Intraspecific variation mediates eco-evolutionary dynamics in the currently changing environments

Habilitation à diriger des recherches

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Eco-evolutionary impacts of global change: from individuals to ecosystems

Species and populations are made up of individuals varying for their genes, their phenotypes and therefore for their potential ecological functions. This intraspecific variation sits at the nexus of evolutionary and ecological dynamics (Hendry 2017). Genetic and phenotypic variations underlie evolutionary responses to changing environments, while environmental conditions shape the degree of variation through plasticity and selection (Lande and Shannon 1996). Accumulating evidences further demonstrated the role of within-species mean values and variations of phenotypes for ecological dynamics at the population, community and ecosystem levels (Hughes et al. 2008, Bolnick et al. 2011, Forsman and Wennersten 2016, Roches et al. 2017, Raffard et al. 2019). From an ecological perspective, at the population level, larger diversity of individuals may for example lead to a generalist population composed of specialist individuals and thus alleviate intraspecific competition (Bolnick et al. 2011) and at the community level, species composed of more diverse individuals could have more diverse species interactions of weaker strenght (Bolnick et al. 2011). For example, in freshwater communities, life-history differences among alewives predators impacted zooplankton community structure, altering the trophic cascade' strength (Post et al. 2008). From an evolutionary perspective, more variable populations may adapt faster to environmental changes, lessening the risk of extinction and leading to phenotypic divergence among environments (Lande 1998, Bolnick et al. 2011, Forsman and Wennersten 2016). More variable populations may therefore be less vulnerable to environmental changes, better colonize novel environments or less prone to extinction than less variable populations (Forsman and Wennersten 2016). It unveils the pivotal function of the phenotype of individuals, its mean and its variation, in the eco-evolutionary dynamics and in the species responses to changing environments (Hawkes 2009, Bestion et al. 2015b, Moran et al. 2016, Legrand et al. 2017).

In a changing world, intraspecific variation may be particularly influential in eco-evolutionary dynamics. The first reason stems directly from an increase of environmental heterogeneity with global changes (Fahrig 2003, Lande et al. 2003, Thompson et al. 2013, Tuff et al. 2016, Cote et al. 2017b). Intraspecific variation considerably matters for the ability of species to cope with varying conditions (Chen et al. 2020). Spatially and temporally varying conditions provide a diversity of ecological niches maintaining a higher degree of phenotypic and genetic variation on one side and reversely magnifying the influence of variation on population performance (e.g., Rainey and Travisano 1998, Forsman and Wennersten 2016). Second, aside from environmental heterogeneity, global changes are shifting averaged abiotic and biotic conditions (Fried et al. 2014) for which species have to adapt to through the selection for the phenotypes the most adapted to novel conditions among available phenotypes. Intraspecific variation allows species to adapt to novel conditions (Lande and Shannon 1996). For example, the degree of dark color polymorphism in a species should be related to its resilience to global warming, with color polymorphic species being more resistant (Roulin 2004). Indeed, melanin-based coloration is linked with several traits (e.g., immunity, competitive ability, thermoregulatory ability, and UV protection) for which the strength of selection should vary with climate change (Roulin 2004). Darker individuals should be favored when changing climates increase UV radiations, when climate warming is associated with an increase in pathogen infections or when darkness reflects individual thermal optimum. On the other hand changes of intraspecific variation may reveal selective pressures being altered by global change and lead to cryptic biodiversity changes within species. For instance, a loss of cryptic evolutionary lineages may greatly exceed those of morphospecies arguing for worse impacts of climate change on biodiversity than previously thought (Bálint et al. 2011). Third, current environmental changes are often shifting species living conditions from benign to stressful conditions. Phenotypic and genotypic variations are likely of greater importance for fitness outcomes in challenging, stressful than in benign environments (Markert et al. 2010, Forsman and Wennersten 2016). Benign conditions may buffer the phenotype-fitness relationships among individuals while challenging conditions should enable a stronger filtering among phenotypes. Altogether, a growing body of studies stresses the importance of investigating and managing biodiversity at the intraspecific level. Hoffmann and Sgrò (2011) propose, for instance, to include evolutionary potential to climate change in conservation planning by prioritizing areas containing high genetic variation across multiple species.

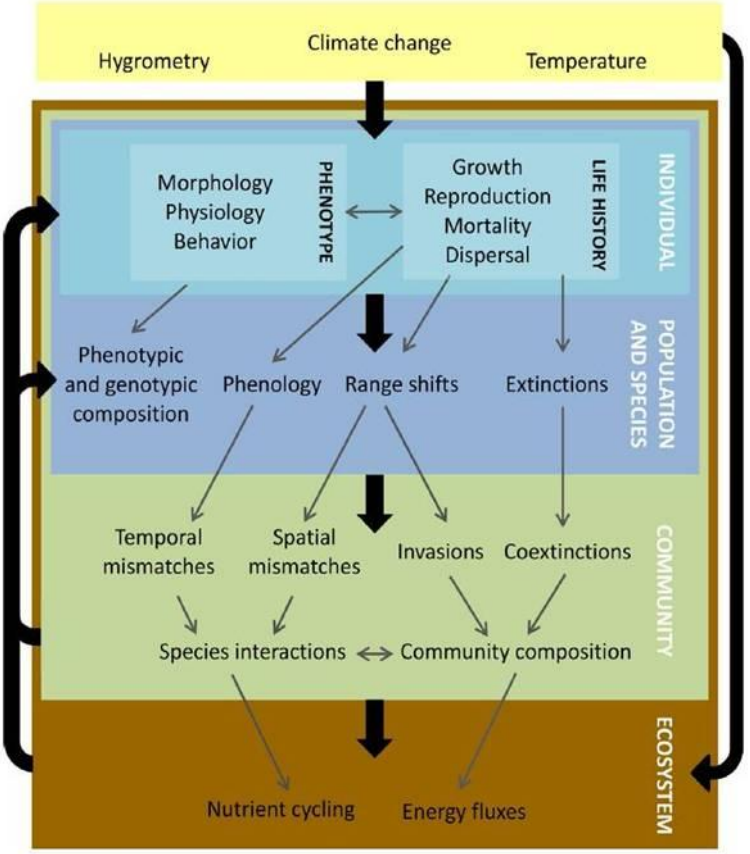


Figure 1: A holistic approach applied to study climate change. From Bestion & Cote 2018.

Accordingly, these last 12 years, my research projects investigated the impacts of global change at different biological levels, from the individual scale to the population, community, and ecosystem responses (see Figure 1 for an illustration about climate change, from Bestion and Cote 2018). This holistic approach is needed to quantify fine-tuned impacts of environmental changes on both evolutionary and ecological processes and the reciprocal feedbacks between intraspecific variation and other levels of biological organization and therefore to accurately predict species' extinction rates and disruption of ecosystem functioning. I applied this approach to three main components of global change, climate change, habitat fragmentation and biological invasions, and in a more anecdotal manner to their synergetic interactions (Brook et al. 2008) and I used experimental approaches coupled with a monitoring of natural populations or with a modeling approach. Below, I will synthesize my recent research studies about climate change, habitat fragmentation and biological invasions. While I also worked on transgenerational effects of predation risks, I will not discuss this part of my research.

Climate warming

The first set of studies relates to the impacts of climate change from the individual to the ecosystem scales. Through three PhD projects and two postdoctoral projects, Elvire Bestion, Félix Pellerin, Emma Fromm, Laurane Winandy, Luis Martin San Jose and I performed either short-term (1 year-long repeated twice) and long-term (>6 year-long) experimental studies to investigate the impacts of warmer climates on the phenotype and life history traits of a lizard species and, to a lesser extent, a newt species, the evolutionary mechanisms behind changes (i.e. within- and transgeneration plasticity, selection) and studied the consequences of these changes on the abundance and dynamics of lizard and newt populations. We further studied the cascading consequences of phenotypic and population changes on the invertebrate and microbial communities interacting with lizards and more recently documented the potential consequences on ecosystem functioning.

A growing number of articles argue that mesocosm experiments are a powerful tool to study the impacts of global changes (Dunne et al. 2004, Legrand et al. 2012, Thompson et al. 2013, Haddad et al. 2015, Rineau et al. 2019). Impacts of global changes are often studied using long-term field monitoring and predictions of future impacts can then be built from these monitoring. However, species responses to increasing temperatures are unlikely to be linear processes. Warm conditions can be beneficial over a given range of temperatures and highly detrimental above a given threshold, hence impacts of past environmental changes may be poorly representative of the impacts of future warming trends (Dunne et al. 2004). Moreover, benefits and damages can vary among life-history traits and across life-stages while most studies in natural populations are constrained to explore specific life stages and life history traits (Zeigler 2013). Combined with field studies, experimental approaches may for example provide an examination of impacts throughout the lifetime or apply stage-dependent treatments to mimic seasonal variation of climatic changes. For example, in a butterfly species, increased temperature positively affected the early survival of larva and the reproduction of females while the survival of overwintering larva was negatively affected (Radchuk et al. 2013). These negative effects had a bigger influence on population viability and times to extinction than the positive effects. Experiments allow to tease apart some tangled factors (e.g. dispersal, survival) and provide a replicated design to control for possible confounding effects (e.g. concomitant habitat degradation) which can be difficult to separate in the field (Stewart et al. 2013, Thompson et al. 2013). However, to accurately predict the impacts in natural systems, mesocosms experiments need to move beyond the constraints of biological realism and ecological complexity inherent to experiments (Stewart et al. 2013, Hendry 2019). Warming experiments are indeed frequently performed indoor to study the impact of temperature increases on physiology and often lack realism, making harder extrapolations to natural systems. Experimental designs that reproduce natural conditions as closely as possible allow more realistic measurements while allowing to tease apart confounding factors and to monitor effects throughout the life cycle.

I therefore used semi-natural warming experiments in the Metatron (https://themetatron.weebly.com/, Figure 2, Legrand et al. 2012) which provide, from my "surely unbiased" point of view, a fine-tuned balance between ecological realism and the necessity to control ecological parameters and therefore permit a good understanding of the complex dynamics underlying the eco-evolutionary feedbacks among biological levels. The Metatron is an experimental system composed of 48 enclosed mesocosms of 100 m² (Ariège, France). Each enclosure acts as a wet meadow ecosystem, with natural vegetation, invertebrate communities and a wide variety of thermal microhabitats (dense vegetation, sun-battered rocks and logs). Mesocosms were naturally enriched with surrounding invertebrates and plants by leaving mesocsoms opened for 1 year after construction. Species diversity within mesocosms is high, with 128 plant species and 123 invertebrate families in total (Bestion et al. 2015a). The distinctive feature of this system is that climatic conditions can be monitored and manipulated. Temperature, illuminance, and hygrometry within each enclosure are indeed monitored every 30 min and can be manipulated through the use of motor-driven shutters and sprinkler systems. In 2012, with Elvire Bestion, we developed experimental treatments to simulate two types of climates: 1) a 'present-day climate' matching current climatic conditions and 2) a 'future climate' with daily temperatures on average 2 and 3°C warmer (mean and maximum daily temperature, respectively, Figure 3), in line with RCP 4.5 climate projections for southern Europe by the end of the century (Stocker et al. 2013).

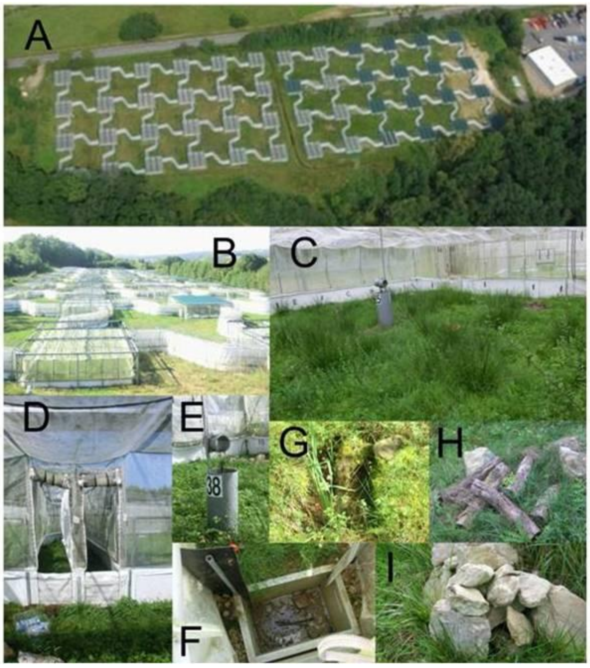


Figure 2: The metatron. A: Aerial view of the structure. B: Close view of the structure. C: Inside view of one enclosure. D: Entrance of the two half-corridors of one enclosure. E: Pole containing the sensors recording temperature, humidity and illuminance inside of the enclosure as well as the sprinkler system, protected with plastic and labeled with the patch identification number. F: Pit-fall trap at the end of one corridor. G: one of the two ponds set in each enclosure. H and I: rock and logs allowing for lizard thermoregulation, set in each corner of the enclosures. From Bestion et al. 2015a

The generated climate regimes follow day-to-day fluctuations in a coordinated manner so that daily fluctuation and seasonality are efficiently reproduced (Figure 3). It is worth noting that temperature differences between the two climate regimes are manipulated during summer and fall, even if there might be a slight residual difference during spring (Figure 3), and that the variance in daily temperature was higher in 'warm climate' enclosures, suggesting that species in warmer conditions may experience a greater variation in thermal microhabitats over the day (Figure 3). Indeed, while maximum daily temperatures varied greatly between treatments, minimum daily temperatures were not significantly different. Each enclosure further contained a wide variety of microhabitats (shaded vegetation, sun-battered rocks and logs, ponds) providing species with thermal refuges (range of mean daily temperatures between microhabitats: 10.0 ± 1.3 °C, 12.9 ± 1.2 °C; respectively for 'present-day' and 'warm' climates). It allows species to evade higher temperatures by shifting their activity timing during the day or hiding to avoid extreme temperatures and prevents direct effects of air temperature going beyond the critical maximum temperature of most terrestrial species (Bennett et al. 2018).

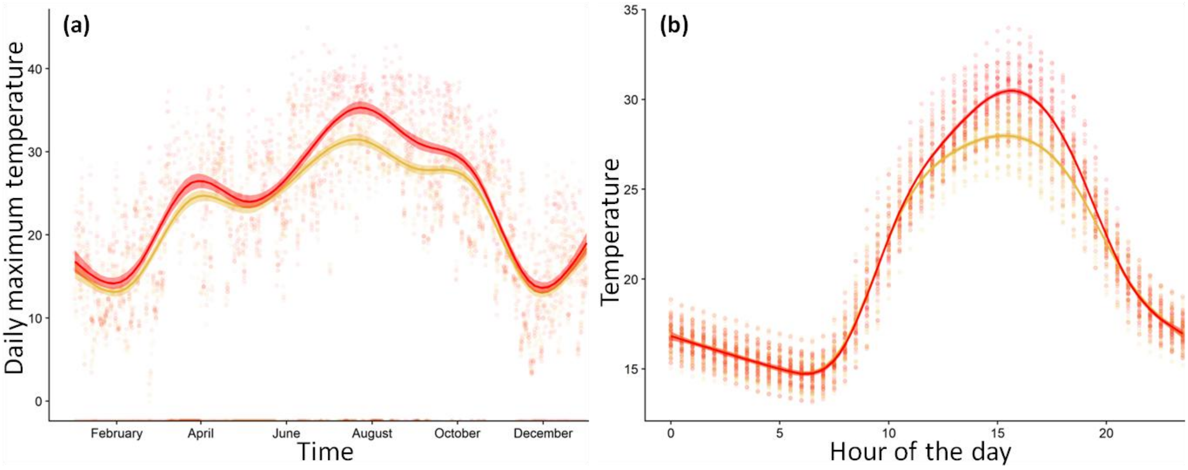


Figure 3: : Mean daily maximum temperature over the year (a) and mean temperature over the day (b) for the experimental years. Mean and 95% interval confidences are shown for present-day treatments (yellow) and warm climates (red).

We used as our model species, the common lizards (*Zootoca vivipara*, Figure 4) and more recently the palmate newt (*Lissotriton helveticus*). This lizard species is widely distributed worldwide and is thus experiencing a large diversity of climatic conditions along altitudinal and latitudinal gradients in the temperate zone. This cold-adapted lizard is now experiencing increased extinction risk in lowland habitats. All of these make the common lizard a good model species to study ectotherms' adaptation to climate warming. Identifying ectotherm responses to warming is crucial considering that they make up most of the biodiversity (Vié et al. 2009). While tropical ectotherms are deemed particularly threatened by changing climates (Tewksbury et al. 2008, Huey et al. 2009), temperate ectotherms are often considered less at risk. This is because tropical ectotherms are believed to live closer to their thermal limits, making more likely the crossing of these limits with warming. Recent studies have even advocated that warmer climates could have some positive impacts on temperate ectotherms and some field and experimental studies came to corroborate this theory even (Chamaillé-Jammes et al. 2006, Le Galliard et al. 2010, Clarke and Zani 2012).

