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### ► To cite this version:

Elvire Bestion, Andrea Soriano-Redondo, Julien Cucherousset, Staffan Jacob, Joël White, et al.. Altered trophic interactions in warming climates: consequences for predator diet breadth and fitness. *Proceedings of the Royal Society B: Biological Sciences*, 2019, 286 (1914), pp.20192227. 10.1098/rspb.2019.2227 . hal-02340138

**HAL Id: hal-02340138**

**<https://hal.science/hal-02340138>**

Submitted on 30 Oct 2019

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

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*Proceedings of the Royal Society B: Biological Sciences*, 2019, 286: 20192227.

doi:10.1098/rspb.2019.2227

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**Keywords:** climate change, niche breadth, diet specialization, stable isotope analysis, gut microbiota, *Zootoca vivipara*

## Abstract

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 diets 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 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.

## 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.

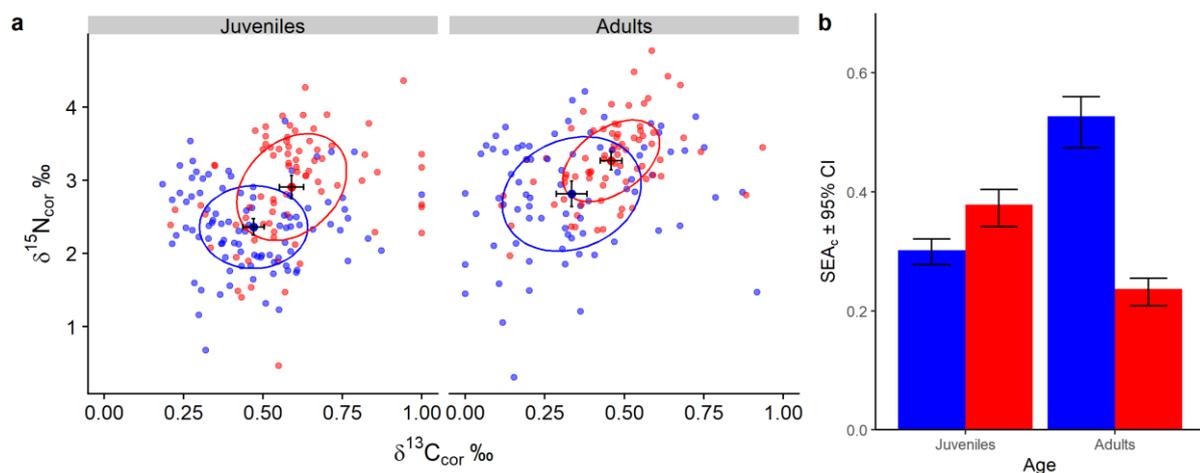
Here we studied the consequences of 2°C-warmer climatic conditions on the trophic niche of a generalist predator, the common lizard (*Zootoca vivipara*). We used a system of semi-natural mesocosms in which climatic conditions can be manipulated to create present-day climatic conditions and +2°C warmer 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 (size-corrected body mass), gut microbiota) and fitness. We characterised 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 positions because warming would decrease the abundance of predatory prey. Alternatively, an increase of 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.

## Results

### 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 (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, Fig. 1). Adults had higher  $\delta^{15}\text{N}_{\text{cor}}$  and  $\delta^{13}\text{C}_{\text{cor}}$  values than juveniles (Table 1, Fig. 1).



### 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: present-day climatic treatment, red: warm climatic treatment. Lines: sample size corrected standard ellipses (SEAc). Large points and errorbars: 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.

### 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, Fig 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,  $p < 0.0001$ , Fig. 1).

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

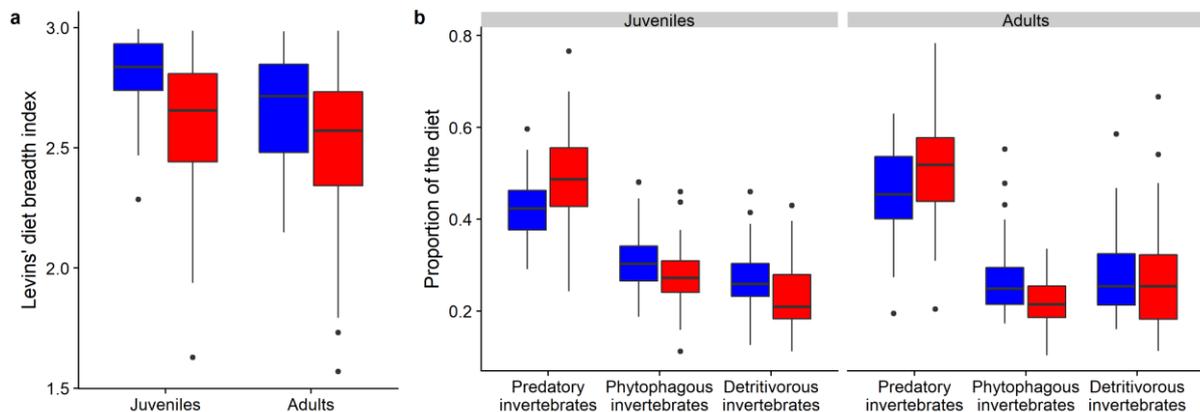
**Table 1: Impact of climatic treatment on lizard corrected stable isotope values, diet and dietary specialization**

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.  $R^2_m$  are 20, 21, 13, 22 and 21 % and  $R^2_c$  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.  $N = 327$ .

Variable	Parameter	Estimate	SE	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
	Age:Climate	0.04	0.12	0.31	0.754	0.14
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
	Age:Climate	-0.01	0.02	0.81	0.420	0.15
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
	Age:Climate	-0.01	0.01	0.51	0.609	0.14
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

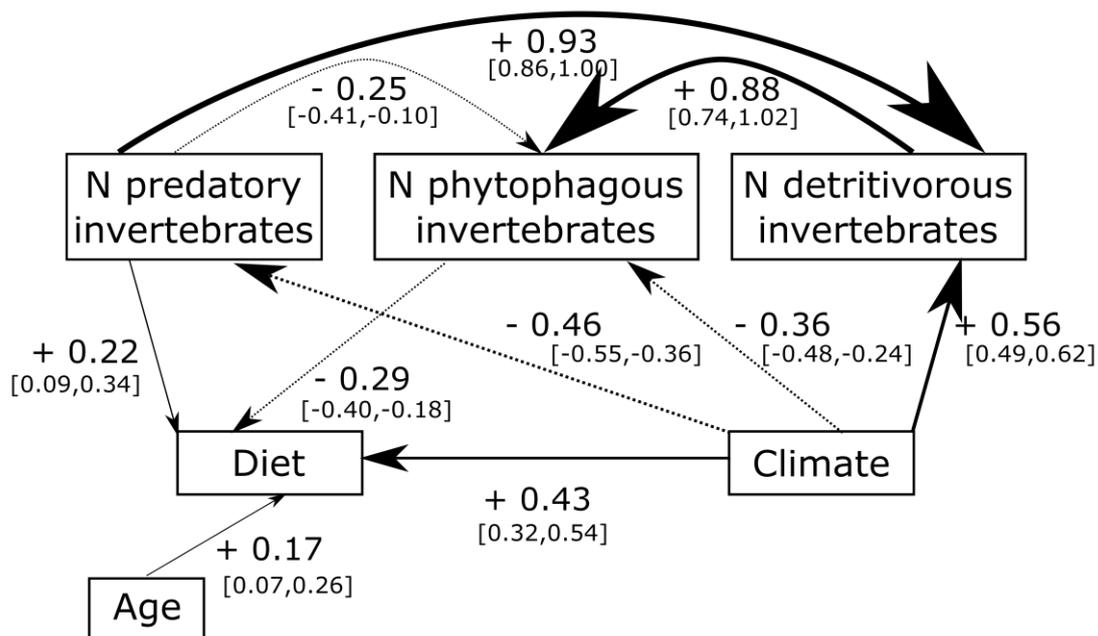
A path analysis was used to disentangle direct effects of climate from climate-dependent changes in prey community on lizard diet, summarized with the first axis of a principal component analysis (Fig 3, Fig S2A). The best model included both a direct positive effect of warmer climate on diet specialization (coef = 0.43, higher specialization) and, to a lower 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) (Fig. 3, Table S2A).



