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Altered trophic interactions in warming climates: consequences for predator diet breadth and fitness

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Species interactions are central in predicting the impairment of biodiversity with climate change. Trophic interactions may be altered through climate-dependent changes in either predator food preferences or prey communities. Yet, climate change impacts on predator diet remain surprisingly poorly understood. We experimentally studied the consequences of 2°C warmer climatic conditions on the trophic niche of a generalist lizard predator. We used a system of semi-natural mesocosms housing a variety of invertebrate species and in which climatic conditions were manipulated. Lizards in warmer climatic conditions ate at a greater predatory to phytophagous invertebrate ratio and had smaller individual dietary breadths. These shifts mainly arose from direct impacts of climate on lizard diets rather than from changes in prey communities. Dietary changes were associated with negative changes in fitness-related traits (body condition, gut microbiota) and survival. We demonstrate that climate change alters trophic interactions through top-predator dietary shifts, which might disrupt eco-evolutionary dynamics.

1. Introduction

Ongoing climate change is a major threat to biodiversity [1] and ecosystem functioning [2]. Climate warming notably alters community and ecosystem functioning through changes in trophic interactions with consequences for the fitness of all species [1,3,4]. This alteration may result from changes in species compositions in prey communities across trophic levels or from changes in the diet of predators.

In ectotherms, all physiological processes are temperature-dependent [5]. Because a rise in temperature causes metabolic rates to increase more rapidly than ingestion rates [6,7], warmer temperatures can lead to energy loss and reduced survival in ectotherm predators. One way to avoid starvation in warmer climates is for predators to increase consumption rate [8], potentially through decreasing their selectivity towards certain prey. Alternatively, predators could shift their diet towards more energy-rich prey [9–11], which could lead to an increased dietary specialization [12].

On the other hand, climate warming may change prey community composition, resulting in modified predator diet [13]. For instance, within the prey community, climate change should disproportionately affect prey species with higher trophic position [13,14], thus forcing their predators to feed on lower trophic levels. Changes in prey community composition with warmer climates might lead dietary generalists to better survive warmer climates as they would be less dependent on specific prey items [15].

Impacts of climate change on predator diet could thus come from temperature-dependent changes in predator energy and nutrient demands or from bottom-up changes in prey communities. Changes in predator diets could subsequently affect predator life-history traits (e.g. body growth and condition [16]) and extended phenotype (e.g. gut microbial communities [17]), leading to changes in fitness. Further, changes in diet should modify predator top-down control of lower trophic levels. Despite the importance of such climate-driven eco-evolutionary dynamics, no study to our knowledge has investigated the two mechanisms underlying climate-dependent changes in predator diet and their consequences on their fitness.

Here, we studied the consequences of 2°C warmer climatic conditions on the trophic niche of a generalist predator, the common lizard (*Zootoca vivipara*). We used a system of semi-natural mesocosms in which climatic conditions can be manipulated to create present-day climatic conditions and +2°C warmer climatic conditions, in line with IPCC predictions [18]. We have previously shown that climatic conditions affected lizard population dynamics, dispersal and gut microbiota [19–21]. We aimed at understanding whether climatic conditions could have affected lizards through changes in diet and subsequent changes in central phenotypic traits (body condition, indicated by size-corrected body mass; gut microbiota) and fitness. We characterized lizard trophic niches through stable isotope analyses, using $\delta^{15}\text{N}$, which is a proxy of trophic position, and $\delta^{13}\text{C}$, which can signal the reliance on different primary producers [22]. We further studied the pathways of climate impacts on lizard niche through structural equation modelling, and investigated potential implications on lizard phenotype and fitness. We predicted that warmer climatic conditions should result in a decrease in lizard trophic position because warming would decrease the abundance of predatory prey. Alternatively, an increase in energy demands at higher temperature should generate a shift towards a more generalized diet. The diet shift should be linked to lizard phenotypic traits, and we should see no impact on lizard fitness when diet shifts can compensate increased energy demands and changes in prey communities.

2. Results

(a) Impact of climatic conditions on lizard and invertebrate stable isotope values

$\delta^{13}\text{C}$ values for both detritivorous and phytophagous invertebrates were higher in warmer climatic conditions, but not for predatory invertebrates, while there were no significant differences between climatic conditions on $\delta^{15}\text{N}$ values from all three invertebrate prey categories (electronic supplementary material, table S1A).

Lizards from warmer climatic conditions had higher $\delta^{13}\text{C}_{\text{cor}}$ values (i.e. $\delta^{13}\text{C}$ corrected for prey $\delta^{13}\text{C}$) and non-significantly

higher $\delta^{15}\text{N}_{\text{cor}}$ values than individuals from present-day climatic conditions (table 1 and figure 1). Adults had higher $\delta^{15}\text{N}_{\text{cor}}$ and $\delta^{13}\text{C}_{\text{cor}}$ values than juveniles (table 1 and figure 1).

(b) Impact of climatic conditions on lizard trophic niche

The population niche breadth, assessed by stable isotope standard ellipse areas (SEAc), was narrower in warmer climatic conditions for adults, while juveniles had a wider population niche breadth in warmer climatic conditions (no 95% CI overlap; figure 1b). Further, climate change led to a differentiation of populations along the two stable isotope axes as overlap among SEAc ellipses was smaller than expected by chance (adults: overlap = 0.13, $p < 0.0001$, juveniles: overlap = 0.08, $p < 0.0001$; figure 1).