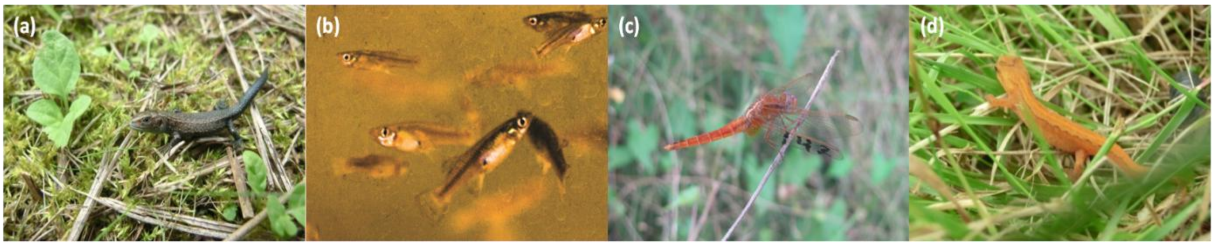


Figure 4: : Main study organisms: (a) a juvenile common lizard (*Zootoca vivipara*), (b) a shoal of western mosquitofish (*Gambusia affinis*), (c) a scarlet dragonfly (*Crocothemis erythraea*), (d) palmate newts (*Lissotriton helveticus*)

For instance, on common lizards, longitudinal studies in French natural populations showed positive effects of recent climate change (Chamaillé-Jammes et al. 2006, Le Galliard et al. 2010). Warmer temperatures caused an increase in adult body size, leading to larger clutch sizes (Chamaillé-Jammes et al. 2006). However, long-term field studies measure the consequences of past warming trends, while continued greenhouse gases emissions will cause even further warming and these studies struggled to conclude on the sole effect of climatic conditions due to concomitant changes in landscape structures and biotic conditions. Accordingly, it has been suggested that changes in population dynamics with climate warming could partly be due to the concomitant degradation of natural habitat (i.e. wetland getting dry, Massot et al. 2008) and that anthropogenic disturbances of habitats may modulate the effects of local climates (Rutschmann et al. 2016a). Furthermore, these field studies rarely monitor precisely plastic and evolutionary responses occurring in natural populations (Rutschmann et al. 2016a, Massot et al. 2017). Our experimental approach in large semi-natural mesocosms may improve our understanding the effects of warming climates in absence of other landscape changes while keeping both abiotic (e.g. temperature) and biotic (e.g. species interactions) triggers of climate impacts.

i. Life styles and impacts on population dynamics and structure

The first suite of traits studied revolves around lizards’ pace-of-life. Rooted in the seminal concept of species life styles and demographic tactics (Sih 1987, Gaillard et al. 1989, Promislow and Harvey 1990), the slow-fast life style gradient saw a recent revival through a within-species appraisal of the concept (Reale et al. 2010).

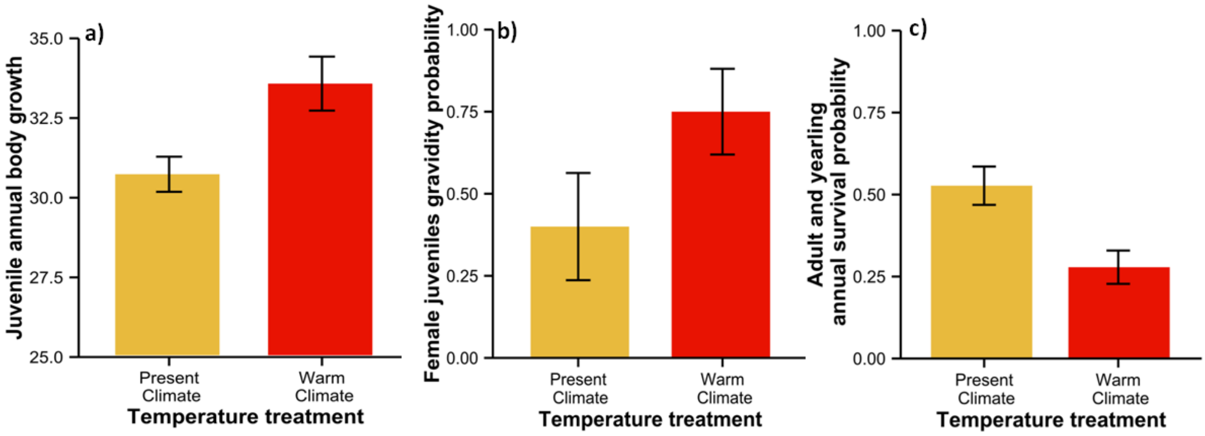
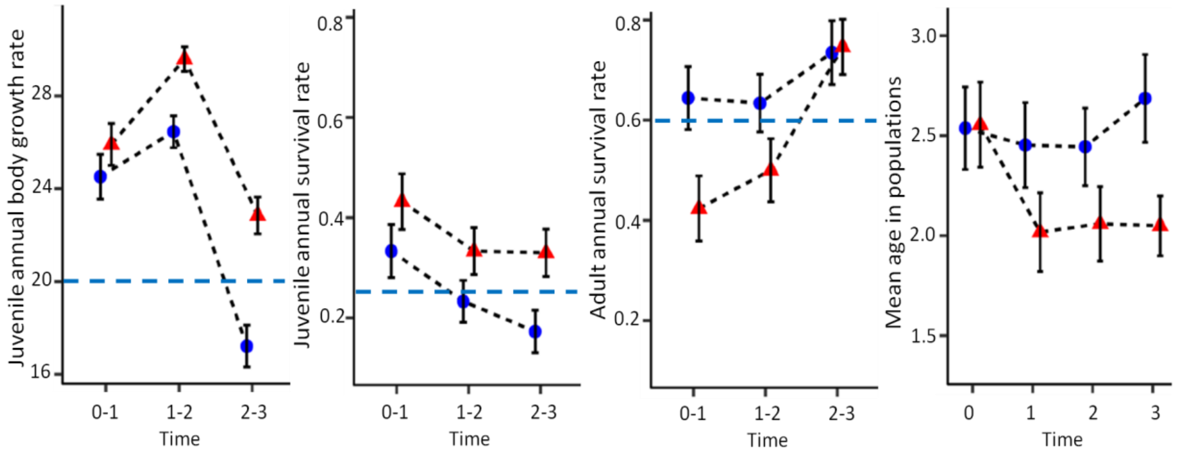


Figure 5: Life history traits with climatic treatments: a) juvenile annual growth rate, b) the probability of female juvenile to be gravid, c) annual survival probability. From Bestion et al. 2015a.

The theory assumes that individuals vary from a slow life style, with a low growth rate, a delayed reproduction onset and a long life, to a fast life style, with a high growth rate, a precocious reproduction and a short life. In common lizards, the life cycle may particularly match this concept. Common lizards have three life stages, juveniles (0-1 year-old), sub-adults (1-2 year-old) and adults (> 2 year-old, up to 10 year-old). In this species, mating supposedly occurs once a year in March and births happen in June-July. As the reproductive onset depends on body size (Promislow et al. 1992), the following march, a large proportion of juveniles are too small to mate (Massot et al. 1992). In experimental populations ~25% of juveniles usually mate during their first spring and the remaining proportion waits for their second spring. We do not know yet the relationship between the age at first reproduction and the lifetime, but the growth - reproductive onset syndrome suggests a life style gradient. The mean position on the gradient is likely to be influenced by climatic conditions through a well-known temperature-dependent growth rate (Atkinson et al. 2008). Our simulated future warmer climates indeed had increased juveniles' growth rates (Bestion et al. 2015a). This faster growth had a carry-on effect on reproduction, with an earlier onset of reproduction of juveniles from warm climates (Figure 5). Contrastingly, warmer climates had strong detrimental effects on adult survival (Figure 5). Anecdotally, warmer climates also led to voltinism for some individuals in this usually univoltine lizard species. Together, these results suggested a shift towards fast life style in warmer climate, with a faster growth, an earlier reproductive onset, and an increased mortality rate, a pattern also supported by results in natural populations (Chamaillé-Jammes et al. 2006, Rutschmann et al. 2016b) even if other climatic parameters such as rainfall also have a strong influence (Le Galliard et al. 2010).

We further examined the consequences on population persistence and structure using a simple modeling of population growth (Bestion et al. 2015a) and a longer term experiment (Pellerin et al. submitted). The modeling shows that these effects translated into a strong decrease in population growth rate in warm climates, which should lead to rapid population extinctions, while present-day climate populations should maintain themselves (Bestion et al., 2015c). An extrapolation of these results suggested that 14–30% of European populations of common lizards might be at risk in the future depending on climate change scenarios (Bestion et al., 2015c), which corroborates recent trends of populations extinctions observed in this species (Sinervo et al., 2010).

Figure 6: Life history traits in juveniles and adults and the mean age in populations with climatic treatments (blue : present-day climate, red: warm climate). The blue dashed lines show values in natural populations from Massot et al. (1992).



We further predicted changes in population age structure on the long term. The observed faster pace-of-life should indeed lead to populations made of younger individuals. In our 3 year-long experiment, we found similar patterns of climate-dependent life history traits, with positive effects on juveniles (growth rate, survival and reproduction) and negative effects on adult survival (Figure 6, Pellerin et al. in preparation). Over the course of the experiment, populations were also becoming younger in warm than in present-day climate (Figure 6). This shift of population age structure towards younger individuals was not associated with a decrease in mean body size in the population (Sheridan and Bickford 2011), but on the contrary with an increase of mean body size. This was surprising given that smaller body size has been advocated to be the third universal ecological response to climate change (Sheridan and Bickford 2011). However this positive effect of climate warming on body size has been found in common lizards’ natural populations (Chamaillé-Jammes et al. 2006) and in other lizards species (Piantoni et al. 2019) and might be explained by a diet generalism allowing to compensate increased metabolic rate and to maintain growth rate after maturity. To sum up, warmer climates induce a faster pace of life of individuals leading to changes in age and size structure which may have a knock-on effect on the structure and persistence of populations. In our 3 year-long experiment, we did not see any strong effect of climate treatments on population density (Pellerin et al. submitted). However three additional experimental years show clear negative effects of warmer climate on population density and persistence (San Jose et al. unpublished data). Several mechanisms may however allow this species, and other reptile species, to soften the negative impacts of climate warming and to adapt to novel climatic conditions as documented in section ii.

With Laurane Winandy, a postdoctoral researcher, we recently added the study of newt’s populations inhabiting the Metatron. After construction, the mesocosms were left opened for vegetal and invertebrate species to colonize them. Newts colonized the mesocosms at that period of them and were then enclosed in the mesocosms therefore undergoing climatic treatments as well. From 2015, during the longer term experiment, we decided to monitored more closely the newt populations and in 2017 and 2021 their phenotype (see below). We found that while the mean abundance in mesocoms was not different between climatic treatments in 2015, the abundance of newts was lower in warmer climate at the adult age class only (Fig. 7).

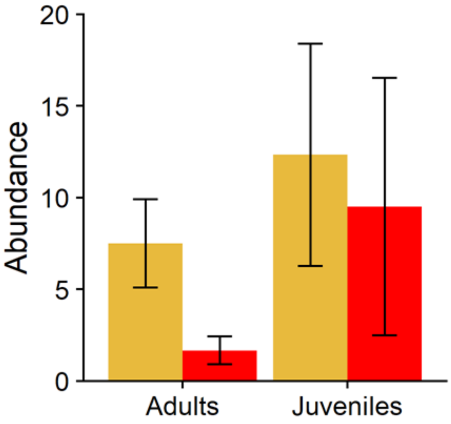


Figure 7: Adundances of adult and juvenile newts in present-day (yellow) and warm climates (red)

As for lizards, the differences observed at the population level were concomitant with phenotypic differences at the individual level.

ii. Thermal phenotype and evolutionary responses to warmer climates

Species can respond to warmer climate by shifting their geographical range or by changing phenotypic and life-history traits to improve their match to novel climatic conditions. Such changes, spanning various traits such as reproductive features (Parmesan 2006) or morphology (Sheridan and Bickford 2011, Zeuss et al. 2014), often enhance species adaptations to warming climates (Boutin and Lane 2014), and may result from a combination of plasticity and microevolution (Merilä and Hendry 2014, Bay et al. 2017, McGaughran et al. 2021). Plastic and selective responses can further interact. Adaptive plasticity can delay extinction and allow enough time for the populations to evolve (Ghalambor et al. 2007, Charmantier et al. 2008, Gibert et al. 2019), but can slow down evolutionary changes by reducing the strength of selection. Alternatively, non-adaptive plasticity can either lead to the rapid extinction of the population or to a rapid evolutionary response by increasing the strength of selection (Ghalambor et al. 2007, Gibert et al. 2019).

Plastic and selective responses

We therefore studied the phenotypic differences between treatments and the plastic and selective responses to our climatic treatments in a one-year long experiment repeated twice (Bestion et al. Submitted). The observed intraspecific variation of pace-of-life is often associated with a variation in other phenotypic traits aside from life history traits (Reale et al. 2010) such as a higher investment in immunity and reproduction, a lower fat storage and a darker coloration (Ducrest et al. 2008, Jacquin et al. 2012).

The association between a fast pace-of-life and a darker color is particularly interesting for lizards' responses to climate warming. In several species (Clusella-Trullas et al. 2007, Paranjpe et al. 2013, Artacho et al. 2013, Roulin 2014), skin darkness vary among individuals consistently over time and may be related to thermal preferences or optimum, with e.g., some individuals preferring higher temperatures and being darker than others. These traits may further form a thermal syndrome, a continuum of correlated thermal traits (Goulet et al. 2017). Common lizards also display consistent differences among individuals in dorsal darkness and thermal preference (Figure 8, Bestion et al. Submitted) which are positively correlated. Individuals preferring higher temperatures also have darker skin abetting them to heat up faster and achieve higher body temperatures. This "hot" syndrome may in addition be related to a faster pace-of-life syndrome. Accordingly, darker females laid eggs earlier in the year than their lighter ones (Pearson's $r = -0.57$ [-0.66, -0.46], $t = -8.86$, $df = 170$, $p < 0.001$ over two years of data) which suggest a faster pace-of-life for darker individuals.

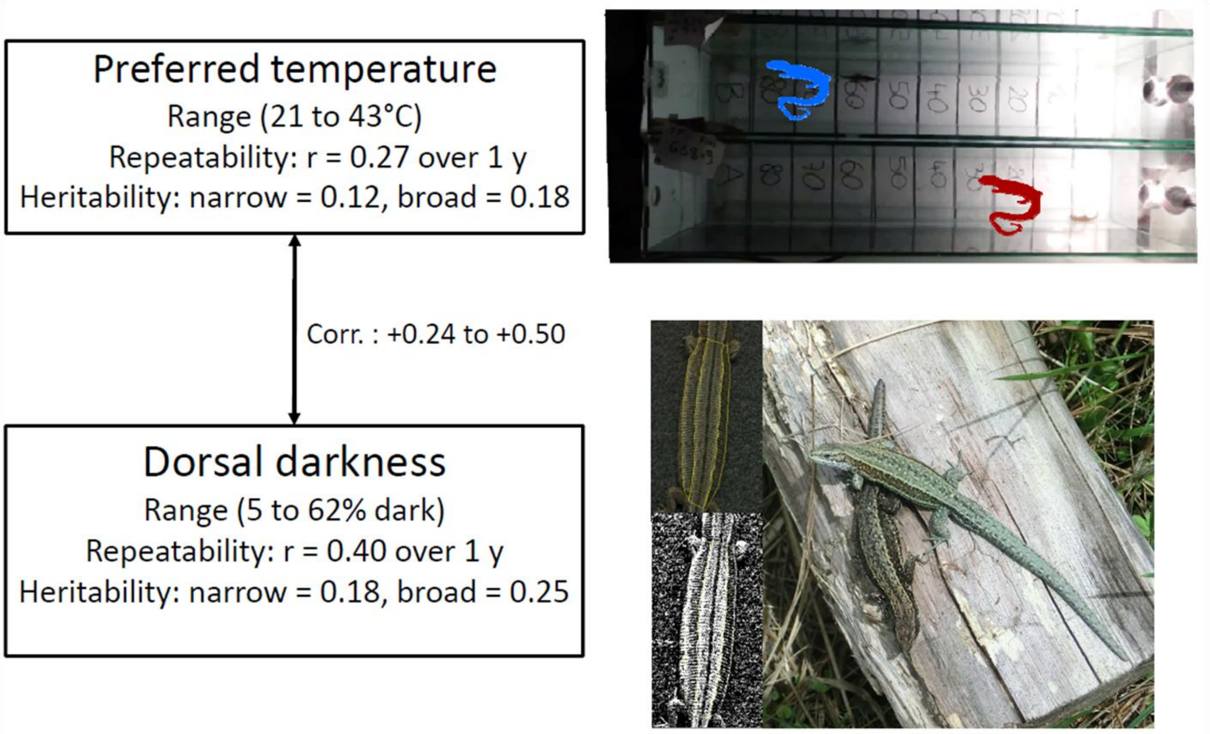
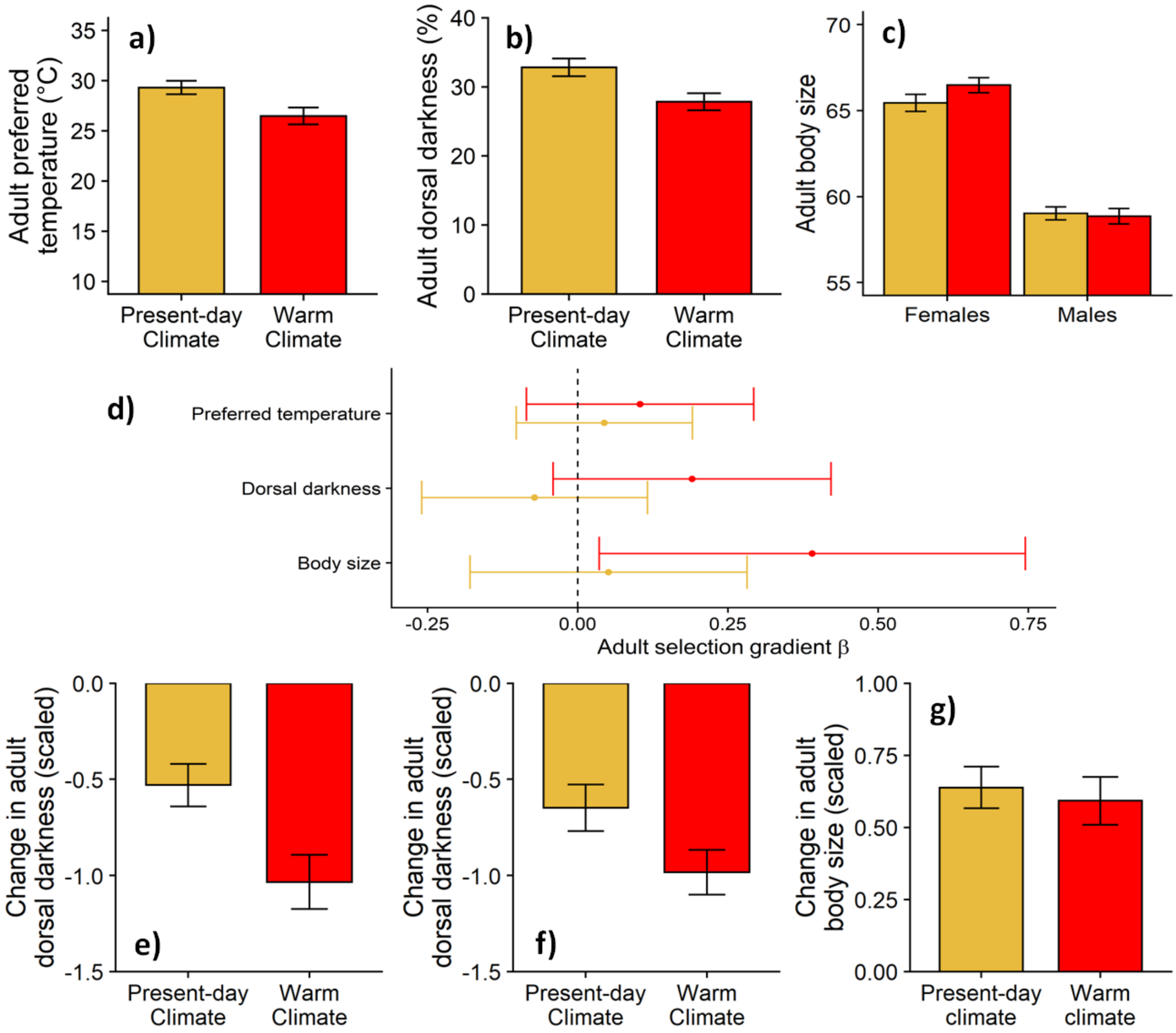