**Figure 2: Impact of climate on lizard diet**

(a) Lizards individual dietary breadth measured by Levins' dietary index (ranging between 1: completely specialized diet to 3: completely generalized diet). (b) Dietary contribution of each putative prey (see Table 1). Blue: present-day climatic treatment, red: warm climatic treatment.  $N = 96$  and  $79$  juveniles in present-day and warm climate respectively, and  $N = 77$  and  $75$  adults.



**Figure 3: Path analysis of the impact of climate on lizard diet**

Diet represents the predator specialization (PCI, Fig. 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 (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).  $N = 327$ .

### Implications of diet change on lizards' body condition, microbiota and survival

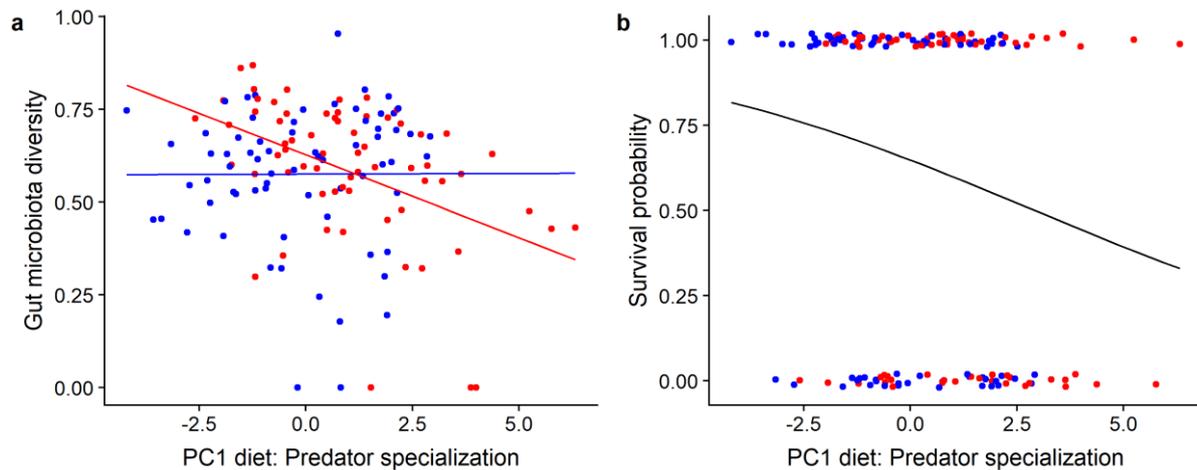
Adult body condition in September was not linked to any of the dietary components (Table 2), while there was an interactive effect of climate and the green-brown food axis (proportion of detritivorous versus phytophagous prey eaten, PC2 axis, Fig S2A) on juvenile body condition ( $p = 0.02$ , Table 2).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

#### **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.  $N = 152$  adults, 175 juveniles.*

Variables	Age	Parameter	Estimate	SE	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 vs 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 vs 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 vs 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

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 ( $p = 0.008$ , Table S4A, Fig 4a).



**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 (Fig. 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 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: present-day climatic treatment, red: warm climatic treatment.  $N = 152$ .

Adult lizard subsequent Winter-Spring survival was negatively correlated to the pre-winter specialization towards predatory invertebrates ( $p = 0.042$ , Fig. 4b, Table 2) 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).

## Discussion

Our study highlights how climatic conditions, prey communities and predator traits interact in driving trophic interactions. Warmer climatic conditions led to higher  $\delta^{13}\text{C}$  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,  $\delta^{15}\text{N}$  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 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 likely 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 (Supplementary 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.

## Methods

### 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, Gasteropods, Isopods 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 nb. 2010-189-16 DREAL). The Station d'Ecologie Theorique 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 x 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 ( $30 \pm 3$  invertebrate families per mesocosm, see below). Climatic conditions within mesocosms are monitored continuously and can be manipulated through motor-driven shutters [19,20].

### 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:  $26.3 \pm 0.3$  °C, WC:  $28.3 \pm 0.2$  °C, mean  $\pm$  SE,  $F_{1,147} = 13$ ,  $p < 0.001$ ; weekly mean of Summer maximum daily temperatures: PC:  $29.1 \pm 0.3$  °C, WC:  $32.4 \pm 0.4$  °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:  $31.4 \pm 4.4$ , WC:  $29 \pm 6.6$ ,  $p = 0.53$ , of phytophagous, PC:  $27.6 \pm 6.5$ , WC:  $37.6 \pm 7.3$ ,  $p = 0.55$ , of detritivorous, PC:  $8.2 \pm 5.4$ , WC:  $5.4 \pm 1.7$ ,  $p = 0.83$ , assessed in May 2013 following the same sampling procedure as below).

We released a total of 612 lizards, 264 adults (including two-and-more year olds (2+yo) and one-year-olds (1yo)) and 348 juveniles. Adults were previously maintained for one 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  $7 \pm 1$  2+yo males,  $12 \pm 1$  2+yo females,  $7 \pm 2$  1yo, and  $35 \pm 3$  juveniles, conforming with local densities in natural populations [20]. We do not expect specific differences between 2+yo and 1yo; in 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 1yo.

### Lizard condition, diet and survival assessment

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 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].

### 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 ( $\emptyset$  8 x 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  $\emptyset$  25 cm sweep net to recover canopy arthropods

and flying insects. Sampling effort led to recover  $295 \pm 91$  invertebrate individuals per enclosure and  $30 \pm 3$  families (Fig S1A). Recovered invertebrates were preserved at  $-20^{\circ}\text{C}$ . 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 (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  $60^{\circ}\text{C}$  for 48h, 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  $\delta^{15}\text{N}$ ).

## Statistical analyses

### 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 v3.4.2 (Table S1A).

We then explored the impact of climate on lizards stable isotope values. Because isotope values for food sources vary among mesocosms (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  $\delta^{13}\text{C}_{\text{cor}}$  and  $\delta^{15}\text{N}_{\text{cor}}$  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 10000 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 10000 permuted ellipses, where  $p$  is the proportion of ellipses with a smaller than observed niche overlap following [24].

### 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 10000 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 ‰ ( $\pm 0.4$  SD) and  $\Delta^{15}\text{N}$ : 0.7 ‰ ( $\pm 0.3$  SD) [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

(Supplementary 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.

#### ***Lizard dietary specialization***

Lizard individual dietary specialization was quantified by calculating Levins' diet breadth index  $B = \frac{1}{\sum p_i^2}$ , where  $p_i$  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.

#### ***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 > 85% of the variance. PC1 correlated positively with the proportion of predatory invertebrates,  $\delta^{15}\text{N}_{\text{corr}}$ , and negatively with Levins' dietary index (Fig S1A), and therefore denotes a dietary specialization toward 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  $\delta^{13}\text{C}_{\text{corr}}$  (Fig 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 Fig. 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 (Fig S2B). Variables were centred and scaled. We first verified whether data was 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 (Fig S2B) through their AIC [51] with the *dsep.test* function from [52,53], and kept the model with the lowest AIC (Table S2A). We then estimated path coefficients and 95% confidence intervals on the best model with linear models.

#### ***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 generalised 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 nb. 2010-189-16 DREAL). The Station d'Ecologie Theorique 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).

