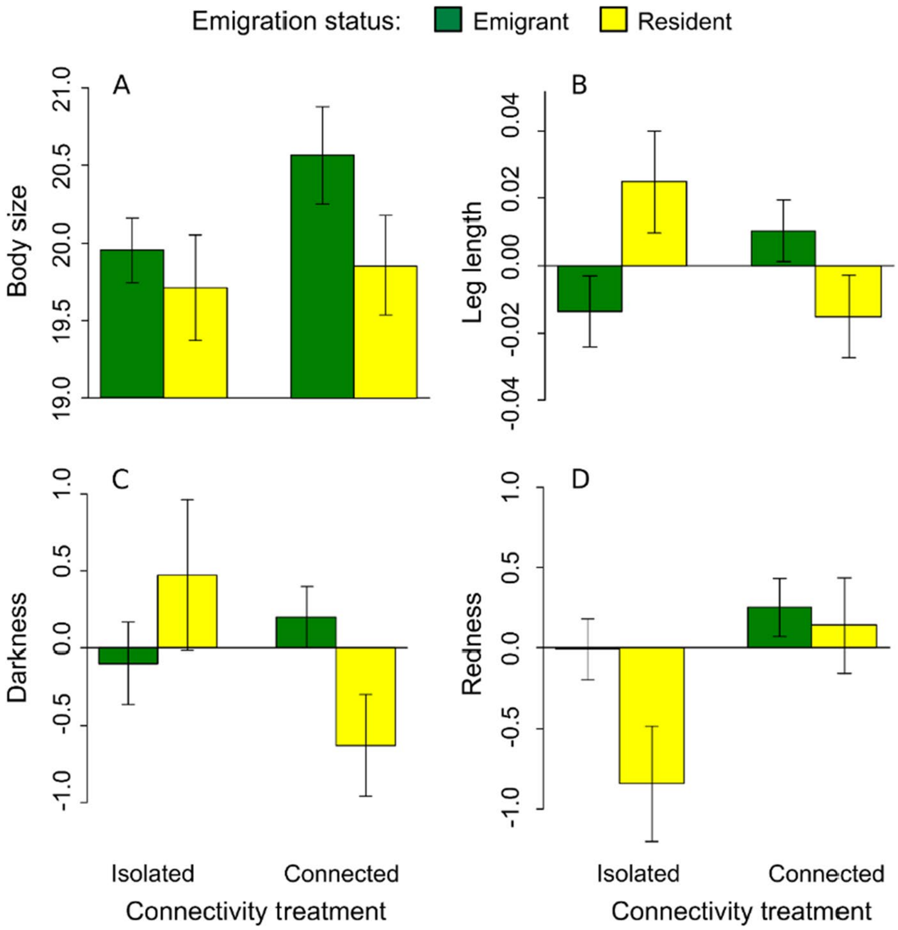

Fig. 5 Interactive effects of connectivity treatment (isolated versus connected) and emigration status (resident versus disperser) on newt phenotypes (mean ± SE): body size (**A**), leg length (**B**), darkness (**C**) and redness (**D**)

tolerance and thermoregulatory behavior, favoring acclimation to warmer temperatures (Fan et al. 2021). Finally, previous studies have showed that compared to cold winters, warm winters more frequently lead to lower survival because they result in depletion of energy reserves in juveniles unable to look for food

(Weinbach et al. 2018). We applied climate treatments only during summer, which could again explain the lack of impact on juvenile abundance. However, unlike adult abundance, which we believe was estimated precisely, estimates for juveniles provide relative abundances among mesocosms due to a lower detection probability of juveniles in dense vegetation than adults in pools.