Figure 8: Illustration and methods to measure thermal preferences (top) and dorsal darkness (bottom). The variation, repeatability and heritability of traits and their correlations in different conditions are given.

If thermal traits are partly genetically determined, warmer climates may exert an upward selection on these thermal traits favoring higher thermal optima in warmer environments and therefore species adaptation to warmer climates. Alternatively, plastic response on these traits may prevent organisms from experiencing damaging temperatures (i.e., overheating costs, Huey et al. 2003, Gvoždík 2011) while buffering population against selection and slowing down population shifts towards higher thermal optima and larger tolerances (the "Bogert effect", Huey et al. 2003, Gunderson and Stillman 2015, Logan et al. 2019). Current evidence suggests low additive genetic variation in behaviors related to thermal preference (Paranjpe et al. 2013, Logan et al. 2018) while darkness is more heritable in several species (Roulin 2016). Indeed, ectotherms adjust their basking behavior to environmental temperatures over time. At a first glance, a lower basking tendency (i.e., low thermal preference) appears as an efficient plastic response to prevent organisms from experiencing damaging temperatures (i.e., overheating costs, Huey et al. 2003, Gvoždík

2011). However, some thermal traits, such as thermal optimum or skin darkness, have a reduced potential for climate-dependent plasticity and may only change through selection (Addo-Bediako et al. 2000, Araújo et al. 2013). In our study, thermal preferences and skin darkness had a low to moderate heritability (Figure 8) and varied with climatic conditions.

Figure 9: Thermal traits 1 year after the climatic treatments (a, b, c), the selection gradient (d) and the plastic changes on thermal traits (e, f, g).



In warmer climates adult individuals preferred lower temperatures, were paler, achieved a lower thermal efficiency and females were bigger 7 months after our 3 month-long treatments (Figure 9). Warmer climates further softened the positive covariance between preferred temperature and dorsal darkness observed in present-day climates from 0.53 to 0.27

(Figure 8). While selection gradients and differentials go in the predicted direction for darkness (i.e., darker skin in warmer climates), selective responses on measured thermal traits were weak and not significantly different between climates while selection for larger body size was significant only in warm climates (Figure 9). Selective responses on thermal traits may have however been softened by a plastic response on these traits. Thermal traits were indeed highly plastic, in particular behavioral choices of thermal microhabitats (Figure 9). Changes of adult thermal traits with climate resulted from climate-dependent phenotypic plasticity, with a lowering of preferred temperature and dorsal darkness of adults after one year in warm climate treatments. This plastic response prevents increased energy expenditure that excessive warming of the body would induce (Angilletta et al. 2002, Artacho et al. 2013) and the risk of overheating, but reduces the time spent foraging. Lizards can indeed retreat to cool refugia when operative temperatures on the surface exceed their physiological limits (Sinervo et al. 2010). However, when heatwaves are chronic, last over a long period of time or induce lasting plastic responses, plasticity may reduce survival rates through a reduced foraging rate (Bestion et al. 2015a). In our study lizards indeed shape their thermal traits 7 months after encountering warmer conditions as our climatic treatments were only active from July to early October and lizard phenotype is assessed the following June. Lizards may thus avoid overheating during the summer, at the expense of thermal efficiency during fall and spring. A further downside of such mitigation responses may be to lower selection pressures on these traits and thus dampen evolutionary adaptation to future warmer climates as suggested by our selective gradients.

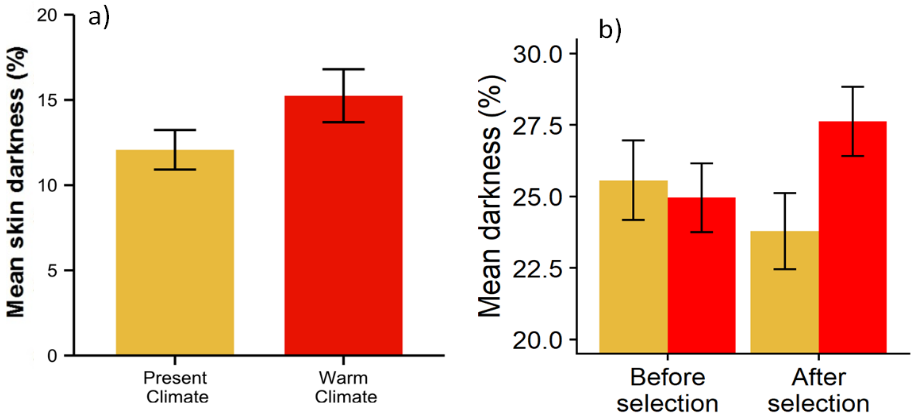


Figure 10: Dorsal darkness 1 year after the climatic treatments in 2012-2013 (a) and before and after survival in 2016 (b) in warm (red) and present-day climates (yellow).

However, results on juveniles may soften this conclusion. Male juveniles were darker at one-year-old in warmer climates (Figure 10) and the expression of 20 melanin-related genes, including key genes promoting melanin synthesis such as KIT (Hou et al. 2000) and HPS4 (Ohishi et al. 2019), were up-regulated in juveniles from warm climates (Figure 11). The difference of darkness could result from an adaptive plasticity, going in the same direction as the adaptive optimum for adults, or from selective processes towards darker colorations and so potentially warmer optima. As warmer climates were actually beneficial for juveniles (see above, Bestion et al. 2015a), it may suggests a selective advantage for warmer optima in juveniles. However, we were unable to measure darkness at birth and to tease apart adaptive plasticity from selection. In 2016, we developed a new method to measure darkness at birth and we are studying the selection on darkness since then in our long-term experiment (San Jose et al. in preparation). The first year, in 2016, we found a selective gradient coherent with a selection for darker colorations in warmer climates. However, this selection gradient varied over years since 2016, which weakens the role of selection in phenotypic shift in juveniles and suggests a fluctuating selection.

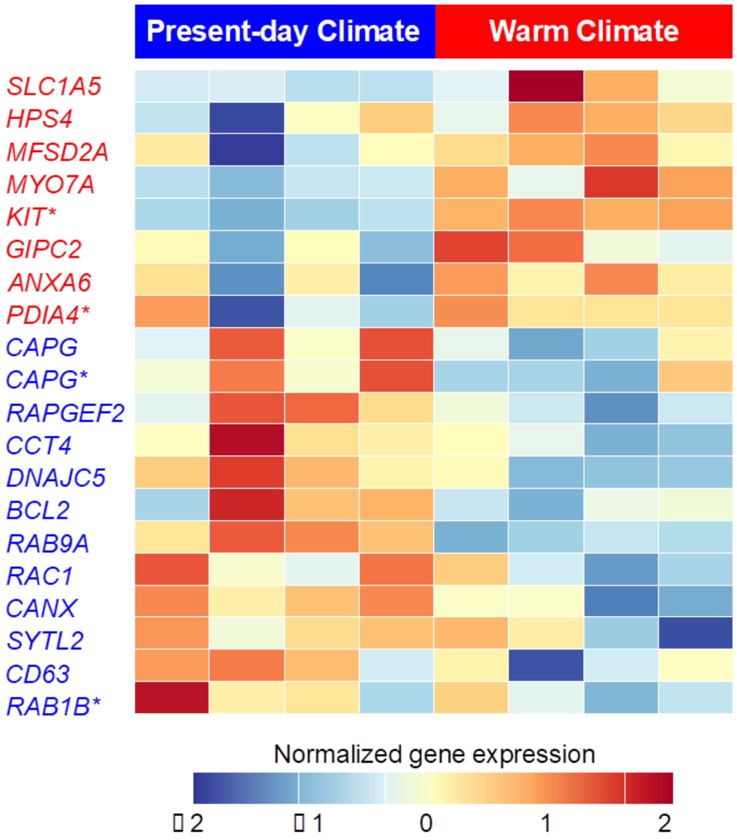


Figure 11: Expression differences in melanin-related genes between juvenile common lizards from “present-day” and “warm” climates

We are now waiting for a larger dataset to better estimate the fluctuating selection and trans- and within-generation plasticity in juveniles. Altogether, we suggest the existence of thermal syndromes involving dorsal darkness and thermal preference that are able to plastically change with warmer temperatures, at least in adults. Such plastic responses might reduce overheating and allow some acclimation of lizard populations to climate change on the short term. However, studied populations were declining in warmer climates (Bestion et al. 2015a) suggesting that acclimation was not strong enough and could additionally interact with selection to shape the evolutionary adaptive potential of ectotherm species in a warming world.

In newts, we quantified phenotypic differences between climate treatments in 2017 and in 2021 (i.e. 2 and 6 years of treatments respectively). While all traits could not be measured both years, we can see some similarity in the phenotypic differences between climates in juvenile newts and in juvenile lizards. In warmer environments, newts were larger, preferred lower temperatures and were darker than in present-day climate (Figure 12), suggesting differences in growth rates and in acclimation or adaptation. However, the evolutionary processes underpinning these differences are harder to appreciate due to the lack of individual monitoring of phenotypic and fitness-related traits.

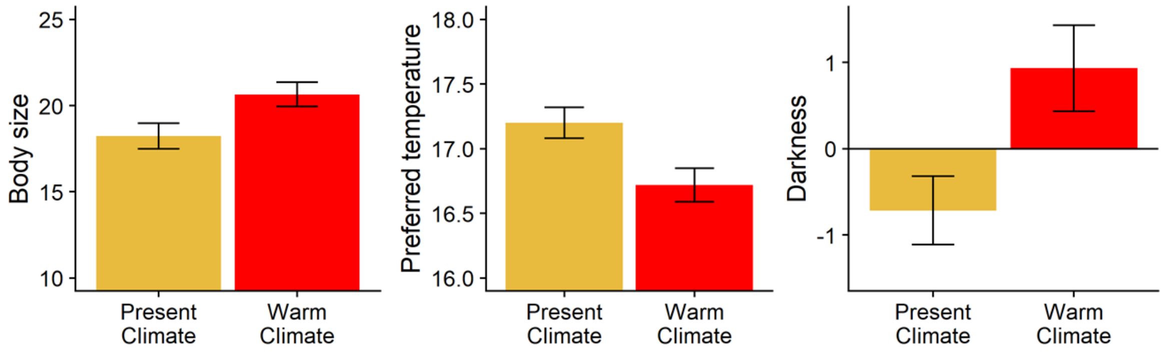


Figure 12: Body size (mm) and thermal traits (thermal preference and dorsal darkness) 1 year after the climatic treatments in juvenile newts.

Dispersal, habitat selection and range shift

We further investigated the role of intraspecific variation in thermal traits on dispersal and habitat selection and the potential consequences on species range shift. Facing warming climate, species can adapt to their new thermal conditions (as studied above) or can shift their range to track their climatic niche (Parmesan 2006, Thomas 2010). Indeed, 68 % of all species have expanded their range polewards due to climate change (Thomas 2010), while numerous range retractions at the southern margins have also been witnessed (Thomas et al. 2006). Conceptual frameworks predict that species less adapted to the new thermal conditions will be the ones that will suffer larger range retractions (Comte et al. 2014). However, these frameworks consider species as uniform ensembles, neglecting the variability in thermal traits among individuals within populations and species. While we could expect thermal phenotype to be assorted along species range and thus differ only among populations, such intrapopulation variation is maintained due to e.g., local spatial and temporal variability in climatic conditions. In the context of global warming, this variation should create within-species and within-population differences in the adaptation to local thermal conditions leading to the departure of phenotypes less adapted to warmer conditions (Clobert et al. 2009a).

We therefore experimentally investigated how individual differences in thermal traits at birth can explain variation in natal and adult dispersal from different climatic conditions in common lizards. In our one-year long experiment, we found that dispersal indeed depended on the fit of individuals to the climatic conditions (Bestion et al. 2015b). Juveniles with low preferred temperatures at birth dispersed more from warmer semi-natural habitats while juveniles with higher preferred temperatures dispersed more from cooler habitats (Figure 13).

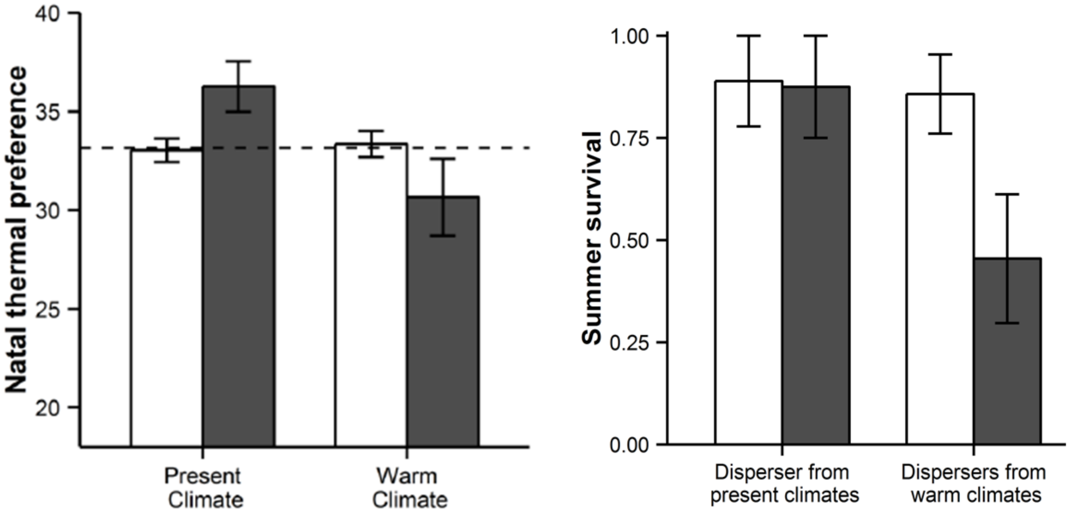


Figure 13: a) Preferred temperature for dispersing (grey bars) and resident (white bars) individuals, mean ± SE. Dashed line: mean juvenile preferred temperature. b) Summer survival for dispersing individuals in post-dispersal warm (grey bars) and present-day (white bars) climates. From Bestion et al. 2015b.

These dispersal decisions partly matched phenotype-dependent survival rates in the different thermal habitats (Figure 13), suggesting an adaptive dispersal for which individuals disperse from habitats less suitable for their phenotype. We further studied this adaptive dispersal in our long-term experiment both in juveniles and adults. While we observed the same patterns in adults, adults with low preferred temperatures dispersed more from warmer climates and vice-versa, juveniles display an adaptive dispersal on dorsal darkness and not on thermal preferences (Figure 14, Pellerin et al. in preparation). However, these two traits are positively correlated and both likely reflect thermal optima and their respective effects on dispersal and on other life history traits might be difficult to tease apart. Overall, our results support the habitat matching theory (Edelaar et al. 2008) in a context of climate change.