**Data accessibility:** data is available on zenodo at [dx.doi.org/10.5281/zenodo.3475402](http://dx.doi.org/10.5281/zenodo.3475402). Data should be cited as: Bestion, E, Soriano-Redondo, A, Cucherousset, J, Jacob, S, White, J, Zinger, L, Fourtune, L, Di Gesu, L, Teyssier, A, Cote, J (2019). Raw data for: "Altered trophic interactions in warming climates: consequences for predator diet breadth and fitness", Bestion et al 2019 Proceedings B. (Version 1). <http://doi.org/10.5281/zenodo.3475402>.

**Author contributions:** EB, JCo and JCu conceived the study and designed the experiment. EB, LDG, AT, and JCo ran the experiment and collected the data. SJ, JW, LDG and LZ extracted and analysed the bacterial data. EB analysed the data with the help of ASR, LF, JCu and JCo. EB led the writing of the manuscript and JC, ASR, JCu, JW, LZ and SJ contributed substantially to the writing of the manuscript.

**Competing interests:** We declare we have no competing interests.

**Funding:** This work was supported by the French Laboratory of Excellence project 'TULIP' (ANR-10-LABX-41; ANR-11-IDEX-0002-02), by an 'Investissements d'avenir' program from the Agence Nationale de la Recherche (ANR-11-INBS-0001AnaEE-Services), by an ANR-12-JSV7-0004-01 to JCo, and by a Young Researchers award from the Bettencourt-Schueller foundation to EB. This work is part of a project that has received funding from the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (grant agreement No 817779 to JCo).

**Acknowledgements:** We thank Olivier Calvez, Olivier Guillaume, Antoine Cave, Bastien Rémurier, Laure Geidel and Alice Fournier for fieldwork assistance and Richard Inger for insightful statistical comments.

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## Supplementary material for

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

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*Proceedings of the Royal Society B*, 2019, 286: 20192227. Doi: 10.1098/rspb.2019.2227

*Electronic supplementary material is available online at*

<https://dx.doi.org/10.6084/m9.figshare.c.4700648>

#### **Contents:**

Section S1: Impact of climatic conditions on invertebrate stable isotope values

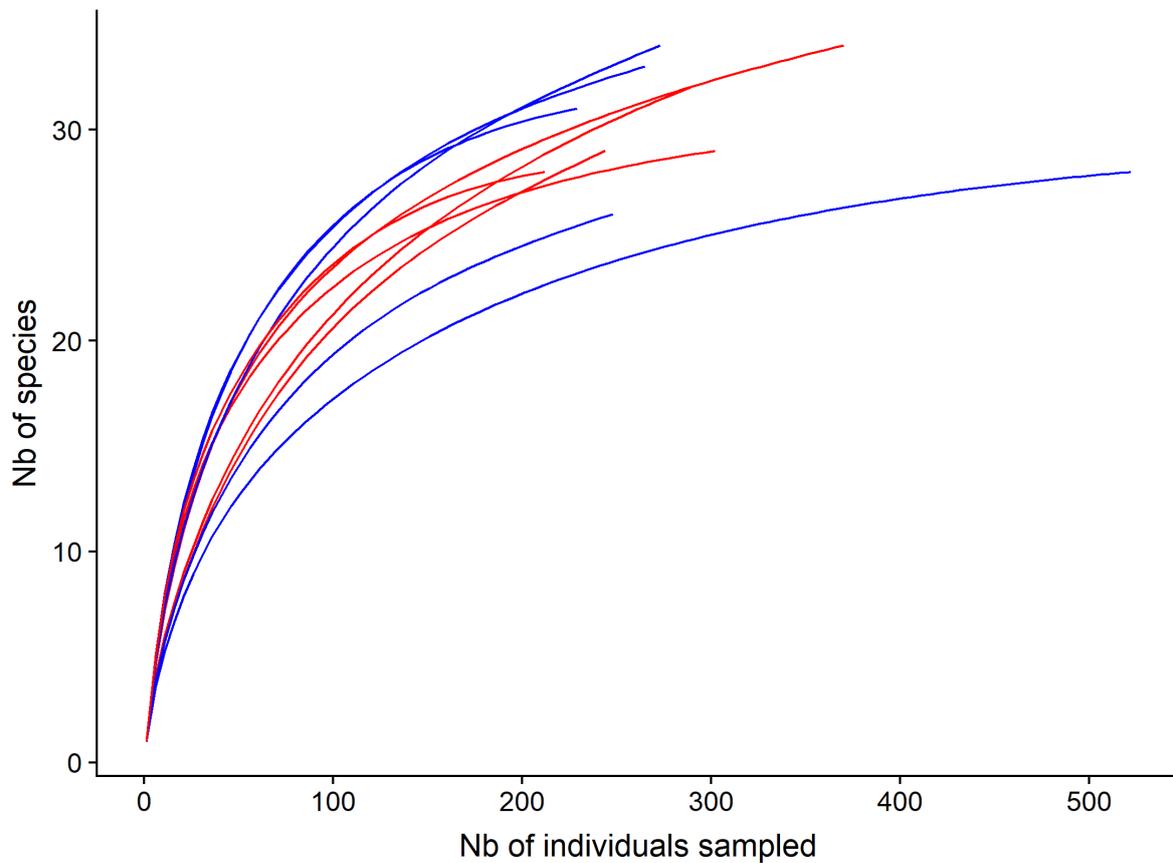
Section S2: Path analysis of the impact of climate and community composition on lizard diet

Section S3: Sensitivity analysis

Section S4: Link between lizards' diet and their gut microbial communities

Section S5: Implications of lizard diet on prey communities

## Supplementary section S1: Impact of climatic conditions on invertebrate stable isotope values



**Figure S1A: Rarefaction curves of invertebrate species richness per mesocosm**

Blue: present-day climate, red: warm climate. While the capture effort was the same among mesocosms, the total number of recovered invertebrates varied due to differences in abundances among enclosures ( $295 \pm 91$  invertebrate individuals sampled per enclosure). However, the shape of the curves show that we were close to saturation for all enclosures, suggesting a relatively good sampling effort.

**Table S1A: Impact of climatic conditions on stable isotope values per invertebrate functional group**

Results from mixed effect models with climatic treatment as a fixed effect and mesocosm as a random intercept. The table presents mean  $\pm$  SE for each climatic condition. Significant effects are in bold.

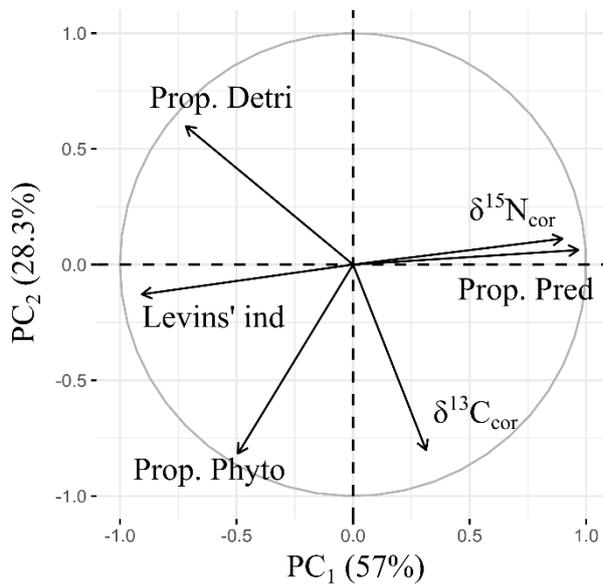
parameter	Detritivorous				Phytophagous				Predatory			
	present	warm	$\chi^2$	p-value	present	warm	$\chi^2$	p-value	present	warm	$\chi^2$	p-value
$\delta^{13}\text{C}$	<b>-26.75</b> $\pm 0.17$	<b>-25.84</b> $\pm 0.20$	<b>11.8</b>	<b>6e-4</b>	<b>-29.47</b> $\pm 0.17$	<b>-28.8</b> $\pm$ <b>7.1</b> <b>0.17</b>	<b>7.1</b>	<b>0.008</b>	-28.26 $\pm 0.15$	-27.96 $\pm 0.27$	0.93	0.33
$\delta^{15}\text{N}$	5.30 $\pm$ 0.30	4.64 $\pm$ 0.28	2.6	0.11	6.64 $\pm$ 0.18	6.20 $\pm$ 0.17	0.9	0.33	8.58 $\pm$ 0.23	8.45 $\pm$ 0.20	0.08	0.78