At the individual level, both adult and juvenile lizards were more specialized in warmer than in present-day climatic conditions (figure 2a and table 1). They consumed fewer phytophagous invertebrates and more predatory invertebrates in warmer climatic conditions than in present-day conditions (table 1 and figure 2b). Prey consumption varied strongly with individual age, with juveniles overall consuming more phytophagous invertebrates and fewer predatory invertebrates than adults.

A path analysis was used to disentangle direct effects of climate from climate-dependent changes in prey community on lizard diet, summarized with the first axis of a principal component analysis (figure 3; electronic supplementary material, figure S2A). The best model included both a direct positive effect of warmer climate on diet specialization (coef = 0.43, higher specialization) and, to a lesser extent, indirect effects, either negative through climate-driven changes in predatory invertebrate abundance (coef = $-0.46 \times 0.22 = -0.10$, lower specialization) or positive through changes in phytophagous invertebrate abundance (coef = $-0.36 \times -0.29 = 0.10$). There was also a positive effect of age on predatory specialization (coef = 0.17) (figure 3; electronic supplementary material, table S2A).

(c) Implications of diet change on lizards' body condition, microbiota and survival

Adult body condition in September was not linked to any of the dietary components (table 2), while there was an interactive effect of climate and the green–brown food axis (proportion of detritivorous versus phytophagous prey eaten, PC2 axis; electronic supplementary material, figure S2A) on juvenile body condition ($p = 0.02$; table 2). Here, juveniles eating more detritivorous prey (i.e. higher scores on PC2) had a lower body condition in warmer climatic conditions only.

Lizard gut microbiota diversity, an important trait for their fitness [21], was linked to their diet. We found a significant interaction between predator specialization and climate on bacterial community diversity, measured by its Shannon index, where lizards highly specialized towards eating predators harboured less diverse communities in warmer climatic conditions, but there was no effect of predator specialization on diversity in present-day climates ($p = 0.008$; electronic supplementary material, table S4A; figure 4a).

Adult lizard subsequent winter–spring survival was negatively correlated to the pre-winter specialization towards predatory invertebrates ($p = 0.042$; figure 4b and table 2)

Table 1. Impact of climatic treatment on lizard corrected stable isotope values, diet and dietary specialization. Model-averaged values using linear mixed models. The global model included climatic treatment and its two-way interactions with age class and sex as fixed effects, and random mesocosm identity. R_m^2 are 20%, 21%, 13%, 22% and 21% and R_c^2 are 37%, 51%, 31%, 29% and 34% for global models of $\delta^{13}C_{cor}$, $\delta^{15}N_{cor}$, prop. predators, prop. phytophagous and diet breadth, respectively. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. $n = 327$.

variable	parameter	estimate	s.e.	z-value	p-value	RI
$\delta^{13}C_{cor}$	intercept	0.46	0.04	11.48	<0.001***	—
	age	-0.13	0.02	6.62	<0.001***	1.00
	climate	0.12	0.06	2.24	0.025*	1.00
	sex	0.02	0.02	0.95	0.344	0.29
	age : climate	0.01	0.04	0.40	0.688	0.20
$\delta^{15}N_{cor}$	intercept	2.38	0.21	11.32	<0.001***	—
	age	0.39	0.06	6.29	<0.001***	1.00
	sex	0.12	0.07	1.70	0.088	1.00
	climate	0.48	0.27	1.80	0.072	0.78
	sex : climate	0.14	0.12	1.19	0.234	0.27
prop. predatory inv.	intercept	0.43	0.02	19.43	<0.001***	—
	age	0.03	0.01	2.90	0.004**	1.00
	sex	0.01	0.01	1.27	0.203	0.83
	climate	0.06	0.03	2.00	0.046*	0.86
	sex : climate	0.02	0.02	1.14	0.253	0.21
prop. phytophagous inv.	intercept	0.31	0.01	30.5	<0.001***	—
	age	-0.05	0.01	6.72	<0.001***	1.00
	sex	-0.01	0.01	1.06	0.290	0.72
	climate	-0.04	0.01	2.67	0.008**	1.00
	sex : climate	-0.01	0.01	1.07	0.283	0.22
dietary breadth	intercept	17.08	0.63	26.98	<0.001***	—
	age	-1.89	0.38	4.93	<0.001***	1.00
	sex	-0.79	0.34	2.31	0.021*	1.00
	climate	-2.47	0.87	2.83	0.005**	1.00
	age : climate	0.66	0.63	1.05	0.294	0.31
	sex : climate	-0.25	0.62	0.40	0.689	0.19

while there was no such relationship in juveniles (table 2). There was no interaction between any of the dietary axes and climatic conditions on survival (table 2).

3. Discussion

Our study highlights how climatic conditions, prey communities and predator traits interact in driving trophic interactions. Warmer climatic conditions led to higher $\delta^{13}C$ values in both lizards and invertebrates. Carbon stable isotopes often signal the relative contributions of different functional groups of primary producers or changes in the environment caused by abiotic conditions like temperature and moisture [22,23], as found in skinks in response to habitat fragmentation [24]. Further, $\delta^{15}N$ values tended to be higher in warmer climatic conditions for lizards but not for invertebrates and higher for

adult lizards relative to juveniles. This suggested that lizards fed on higher trophic levels in warmer conditions, as found in trout [12]. Because we corrected lizard stable isotope signature by those of their prey, the differences in lizard stable isotope values result from a difference in the prey species consumed by lizards and not from a shift in invertebrate values.