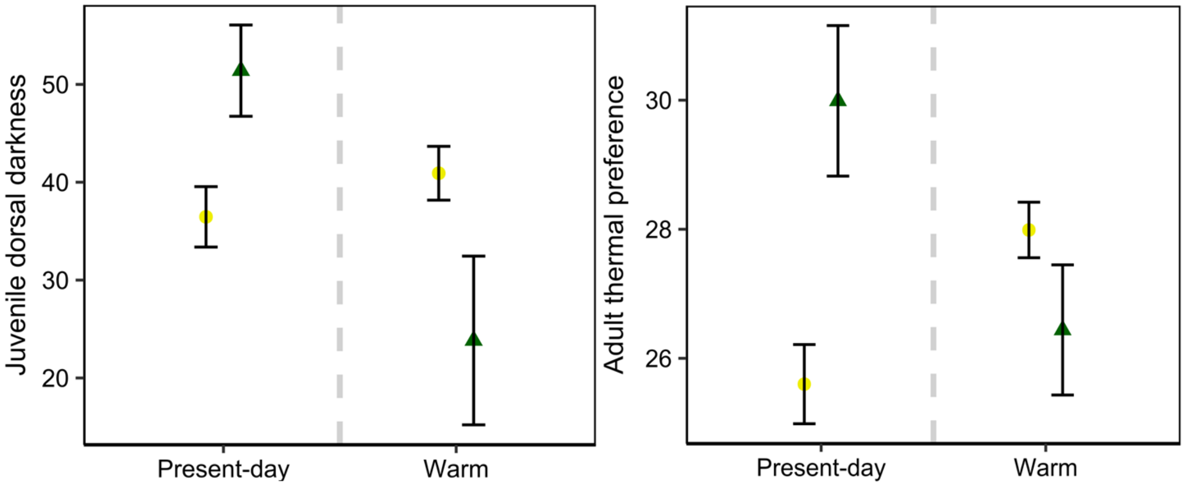


Figure 14: Juvenile dorsal darkness (a) and adult thermal preference (b) of dispersing (green triangles) and resident (yellow circle) individuals from present-day and warm climates.

In a range shift perspective, the dispersal syndromes linking thermal traits and dispersal can impact the composition of phenotypes and local adaptation at range edges, and therefore the success and speed of range shift, expansion and retraction. As thermal traits are partly genetically inherited and linked to various other life-history traits (see above), dispersal syndromes may thus have strong consequences on species range shift (Duckworth and Badyaev 2007a, Cote et al. 2010b, Jacob et al. 2015). Individuals with thermal requirements ill-adapted to local conditions could disperse to match their habitat choice (Edelaar et al. 2008), and this should promote rapid local adaptation to climatic conditions at both warm and cold margins. We therefore studied through an individual-based modeling to study the impacts of dispersal thermal syndromes on range shift (Pellerin et al. 2019).

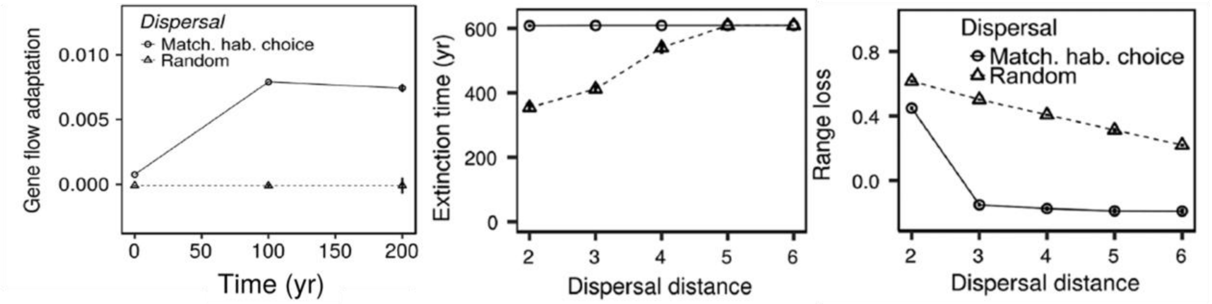


Figure 15: Effects of random dispersal and matching habitat choice on adaptive gene flow (a), species extinction time (b) and the proportion of range lost (c) Triangles and circles show random dispersal scenario and matching habitat choice respectively. From Pellerin et al. 2019.

Felix Pellerin, Robin Aguilée, Elvire Bestion and I developed an individual-based model including either random dispersal or temperature-dependent matching habitat choice and a structured population landscape with a climate warming occurring at different paces. In the random dispersal scenario, individuals disperse at a constant probability and settled randomly in surrounding patches at a given distance. In the habitat matching scenario, the departure probability of each individual depended on its expected lifetime reproductive success and was exclusively driven by local thermal adaptation, that is the match between individual thermal phenotype and local temperature. We monitored population composition and distribution through space and time under climate change. Relative to random dispersal, matching habitat choice induced an adaptive gene flow that lessened spatial range loss during climate warming by improving populations' viability within the range (i.e. limiting range fragmentation) and by facilitating colonization of new habitats at the cold margin (Figure 15). Our results highlight the need to implement more realistic mechanisms of dispersal such as matching habitat choice into models predicting the impacts of ongoing climate change on biodiversity.

iii. Variation in diet and consequences on microbial and invertebrate communities

As outlined above, climatic conditions can modify the phenotype and performance of individuals through intergenerational and lifetime phenotypic plasticity, through microevolutionary changes, or through gene flow among populations (Gienapp et al. 2008, Merilä and Hendry 2014, Urban et al. 2014). It is now clearly established that these changes can take place on a shorter time-scale than previously thought (Pelletier et al. 2009) and consequently can spread throughout the whole ecological network due to alteration of interspecific interactions (e.g. mutualistic, parasitic, trophic, Brose et al. 2012). For instance, changes in the abundance or the diet of apex predators can bear on consequences at other trophic levels, by reducing competitive exclusion or regulating herbivore abundance (Estes et al. 2011, Marino et al. 2018). An illustration is the impact of water temperature on salmonid fish (Salvelinus malma) feeding activity, modifying their top-down control on caddisfly (*Glossoma* spp.) larvae and periphyton abundance in freshwater streams (Kishi et al. 2005). These alterations of species interactions may further translate into indirect changes of energy fluxes and nutrient cycles at the ecosystem level via modifications of important ecosystem processes, such as primary productivity and organic matter decomposition (Cardinale et al. 2012, Crowther et al. 2015).

Elvire and I therefore studied whether the changes in pace-of-life and thermal traits were associated with trophic traits, i.e. traits with a role in trophic interactions, and with alterations in the communities of species interacting with lizards. Accordingly, we studied the changes of trophic niche and the diet of common lizards with climatic conditions (Bestion et al. 2019b). Because a rise in temperature causes metabolic rates to increase more rapidly than ingestion rates (Rall et al. 2010, Vucic-Pestic et al. 2011), 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 (Zhang et al. 2018), potentially through decreasing their selectivity towards certain prey. Alternatively, predators could shift their diet towards more energy-rich prey (Boersma et al. 2016, Carreira et al. 2016, Vejříková et al. 2016) which could lead to an increased dietary specialization (O'Gorman et al. 2016). Climate warming may also change prey community composition resulting in modified predator diet (Petchey et al. 1999). For instance, within the prey community, climate change should disproportionately affect prey species with higher trophic position (Petchey et al. 1999, Voigt et al. 2003), 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 (Lurgi et al. 2012). We characterized lizard trophic niches through stable isotope analyses, using $\delta^{15}N$, which is a proxy of trophic position, and $\delta^{13}C$, which can signal the reliance on different primary producers (Newsome et al. 2007). Warmer climatic conditions led to lizards feeding on higher trophic levels in warmer conditions (i.e. higher $\delta^{15}N$), being more specialized and eating less phytophagous and more predatory invertebrates (Figure 16).

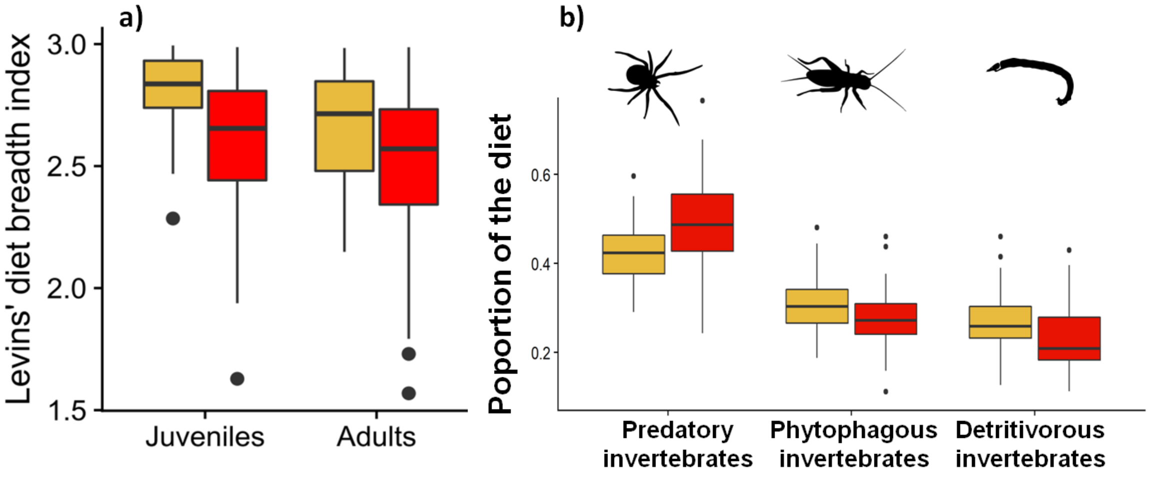


Figure 16: Lizards diet breath (a) and the proportion of predatiory, phytophagous and detritivorus invertebrates in lizards diet(b) in present-day (yellow) and warm (red) climates. From Bestion et al. 2019.

We further studied the pathways of climate impacts on lizard niche through structural equation modeling and teased apart the direct effect of climates on lizards diet from an effect mediated by changes in prey communities. 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 and diversity. Warmer climatic conditions actually decreased lizard specialization towards predators through a lower abundance in predatory invertebrates. However, this negative indirect impact of warmer climatic conditions was quite weak (estimate: -0.10), and overwhelmed by a strong (estimate: 0.43) direct positive impact of climate on the specialization for predatory invertebrates. This suggests that lizards "actively" shifted their diet in warmer climatic conditions, even if we do not know yet whether these changes results from plasticity or selection for specialized diets. Several hypotheses about elemental stoichiometry could drive diet shifts with temperature. Because temperature is linked to metabolic rates (Brown et al. 2004), higher temperatures should lead to a higher demand for carbon (respiration) than for nitrogen and phosphorus (Cross et al. 2015). This has led several species, from copepods to fish, to switch towards greater herbivory owing to the higher C content of plants (Boersma et al. 2016, Carreira et al. 2016, Vejříková et al. 2016). Conversely, higher temperatures should lead to higher protein denaturation rates, thus increasing N demands (Lemoine et al. 2013) as found in grasshoppers (Schmitz et al. 2016). Finally, as growth rate is linked to phosphorus demand, increased growth rates with warming would thus lead to increased P demands (Elser et al. 1996, Persson et al. 2011). Given that invertebrate predators display a higher N and P content than herbivores for a similar C content (González et al. 2017), 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 (Bestion et al. 2015a), they might shift towards eating predators to fulfill their phosphorus demands. On the contrary, adult growth is much slower, but they also suffer more from warmer climates, with a decreased survival (Bestion et al. 2015a). Warmer climates might mean more maintenance costs to repair proteins (Lemoine et al. 2013), 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 and particularly the potential evolutionary processes behind diet shifts.

We further investigated whether changes in lizards' diet may have negative or positive effects on lizards' fitness and whether it could explain observed impacts on life history traits (see above). We focused on lizards' body condition, survival and gut microbiome. We studied gut microbiome as gut microbial systems play multiple essential fitness-related functions for hosts (e.g., digestion, Yatsunenko et al. 2012 and immunity, Olszak et al. 2012), and a disruption of these communities might cause potential dysbioses with strong consequences for hosts (Turnbaugh et al. 2007). We summed-up diet changes (degree of specialization and proportion of predatory invertebrates in the diet) with a PCA and linked PCA scores to body condition and gut microbiome and post-measurement survival. These results are therefore correlative and should be carefully discussed.

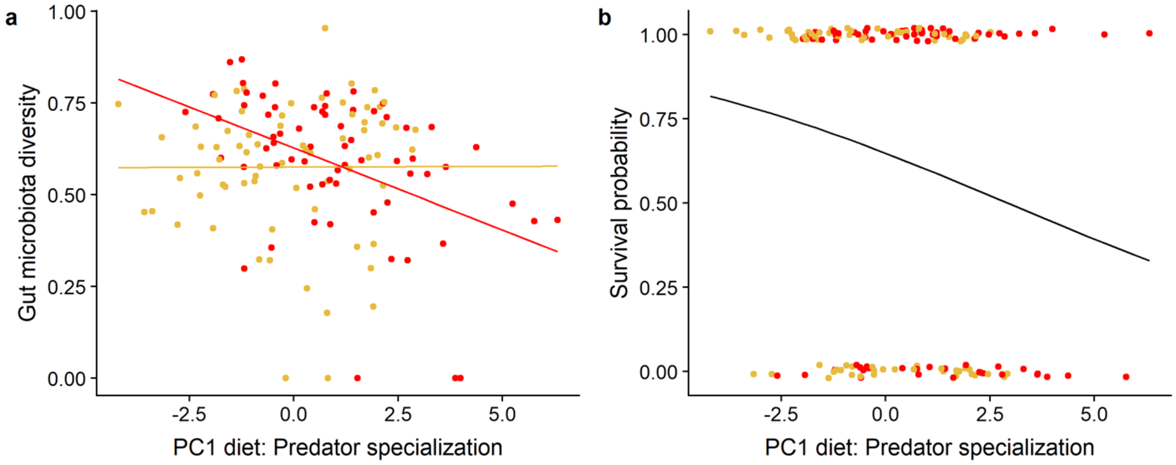


Figure 17: Relationship between diet specialization for predatory invertberates and gut microbial diversity (a) and survival (b) in lizards from present-day (yellow) and warm (red) climates. From Bestion et al. 2019

The survival of adult lizards over the winter and the spring was negatively correlated to the pre-winter specialization towards predatory invertebrates (Figure 17) while there was no such relationship in juveniles. These results match the previously observed effects of warmer climatic conditions on juveniles’ and adults’ life history traits, where climate change favored growth in juveniles but reduced survival in adults (Bestion et al. 2015a). 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 (Brown et al. 2004). 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 (Brose et al. 2006). 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 (Bestion et al. 2015a).

This negative impact may be further worsened by phenotypic changes concomitant with diet shift. The predator specialization was indeed linked to a lower gut microbiome diversity in warm climatic conditions (Figure 17). Such lower microbiome diversity might be involved in the lower survival. Because higher gut microbiome diversity is often beneficial to their hosts (Bolnick et al. 2014), a reduced diversity due to climate-driven dietary changes should be detrimental, particularly if it affects essential functions such as immunity or digestion. We further studied changes in gut microbial communities on our two short-term experiments and our long-term experiment. In our short-term experiments, we repeatedly found the same patterns; a much lower microbial diversity in the gut of lizards inhabiting warmer climates associated with a change the relative abundances among the 5 major phyla. (Figure 18, Bestion et al. 2017).

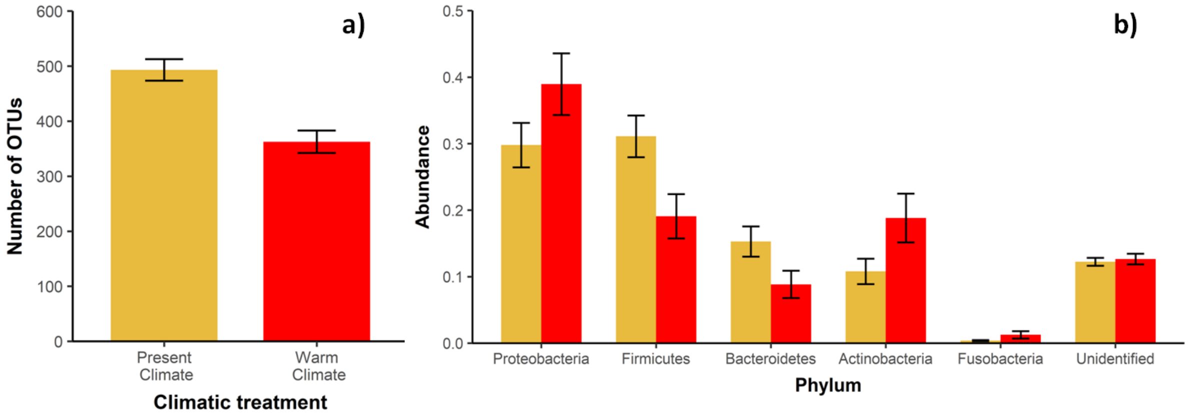


Figure 18: Number of OTUs (a) and relative abundance among phylum (b) in the gut microbiome of lizards from present-day (yellow) and warm (red) climates. From Bestion et al. 2017.