Climate change can induce multiple phenotypic changes in species. Decreased body size has emerged as a universal response in many organisms to climate warming but seems less pronounced in amphibians (Li et al. 2013) and was not observed in our study. In accordance with other taxa, Reading (2007) found that, compared to cold winters, mild winters reduced body size and condition in common toads by depleting more energy reserves during hibernation. Alternatively, in some frog species, body size was increased in warmer habitats (Tryjanowski et al. 2006), which could be explained by either a positive effect of insect prey availability on growth rate (i.e. developmental plasticity), or by an adaptive role of larger body size in desiccation resistance (i.e. selection). In a previous study using the same experimental system, we found that after 3 years of treatment, common lizards inhabiting warm mesocosms were bigger than in the present-day climate, mainly because of accelerated growth rate at the juvenile stage (Pellerin et al. 2022). In our study, the absence of a climate effect on body size may result from the summertime climatic manipulation or from opposite effects of energetic saving and prey availability.

Adult newts and, to a smaller extent, juvenile newts were darker in warm climates. Climate warming is predicted to induce a darker skin for UV protection or a paler skin to avoid overheating (Roulin 2014), with the resulting effect depending on the cost–benefit balance between UV protection and overheating. In our experiment, the climatic treatment was created with shutters that automatically closed above certain temperature thresholds, so the warmer treatment implied more exposure to the sun and UV radiation. Amphibian skin is particularly thin and UV radiation can induce strong damage that can directly affect survival (reviewed by Blaustein et al. 2010). Coloration traits have been shown to be highly plastic in amphibians (Nilsson Sköld et al. 2013) and the development of darker skin under UV exposure has been observed in several amphibian species (Garcia et al. 2004; Blaustein et al. 2010).

Juvenile newts in our study were also less red in warmer than in present-day climates. In amphibians, the red pigments, mostly carotenoids, are acquired through dietary sources (Mochida et al. 2013). In red-eyed tree frogs (*Agalychnis callidryas*), a diet rich in carotenoids leads to redder skin and has a positive effect on juvenile development and female fecundity (Ogilvy et al. 2012). Warm climates may reduce newt's prey availability and diversity, and hence access to dietary pigments. Carotenoids may also provide protection against the pro-oxidative effects of UV induced by our warming treatment (Ogilvy and Preziosi 2012) and making carotenoids less available for skin color. Regardless of the exact determinant, redder individuals are often considered healthier, advantaged against predators (i.e., toxicity signal, (Mochida et al. 2013), and have higher reproductive success (Ogilvy and Preziosi 2012). Overall, the decrease of red pigments in juveniles from our experiment suggests the potential for negative effects from warmer conditions.

Connectivity mitigates the effects of climate warming

Interestingly, access to microclimatic refuges negated the effect of warming on newt abundance and suggests a mitigating effect of these refuges for population persistence (Scheffers et al. 2013). Newts in our study may have migrated to the cooler climate habitats during the warmer season to prevent overheating, as found in other ectotherms (Chukwuka et al. 2021). However, we could not monitor movements between microclimates because newts were not individually marked. Movements could also have allowed a reorganization of individuals according to their thermal optimum, with the phenotypes less adapted to warm climate settling in cooler habitats and vice-versa (Bestion et al. 2015a). Such adaptive dispersal could reduce the negative impacts of warming climate on (meta)population persistence (Pellerin et al. 2019), and is a likely hypothesis given the changes in phenotypic composition in connected populations.

Contrary to patterns observed in isolated habitats, newts were paler in the warm climate than in the present-day climate in connected habitats. Darker newts may have moved from the warm climate to the present-day climate to prevent overheating (Roulin

2014), and paler individuals may have moved to the warmer climate to meet their thermal needs. In amphibians, smaller sized juveniles are at greater risk of desiccation and their strictly terrestrial lifestyle may lead them to search for terrestrial microclimatic refuges (Enriquez-Urzelai et al. 2019). Darker individuals may therefore seek microclimatic refuges to prevent overheating. In contrast to juveniles, darker adults could avoid risk of overheating by remaining in the water during summer, while still remaining more protected against UV radiation.