Warmer climatic conditions reduced the relative proportion of phytophagous versus predatory invertebrates in lizard diets. This dietary shift was mainly due to a direct effect of climatic conditions on the lizards and to a lesser extent by climate-driven changes in prey abundance. Because climate change should impact species at higher trophic levels more [14], we could have expected lizards to decrease their trophic position due to a decline in the abundance of predatory invertebrates. Warmer climatic conditions indeed decreased lizard specialization towards predators through a lower abundance in predatory invertebrates. However, this

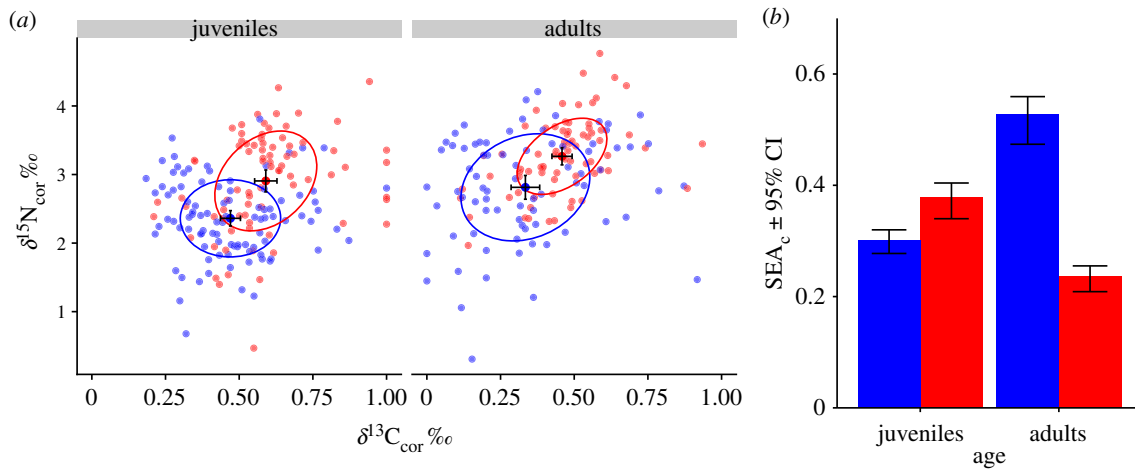


Figure 1. Impact of climate on lizard corrected stable isotope values and population niche breadth. (a) Bivariate plot of lizard corrected $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values by age. Blue (dark grey in print), present-day climatic treatment; red (light grey in print), warm climatic treatment. Lines: sample size-corrected standard ellipses (SEAc). Large points and error bars: treatment mean and 95% CI. (b) Area of the SEAc for each treatment by age with bootstrapped 95% CIs. $n = 96$ and 79 juveniles in present-day and warm climate, respectively, and $n = 77$ and 75 adults. (Online version in colour.)

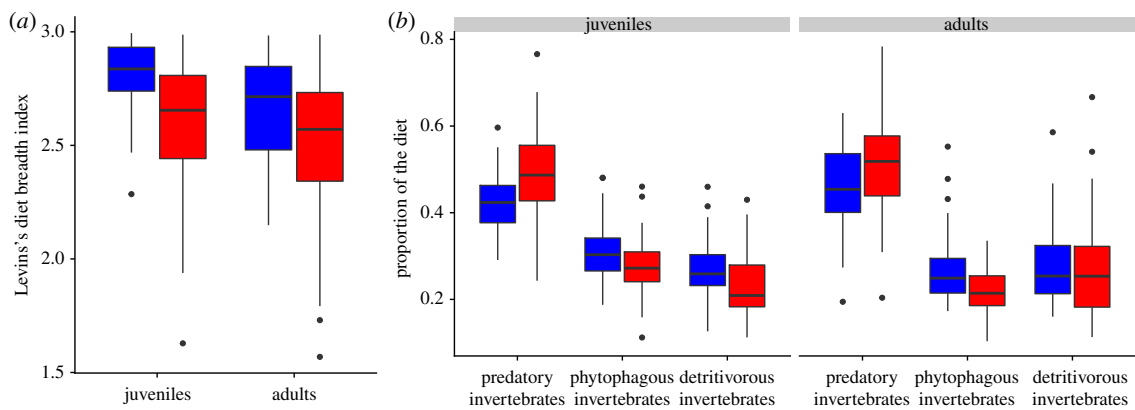


Figure 2. Impact of climate on lizard diet. (a) Lizards individual dietary breadth measured by Levin's dietary index (ranging between 1, completely specialized diet, and 3, completely generalized diet). (b) Dietary contribution of each putative prey (table 1). Blue (dark grey in print), present-day climatic treatment; red (light grey in print), warm climatic treatment. $n = 96$ and 79 juveniles in present-day and warm climate, respectively, and $n = 77$ and 75 adults. (Online version in colour.)