Interestingly, the pre-winter low microbial diversity was also positively related to the survival over the winter and the spring, suggesting that the loss of diversity induced by warmer climates may underlie the relationship between diet specialization and survival (Figure 16b). However, changes in gut microbiome might be the consequence or the cause of the observed dietary shifts or of a third unknown phenotypic change and so the impacts on survival may result from the diet shift, the loss of microbial diversity, a third unidentified factor or a combination of them. Future studies should disentangle the different hypotheses through the manipulation of either gut microbiome or lizard diet. It will allow us to estimate the additive and overlapping effects of climate warming itself, climate-driven bacterial richness loss and climate-driven diet shift and to better predict the potential extinction vortices of lizard populations in warmer climates. As a first step, Emma From is currently analyzing for her PhD project the temporal dynamics of gut microbiome in the 6 year-long experiment and couple this dynamics with concomitant changes in potential drivers of lizard microbiome changes [i.e. trophic related traits (lizard diet, prey community & prey microbiome changes), reproduction relative traits (lutch sizes & number of partners), social interactions relative traits (local density & individual sociability]. While these analyses are ongoing, Emma found again a negative effect of warmer climate on gut microbial diversity (Fromm et al. In preparation). However, this effect varied among years (Figure 19) with no difference between treatments the first and larger difference the last two experimental years available for analyses. The overall pattern matches the pattern repeatedly found in our short-term experiments, but not the temporal pattern. Our short-term experiments indeed showed a negative impact of warmer climates on microbial diversity after a couple of month and after a year (Bestion et al. 2017b, 2019b) while negative impacts appeared after two years in our long-term experiment. This temporal discrepancy may result from temporal variation in local climate and therefore treatments efficiency or in biotic conditions.

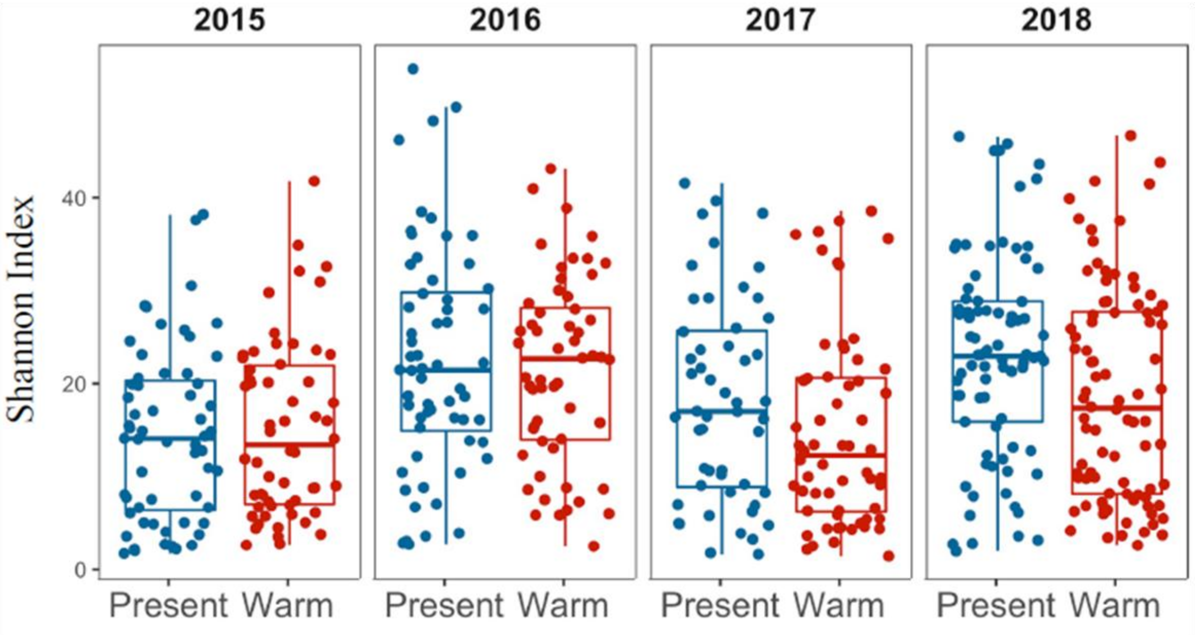


Figure 19: Shannon indexes in the gut microbiome of lizards from present-day (blue) and warm (red) climates. 2015 is the pre-experimental year.

This temporal variation further questioned us on the similarity of climate effects over the years above and beyond the diversity changes. Alpha diversity is indeed only one dimension of microbiome communities which can sometimes poorly describe the changes of structure and functional diversity of communities and its consequences for hosts (Johnston and Burnet 2016, Worsley et al. 2021). Using our entire experimental dataset (2012-2021), Emma is currently investigating this fluctuating effect of climate treatments on alpha, beta and functional diversities and its potential drivers.

Another ongoing objective is to study the consequences of diet and microbiome changes on the communities of species interacting with lizards (plant and invertebrates communities). In our last study, results suggested that prey abundances were moderately affected by lizard diet, with a slightly lower density of phytophagous invertebrates while lizards tend to feed more on them. This moderate 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. Accordingly my future project will focus on the top-down and bottom-up effects and their changes with climatic conditions. To do so, we will quantify climate-dependent impacts - in presence or absence of lizard populations, as an apex predator - on species abundance, and taxonomic and functional diversities for different components of ecological networks: primary & secondary consumers, primary producers, detritivores, decomposers and relate these changes to changes in key soil ecosystem functions.

iv. Consequences on the structure and functions of plant and soil communities

A last objective of my current and future research is therefore to investigate climate-induced changes in community structure, species interactions and ecosystem functioning in presence and absence of apex predators. Preliminary results show small changes in invertebrate diversity with a slightly higher number of invertebrate families and lower plant diversity only in presence of lizards' populations (Figure 20). However, these weak effects vary and seem not to accumulate over time. However, further analyses should investigate more precisely the changes in community structure, functional diversity and the relationship between invertebrate and plant communities.

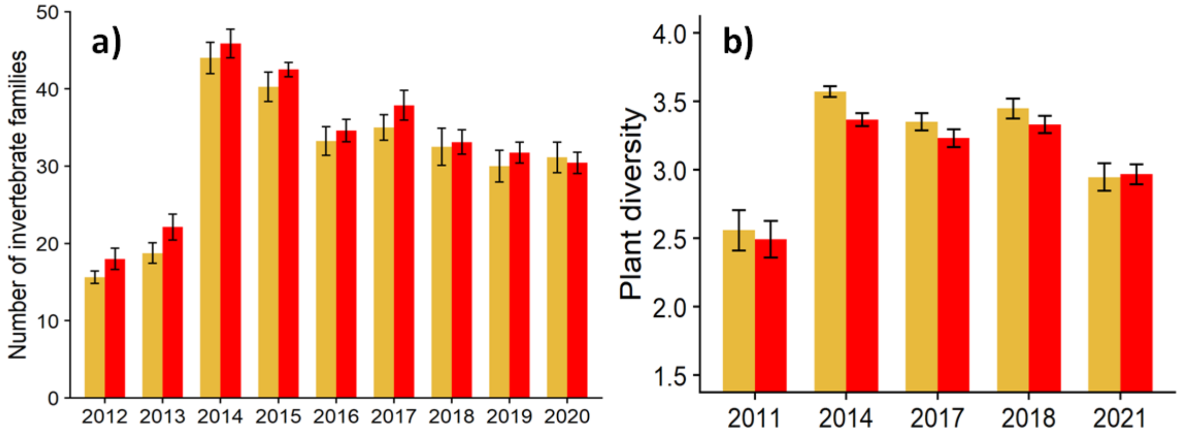


Figure 20: Number of invertebrate families (a) and plant diversity (shannon index, b) in enclosures of warm (red) and present-day climates.

The alterations of community structure and species interactions may further translate into indirect changes of energy fluxes and nutrient cycles at the ecosystem level via modifications of important ecosystem processes, such as primary productivity and organic matter decomposition (Cardinale et al. 2012, Crowther et al. 2015). Thanks to a collaboration with Lucie Zinger, Alain Brauman and a newly recruited postdoctoral researcher, we will be studying soil ecosystem functions and microbial communities. After 10 years of climate manipulation, we quantified soil respiration in situ (*i.e.*, tea bags methods) and ex-situ (*i.e.*, respiration profiles on different substrates), decomposition rate and N and C cycle. The dataset is being analyzed, but first results suggest a stronger soil respiration both in situ and ex situ in warm climates (Figure 21) which might suggest changes in microbial abundances or diversity as repeatedly reported in response to warmer climates (Zhou et al. 2020). We are now running metabarcoding analyses to study such changes, relate them to changes in soil functions and investigate changes in biodiversity-ecosystem functions relationships with climate.

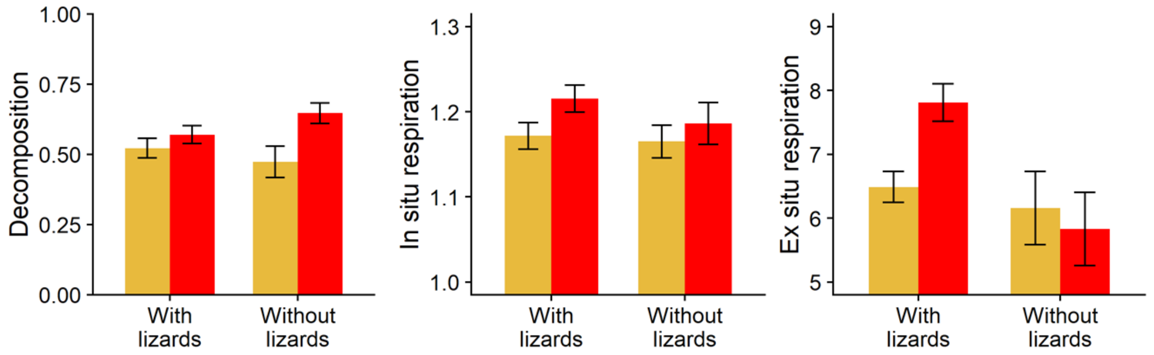


Figure 21: Soil decomposition (a) and in situ (b) and ex situ (c) respiration for enclosures in warm (red) and present-day (yellow) enclosures hosting or not lizards population.

Habitat fragmentation

Habitat conversion from natural ecosystems to agriculture, forestry and human settlements has taken over large amounts of land, leaving species with an increasingly shrinking world (Foley et al. 2005, Newbold et al. 2015). Beyond direct negative effects on taxonomic, functional and genetic diversity (Foley et al. 2005, Newbold et al. 2015), this indirectly erodes biodiversity through the fragmentation of large, continuous habitats into smaller isolated patches in a heterogeneous matrix (Fahrig 2003, Haddad et al. 2015, Wilson et al. 2015, Thompson et al. 2017). Fragmentation modifies landscapes in four ways: reducing habitat quantity; increasing the number of patches; decreasing their size; and increasing isolation (Fahrig 2003) with diverse effects on population dynamics. Smaller patches have smaller populations, increasing stochastic risks of extinction from demographic and genetic processes, e.g. inbreeding depression, leading to an extinction vortex (e.g. Gilpin 1986, Fagan and Holmes 2006). Interestingly, while intraspecific genetic and phenotypic variations likely mediate many impacts of fragmentation and species eco-evolutionary responses, their roles remain nonetheless poorly understood. As outlined in the introduction, the role of intraspecific variation was in the first instance outlined from evolutionary dynamics rather than from ecological ones and it may explain the weak focus in fragmentation studies. We indeed recently reviewed fragmentation studies on arthropods (Bestion et al. 2019a) and we identified a striking gap in the study of genetic and eco-evolutionary dynamics. These last years, I therefore studied the roles of intraspecific variation and more specifically of dispersal variation.

i. Condition- and phenotype-dependent dispersal

Dispersal between patches (Fahrig and Merriam 1994, Baguette et al. 2013), enables recolonization after local extinction and may reduce the likelihood of stochastic extinctions (Fahrig and Merriam 1994, Bowne and Bowers 2004, Baguette et al. 2013). However, fragmentation increases inter-patch distances and thus magnifies dispersal risks. Consequently fragmentation may reduce movements among patches (Fahrig 2007) and worsen the extinction vortex. Contrariwise, some modeling studies suggest that highly fragmented landscapes may select for higher dispersal (Olivieri et al. 1995, Gandon and Michalakis 1999, Travis and Dytham 1999) and an increased dispersal may even hamper persistence, given trade-offs with reproduction (Baguette and Schtickzelle 2006), effects on synchrony (Heino et al. 1997), or the swamping of local adaptation (Lenormand 2002). Understanding how dispersal will change with fragmentation, and more generally its role in species responses, is essential for forecasting the fate of populations and communities (Caplat et al. 2016). The precise influence of dispersal should however depend on its variation among individuals.

Dispersal largely vary among individuals' phenotypes and environments (i.e. condition- and/or phenotype-dependent dispersal or conditional dispersal syndromes) at each of the three dispersal steps: departure (emigration), transience, and settlement (immigration, Clobert et al. 2009). Habitat fragmentation may shape local and global selective pressures acting on a large array of phenotypic traits known to covary with dispersal behaviors and could therefore modify dispersal syndromes (i.e. dispersers' phenotypic specializations and its dependency on environments) on top of changing or not dispersal propensity (Cote et al. 2017b, Cheptou et al. 2017). It results in non-random fluxes with consequences far beyond dispersal itself, redistributing phenotypes and genotypes across habitats in heterogeneous landscapes and causing cryptic changes in functional biodiversity within metapopulations and metacommunities (Stevens et al. 2014). As individual traits drive the role of organisms in ecosystems (Roches et al. 2017, Raffard et al. 2017), the redistribution may indeed influence local demography, food webs and ecosystem functioning in heterogeneous landscapes (Hawkes 2009, Moran et al. 2016, Dahirel et al. 2017, Legrand et al. 2017).

A first part of my work aimed at identifying dispersal syndromes in patchy habitat and its dependency on environmental conditions between habitat patches, often referred as matrix, and within local patches. I indeed assumed that, by reducing movements, fragmentation will reduce variability (at any one point in time) of conditions within patches, but increase variability among patches, in heterogeneous landscapes. The heterogeneity in biotic and abiotic conditions experienced by individuals may therefore influence dispersal propensity and dispersal syndromes. I have been studying dispersal syndrome since my PhD studies in the context of fragmentation, biological invasion and more recently climate change (Bestion et al. 2015b, Pellerin et al. 2019). I recently had the opportunity to co-lead a cross-species experiment to test variation in dispersal with environmental conditions and individual phenotypes across 17 species ranging from protozoa to vertebrates (Fronhofer et al. 2018, Cote et al. Submitted). Though we did not manipulate the matrices between habitats, we experimentally investigate how dispersal propensity varies with individuals' phenotype and local bottom-up and top-down environmental stressors, here food limitation and predation risk, in two- or three-patch systems. Challenging local conditions, a low food availability and a risk of predation, increased dispersal propensity across species from 9% to 16% and from 9% to 12% respectively (Fronhofer et al. 2018).

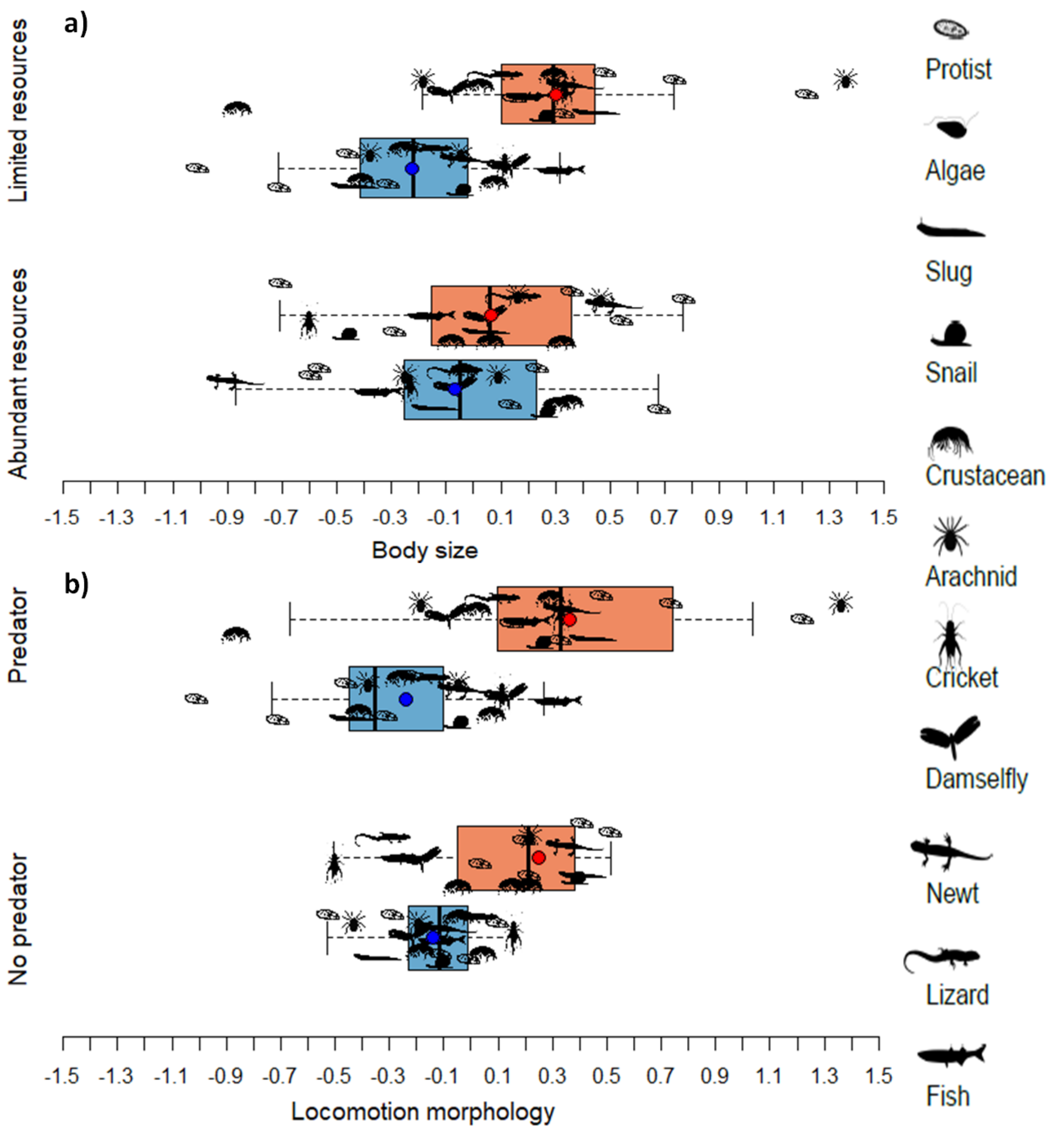


Figure 22: Standardized body size (a) and locomotion morphology (b) differences between residents (in blue) and dispersing individuals (in red) in benign or challenging environments, either food availability or predation risk, for the 17 species tested.