**Table S1B: Mean and SD stable isotope values per invertebrate functional group and mesocosm**

The detritivorous group is composed of the 3 locally dominant families: Isopodae, Julidae and Lumbricidae, representing 82% of the total detritivorous invertebrate abundance. The phytophagous group is composed of Cercopidae, Crysomelidae, Delphacidae, Formicidae, Tipulidae, Gryllidae, Arionidae, (69% of the phytophagous invertebrate abundance). The predator group is composed of spiders (Araneidae, Clubionidae, Lycosidae, Salticidae, Tetragnathidae, Theridiidae, Thomisidae), Carabidae, Nabidae and Staphilinidae (86 % of the predatory invertebrate abundance).

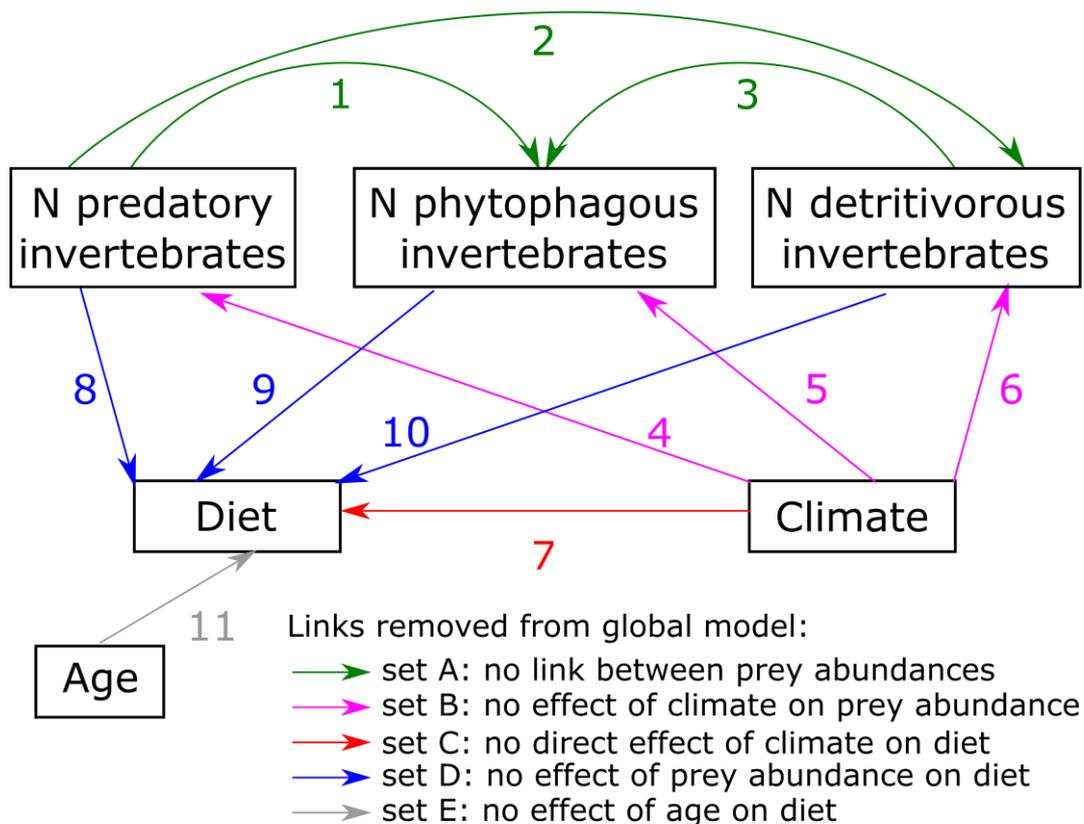
Group	Mesocosm	Climate	Mean $\delta^{15}\text{N}$	SD $\delta^{15}\text{N}$	Mean $\delta^{13}\text{C}$	SD $\delta^{13}\text{C}$
detritivorous	26	present-day	4.50	0.77	-26.82	0.79
detritivorous	28	present-day	5.75	1.62	-26.76	0.98
detritivorous	33	present-day	5.50	0.42	-27.04	0.46
detritivorous	41	present-day	6.05	2.18	-26.66	0.94
detritivorous	45	present-day	4.17	2.33	-26.36	1.71
detritivorous	25	warm	4.82	1.13	-26.31	0.98
detritivorous	29	warm	4.88	1.96	-26.42	0.57
detritivorous	32	warm	4.80	1.30	-25.60	1.44
detritivorous	38	warm	4.93	2.20	-25.43	0.56
detritivorous	46	warm	3.86	1.77	-25.70	1.47
phytophagous	26	present-day	5.97	1.06	-29.09	1.21
phytophagous	28	present-day	7.20	1.04	-29.44	1.05
phytophagous	33	present-day	7.35	2.11	-29.90	1.37
phytophagous	41	present-day	6.64	0.61	-29.54	0.93
phytophagous	45	present-day	6.41	0.80	-29.66	1.65
phytophagous	25	warm	4.79	1.02	-28.60	1.18
phytophagous	29	warm	6.03	0.83	-28.77	1.43
phytophagous	32	warm	7.78	0.93	-28.73	2.09
phytophagous	38	warm	6.16	0.93	-28.85	0.84
phytophagous	46	warm	6.11	1.04	-29.02	1.10
predatory	26	present-day	8.19	1.69	-28.12	0.96
predatory	28	present-day	10.03	0.93	-27.86	0.85
predatory	33	present-day	7.38	0.88	-28.60	0.76
predatory	41	present-day	9.21	1.04	-28.55	0.73
predatory	45	present-day	7.67	1.50	-27.93	2.15
predatory	25	warm	7.28	0.90	-27.08	3.03
predatory	29	warm	7.41	0.63	-28.33	0.54
predatory	32	warm	10.19	0.82	-28.38	0.63
predatory	38	warm	8.03	0.76	-27.78	0.51
predatory	46	warm	8.56	0.76	-27.93	2.66

## Supplementary section S2: Path analysis of the impact of climate and community composition on lizard diet



### Figure S2A: Principal component analysis of lizard diet

The first axis of the PCA represents 57 % of the variance, and is mainly linked to the proportion of predatory invertebrates in the diet (+0.52 loading), the Levins' dietary index (-0.49 loading), and the corrected  $\delta^{15}\text{N}$  values (+0.49), while the proportion of phytophagous (-0.27), detritivorous invertebrates (-0.39) and the  $\delta^{13}\text{C}$  values (0.17) have less importance. This first principal component is hereafter named predatory specialization. The second axis of the PCA represents 28 % of the variance and is mainly linked to the proportion of phytophagous invertebrates (-0.63), of detritivorous invertebrates (+0.46) and the  $\delta^{13}\text{C}$  values (-0.62), while the proportion of predatory invertebrate (0.05) and the  $\delta^{15}\text{N}$  values (0.09) are less represented. This axis will be referred to as the green-brown diet axis.