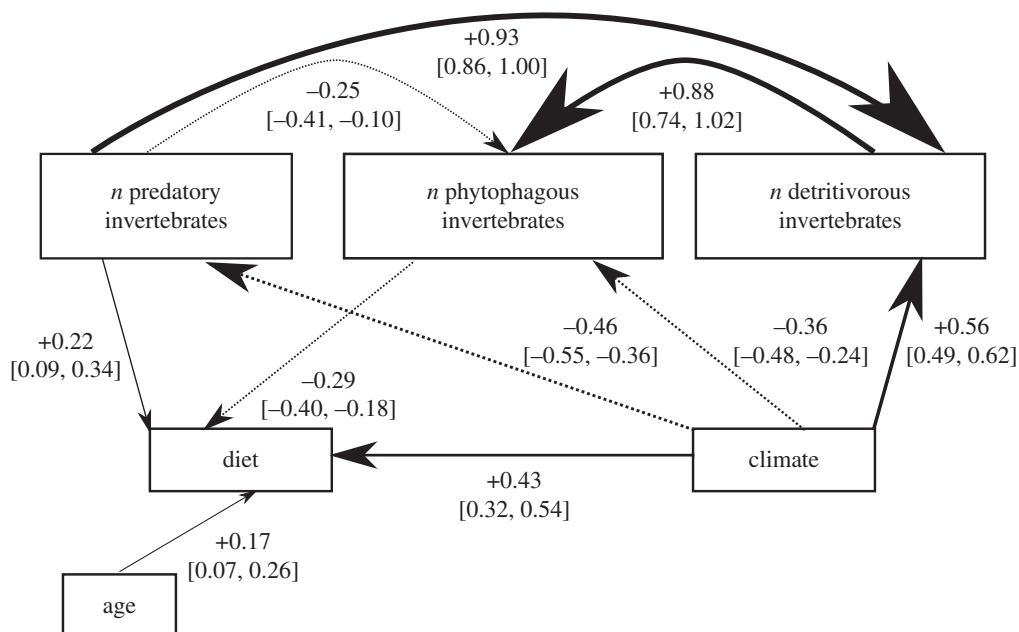


Figure 3. Path analysis of the impact of climate on lizard diet. Diet represents the predator specialization (PC1; electronic supplementary material, figure S2A). The best path model includes direct effect of climate and indirect effect of climate through changes in predatory and phytophagous invertebrate abundances, but not on detritivorous invertebrate abundances (electronic supplementary material, table S2A). Solid and dashed lines represent positive and negative values, respectively, and their width is proportional to the value of the path coefficient (shown with mean and 95% CI). $n = 327$.

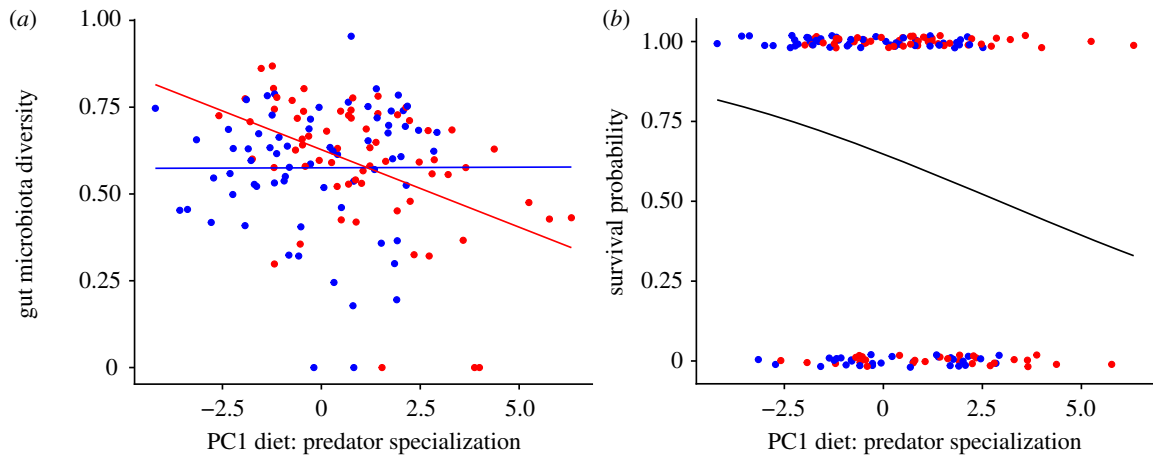


Figure 4. Link between dietary specialization and adult gut microbial community diversity and future survival. (a) Gut bacterial community diversity (Shannon index) as a function of adult predator specialization (electronic supplementary material, figure S2A). High values of the principal component denote lizards with a high level of specialization towards eating predators. There is a significant interaction between predator specialization and climatic conditions (see electronic supplementary material, table S4A). $n = 135$. (b) Survival probability as a function of adult predator specialization. There is no interaction between predator specialization and climatic conditions (table 2). Blue (dark grey in print), present-day climatic treatment; red (light grey in print), warm climatic treatment. $n = 152$.