More interestingly, while dispersal was overall positively related to body size, activity level and morphological apparatus for locomotion (e.g. wing size, feet size, and body elongated shape), challenging conditions enhanced the association between dispersal and phenotype. For example, dispersing individuals were larger and had a more pronounced locomotion morphology than residents mostly when resources availability was low and in presence of predation risk respectively (Cote et al. Submitted, Figure 22). In a patchy and heterogeneous landscape, predation occurrence and food availability may largely vary among patches creating refuges for prey or competitors (Fahrig 2017) and producing variable environmental cues and selection pressures shaping, plastically or evolutionary, dispersal syndromes (Cote et al. 2017b).

A related objective was therefore to quantify the relative influence of environmental and genetic drivers on the variation of dispersal behavior and syndrome. As a first step, Luis and I used the database from the Metatron experiment in which we quantified dispersal behavior for 7 years of individuals with a full pedigree and released in varying environmental conditions (San-Jose et al. Submitted).

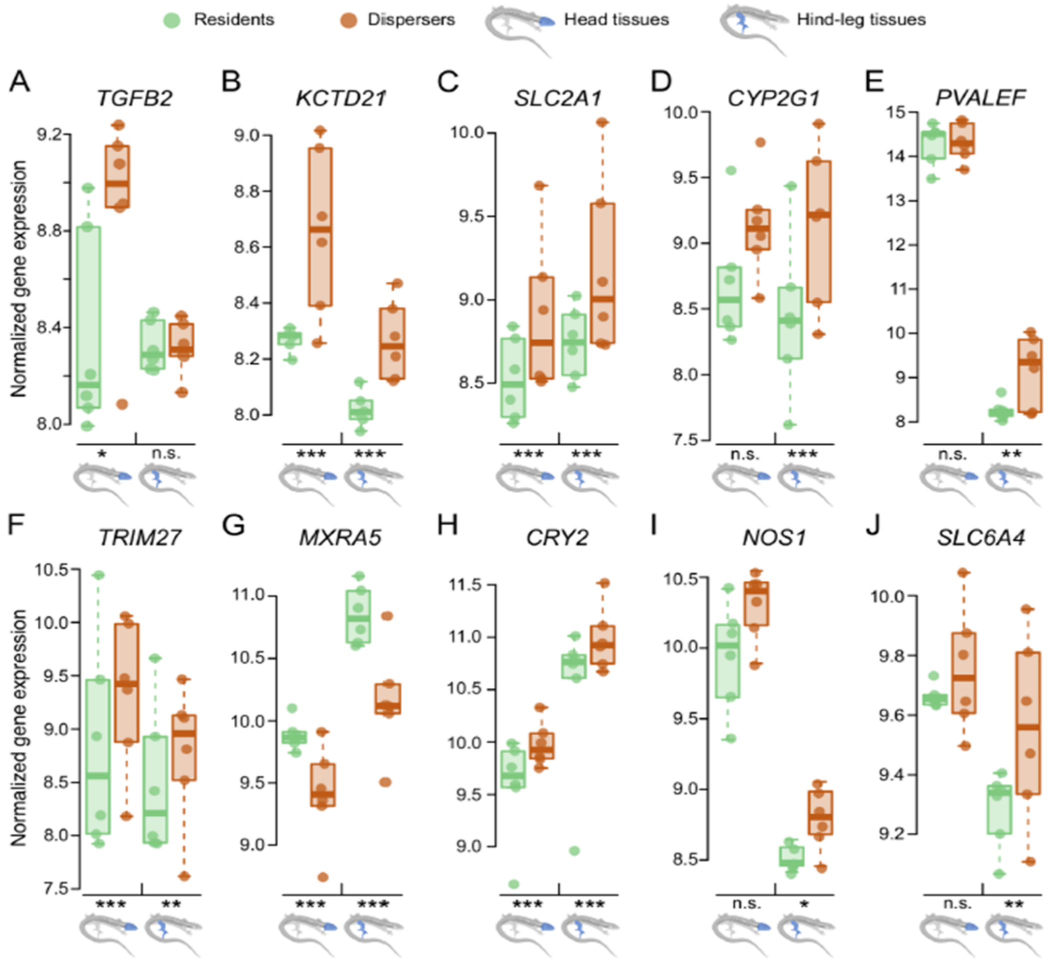


Figure 23: Genes differentially expressed in the head and hind-leg tissues of disperser and resident common lizards. Gene expression in the head and hind-leg tissues of resident (light green dots and box and-whisker plots) and disperser lizards (dark brown dots and box-and-whisker plots) for a subset of the differentially expressed genes.

Using quantitative genetics, we show that we found support for a low-to-moderate heritability of dispersal (0.17 – 0.35), with maternal (< 0.01) and natal environment effects (0.08-0.14) having a smaller contribution than additive genetic variation. To better understand the genetic drivers, we complemented our approach with a RAD and a RNA sequencing on a subset of individuals. We found that dispersal behavior was related to the variation in the Carbonic Anhydrase (CA10) gene and with the expression of several genes involved in neurotransmitters regulation (serotonin and nitric oxide) and the circadian clock (Figure 23). Our next objective is to quantify with our database the influence of well-known environmental drivers of dispersal (i.e. population density, relatedness, climatic conditions and food availability). With Delphine Legrand, we are additionally running a project with 12 including insects, molluscs and vertebrates species to compare the influence of previously identified genetic pathways on dispersal behavior (e.g. dopamine, serotonin and glucocorticoid receptors or transporters, *foraging* and *Pgi* genes).

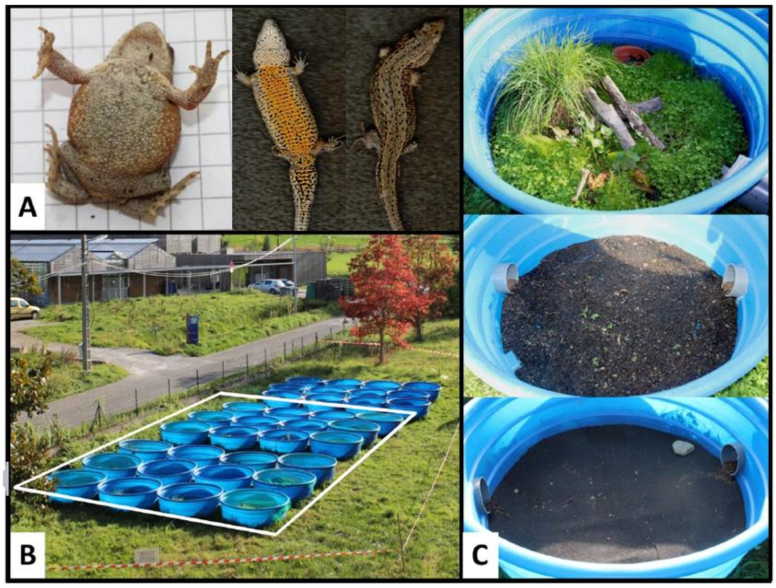


Figure 24: A) Common toads and common lizards used for the experiments, B) Four cattle tanks (1.7 m each) connected in a row with living habitats in the first and the last tank, C) The two intermediate tanks (~the size of a road) are made of vegetation, bare ground or fake tarmac. From Winandy et al. 2019

A subsequent objective was to study the variation of dispersal strategies and syndromes in the context of landscape fragmentation and predict its consequences on the dynamics of spatially-structured populations. The dispersal propensity and the phenotype-dispersal covariations may vary with the landscape impediments to movements on top of the local conditions met before the movement (Cote et al. 2017b). We tested these hypotheses using side experiments on common toads (*Bufo bufo*) and on common lizards on which we measured phenotypic traits (body size, feet length, body mass) and manipulated predation risk in local, departure patches and the viscosity of the matrix between living patches, either natural vegetation, bare ground or a fake tarmac (Figure 24). On common lizards, the dispersal propensity was related to the viscosity of the matrix and the risk of predation while the dispersal syndrome was not. While a road matrix largely reduce the speed of movements in safe environments compare to vegetalized matrices, the presence of predation risk largely reduced this effect (Figure 25). This result suggests that local conditions may modify the effect of fragmentation on species movements, in that case forcing individuals to cross hostile environments to escape predators, and may therefore change the dynamics of metapopulations (see section ii).

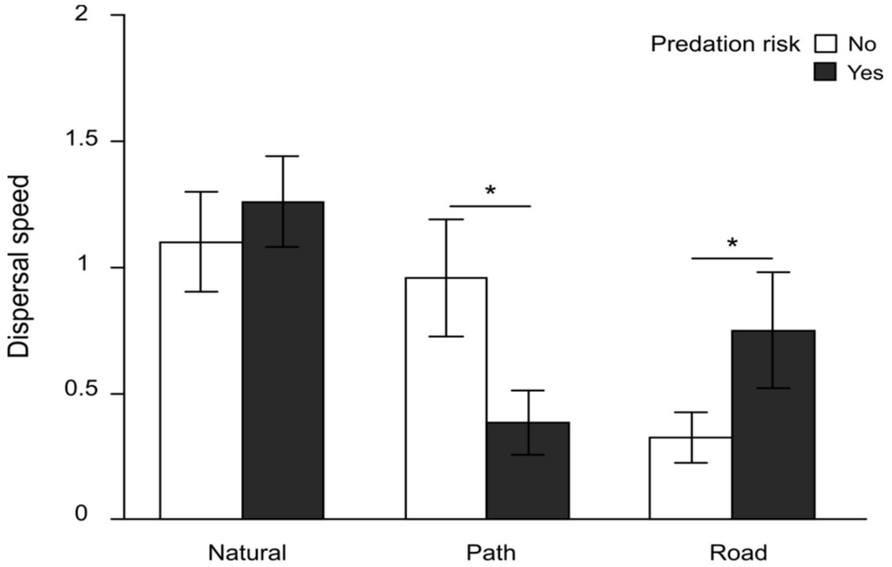


Figure 25: The speed of movements depending on the matrix between habitats and the risk of predation in the local, departure habitats

In toads, the dispersal syndrome, dispersers having longer legs than residents, depended on the interaction between matrix permeability and predation risk and resulted in differences in mass loss (i.e. dispersal costs) among matrix types. Dispersers lost more mass on average than residents, but this effect was weaker when dispersers had longer legs than residents and when they crossed the most permeable matrix in the presence of predation risk (Winandy et al. 2019). This result suggests that the dispersal syndrome is an adaptation to dispersal, reducing its costs, and that conditions locally and in the “landscape” may alter the strategies of individuals dispersing (Winandy et al. 2019).

Through a decrease in connectivity among habitat patches and a variation in local conditions, the fragmentation can plastically and evolutionary alter the intraspecific variation of dispersal among environmental contexts, populations and individuals. It may further select for or against phenotypes better skilled to move depending on the permeability of matrices and the costs-benefits balance of dispersal. Felix Pellerin tested this hypothesis during his PhD by creating connected and unconnected pairs of warm and present-day enclosures. While the main goal was to study synergetic effects of climate and connectivity on population dynamics (see section ii), a related project aimed at studying the effects of connectivity on activity levels and leg lengths, two phenotypic traits linked to movement ability in terrestrial vertebrates (e.g. (Cote et al. 2010a, Submitted, Cayuela et al. 2020). At the beginning of the experiment, founding individuals in isolated and connected populations displayed similar activity levels and leg length. The most striking results concern the leg length relative to body size even if similar results were found for activity levels. The relative leg length in adults decreased in all connectivity and climate treatments (Figure 26). However, leg lengths in adults were larger in connected populations compared to isolated populations the first two years of connectivity treatment and were larger in warm climates than in present-day climates only in connected populations (Figure 26).

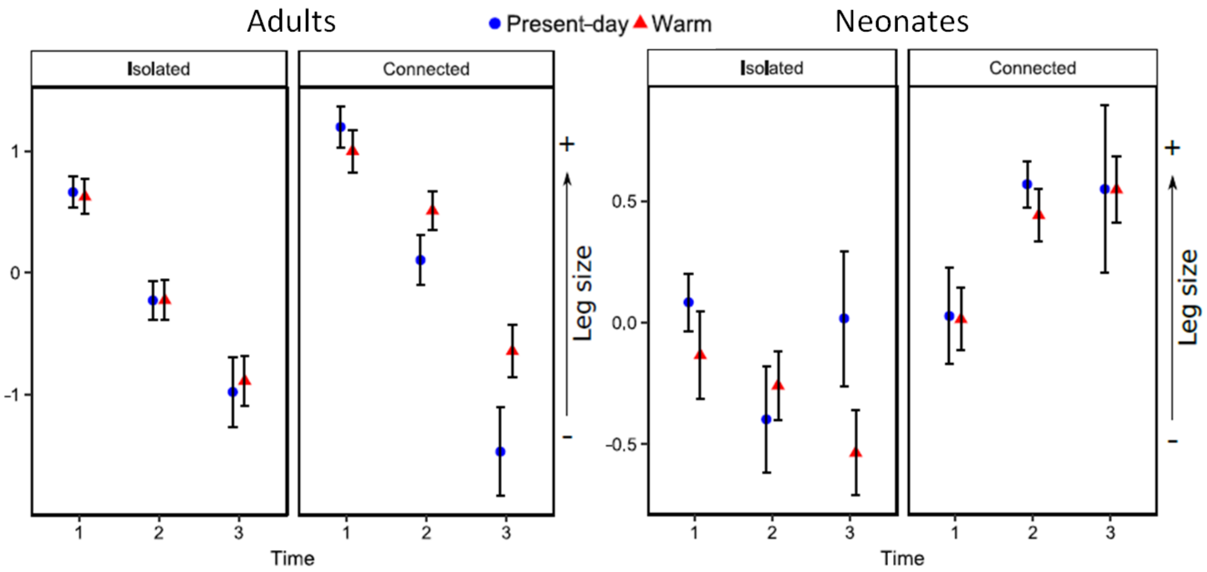


Figure 26: The leg sizes, relative to body size, in connected and isolated enclosures of warm and present-day climates over time (1 to 3 years of treatments).

As dispersal rates were larger in the direction of present-day to warm climates habitats, an association between dispersal propensity and leg length could lead to a spatial reorganization of phenotypes among climates. The association between dispersal propensity and leg length was however not obvious in our dataset but, as we estimated dispersal status from capture-mark-recapture, we might have included individuals performing a round trip as residents. A first objective is now to refine our dispersal estimate using paternity assignment to detect unidentified movements during the mating season. A spatial reorganization would however not lead to differences in average phenotype between connected and isolated habitats. Still we observed increased mean leg lengths in connected habitats relative to isolated habitats. This difference suggests a plastic change in leg length or an extremely fast evolution. While this latter hypothesis is quite unlikely, the results on newborns were quite surprising (Figure 26). From the second year of experiment, the legs were larger in newborns from mothers inhabiting connected habitats than from mothers inhabiting isolated habitats. We are currently estimating the selective gradients from the potential fitness benefits and costs associated with longer legs and the within- and transgenerational plasticity of this phenotypic trait. Due to technical limitations, pairs of connected or unconnected enclosures were made of a warm climate and a present-day climate and therefore our design mimics a habitat with variable microclimates connected or not. A working hypothesis is that longer legs facilitate movements between climates to maximize the heat absorption while limiting overheating. Furthermore, we are currently running a common garden experiment on two generations and a genomic analysis to quantify the evolved part of phenotypic differences observed.

ii. Consequences on (meta)population dynamics

Thanks to this design, we could further study the role of habitat connectivity on the effects of climatic conditions on life history traits and population structure (isolated habitats: Figure 6, connected habitats: Figure 27, Pellerin et al. submitted). The impacts of climate change are often studied independently of other contemporary environmental changes while they often co-occur and may interact synergistically or antagonistically (Opdam and Wascher 2004, Brook et al. 2008, Scheffers et al. 2014, Suggitt et al. 2018). Fragmentation may for example strengthen the impacts of climate change by making access to microclimatic refuges more difficult, increasing the impacts of stochastic climatic extreme events, slowing down the range expansion at margins or preventing a spatial reorganization of phenotypes allowing species to persist. Alternatively, the connectivity among habitats may swamp local adaptation to new climates by allowing gene flow (Lenormand 2002) or accelerate the extinction of populations in warmer microhabitats by allowing a source-sink dynamics (Gundersen et al. 2001).