### Figure S2B: Diagram of the global path analysis model and sub-models

The global path, containing all links, represents our first biological hypothesis, that is that diet is affected by age, a direct effect of climate and an indirect effect of climate through differences in abundances of prey types, while the abundances of prey types are linked together. A first set of models, set A, removing links 1 to 3 and their combinations, tests whether the abundances of prey types are actually dependent on each other. A second set of models, set B, removing links 4 to 6 and their combinations, represents the direct impact of climate on diet, while prey abundances affect diet independently of climate as climate does not affect prey abundance. A third set of models, set C, removing link 7, represent the hypothesis of an indirect effect of climate only, through climate-driven changes in prey abundances. A fourth set of models, set D, removing links 8 to 10 and their combinations, represents the direct impact of climate on diet, while prey abundances are affected by climate but do not affect lizard diet. Finally, a fifth set of models, set E, removing link 11, represents no impact of age on diet. We compared the fitted models from each of the 5 sets of models through their AIC with the `dsep.test` function and kept the model with the lowest AIC. The best model was a model from the fourth set of model, removing link 10 (Table S2A). We tested whether a better model could be made by combining the paths from the best model of set D (minus link 10, AIC = 46.02) and the best model of set A (minus link 1, AIC = 56.86). The AIC difference between the best model (minus link 10) and this new model (minus links 10+1) was >10 points (AIC = 56.06).

**Table S2A: C-test statistic, p-value and AIC of the path sub-models**

The table ranks the global model and all of the sub-models tested (see Fig S1B) by their AIC. The best model includes all links but the 10<sup>th</sup> link, that is the effect of the abundance of detritivorous invertebrates on the diet. Its p-value is > 0.05, which means that it fits well the data.

Set	Links missing from the path	Ctest	df	p-value	AIC
D	10	10.02	10	0.439	46.02
Global model	None	8.82	8	0.358	46.82
D	8	13.62	10	0.191	49.62
D+A	10+1	22.06	12	0.0368	56.06
A	1	20.86	10	0.0221	56.86
D	8+10	24.69	12	0.0164	58.69
E	11	23.81	10	0.00813	59.81
D	9	32.26	10	3.62e-4	68.26
C	7	37.58	10	4.5e-5	73.58
D	9+10	39.88	12	7.52e-5	73.88
D	8+9+10	42.11	14	1.19e-4	74.11
D	8+9	40.75	12	5.39e-5	74.75
B	5	46.29	10	1.27e-6	82.29
B	4	88.29	10	1.17e-14	124.29
B	4+5	125.76	12	0	159.76
A	3	135.81	10	0	171.81
B	6	204.67	10	0	240.67
A	1+3	235.94	12	0	269.94
B	5+6	242.14	12	0	276.14
B	4+6	284.14	12	0	318.14
B	4+5+6	321.61	14	0	353.61
A	2	394.49	10	0	430.49
A	1+2	406.53	12	0	440.53
A	2+3	521.47	12	0	555.47
A	1+2+3	707.54	14	0	739.54

### Supplementary section S3: sensitivity analysis

Best practices in stable isotope ecology recommend the use of trophic enrichment factor if possible from the same species, or failing that for a species ecologically and taxonomically close [1]. There is very few data available for trophic enrichment factors in reptiles, and the only study giving both  $\Delta^{13}\text{C}$  and  $\Delta^{15}\text{N}$  values for trophic enrichment factors in lizards is for another species, *Urosaurus ornatus*[2,3]. Fortunately, this species is quite ecologically similar, with a small body size (up to 59 mm snout-vent length), and feeding on a similar range of invertebrates such as Araneae, Coleoptera, Orthoptera, Heteroptera, Homoptera, Diptera and Hymenoptera [2–4]. However, the true TEF for common lizards might still be different from the one of tree lizards. To ensure the reliability of our results, we hence ran a sensitivity analysis around the values of *Urosaurus ornatus* TEF.

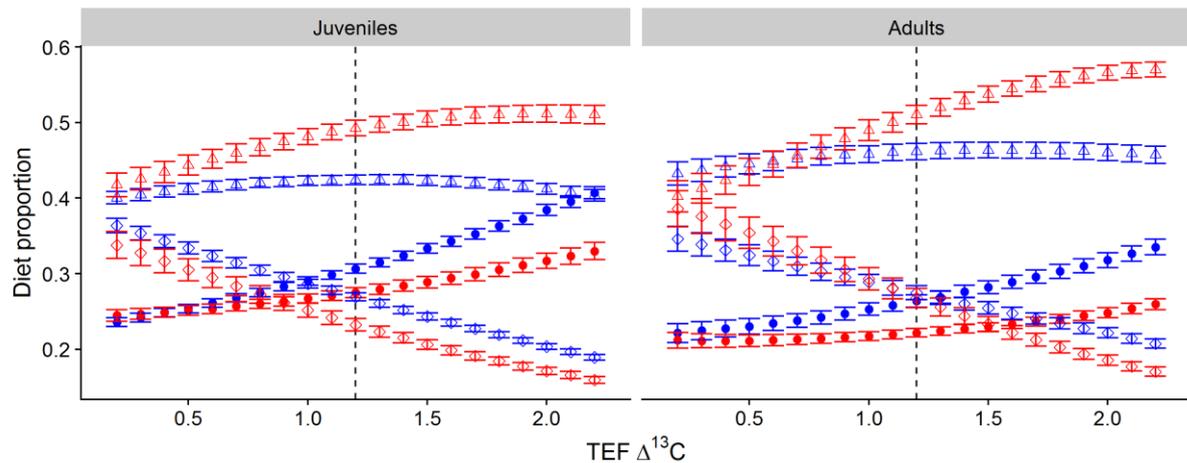
We varied the TEF by 0.1 ‰ steps up to +1 and -1‰ from the values found by Lattanzio & Miles (2016a, b):  $\Delta^{13}\text{C}$  1.2 ‰ ( $\pm 0.4$  SD) and  $\Delta^{15}\text{N}$ : 0.7 ‰ ( $\pm 0.3$  SD). We studied how changing the TEF changed the proportion of each prey source eaten by the lizards and the Levins' dietary index; and how it impacted the dietary differences between climatic conditions (Figures S3A-S3D, Tables S3A-S3B). Because there were no significant interactions between climatic conditions and age class or sex in the original models (Table 1), our analyses did not take into account interactions to simplify the models. We fitted models with climate, age, sex and random mesocosm identity to test the climate effect. Not surprisingly, changes in the TEF lead to changes in the proportion of each invertebrate group eaten (Fig S3A-S3B), however the differences between climatic conditions are relatively robust to changes in TEF.  $\Delta^{13}\text{C}$  TEFs higher than the reference value of 1.2 ‰ lead to more significant differences in the proportion of predatory and phytophagous invertebrates eaten, while TEFs lower than 1.2 ‰ lead to non-significant differences in the proportion of predatory invertebrates and TEFs lower than 1.1 ‰ lead to non-significant differences in the proportion of phytophagous invertebrates (Table S3A, Fig S3A).  $\Delta^{15}\text{N}$  TEFs higher than the reference value of 0.7 ‰ lead to significant differences in the proportion of predatory invertebrates, while TEFs up to 0.9 ‰ or lower lead to significant differences in the proportion of phytophagous invertebrates (Table S3B, Fig S3B). The differences in the Levins' dietary index are the most robust to variation in TEF, with significant differences apart from very low values of  $\Delta^{13}\text{C}$  TEF and very high and very low values of  $\Delta^{15}\text{N}$  TEF (Fig S3C-S3D, Table S3A-S3B). Overall, these results suggest that the differences between climatic conditions in lizard dietary habits are robust to variation in the trophic enrichment factor, particularly for values of  $\Delta^{13}\text{C}$  TEF higher than 1.2 ‰ and values of  $\Delta^{15}\text{N}$  TEF lower than 0.7 ‰. These values are consistent with TEF values for other reptiles, with  $\Delta^{13}\text{C}$  TEF values as high as 2.29 ‰ for snakes' muscle [5], and 1.06 ‰ for crocodiles' muscle [6], although another study on lizards found extremely low values of -1.9 ‰ for lizards' muscle, without characterizing  $\Delta^{15}\text{N}$  TEF [7], and with  $\Delta^{15}\text{N}$  TEF values as low as -2.50 ‰ for crocodiles' muscle [6]. Other studies have used a meta-analysis on birds'  $\Delta^{15}\text{N}$  TEF to approximate lizards' trophic enrichment [8], which would amount to a TEF of 0.8 ‰ for birds' muscle[9], very close to the 0.7 ‰ value used in this study.