Table 2. Implication of lizard diet on their body condition and future survival. Model-averaged values with linear (body condition) and generalized (survival, binomial family) linear mixed models. Global models included two-way interaction between each dietary component and climate, and for juveniles, continuous birthdate, plus random mesocosm identity. Numeric variables were centred and scaled. The global models explained 24%, 16%, 12% and 3% of the marginal variance, and 29%, 16%, 21% and 15% of the conditional variance, respectively, for adult body condition, juvenile body condition, adult survival and juvenile survival. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. $n = 152$ adults, 175 juveniles.

variables	age	parameter	estimate	s.e.	z-value	p-value	RI
September body condition	adults	intercept	-0.21	0.07	3.22	0.001**	
		sex	0.54	0.08	6.57	<0.001***	1.00
		PC1 diet: predator specialization	-0.03	0.04	0.69	0.488	0.24
		PC2 diet: detri versus phyto	0.03	0.04	0.61	0.544	0.22
	juveniles	intercept	-0.06	0.03	2.21	0.027*	
		PC1 diet: predator specialization	0.02	0.02	1.4	0.163	0.48
		PC2 diet: detri versus phyto	0.03	0.02	1.54	0.123	0.42
		sex	0.14	0.03	4.67	<0.001***	1.00
		climate	-0.05	0.03	1.33	0.184	0.67
		climate*PC2 diet	-0.07	0.03	2.33	0.020*	0.42
winter-spring survival	adults	intercept	0.11	0.33	0.32	0.748	
		PC1 diet: predator specialization	-0.44	0.21	2.03	0.042*	1.00
		sex	0.88	0.38	2.3	0.021*	1.00
		climate	0.34	0.53	0.63	0.526	0.23
		PC2 diet: detri versus phyto	0.10	0.20	0.49	0.622	0.21
	juveniles	intercept	-0.44	0.29	1.49	0.137	
		PC1 diet: predator specialization	0.20	0.19	1.01	0.313	0.21
		climate	-0.35	0.5	0.7	0.482	0.16
		date of birth	0.07	0.16	0.45	0.649	0.14
		sex	0.09	0.32	0.27	0.787	0.13

negative indirect impact of warmer climatic conditions was quite weak (-0.10), and overwhelmed by a strong (0.43) direct positive impact of climate on predator specialization. This suggests that lizards actively shifted their diet in warmer climatic conditions. Such a dietary shift has been found in brown trout (*Salmo trutta*) from a natural thermal gradient, where the trophic position of brown trout increased with

temperature [12]. Several hypotheses about elemental stoichiometry could drive diet shifts with temperature. Because temperature is linked to metabolic rates [5], higher temperatures should lead to a higher demand for carbon (respiration) than for nitrogen and phosphorus [25]. This has led several species, from copepods to fish, to switch towards greater herbivory owing to the higher C content of plants [9–11]. Conversely, higher

temperatures should lead to higher protein denaturation rates, thus increasing N demands [26], as found in grasshoppers [27]. Finally, as growth rate is linked to phosphorus demand, increased growth rates with warming would thus lead to increased P demands [28,29]. Given that invertebrate predators display a higher N and P content than herbivores for a similar C content [30], a shift towards eating more predators should not be linked to increased C demands but instead to higher N and/or P demands. As juveniles grow faster in warm climates [20], they might shift towards eating predators to fulfil their phosphorus demands. On the contrary, adult growth is much slower, but they also suffer more from warmer climates, with a decreased survival [20]. Warmer climates might mean more maintenance costs to repair proteins [26], which might explain their shift towards N- and P-rich predatory invertebrates. Future work should aim at better understanding the mechanism of climate-induced lizard dietary shifts.

Lizard individual dietary breadth declined with warmer climatic conditions (i.e. both adults and juveniles became more specialized). Although this lower niche breadth at the individual level translated into narrower niche breadth at the population level in adults, juvenile diet specialization in warmer climatic conditions led to a wider population niche breadth. This result suggests that warmer climatic conditions induced a shift in juveniles from a homogeneous generalist population composed of generalist individuals to a heterogeneous generalist populations made of individuals specialized on different groups of prey [31]. On the contrary, the greater specialization of adult lizards at the individual level in warm climates resulted into a lower population niche breadth, suggesting that all adult individuals shifted their diet towards eating more predatory invertebrates. These results match the previously observed effects of warmer climatic conditions on juveniles' and adults' life-history traits, where climate change favoured growth in juveniles but reduced survival in adults [20]. Here, individual dietary specialization towards predators had an overall negative impact on adult winter–spring survival, while there was no impact on juvenile survival. The difference between adults and juveniles could be due to differences in metabolic demands, translating into different foraging strategies and thus intraspecific competition. Metabolic rates scale with body size and temperature in ectotherms [5]. Juvenile metabolic demands probably increased in warmer climatic conditions, which might push them to consume a higher biomass of prey. Juveniles' small size limits the size of prey they can eat, including the biggest and potentially more dangerous predatory invertebrates [32]. Accordingly, juveniles were here found to eat on lower trophic levels than adults. The observed increased growth rate in warmer climatic conditions [20] might allow juveniles to choose from a wider array of prey including bigger predatory invertebrates. Because different juveniles focus on different prey items (as shown by the larger population niche breadth), they should avoid increased competition and thus overcome their increased energy demands in warmer climates.