In our experimental study, the connectivity between habitat patches largely influenced the effects of climatic conditions on life history traits and population structure. When we allowed populations in warm and present-day climate to be connected, there was a striking change in the observed impacts of climate change on population dynamics (Figure 27). In connected habitats, impacts on juvenile growth rate and survival were weaker compared to isolated populations and adult survival was even enhanced in warmer climates compared to present-day climates (Figure 27). When individuals had access to a cooler microclimate, the effect of warm climate on population age structure was also offset (Figure 27) and the density of present-day populations became lower than the density of warm populations. These differences may be due to an uneven flow of individuals between climates (Figure 27). We observed a strongly biased dispersal from present-day climate populations to warm climate populations. The flow of individuals affected the dynamics of populations in the two climates, counterbalancing the influence of warm climate on population age structure and decreasing the density in present-day climates. As the bias in dispersal was stronger in adults than in juveniles, it could have both decreased the density and the mean age in connected populations of present-day climates. We could have expected adults to disperse more from warm climate given the lower survival in warmer climates in isolated populations. However, slightly warmer conditions may be attractive for an ectotherm species while the costs of living in may be less predictable for a potential immigrant (i.e. physiological exhaustion and heatwave). One hypothesis is that lizards prefer living in the warmer environments. Warmer habitats would become denser and present-day habitats would be inhabited by less competitive individuals, explaining the lower survival rate in these habitats (Figure 27).

However, we only recorded individual position once a year before hibernation. We may therefore quantify only permanent individual movements (aka dispersal) and underestimate seasonal and daily movements to avoid overheat. An alternative and non-exclusive explanation is that individuals used present-day mesocosms as a thermal refuge to avoid temporary heatwaves and made the most of the advantages of warmer environments without the overheating costs. Intra annual movements between microclimates would thus limit the effect of warmer climatic conditions on survival and population dynamics, but the additional costs of regular movements (e.g. energetic costs, inaccurate information) may have led to negative impacts to the metapopulations on the whole (population growth λ, Isolated populations: 0.97 [0.77-1.17], connected populations: 0.76 [0.56-0.96]).

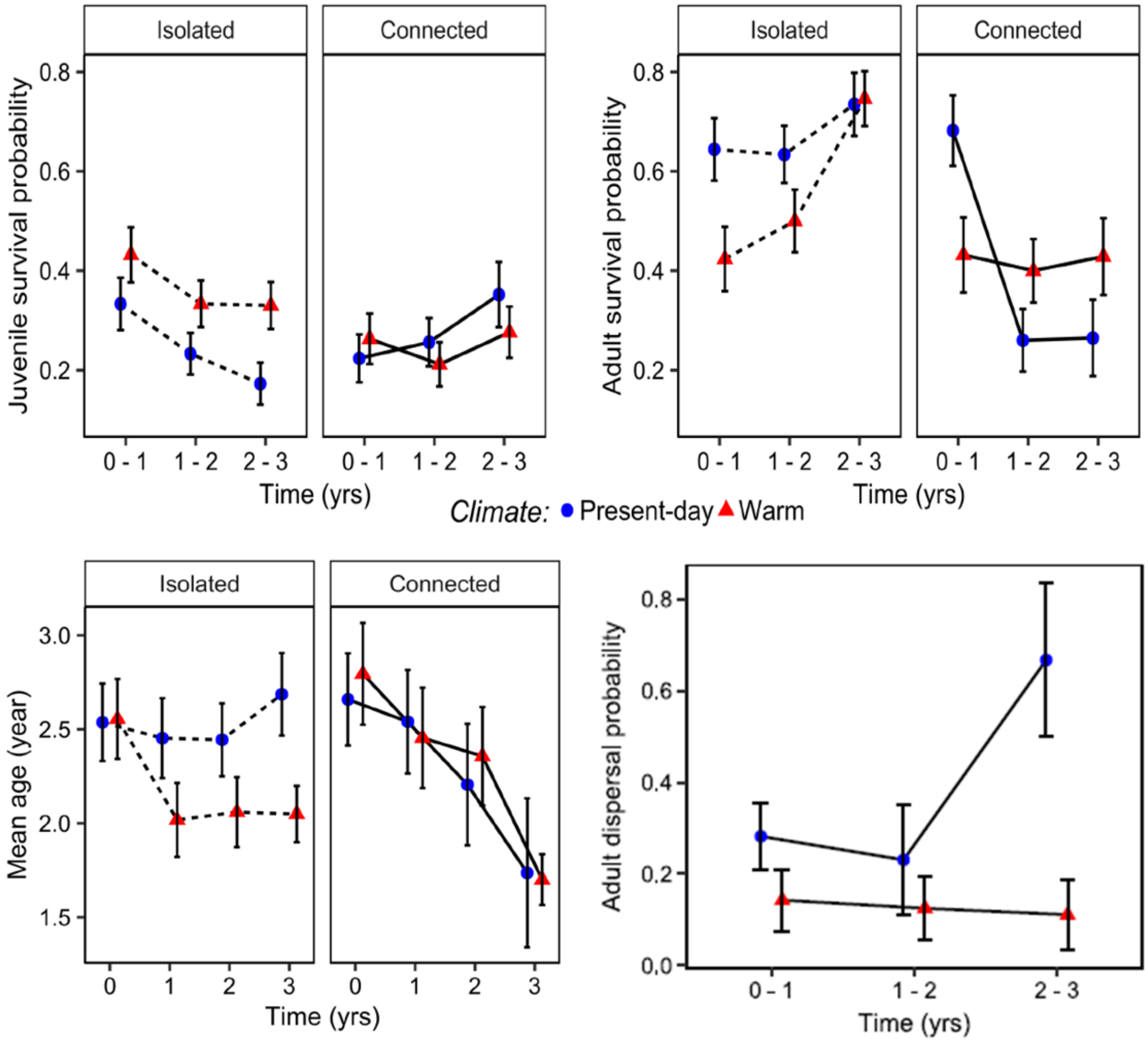


Figure 27: Life history traits in juveniles and adults and the mean age in populations with climatic treatments (blue : present-day climate, red: warm climate) in isolated and connected habitats.

A final explanation relates to conditional dispersal syndromes, i.e. a climate-dependent phenotypic bias in dispersers as outlined above (Figure 13 & 14). Such a syndrome conditional on local climatic conditions can cause a biased flow and then different distributions of phenotypes and genotypes in microhabitats. The pattern observed on thermal phenotype suggests that movements should have improved the adaption of lizards to local warmer climates as suggested by a relative better survival in warm climate relative to present-day climates in connected populations. However adaptive dispersal should improve survival in connected populations compared to isolated populations while the survival in connected populations was weaker, in particular in present-day climates. The previous explanations may potentially lead to this pattern. The preferences towards warmer habitats may be an optimal decision on a short time frame and a suboptimal one when it comes to heat waves. Rapid anthropogenic changes may generate source-sink dynamics with individuals perceiving warm habitats as source habitats (Remeš 2000, Delibes et al. 2001). In our study, habitats with a present-day climate and warm habitats are not strictly speaking sources and sink habitats respectively because warmer climates has a negative effect only on adults and a positive effect on juveniles. However a similar process may be at play with adults being attracted towards warmer habitats in which they might suffer from physiological exhaustion. Facing a heat wave in warmer habitats, individuals with high thermal optimum may sustain these climatic conditions while others may go back and forth between thermal habitats or settled definitively in the coolest habitats. These latter strategies may come with the costs of movements or of temporary overheating and therefore with an overall weaker survival. It may unbalance the source populations and then the whole system. As for source-sink dynamics, we could have expected a selective change towards phenotypes better selecting thermal habitats (Holt 1995) or better adapted to warm habitats (Dias 1996). However, our experiment may be too short to observe such a microevolution. On top of a continuous monitoring of movements, unfortunately available, running the experiment on a longer period of time is again a suitable next step. It would help us better understanding the influence of thermal phenotypes and habitat choice in the complex interaction between climate change and habitat fragmentation on population dynamics.

Environmental variation leads to spatially heterogenous warming at the landscape scale with thermal refugia where species can persist to regional climate warming (Ashcroft et al. 2009). The connectivity between habitats could buffer the impact of warm climatic conditions on population dynamics by allowing access to refuge areas (Scheffers et al. 2014, Suggitt et al. 2018). However, contrary to our expectations, our results show that the movements between microclimates may be costly and depopulate areas less impacted by climate warming by creating a pseudo source-sink dynamics. Given the ongoing habitat fragmentation, the landscape structure should be considered while quantifying and predicting alterations of population dynamics and species adaptation to warming climates.

In the side experiments on dispersal variation in patchy environments (Figure 22, 24-25), we also investigated the consequences of dispersal variation with local conditions on metapopulation dynamics. We supplemented the multi-species coordinated experiment with two simple illustrative models to test the influence of context-dependent dispersal, *i.e.* the dependency of dispersal to predation risk and to resource availability, and of context-dependent dispersal syndrome, *i.e.* the change of size-dependent dispersal with food availability. Firstly, with Emanuel Fronhofer, we developed a simple food chain model in a two-patch system with a basal resource, a focal consumer, a top predator and two dispersal modes for the focal consumers. The dispersal of focal consumers either depended simultaneously on the predator and the basal resource populations, as found in our multi-species experiment (Fronhofer et al. 2018) or not. Simultaneous resource- and predator-dependent emigration of the consumer greatly reduced local fluctuations of consumer population dynamics through time and even had cascading effects on the fluctuations of resource and predator populations (Figure 28). These smaller fluctuations may increase the stability of regional metacommunities.

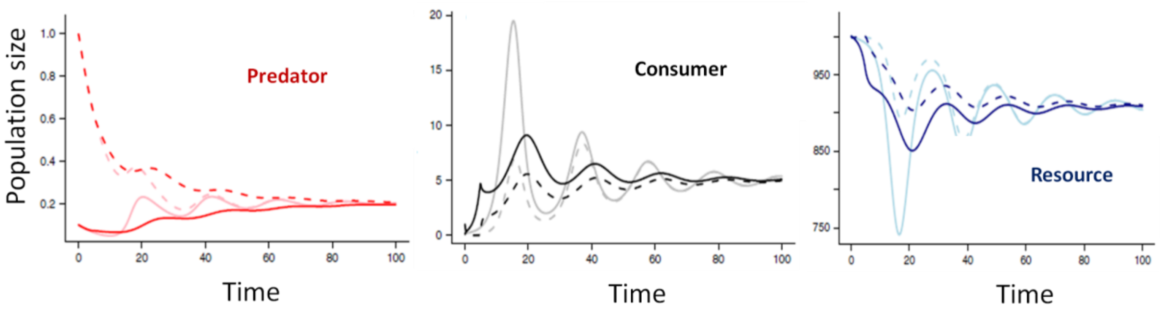


Figure 28: Consequences of conditional dispersal for local and regional metacommunity dynamics. The dynamics of a top predator, a focal species and a resources for both patches (patch 1: solid lines; patch 2: dashed lines) and for the random dispersal (light colours) and conditional (dark colours) dispersal are shown. From Fronhofer et al. 2018.

Secondly, with Bart Haegeman, we illustrated how a context-dependent dispersal syndrome could influence ecological dynamics with a simple, proof-of-concept metacommunity model (Cote et al. Submitted). We studied the consumption rate and density of a sessile resource interacting with a consumer dispersing across a patchy landscape according to its body size and local resource availability, following one of our empirical results (Figure 22). We assumed that individuals' resource consumption rate was positively correlated with body size (Peters 1986) and compared four dispersal scenarios exploring our main experimental results: that dispersers and residents differ in body size (i.e., they exhibit a dispersal syndrome), and that this difference varies with local resource availability (i.e., it is context-dependent; see results). We studied the consequences of these scenarios on the temporal mean and coefficient of variation of resource consumption and population density per patch. Compared to scenarios where dispersal was independent of phenotypes and resources, the dependencies of dispersal on individual body size, resource availability or both had positive additive effects on the temporal mean of consumption rate, and consequently negative effects on resource density (Figure 29). More importantly for metacommunity stability, the temporal variation in consumption rate and resource density was strongly decreased by context-dependent dispersal syndrome (Figure 29), suggesting it can have a balancing role on resource consumption among patches of varying resources in structured landscapes and promote the stability of the whole metacommunity.

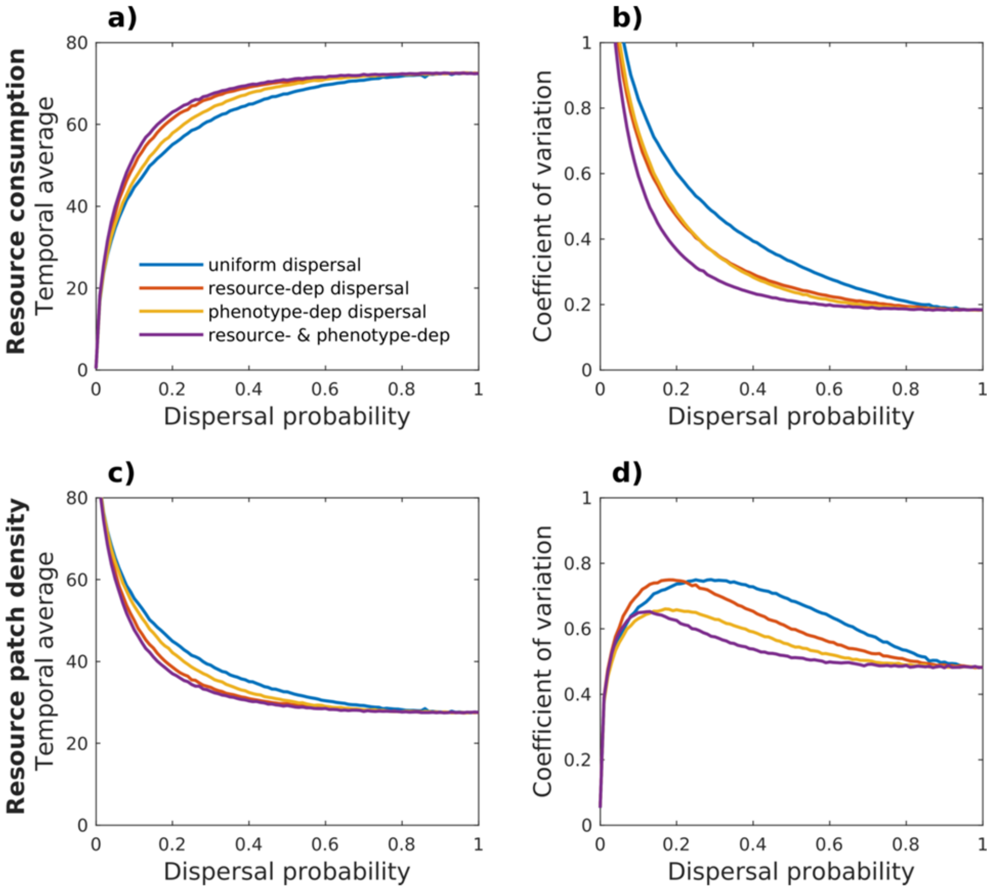


Figure 29: Theoretical illustration of the temporal average and coefficient of variation of resource consumption and density in relation to the dependencies of consumers' dispersal to patch resource density, individual consumption rate, or both.

Finally, we studied the consequences of a dependence of dispersal on the viscosity of the matrix and the risk of predation in interaction as shown in common lizards (Figure 25). As a reminder, the predation risk cancelled the effect of roads on lizards' dispersal propensity. Based on our experimental results, we modeled with Sylvain Moulherat, the consequences of fragmentation and predation risk on the dynamics of a metapopulation of lizards located in the Cevennes (figure 30).

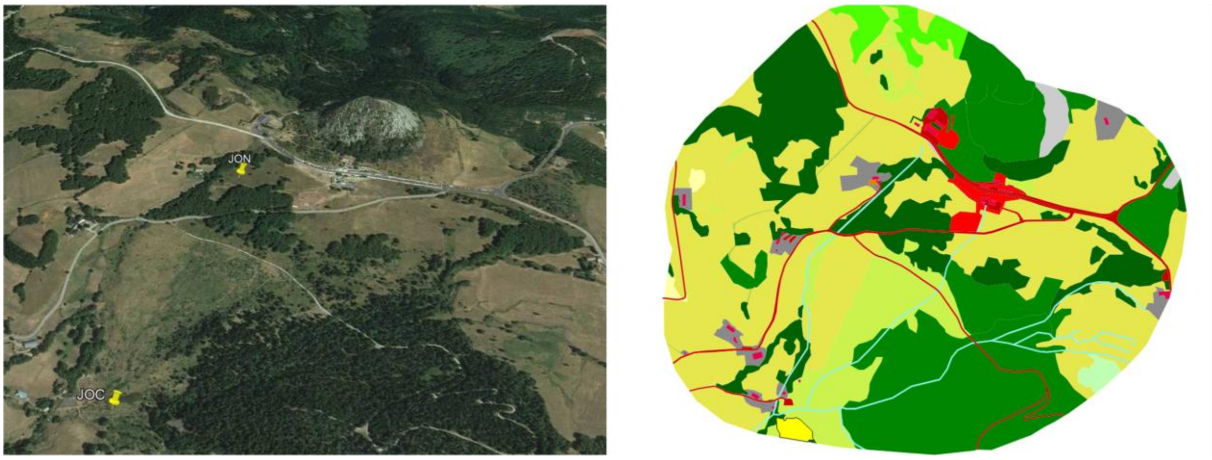


Figure 30: A metapopulation of lizards located in the Cevennes. Left: the real picture. Right: the graphical respresentation of patches and environmental types.