Another issue is that TEF could change with temperature. Although there is no literature on variation in TEF with temperature in reptiles, one study shows that a +5°C increase in temperature can lead to both a -0.6 ‰ decrease in  $\Delta^{15}\text{N}$  TEFs and a +0.4 ‰ increase in  $\Delta^{13}\text{C}$  TEFs in fish [10]. We thus studied how a decrease in  $\Delta^{15}\text{N}$  TEFs (resp. an increase in  $\Delta^{13}\text{C}$  TEFs) in warm climates compared to present-day climates could affect our results. We first studied a change in  $\Delta^{15}\text{N}$ .  $\Delta^{13}\text{C}$  was thus fixed at 1.2 ‰ and  $\Delta^{15}\text{N}$  was fixed at the reference value of 0.7 ‰ in present-day climate, but was allowed to vary between 0.7-0 and 0.7-0.6 ‰

in warm climates (Table S3C). We then repeated the analysis focusing on changes in  $\Delta^{13}\text{C}$ .  $\Delta^{15}\text{N}$  was thus fixed at 0.7 ‰ and  $\Delta^{13}\text{C}$  was fixed at the reference value of 1.2 ‰ in present-day climate, but was allowed to vary between 1.2+0 and 1.2+0.6 ‰ in warm climates (Table S3D). Our results are very robust to potential variations in TEF with temperature, with impacts of climate on the proportion of predatory invertebrates eaten becoming more significant, and impacts of climate on the proportion of phytophagous invertebrates eaten being mainly robust, except for very high increases in  $\Delta^{13}\text{C}$  for which the impact of climate on the proportion of phytophagous invertebrates became non-significant (Table S3C-S3D). The differences in Levins' index were always significant (Table S3C-S3D).

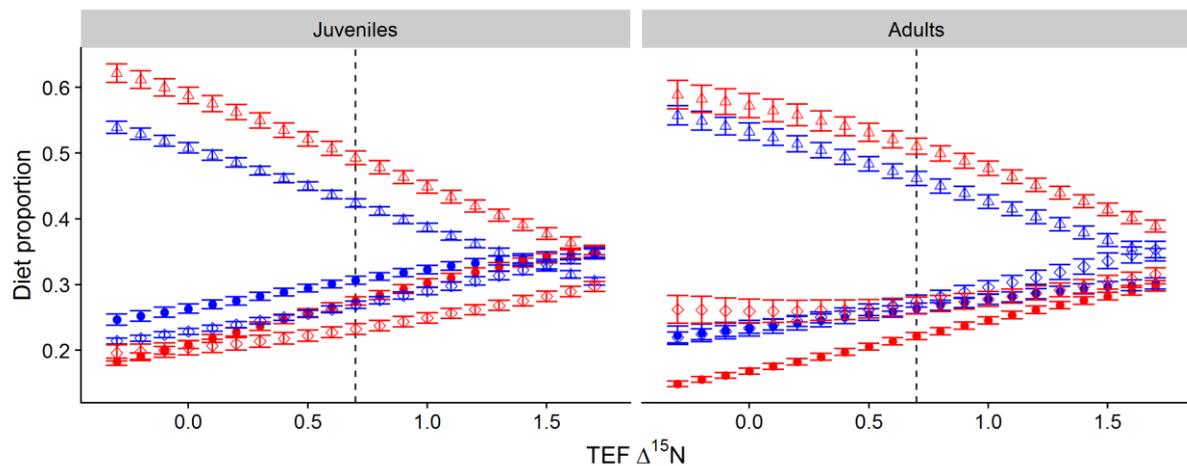
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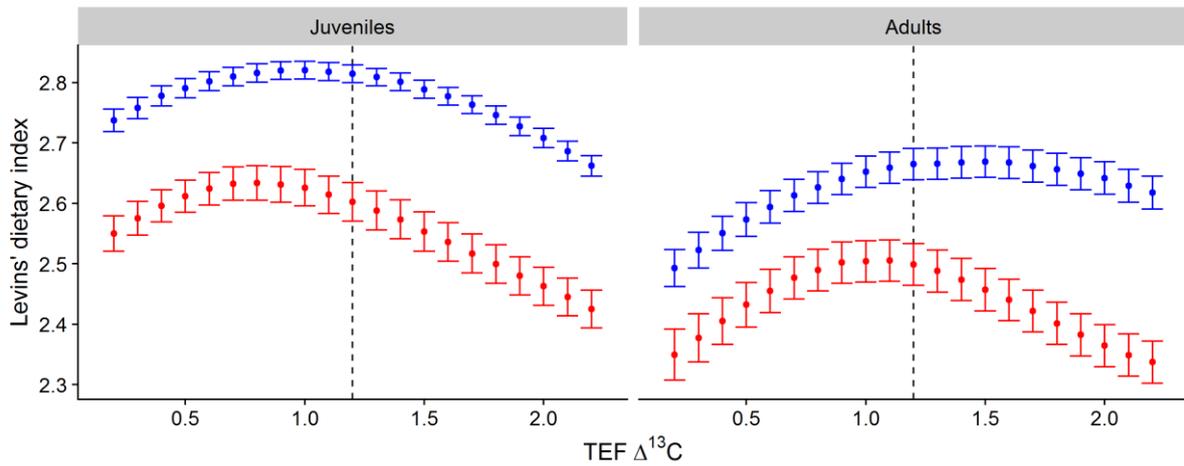
**Figure S3A: Impact of variation on the  $\Delta^{13}\text{C}$  TEF on the proportion of each of the 3 prey sources eaten by lizards from warm (in red) and present-day (blue) climates (mean values  $\pm$  SEM).**

$\Delta^{15}\text{N}$  is fixed at 0.7 ‰ and  $\Delta^{13}\text{C}$  varies by +1 and -1 from 1.2 ‰ (value from Lattanzio and Miles, dashed line). Triangles are predatory invertebrates, filled circles are phytophagous invertebrates, and diamonds are detritivorous invertebrates.

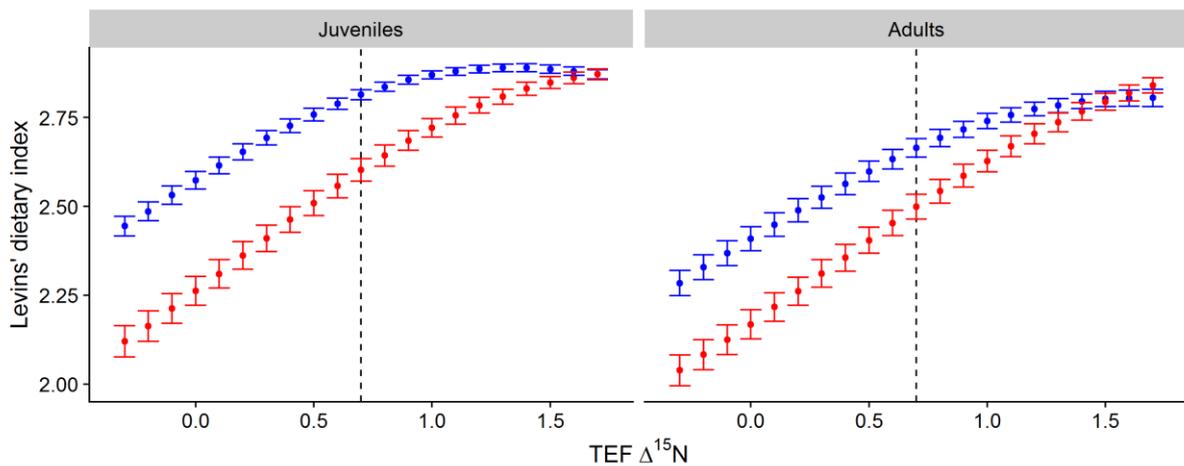


**Figure S3B: Impact of variation on the  $\Delta^{15}\text{N}$  TEF on the proportion of each of the 3 prey sources eaten by lizards from warm (in red) and present-day (blue) climates (mean values  $\pm$  SEM).**

$\Delta^{13}\text{C}$  is fixed at 1.2 ‰ and  $\Delta^{15}\text{N}$  varies by +1 and -1 from 0.7 ‰ (value from Lattanzio and Miles, dashed line). Triangles are predatory invertebrates, filled circles are phytophagous invertebrates, and diamonds are detritivorous invertebrates.