Connectivity between microclimates further mitigated the effect of warm climate on red coloration. This suggests that the possibility to reach a cooler microclimate can decrease oxidative stress and may leave more carotenoids available for the skin (Ogilvy and Preziosi 2012) or increase the availability of prey that provide the pigments. Information on food availability and diet preference of newts in the two climatic treatments would allow a better understanding of the underlying mechanisms.

Emigration propensity and dispersal syndrome

We found that newts from populations with present-day climate temperatures emigrated slightly more often from warmer than from cooler conditions, while newts from populations with warmer climates emigrated equally under both thermal conditions. This might suggest an acclimation to warmer temperatures by newts from warm climates induced by developmental plasticity. Acclimation to warm temperatures has previously been shown in several newt species through locomotor activity, metabolic rate and critical thermal maximum, and these plastic responses can mitigate the impacts of climate change to some extent (Gvoždík et al. 2007; Winterová and Gvoždík 2021). Acclimation to warmer temperatures could also result from natural selection, but given the short duration of this study this explanation is unlikely.

While dispersal can facilitate colonization of areas with suitable climatic conditions, this depends on the phenotypic specialization of the dispersers, which modulates their success in travelling or adapting to novel conditions (Clobert et al. 2009). In this study we assessed dispersal syndrome by measuring traits that enhance movement (body size and leg length) on the one hand, and traits related to local adaptation/acclimation (coloration) and movement propensity on the other. In connected populations, we found evidence of dispersal syndrome among almost all the traits measured. Emigrant newts were bigger, had longer legs and were darker than residents. Body size and leg length are the main common enhancing traits of dispersers, and this phenomenon has been well-documented in other amphibians (Denoël et al. 2018; Winandy et al. 2019). The positive association between darkness in coloration and dispersal has been mostly described in birds (Roulin 2014; Saino et al. 2014), and may arise as a by-product of correlation with other physiological, morphological and behavioral traits. For example, darkness is positively correlated to boldness and exploration (Mafli et al. 2011; Mateos-Gonzalez and Senar 2012), two behavioral traits often associated to a higher dispersal propensity. Yet habitat isolation largely altered these syndromes in our study. Emigrants had shorter legs than residents but did not differ in body size and darkness. As found in other species (Cote et al. 2022), specific environmental conditions can disrupt the relationships between phenotypic traits and dispersal and may result in additional dispersal costs (Winandy et al. 2019). While the higher abundance of newts in connected populations in our study could suggest adaptive movements, a longer-term follow-up of the fitness of individuals of different phenotypes and emigration decisions is needed to validate this hypothesis. The interaction between the phenotype and environmental conditions is complex, and challenging environments such as warmer and more fragmented habitats can modify dispersal syndrome. This could have consequences for the success of range shifts and, to a greater extent, on phenotypic composition and/or survival of populations (Pellerin et al. 2019).

Conclusion

The spatial configuration of habitats in the landscape can influence the response of organisms to warming climates (Opdam and Wascher 2004). In this study, we found interactive effects of these factors on newt populations: when newts do not have the opportunity to escape warmer temperature, their abundance declines and the phenotypic composition of populations is altered, while microclimate connectivity seems to alleviate these effects. We cannot tease apart the effects of genetic selection and phenotypic plasticity on the observed phenotypic changes. Yet coloration traits have been shown to be highly plastic in amphibians (Nilsson Sköld et al. 2013). By buffering the adverse effects of high temperatures, phenotypic plasticity can be a first step of population persistence (Seebacher et al. 2014). Indeed, in amphibians, thermal acclimation through behavioral thermoregulation or physiological heat tolerance can act as efficient compensatory mechanisms (Gvoždík et al. 2007). We did not measure these thermal traits in our study, so we do not know if newts developed thermal compensation in warmer climates. Yet even the most plastic traits may prove insufficient to fully compensate for the consequences of overheating in ectotherms (Gunderson and Stillman 2015). In this case, emigration of less adapted phenotypes to a habitat that better matches their phenotype could be a way of ensuring population persistence, a hypothesis which needs to be validated through long term monitoring of the survival and reproduction of individuals (Merilä and Hendry 2014).