Adult individuals already eat more predatory invertebrates than juveniles. They might be more constrained in their metabolic response to climate and forced to specialize even more on larger, more rewarding prey. Such large prey are however rarer, thus lowering encounter rates. The resulting stronger competition may lead to lower *per capita* intake and decreased survival [20]. This negative impact may be further worsened by phenotypic changes concomitant with diet shift. The

predator specialization was indeed linked to a lower gut microbiota diversity in warm climatic conditions. Such lower microbiota diversity might explain reported impacts of climate on lizard microbiota and survival. We previously showed that warmer temperatures lead to a less diverse microbiota which was correlated with a lower subsequent survival [21]. Because higher gut microbiota diversity is often beneficial to their hosts [17], a reduced diversity due to climate-driven dietary changes should be detrimental, particularly if it affects essential functions such as immunity or digestion [33]. On the other hand, changes in gut microbiota might not be the consequence but the cause of the observed dietary shifts if it changes the relationship between digestive performance and temperature. For instance, in salamanders, the relative abundance of some bacterial taxa was correlated to energy assimilation, and both depended on temperature [34]. Thus, the link we previously observed between lizard gut microbiota and survival would be the consequence of the microbiota-induced dietary shift. Future studies should disentangle whether climate-dependent diet shift induced microbiota changes or the other way around.

We further found that prey abundances were weakly affected by lizard diet, with a slightly lower density of phytophagous invertebrates when lizards tend to feed more on them (electronic supplementary material, section S5). This weak top-down impact on prey communities may however strengthen in the long term, and interact with the observed bottom-up effects of prey abundance on lizard diet. The climate-driven changes in predator physiology could then lead to changes in the whole food web structure and functioning from bacteria to invertebrate communities through both top-down and bottom-up effects. For instance, in pitcher plants, higher temperature leads to increased importance of top-down versus bottom-up effects on protozoan communities [35]. Together, these results show the importance of considering bottom-up and top-down drivers of trophic interactions to further understand how climate change affects species and communities [36]. Given the importance of trophic interaction strength on prey population dynamics, and the potential for climate change to affect trophic interaction strength [37], further work should focus on how climate-induced changes in diet will affect trophic interaction strength in a multi-species context.

4. Methods

(a) Species and experimental system

The common lizard (*Zootoca vivipara*; Jacquin 1787) is a small (snout–vent length 50–70 mm) lizard foraging actively on a wide variety of invertebrate species including Araneae, Coleoptera, Orthoptera, Heteroptera, Homoptera, Diptera, Hymenoptera, Gasteropoda, Isopoda and Lepidoptera caterpillars [38,39]. Lizards used in this study are part of a wider study on the consequences of climate change on populations [19–21], and descend from lizards captured in nature (capture licence no. 2010-189-16 DREAL). The Station d'Ecologie Théorique et Experimentale has a national agreement for use of animals in the laboratory (number B09583), and our experiments are made in accordance with 2013 French ethics regulations (permits number APAFIS#15897-2018070615164391 v3 and APAFIS#19523-201902281559649 v3). Lizards were individually marked by toe-clipping at birth and were maintained in the Metatron, an infrastructure composed of 48 semi-natural caged enclosures acting as mesocosms (Ariège, France, 43°01' N,

1°05' E). Each mesocosm is 10 × 10 m and is fully enclosed by tarpaulin and fine-meshed nets; it acts as a mini-ecosystem, with natural vegetation and invertebrate communities, and a wide variety of thermal micro-habitats (dense vegetation, rocks and logs, ponds [19,20]). Diversity within these caged habitats is relatively high (30 ± 3 invertebrate families per mesocosm, see below). Climatic conditions within mesocosms are monitored continuously and can be manipulated through motor-driven shutters [19,20].

(b) Experimental procedure

In June 2013, we allocated lizards to 10 enclosures, five attributed to a 'present-day climate' treatment and five to a 'warm climate' treatment, on average 2°C warmer (weekly mean of summer daily temperatures, PC: 26.3 ± 0.3°C, WC: 28.3 ± 0.2°C, mean ± s.e., $F_{1,147} = 13$, $p < 0.001$; weekly mean of summer maximum daily temperatures: PC: 29.1 ± 0.3°C, WC: 32.4 ± 0.4°C, $F_{1,147} = 35$, $p < 0.001$), coherent with climate change projections for southern Europe [18] (see [20] for more details about climatic treatments). There was no difference between treatments in the abundance of invertebrate prey communities at the beginning of the experiment (difference in abundance of predatory invertebrates between enclosures, PC: 31.4 ± 4.4, WC: 29 ± 6.6, $p = 0.53$, of phytophagous, PC: 27.6 ± 6.5, WC: 37.6 ± 7.3, $p = 0.55$, of detritivorous, PC: 8.2 ± 5.4, WC: 5.4 ± 1.7, $p = 0.83$, assessed in May 2013 following the same sampling procedure as below).

We released a total of 612 lizards, comprising 264 adults and 348 juveniles. The adults included lizards aged 1 year (1 yo) and 2 years or older (2+ yo). Adults were previously maintained for 1 year inside the Metatron and recaptured in May 2013 to monitor female parturition in laboratory. Juveniles were born in terraria between June and July 2013 (see [20] for more details). Before being released into the Metatron, all lizards were measured, weighted and marked and a tail tip was taken from adults (but not from juveniles as they were too small to be sampled at birth) for stable isotope analyses. This procedure enables non-lethal sampling. Lizards were then released into the Metatron controlling for body size [20]. There were no differences in stable isotope values before the climatic treatments were applied ($\delta^{15}\text{N}$: $\chi^2 = 0.27$, $p = 0.61$, $\delta^{13}\text{C}$: $\chi^2 = 0.78$, $p = 0.38$). Each population included 7 ± 1 2+ yo males, 12 ± 1 2+ yo females, 7 ± 2 1 yo and 35 ± 3 juveniles, conforming with local densities in natural populations [20]. We do not expect specific differences between 2+ yo and 1 yo; by contrast, juveniles both have a different diet [38] and react differently to climate [20] from adults. Consequently, we defined two age categories, i.e. juveniles and 'adults', the latter corresponding to 2+ yo and 1 yo.