**Figure S3C: Impact of variation on the  $\Delta^{13}\text{C}$  TEF on Levins' dietary index of lizards from warm (in red) and present-day (blue) climates (mean values  $\pm$  SEM).**  $\Delta^{15}\text{N}$  is fixed at 0.7 ‰ and  $\Delta^{13}\text{C}$  varies by +1 and -1 from 1.2 ‰ (value from Lattanzio and Miles, dashed line).



**Figure S3D: Impact of variation on the  $\Delta^{15}\text{N}$  TEF on Levins dietary index of lizards from warm (in red) and present-day (blue) climates (mean values  $\pm$  SEM).**  $\Delta^{15}\text{N}$  is fixed at 0.7 ‰ and  $\Delta^{13}\text{C}$  varies by +1 and -1 from 1.2 ‰ (value from Lattanzio and Miles, dashed line).

**Table S3A: Impact of variation in the  $\Delta^{13}\text{C}$  TEF on the difference between climatic conditions in the proportion of predatory and phytophagous prey eaten, as well as the Levins' index.**

$\Delta^{15}\text{N}$  is fixed at 0.7 ‰ and  $\Delta^{13}\text{C}$  varies by +1 and -1 from the reference value of 1.2 ‰ in 0.1 ‰ steps. For each value of  $\Delta^{13}\text{C}$ , we apply a linear mixed model of the dependent variable as a function of climatic conditions, age, sex and random mesocosm identity. We report  $\chi^2$  and p-values for the climatic effect. Significant effects are in bold.

$\Delta^{13}\text{C}$ TEF	Predatory inv.		Phytophagous inv.		Levins' index	
	$\chi^2$	p-value	$\chi^2$	p-value	$\chi^2$	p-value
0.2	0.03	0.87	0.03	0.86	3.04	0.081
0.3	0.01	0.92	0.07	0.78	<b>4.23</b>	<b>0.04</b>
0.4	0	0.99	0.15	0.69	<b>6.06</b>	<b>0.014</b>
0.5	0.01	0.92	0.26	0.61	<b>7.44</b>	<b>0.0064</b>
0.6	0.05	0.82	0.51	0.48	<b>8.06</b>	<b>0.0045</b>
0.7	0.15	0.70	0.81	0.37	<b>7.14</b>	<b>0.0075</b>
0.8	0.34	0.56	1.33	0.25	<b>6.48</b>	<b>0.011</b>
0.9	0.69	0.41	2.26	0.13	<b>5.87</b>	<b>0.015</b>
1.0	1.31	0.25	3.58	0.058	<b>5.83</b>	<b>0.016</b>
1.1	2.22	0.14	<b>5.06</b>	<b>0.024</b>	<b>6.01</b>	<b>0.014</b>
1.2* ref	3.57	0.059	<b>7.07</b>	<b>0.0079</b>	<b>6.65</b>	<b>0.0099</b>
1.3	<b>5.35</b>	<b>0.021</b>	<b>9.23</b>	<b>0.0024</b>	<b>7.75</b>	<b>0.0054</b>
1.4	<b>7.63</b>	<b>0.0057</b>	<b>11.27</b>	<b>7.9e-4</b>	<b>9.51</b>	<b>0.002</b>
1.5	<b>10.41</b>	<b>0.0013</b>	<b>13.09</b>	<b>3e-4</b>	<b>11.59</b>	<b>6.6e-4</b>
1.6	<b>13.2</b>	<b>2.8e-4</b>	<b>13.6</b>	<b>2.3e-4</b>	<b>14.39</b>	<b>1.5e-4</b>
1.7	<b>15.86</b>	<b>6.8e-5</b>	<b>14.45</b>	<b>1.4e-4</b>	<b>16.51</b>	<b>4.8e-5</b>
1.8	<b>18.03</b>	<b>2.2e-5</b>	<b>14</b>	<b>1.8e-4</b>	<b>19</b>	<b>1.3e-5</b>
1.9	<b>19.94</b>	<b>8e-6</b>	<b>13.18</b>	<b>2.8e-4</b>	<b>20.72</b>	<b>5.3e-6</b>
2.0	<b>21.13</b>	<b>4.3e-6</b>	<b>12.81</b>	<b>3.4e-4</b>	<b>21.44</b>	<b>3.6e-6</b>
2.1	<b>21.92</b>	<b>2.8e-6</b>	<b>11.77</b>	<b>6e-4</b>	<b>21.6</b>	<b>3.4e-6</b>
2.2	<b>22.15</b>	<b>2.5e-6</b>	<b>10.78</b>	<b>0.001</b>	<b>21.52</b>	<b>3.5e-6</b>

**Table S3B: Impact of variation in the  $\Delta^{15}\text{N}$  TEF on the statistical significance of the difference between climatic conditions in the proportion of predatory and phytophagous prey eaten, as well as the Levins' index.**

$\Delta^{13}\text{C}$  is fixed at 1.2 ‰ and  $\Delta^{15}\text{N}$  varies by +1 and -1 from the reference value of 0.7 ‰ in 0.1 ‰ steps. For each value of  $\Delta^{15}\text{N}$ , we apply a linear mixed model of the dependent variable as a function of climatic conditions, age, sex and random mesocosm identity. We report  $\chi^2$  and p-values for the climatic effect. Significant effects are in bold.

$\Delta^{15}\text{N}$ TEF	Predatory inv.		Phytophagous inv.		Levins' index	
	$\chi^2$	p-value	$\chi^2$	p-value	$\chi^2$	p-value
-0.3	0.57	0.45	<b>2.82</b>	<b>0.093</b>	2.64	0.1
-0.2	0.67	0.41	<b>3.11</b>	<b>0.078</b>	2.96	0.086
-0.1	0.83	0.36	<b>3.43</b>	<b>0.064</b>	3.29	0.07
0	0.97	0.32	<b>3.8</b>	<b>0.051</b>	3.66	0.056
0.1	1.18	0.28	<b>4.37</b>	<b>0.037</b>	<b>4.04</b>	<b>0.044</b>
0.2	1.43	0.23	<b>4.94</b>	<b>0.026</b>	<b>4.37</b>	<b>0.036</b>
0.3	1.74	0.19	<b>5.59</b>	<b>0.018</b>	<b>4.82</b>	<b>0.028</b>
0.4	2.1	0.15	<b>6.66</b>	<b>0.0099</b>	<b>5.27</b>	<b>0.022</b>
0.5	2.55	0.11	<b>7.21</b>	<b>0.0072</b>	<b>5.68</b>	<b>0.017</b>
0.6	3.08	0.079	<b>7.76</b>	<b>0.0053</b>	<b>6.3</b>	<b>0.012</b>
0.7* ref	3.57	0.059	<b>7.07</b>	<b>0.0079</b>	<b>6.65</b>	<b>0.0099</b>
0.8	<b>4.10</b>	<b>0.043</b>	<b>5.71</b>	<b>0.017</b>	<b>7.2</b>	<b>0.0073</b>
0.9	<b>4.68</b>	<b>0.031</b>	<b>4.13</b>	<b>0.042</b>	<b>7.85</b>	<b>0.0051</b>
1	<b>5.01</b>	<b>0.025</b>	2.55	0.11	<b>8.12</b>	<b>0.0044</b>
1.1	<b>5.31</b>	<b>0.021</b>	1.46	0.23	<b>8.14</b>	<b>0.0043</b>
1.2	<b>5.45</b>	<b>0.02</b>	0.73	0.39	<b>7.41</b>	<b>0.0065</b>
1.3	<b>5.55</b>	<b>0.018</b>	0.35	0.55	<b>6</b>	<b>0.014</b>
1.4	<b>5.43</b>	<b>0.02</b>	0.14	0.7	3.5	0.061
1.5	<b>5.24</b>	<b>0.022</b>	0.03	0.86	0.72	0.40
1.6	<b>4.91</b>	<b>0.027</b>	0	1	0	0.97
1.7	<b>4.44</b>	<b>0.035</b>	0.02	0.88	0.4	0.53