Landscape connectivity to microclimatic refuges seems to be a key factor that could buffer species against regional extirpation (Suggitt et al. 2018). Access to microclimatic refuges can be particularly important in the case of amphibians such as newts that have relatively limited dispersal capacity. Conservation of microclimatic areas like forests and wetlands as well as maintaining landscape connectivity should be a primary consideration to reduce the impact of climate warming on amphibian diversity (Scalercio et al. 2009; Frey et al. 2016).

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Author contributions JC, LW and DL designed the study. LW, FP and LDG performed the experiment. JC analyzed the pictures on ImageJ. LW performed the statistical analysis and wrote the first version of the manuscript. All authors contributed substantially to manuscript revisions and gave final approval for publication.

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Data availability The datasets analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare no conflict of interest.

References

Balogová M, Gvoždík L (2015) Can newts cope with the heat? Disparate thermoregulatory strategies of two sympatric species in water. PLoS ONE 10(5):e0128155

Bates D, Mächler M, Bolker B, Walker S (2008) Fitting mixed-effects models using the lme4 package in R. In: International Meeting of the Psychometric Society

Bestion E, Clobert J, Cote J (2015a) Dispersal response to climate change: scaling down to intraspecific variation. Ecol Lett 18:1226–1233

Bestion E, Teyssier A, Richard M et al (2015b) Live fast, die young: experimental evidence of population extinction risk due to climate change. PLoS Biol 13:e1002281

Blaustein AR, Walls SC, Bancroft BA et al (2010) Direct and indirect effects of climate change on amphibian populations. Diversity 2:281–313

Burraco P, Orizaola G, Monaghan P, Metcalfe NB (2020) Climate change and ageing in ectotherms. Glob Change Biol 26:5371–5381

Cayuela H, Arsovski D, Bonnaire E et al (2016) The impact of severe drought on survival, fecundity, and population persistence in an endangered amphibian. Ecosphere 7:e01246

Cayuela H, Grolet O, Joly P (2018) Context-dependent dispersal, public information, and heterospecific attraction in newts. Oecologia 188:1069–1080

Chukwuka CO, Mello RS, Cree A, Monks JM (2021) Thermal heterogeneity of selected retreats in cool-temperate viviparous lizards suggests a potential benefit of future climate warming. J Therm Biol 97:102869

Clobert J, Le Galliard J-F, Cote J et al (2009) Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. Ecol Lett 12:197–209

Cote J, Bestion E, Jacob S, Travis J, Legrand D, Baguette M (2017) Evolution of dispersal strategies and dispersal syndromes in fragmented landscapes. Ecography 40:56–73

Cote J, Dahirel M, Altermatt F et al (2022) Dispersal syndromes in challenging environments: a cross-species experiment. Ecol Lett 25:2675–2687

Denoël M (2006) Seasonal variation of morph ratio in facultatively paedomorphic populations of the palmate newt *Triturus helveticus*. Acta Oecologica 29:165–170

Denoël M, Dalleur S, Langrand E et al (2018) Dispersal and alternative breeding site fidelity strategies in an amphibian. Ecography 41:1543–1555

Díaz SM, Settele J, Brondízio E et al (2019) The global assessment report on biodiversity and ecosystem services: summary for policy makers

Enriquez-Urzelai U, Bernardo N, Moreno-Rueda G et al (2019) Are amphibians tracking their climatic niches in response to climate warming? A test with Iberian amphibians. Clim Change 154:289–301

Fan XL, Lin ZH, Scheffers BR (2021) Physiological, developmental, and behavioral plasticity in response to thermal acclimation. J Therm Biol 97:102866

Frey SJ, Hadley AS, Johnson SL et al (2016) Spatial models reveal the microclimatic buffering capacity of old-growth forests. Sci Adv 2:e1501392