(c) Lizard condition, diet and survival assessment

In mid-September 2013, we recaptured all surviving lizards during multiple capture–recapture sessions. Captured lizards were measured for snout–vent length and body mass, which allowed us to assess body condition as the residuals of body mass by snout–vent length [16]. We also measured lizards extended phenotype as their gut microbiota community (in adults only as juveniles were too small to be sampled). Sampling, molecular and bioinformatics methods were identical to [21].

We took a tail tip for stable isotope analyses. Tail tips were clipped at the start of the experiment and they regrew the tail during the experiment, thus the stable isotope values from the regrown tissue captured diet composition during the study period [40,41]. Lizards were then released to hibernate in the Metatron.

Finally, we measured lizard winter–spring survival through repeated capture sessions in May 2014 allowing to capture all individuals [20].

(d) Prey invertebrate community sampling

End of September 2013, we surveyed the invertebrate community to estimate relative invertebrate diversity and abundance within each mesocosm. We set up two pitfall traps (diameter 8 × 12 cm glass jars) within each mesocosm [20], a sampling effort in agreement with the literature [42]. Pitfall traps were placed at least 1.5 m from the border of the mesocosms to prevent edge effects, in areas representative of the mesocosms' plant cover, and separated by at least 5 m. Traps were left for 5 sunny days to trap crawling arthropods. We also performed two net-sampling sessions on sunny days with a sweep net (diameter 25 cm) to recover canopy arthropods and flying insects. Sampling effort led to recover 295 ± 91 invertebrate individuals per enclosure and 30 ± 3 families (electronic supplementary material, figure S1A). Recovered invertebrates were preserved at −20°C.

Invertebrate individuals were identified to the family level under a binocular microscope. We then attributed families to a functional trophic group (predatory, detritivorous and phytophagous invertebrates) and calculated abundance per group. We selected 22 invertebrate families from the most abundant families relevant to lizard diet [38] for stable isotope analyses. These families represented 72% of the individuals sampled in the mesocosms (electronic supplementary material, table S1B). Samples from lizards (tail tip) and invertebrates (whole organisms, composed of pooled items ($n = 3–20$) to account for interindividual variation within mesocosms) were oven-dried at 60°C for 48 h, ground and sent to Cornell Stable Isotope for carbon and nitrogen stable isotope analyses ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$). Within trophic group variability in stable isotope values was low compared with between-group variability (ANOVA, $F_{2,253} = 91$, $p < 0.001$ for $\delta^{13}\text{C}$, and $F_{2,253} = 116$, $p < 0.001$ for $\delta^{15}\text{N}$).

(e) Statistical analyses

(i) Stable isotope analyses

We first studied whether climatic conditions affected prey stable isotope values with a mixed effect model of $\delta^{13}\text{C}$ (resp. $\delta^{15}\text{N}$) depending on climatic treatment plus a random mesocosm effect for each of the prey sources with *lmer* package in R v. 3.4.2 (electronic supplementary material, table S1A).

We then explored the impact of climate on lizards stable isotope values. Because isotope values for food sources vary among mesocosms (electronic supplementary material, table S1A,B), and to be able to perform between-mesocosm comparisons, we performed a baseline correction of isotopic values previous to exploring climatic effects. $\delta^{15}\text{N}$ values were corrected by subtracting the mean $\delta^{15}\text{N}$ values of the primary consumers (phytophagous and detritivorous invertebrates) from each mesocosm ($\delta^{15}\text{N}_{\text{corr}}$). $\delta^{13}\text{C}$ values were corrected ($\delta^{13}\text{C}_{\text{corr}}$) following [43] by calculating the relative contribution of carbon originating from phytophagous invertebrates to lizards using a two end-member mixing model. We then fitted a global linear mixed model on $\delta^{13}\text{C}_{\text{corr}}$ and $\delta^{15}\text{N}_{\text{corr}}$ with climatic treatment and its two-way interactions with age class (juvenile or adult) and sex as fixed effects and mesocosm identity as random intercept. We then compared the global model to all derived simpler models with AIC using dredge function from *MuMIn* package to fit all combinations of fixed variables. As several models had close AICs, we used a model averaging method [44].

To address the consequences of climate treatment on the stable isotope niche of lizard populations, we calculated standard ellipse areas (SEAc) of juveniles and adults in each treatment using $\delta^{13}\text{C}_{\text{corr}}$ and $\delta^{15}\text{N}_{\text{corr}}$ with *siar* package [45]. We tested for differences in SEAc between treatments by drawing 10 000 bootstrapped samples resampling individual lizards from the two treatments to generate 95% CIs following [24]. We tested for differentiation in the stable isotope niche between climates (overlap area between ellipses) using a permutation test

drawing 10 000 permuted ellipses, where p is the proportion of ellipses with a smaller than observed niche overlap following [24].