**Table S3C: Impact of variation in the  $\Delta^{13}\text{C}$  TEF between warm and present-day climatic conditions on the statistical significance of the difference between climatic conditions in the proportion of predatory and phytophagous prey eaten, as well as the Levins' index.**

$\Delta^{15}\text{N}$  is fixed at 0.7 ‰ and  $\Delta^{13}\text{C}$  is fixed at the reference value of 1.2 ‰ in present-day climate, but is allowed to vary between 1.2 + 0 and 1.2 + 0.6 ‰ in warm climates. For each value of  $\Delta^{15}\text{N}$ , we apply a linear mixed model of the dependent variable as a function of climatic conditions, age, sex and random mesocosm identity. We report  $\chi^2$  and p-values for the climatic effect. Significant effects are in bold.

$\Delta^{13}\text{C}$ TEF	Predatory inv.		Phytophagous inv.		Levins' index	
	$\chi^2$	p-value	$\chi^2$	p-value	$\chi^2$	p-value
+0* ref	3.57	0.059	<b>7.07</b>	<b>0.0079</b>	<b>6.65</b>	<b>0.0099</b>
+0.1	<b>5.22</b>	<b>0.022</b>	<b>6.13</b>	<b>0.013</b>	<b>7.69</b>	<b>0.0056</b>
+0.2	<b>7.17</b>	<b>0.0074</b>	<b>4.74</b>	<b>0.03</b>	<b>9.57</b>	<b>0.002</b>
+0.3	<b>9.24</b>	<b>0.0024</b>	3.67	0.055	<b>12.03</b>	<b>5.2e-4</b>
+0.4	<b>11.25</b>	<b>7.9e-4</b>	2.4	0.12	<b>15.37</b>	<b>8.8e-5</b>
+0.5	<b>12.86</b>	<b>3.4e-4</b>	1.55	0.21	<b>18.47</b>	<b>1.7e-5</b>
+0.6	<b>14.2</b>	<b>1.6e-4</b>	0.79	0.37	<b>22.28</b>	<b>2.4e-6</b>

**Table S3D: Impact of variation in the  $\Delta^{15}\text{N}$  TEF between warm and present-day climatic conditions on the statistical significance of the difference between climatic conditions in the proportion of predatory and phytophagous prey eaten, as well as the Levins' index.**

$\Delta^{13}\text{C}$  is fixed at 1.2 ‰ and  $\Delta^{15}\text{N}$  is fixed at the reference value of 0.7 ‰ in present-day climate, but is allowed to vary between 0.7-0 and 0.7-0.6 ‰ in warm climates. For each value of  $\Delta^{15}\text{N}$ , we apply a linear mixed model of the dependent variable as a function of climatic conditions, age, sex and random mesocosm identity. We report  $\chi^2$  and p-values for the climatic effect. Significant effects are in bold.

$\Delta^{15}\text{N}$ TEF	Predatory inv.		Phytophagous inv.		Levins' index	
	$\chi^2$	p-value	$\chi^2$	p-value	$\chi^2$	p-value
-0* ref	3.57	0.059	<b>7.07</b>	<b>0.0079</b>	<b>6.65</b>	<b>0.0099</b>
-0.1	<b>4.50</b>	<b>0.034</b>	<b>11.24</b>	<b>8e-4</b>	<b>8.89</b>	<b>0.0029</b>
-0.2	<b>5.21</b>	<b>0.022</b>	<b>16.61</b>	<b>4.6e-5</b>	<b>11.02</b>	<b>9e-4</b>
-0.3	<b>5.61</b>	<b>0.018</b>	<b>23.44</b>	<b>1.3e-6</b>	<b>13.16</b>	<b>2.9e-4</b>
-0.4	<b>5.87</b>	<b>0.015</b>	<b>32.1</b>	<b>1.5e-8</b>	<b>15.09</b>	<b>1e-4</b>
-0.5	<b>5.97</b>	<b>0.015</b>	<b>42.77</b>	<b>6.2e-11</b>	<b>16.97</b>	<b>3.8e-5</b>
-0.6	<b>5.88</b>	<b>0.015</b>	<b>54.84</b>	<b>1.3e-13</b>	<b>18.84</b>	<b>1.4e-5</b>

## Supplementary section S4: Link between lizards' diet and their gut microbial communities

**Table S4A: Link between lizard diet and their gut microbial community diversity**

Analyses of the effect of diet on adult lizard microbial community diversity (measured by Shannon index) using a linear mixed model with a model averaging approach. The global model included the interaction between each of the two dietary axes and climatic conditions, sex, sample sequencing depth plus mesocosm identity as a random effect. All numeric variables were centred and scaled. The global model explained 24% of the marginal variance and 29% of the conditional variance. Stars denote significance levels: \* :  $p < 0.05$ , \*\* :  $p < 0.01$ , \*\*\* :  $p < 0.001$ . N = 135 adults.

Parameter	Estimate	SE	z-value	p-value	RI
Intercept	0.62	0.03	20.64	<0.001***	-
Sample sequencing depth	-0.04	0.01	2.78	0.005**	1
PC1_diet	0.00	0.02	0.03	0.978	1
Sex	-0.09	0.03	3.17	0.002**	1
Climate	0.03	0.04	0.82	0.410	1
PC1_diet:Climate	-0.09	0.03	2.67	0.008**	1
PC2_diet	0.02	0.01	1.35	0.178	0.43

## **Supplementary section S5: implications of lizard diet on prey communities**

We tested whether climate-driven changes in lizard diets could affect prey abundances and family richness in the mesocosms. For each prey type, we fitted a linear model of the prey abundance (resp. richness) in the mesocosm as a function of the mean diet (predatory specialization axis or green-brown food axis) of the lizards in this mesocosm.

Lizard predatory specialization (PC1 axis, Fig S2A) was not linked to predatory ( $t = -0.38$ ,  $df = 8$ ,  $p = 0.71$ ), phytophagous ( $t = -0.96$ ,  $df = 8$ ,  $p = 0.36$ ) and detritivorous invertebrate abundance ( $t = 0.34$ ,  $df = 8$ ,  $p = 0.74$ ), but lizard green-brown food axis (proportion of detritivorous versus phytophagous prey eaten, PC2 axis, Fig S2A) tended to positively correlate with phytophagous invertebrate abundance ( $t = 2.2$ ,  $df = 8$ ,  $p = 0.058$ ), while there was correlation between green-brown axis and predatory ( $t = -0.08$ ,  $df = 8$ ,  $p = 0.94$ ) or detritivorous ( $t = 0.17$ ,  $df = 8$ ,  $p = 0.87$ ) invertebrate abundance. There was no link between any of the dietary metrics and the number of invertebrate families from each prey type ( $p > 0.20$  for all).