Fronhofer EA, Legrand D, Altermatt F et al (2018) Bottom-up and top-down control of dispersal across major organismal groups. Nat Ecol Evol 2:1859–1863

Garcia TS, Stacy J, Sih A (2004) Larval salamander response to UV radiation and predation risk: color change and microhabitat use. Ecol Appl 14:1055–1064

Gunderson AR, Stillman JH (2015) Plasticity in thermal tolerance has limited potential to buffer ectotherms from global warming. Proc R Soc B 282:20150401

Gvoždík L (2015) Mismatch between ectotherm thermal preferenda and optima for swimming: a test of the evolutionary pace hypothesis. Evol Biol 42:137–145

Gvoždík L (2022) Thermoregulatory opportunity and competition act independently on life-history traits in aquatic ectotherms. Funct Ecol 36:2520–2530

Gvoždík L, Puky M, Šugerková M (2007) Acclimation is beneficial at extreme test temperatures in the Danube crested newt, *Triturus dobrogicus* (Caudata, Salamandridae). Biol J Linn Soc 90:627–636

Huey RB, Kearney MR, Krockenberger A et al (2012) Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. Philos Trans R Soc B 367:1665–1679

Joly P, Miaud C (1989) Fidelity to the breeding site in the alpine newt *Triturus alpestris*. Behav Proc 19:47–56

Kristín P, Gvoždík L (2014) Aquatic-to-terrestrial habitat shift reduces energy expenditure in newts. J Exp Zool A 321:183–188

Lê S, Josse J, Husson F (2008) FactoMineR: an R package for multivariate analysis. J Stat Softw 25:1–18

Legrand D, Guillaume O, Baguette M et al (2012) The Metatron: an experimental system to study dispersal and metaecosystems for terrestrial organisms. Nat Methods 9:828–833

Legrand D, Trochet A, Moulherat S et al (2015) Ranking the ecological causes of dispersal in a butterfly. Ecography 38:822–831

Lenoir J, Svenning J-C (2015) Climate-related range shifts–a global multidimensional synthesis and new research directions. Ecography 38:15–28

Li Y, Cohen JM, Rohr JR (2013) Review and synthesis of the effects of climate change on amphibians. Integr Zool 8:145–161

Lüdecke D, Lüdecke MD (2019) Package ‘sjstats.’ Statistical functions for Regression Models, Version 0.17, 3

Lüdecke D, Ben-Shachar MS, Patil I et al (2021) performance: an R package for assessment, comparison and testing of statistical models. J Open Source Softw 6:3139

Mafli A, Wakamatsu K, Roulin A (2011) Melanin-based coloration predicts aggressiveness and boldness in captive eastern Hermann’s tortoises. Anim Behav 81:859–863

Masson-Delmotte V, Zhai P, Pirani A, Connors SL, Péan C, Berger S et al (2021) Climate change 2021: the physical science basis. Contribution of working group I to the sixth assessment report of the intergovernmental panel on climate change, 2

Mateos-Gonzalez F, Senar JC (2012) Melanin-based trait predicts individual exploratory behaviour in siskins, *Carduelis spinus*. Anim Behav 83:229–232

McGaughran A, Laver R, Fraser C (2021) Evolutionary responses to warming. Trends Ecol Evol 36:591–600

Merilä J, Hendry AP (2014) Climate change, adaptation, and phenotypic plasticity: the problem and the evidence. Evol Appl 7:1–14

Milling CR, Rachlow JL, Olsoy PJ et al (2018) Habitat structure modifies microclimate: an approach for mapping fine-scale thermal refuge. Methods Ecol Evol 9:1648–1657

Mochida K, Kitada M, Ikeda K et al (2013) Spatial and temporal instability of local biotic community mediate a form of aposematic defense in newts, consisting of carotenoid-based coloration and tetrodotoxin. J Chem Ecol 39:1186–1192