(ii) Lizard diet composition

We then used stable isotope values to calculate the dietary contribution of each prey type to each individual lizard using a Bayesian mixing model with *Simmr v0.3* [46] with the recommended values of 10 000 iterations, a burning of 1000, a thinning of 10 and default priors (no prior information). As there is no specific trophic enrichment factor (TEF) for the common lizard available in the literature, we used TEF of tree lizards (*Urosaurus ornatus*), a species ecologically close to the common lizard: $\Delta^{13}\text{C}$ 1.2 ‰ (± 0.4 s.d.) and $\Delta^{15}\text{N}$: 0.7 ‰ (± 0.3 s.d.) [47,48]. However, we ran sensitivity analyses varying the TEF by $\pm 1\%$ around these values to check the consistency of our results, and we also checked for potential impacts of a change in TEF with temperature on our results, showing a robustness to variation in TEF (electronic supplementary material, section S3). To account for potential differences in prey stable isotope signatures from the different mesocosms (climate-induced or not), we estimated diet composition by mesocosm, given that lizards only had access to the prey of their own mesocosm.

We explored the impact of climate on the mean proportion of each prey category consumed by the lizards using linear mixed models with the same structure as described above. Because proportions are not independent, we focused on the two preferred prey categories only [38], the predators and the phytophagous invertebrates, to prevent issues related to non-independency of statistical models.

(iii) Lizard dietary specialization

Lizard individual dietary specialization was quantified by calculating Levins's diet breadth index $B = 1 / \sum pi^2$, where pi is the mean proportion of the i th prey [49]. This metric measures whether an individual is a perfect generalist ($B = 3$, eating each of the 3 prey categories evenly), a perfect specialist ($B = 1$, eating only one category of prey) or in between. We explored the impact of climate on individual dietary specialization (exp-transformed to avoid heteroscedasticity) with the same model structure as above.

(iv) Path analyses of lizard diet

We aimed to understand whether impacts of climate on lizard diets were driven by intrinsic effects of climate on the lizards themselves, or by climate-driven changes in prey abundances. We first summarized the variables linked to lizard diet into a principal component analysis, whose two first axes explained greater than 85% of the variance. PC1 correlated positively with the proportion of predatory invertebrates, $\delta^{15}\text{N}_{\text{corr}}$ and negatively with Levins's dietary index (electronic supplementary material, figure S1A), and therefore denotes a dietary specialization towards predator invertebrates (hereafter called predator specialization axis). PC2 was positively linked to the proportion of detritivorous invertebrates, and negatively to the proportion of phytophagous and to $\delta^{13}\text{C}_{\text{corr}}$ (electronic supplementary material, figure S1A), and denotes inputs from the green and brown food webs (hereafter called green–brown food axis). As only PC1 was linked to climate (impact of climate on PC1: $t = 2.161$, $p = 0.031$; on PC2: $t = 0.07$, $p = 0.94$), we only analysed impacts on this first axis.

We used path analysis using *ggm* package to build several causal models corresponding to the different biological hypotheses investigated ([50], see electronic supplementary material, figure S2B). The global model included the impact of climate on the abundance of the three prey groups, an impact of prey groups abundance on each other and the impact of lizard age, climate and abundance of the three prey categories on lizard diet, represented by PC1 axis (electronic supplementary material, figure S2B). Variables were centred and scaled. We first verified whether data were well supported according to the d-sep test in which conditional dependencies were tested through linear regressions [50]. We then compared the fitted models from the different sets of hypotheses (electronic supplementary material, figure S2B) through their AIC [51] with the *dsep.test* function from [52,53], and kept the model with the lowest AIC (electronic supplementary material, table S2A). We then estimated path coefficients and 95% confidence intervals on the best model with linear models.

(v) Implications of lizard diet on lizard phenotype and fitness

Finally, we studied whether lizard condition in September (body condition and gut microbiota diversity (Shannon index), through linear mixed models) and future winter–spring survival (through generalized mixed models with binomial family) was linked to their dietary habits for adults and juveniles, respectively.

Global models included the PC1 and PC2 diet and their interaction with climate, sex, juveniles' date of birth (Julian days) and for gut microbiota, sample sequencing depth (to control for differences in bacterial load) plus random mesocosm identity. Numeric variables were centred and scaled.

Ethics. The lizards used in this study are part of a wider study on the consequences of climate change on populations, and descend from lizards captured in the field (capture licence no. 2010-189-16 DREAL). The Station d'Ecologie Théorique et Experimentale has a national agreement for use of animals in the laboratory (number B09583), and our experiments are made in accordance with 2013 French ethics regulations (permits APAFIS#15897-2018070615164391 v3 and APAFIS#19523-201902281559649 v3).

Data accessibility. Data are available on Zenodo at <https://doi.org/10.5281/zenodo.3475402> [54].

Authors' contributions. E.B., J.Co. and J.Cu. conceived the study and designed the experiment. E.B., L.D.G., A.T. and J.Co. ran the experiment and collected the data. S.J., J.W., L.D.G. and L.Z. extracted and analysed the bacterial data. E.B. analysed the data with the help of A.S.-R., L.F., J.Cu. and J.Co. E.B. led the writing of the manuscript and J.Co., A.S.-R., J.Cu., J.W., L.Z. and S.J. contributed substantially to the writing of the manuscript.

Competing interests. We declare we have no competing interests.

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