Nilsson Sköld H, Aspengren S, Wallin M (2013) Rapid color change in fish and amphibians–function, regulation, and emerging applications. Pigment Cell Melanoma Res 26:29–38

Ogilvy V, Preziosi RF (2012) Can carotenoids mediate the potentially harmful effects of ultraviolet light in *Silurana* (*Xenopus*) *tropicalis* larvae? J Anim Physiol Anim Nutr 96:693–699

Ogilvy V, Preziosi RF, Fidgett AL (2012) A brighter future for frogs? The influence of carotenoids on the health, development and reproductive success of the red-eye tree frog. Anim Conserv 15:480–488

Opdam P, Wascher D (2004) Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. Biol Conserv 117:285–297

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42

Pellerin F, Cote J, Bestion E, Aguilée R (2019) Matching habitat choice promotes species persistence under climate change. Oikos 128:221–234

Pellerin F, Bestion E, Winandy L et al (2022) Connectivity among thermal habitats buffers the effects of warm climate on life-history traits and population dynamics. J Anim Ecol 91:2301–2313

Pittman SE, Osbourn MS, Semlitsch RD (2014) Movement ecology of amphibians: a missing component for understanding population declines. Biol Conserv 169:44–53

Reading CJ (2007) Linking global warming to amphibian declines through its effects on female body condition and survivorship. Oecologia 151:125–131

Román-Palacios C, Wiens JJ (2020) Recent responses to climate change reveal the drivers of species extinction and survival. Proc Natl Acad Sci 117:4211–4217

Roulin A (2014) Melanin-based colour polymorphism responding to climate change. Glob Change Biol 20:3344–3350

Saino N, Romano M, Scandolara C et al (2014) Brownish, small and lousy barn swallows have greater natal dispersal propensity. Anim Behav 87:137–146

Scalercio S, Russo M, Dapporto L (2009) Wetlands are refuge areas that delay global warming-induced range shift of Lepidoptera. In: Handbook of nature conservation: global, environmental and economic issues. Nova Publishers, New York, pp 393–406

Scheffers BR, Phillips BL, Laurance WF et al (2013) Increasing arboreality with altitude: a novel biogeographic dimension. Proc R Soc B 280:20131581

Seebacher F, Beaman J, Little AG (2014) Regulation of thermal acclimation varies between generations of the short-lived mosquitofish that developed in different environmental conditions. Funct Ecol 28:137–148

Sillero N (2021) Climate change in action: local elevational shifts on Iberian amphibians and reptiles. Reg Environ Change 21:1–13

Suggitt AJ, Wilson RJ, Isaac NJ et al (2018) Extinction risk from climate change is reduced by microclimatic buffering. Nat Clim Chang 8:713–717

Thompson RM, Beardall J, Beringer J et al (2013) Means and extremes: building variability into community-level climate change experiments. Ecol Lett 16:799–806

Tryjanowski P, Sparks T, Rybacki M, Berger L (2006) Is body size of the water frog *Rana esculenta* complex responding to climate change? Naturwissenschaften 93:110–113

Urban MC (2015) Accelerating extinction risk from climate change. Science 348:571–573

Urban MC, Richardson JL, Freidenfelds NA (2014) Plasticity and genetic adaptation mediate amphibian and reptile responses to climate change. Evol Appl 7:88–103

Verell PA (1987) The directionality of migrations of amphibians to and from a pond in southern England, with particular reference to the smooth newt, *Triturus vulgaris*. Amphib-Reptil 8:93–100

Weinbach A, Cayuela H, Grolet O et al (2018) Resilience to climate variation in a spatially structured amphibian population. Sci Rep 8:1–9

Winandy L, Cote J, Di Gesu L et al (2019) Local predation risk and matrix permeability interact to shape movement strategy. Oikos 128:1402–1412

Winterová B, Gvoždík L (2021) Individual variation in seasonal acclimation by sympatric amphibians: a climate change perspective. Funct Ecol 35:117–126