We created four scenario, two scenario with a continuous landscape in which the roads and paths were replaced by an environment type suitable to lizards and two fragmented scenarios maintaining the roads and paths. The movements throughout the landscapes and across roads and paths were parameterized with our experimental results. For fragmented and continuous landscapes, one scenario used the dispersal parameters observed in presence of predation risk and the second one without predation risk. As expected, we first found that, in absence of predation risk, the movement impediments on roads and paths strongly decreased the total population size in the landscape through higher local extinction and lower rescue effects (Figure 31). More unexpected, we found that, through its incentive effects on movement, predation risk in fragmented landscapes may largely reduce and even slightly reverse the effect of human infrastructure of metapopulation dynamics (Figure 31). We built this simplistic model to highlight the importance of considering environmental changes concomitant with fragmentation and conditional dispersal in our understanding of spatially structure populations. The purpose of this model is not to provide accurate predictions about common lizards or any ectotherm species, but to warn policy makers to consider scenarii implementing more complex rules for dispersal.

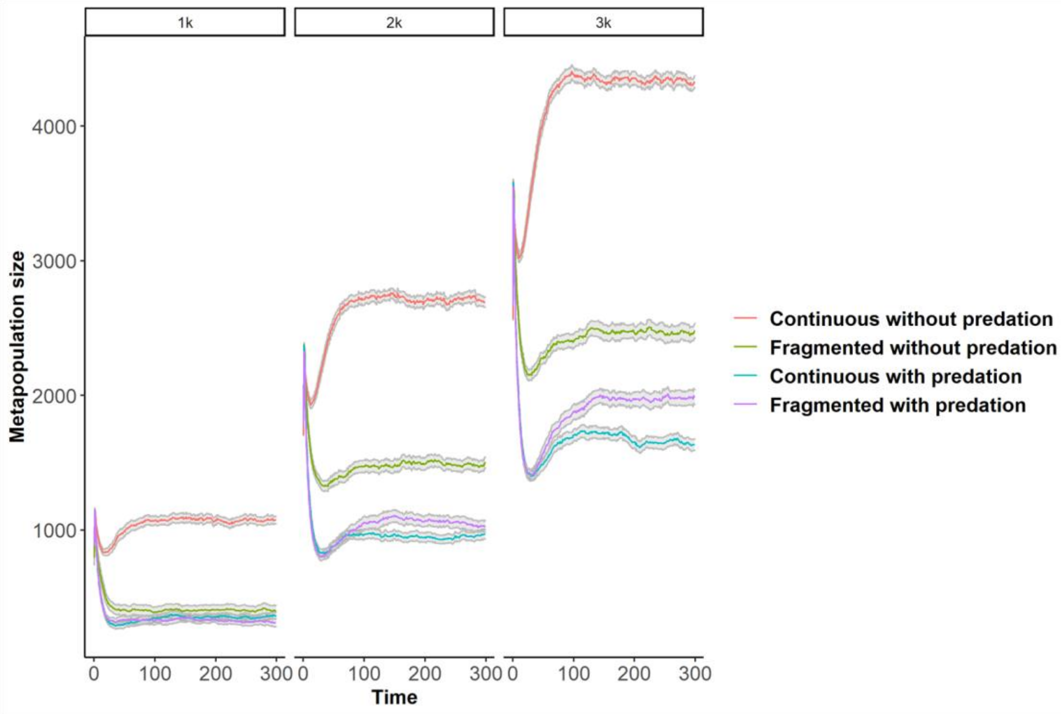


Figure 31: Metapopulation dynamics for 3 initial densities (1k, 2k and 3k individuals) and three scenarii varying for predation risk and landscape fragmentation

Overall, my studies about fragmentation focused on my oldest and dearest research topic, the intraspecific variation of dispersal, including environmental and phenotypic dependencies and their interaction, and its impacts on ecological dynamics. For several decades, ecologists have emphasized the importance of taking into account individual variation to understand population dynamics, species interactions, coexistence and extinction (MacArthur 1972, Lomnicki 1978, Sih 1987, Sutherland 1996). Interestingly, while dispersal is a key functional trait that varies in a non-stochastic manner among individuals and environments, predictive studies of global changes still often modeled dispersal through its very basic features (e.g., movement rate, dispersal distance). This often-written statement is nowadays outdated regarding the environmental dependencies of dispersal and to a lesser extent its phenotypic dependencies, but is still fully valid for the interplay between environmental and phenotypic dependencies and the related matching habitat choice. This interplay is however of major importance in an era of global changes where environmental conditions are constantly changing and where the (re)colonization – extinction dynamics are recurrent.

Biological invasions and range expansion

In this respect, biological invasions are a particularly interesting component of global change. A biological invasion occurs when a species is transported and introduced beyond its native range, spreads and establishes self-sustained populations into new habitats. Biological invasions have important negative impacts on native biota across levels of biological organizations ranging from genes to ecosystems (e.g. Ruiz et al. 1997, Mack et al. 2000). Invasions result from the intentional or accidental introduction of species beyond their native range. Because some processes are similar, I also studied range expansion in response to environmental changes (but see Urban 2020). Human activities profoundly change the abiotic and biotic habitats (Díaz et al. 2020) and force species to invade and to adapt to novel habitats beyond their native range (Tuomainen and Candolin 2011), provide species with suitable climatic conditions in habitats beyond the native range (Stachowicz et al. 2002) and lead to range expansion or shift if species cannot adapt to novel local conditions (Figuerola 2007). I will therefore include my studies on range expansion into this section on invasions, even if I acknowledge the important differences between climate-driven range expanded and invasive species (Urban 2020).

Investigations in biological invasions have mainly focused on determining the biological and ecological characteristics underlying the success of non-native species in the different stages of invasions (Facon et al. 2006, Gurevitch et al. 2011). Invasion is a multi-stage process: introduction, establishment in novel habitats, population growth to high density, spread from the place of introduction and so dispersal, and potential high impact on the invaded community (Lodge 1993). For instance, non-native species have higher dispersal rate, disperse over longer distance or display higher reproductive rates than native species (Lodge 1993, Kolar and Lodge 2001, Moyle and Marchetti 2006). A relatively more "recent" approach focused on the role of intraspecific variation in biological invasions and range expansion (Cote et al. 2010b, Cucherousset and Olden 2011, Chapple et al. 2012, Juette et al. 2014, Forsman 2014, Moran et al. 2016, Chuang and Peterson 2016). The phenotype and genotype of individuals shape their life history traits and the way they cope with novel conditions and could therefore confer upon individuals differential abilities to succeed the different stages of invasions.

First, upon introduction, individuals are caught in their native range for intentional introduction or are accidentally transported to habitats beyond their native distribution. Studies have demonstrated that captured individuals, for intentional introductions, and individuals entering transport vectors (e.g. freight, cargo), for accidental introductions, can have a biased phenotype and genotype (Biro and Post 2008, Chapple et al. 2012). The composition of introduced individuals can thus be biased towards specific phenotypes and genotypes. Second, a non-native species has to establish populations in newly and unfamiliar colonized habitats. Invaders face strong environmental pressures in their new environments and only those able to forage on novel items, to avoid novel predators, to resist to novel parasites and pathogens and to deal with new abiotic conditions can survive and establish self-sustained populations. Similarly studies have demonstrated the role in the establishment success of phenotypic traits like behavioral flexibility, innovation, aggression and diet specialization (Sol and Lefebvre 2000, Cucherousset et al. 2012, Pintor et al. 2014). Third, following establishment, non-native individuals might spread and this spread can be human-mediated or not. The spread of nonnative individuals, natural or human-mediated, is characterized by a higher dispersal propensity which is often associated with a suite of phenotypic traits, as demonstrated above. Even if transport from native areas, introduction and establishment were not biased towards a phenotype, the dispersal syndrome would lead to a biased composition in the invaded areas. It is worth noting that different phenotypic dimensions may influence different stages. For example, inconspicuous individuals may succeed better an unintentional transportation (Chapple et al. 2012) while aggressive individuals may compete better with local competitors in invaded areas (Duckworth and Badyaev 2007b). A phenotypic trait may even influence different stages in opposite ways, with for example a high level of aggressiveness slowing down the population growth to high density (Duckworth 2008a). This multi-facets process may lead to an evolutionary or plastic coupling of phenotypic traits, a temporary plastic expression of optimal traits' values or a mix of phenotypic specializations in groups of invaders. Overall, individuals settling out of their native range likely display a particular array of phenotypic characteristics and life history traits (Chuang and Peterson 2016) and may exhibit different biological and ecological features that could modify their biological interactions with novel competitors, prey or predators (Juette et al. 2014). These differences may play a crucial role in driving the intensity and the propagation of ecological impacts across levels of biological organizations. I will illustrate below my research on these topics.

i. Phenotypic variation during invasion stages

Shifts in the distribution of invasive and range-expanding species therefore often go along with differences in phenotypic traits (reviewed by Chuang and Peterson 2016), whereby individuals in newly colonized areas typically show, for example, greater dispersal ability, reproductive investment, or levels of foraging activity, which lead to a faster pace of life, compared with their counterparts in long-established populations (Hill et al. 1999, Martin and Fitzgerald 2005, Duckworth 2008b, Pintor et al. 2008, Alford et al. 2009, Therry et al. 2014). I studied two main non-exclusive mechanisms that can explain the phenotypic differences. Not surprisingly, I was first interested in non-random dispersal. The spread from the source populations (i.e. introduction or native areas) is led by a non-random subset of individuals that are characterized by a phenotype that favor a better colonization capacity, which includes, for example, high risk-taking behavior and metabolic rate (Cote et al. 2010; Carere and Gherardi 2013). Second, the abiotic and biotic conditions at species' invasion and range fronts, the newly colonized areas, are often novel to species and so more challenging than those in native areas (Hardie and Hutchings 2010). They may shape organism phenotype through plasticity or selection. For instance, during northward range expansions, organisms face strong shifts in climatic conditions. Ectotherms at higher latitudes often have darker colors which is advantageous for thermoregulation at lower temperatures (Clusella Trullas et al. 2007).

A large part of my work on this topic comes from my postdoctoral studies and follow-up articles. Using a major invasive species worldwide, *Gambusia affinis*, we ran a suite of studies examining the role of behavioral variation (aka personality) in the propensity to dispersal. Individuals vary in their shoaling tendency and this individual tendency is partly stable over several months, a substantial portion of this small fish's lifetime. Asocial individuals tend to shoal less and exhibit weaker choosiness for shoal characteristics (Cote et al. 2010a, 2012). Using artificial streams, we showed that dispersal behavior varies among individuals in a repeatable manner and is linked to between-individual differences in sociability (Cote et al. 2010a, 2011, 2013, Figure 32). Asocial individuals were more likely to leave their initial population and disperse farther. Furthermore, we showed that group composition in terms of sociability types also matters for individual dispersal decisions in a similar way (Cote et al. 2011), the less sociable the group was, the more any individual dispersed from the group regardless of their own personality type. These results suggest that individuals at the front of a spread would not be a random subset. This could result in higher invasion success and can hasten the spread of an invasion (see section ii below).

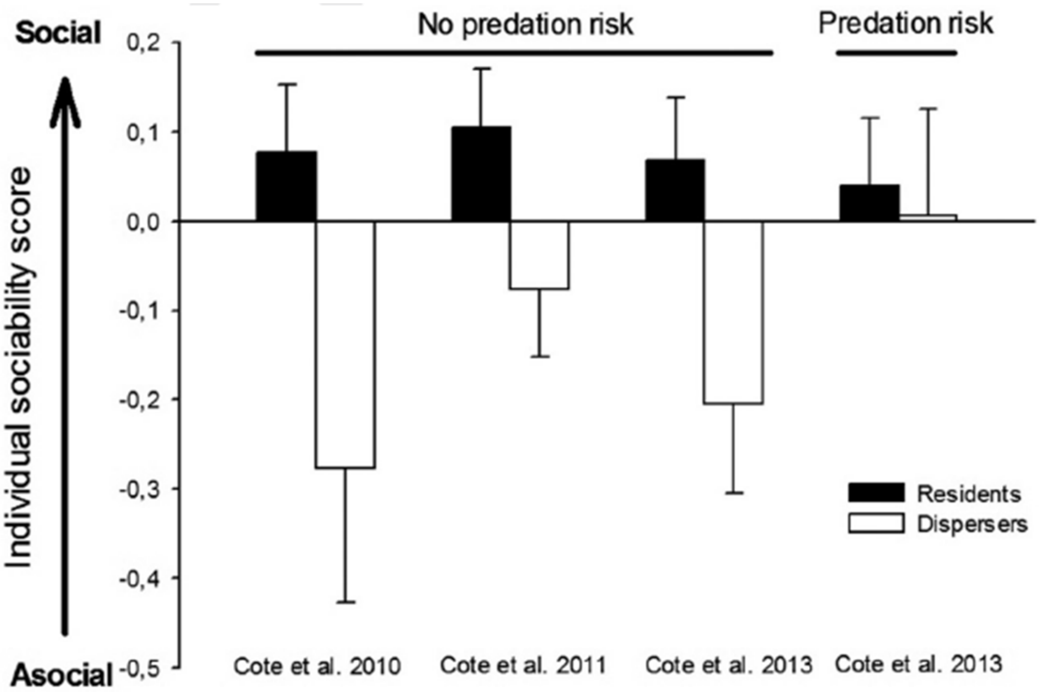
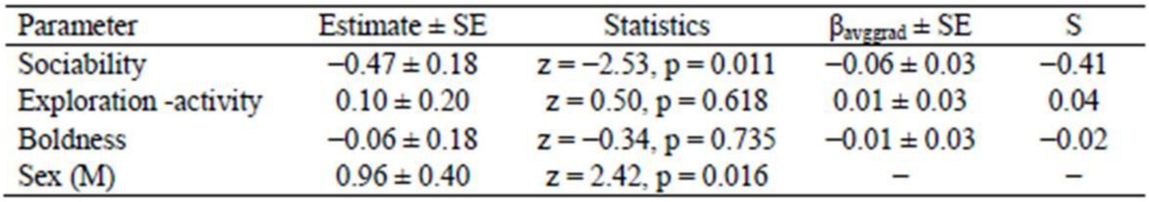


Figure 32: Pre-dispersal sociability score in dispersing and resident *G. affinis* individuals . The dispersal behavior was tested with and without predation risk. From Rehage et al. 2016

This behavioral dispersal syndrome was observed repeatedly in independent studies, with the one exception of predation risk in the initial habitat (Figure 32). When mosquitofish were released into a pool containing a caged novel predator, sociability was no longer related to dispersal tendency. This result suggests that personality-dependent spread is likely to vary with environmental conditions encountered during invasion. We therefore studied the interplay between sociability and predation which investigates both the impacts of phenotypic bias (see section ii below) and the selective process at the front, the second mechanism mentioned above. We found that survival in the presence of predators was negatively related to social tendencies, with asocial individuals surviving better when exposed to novel predators at low mosquitofish density, the conditions encountered at the expanding edges (Brodin et al. 2019, Table 1). Being part of a social group is often thought to be the best predator avoidance strategy due to the confusion and dilution effects (Krause and Ruxton 2002). However, groups of individuals also attract more predators than single individuals (Botham et al. 2005), in particular for naïve predators, and the benefit of shoaling should depend on a benefit-cost balance where confusion-dilution is the benefit and predator attraction is the cost. At low density, as in our study, the benefits of safety in numbers were weaker than the costs of attracting predators. Asocial individuals might be safer alone than in groups. We only tested the sociability-survival relationship with a novel predator at low density and so we cannot firmly conclude on this explanation. However this result suggest a selection for less social individuals in conditions mimicking the newly colonized areas (Table 1) which would reinforce the phenotypic bias created by dispersal syndromes.



Parameter	Estimate ± SE	Statistics	$\beta_{avggrad}$ ± SE	S
Sociability	−0.47 ± 0.18	$z = -2.53$, $p = 0.011$	−0.06 ± 0.03	−0.41
Exploration -activity	0.10 ± 0.20	$z = 0.50$, $p = 0.618$	0.01 ± 0.03	0.04
Boldness	−0.06 ± 0.18	$z = -0.34$, $p = 0.735$	−0.01 ± 0.03	−0.02
Sex (M)	0.96 ± 0.40	$z = 2.42$, $p = 0.016$	−	−

Table 1: Survival selection gradients and selection differential (S) on sociability and exploration. We estimated selection gradients using these predictors. Logistic coefficients were recalculated to average gradient vectors βavggrad according to the methods of Janzen and Stern (1998). From Brodin et al. 2019.

Thanks to a pan-European Biodiversa project, co-led with Simon Banchet, I could tackle the same questions on a range-expanding dragonfly, *Crocothemis erythraea*. *C. erythraea* is a dragonfly species with a predominantly African distribution but with a small historical European breeding range confined to the Mediterranean area (Dijkstra and Lewington 2006). Triggered by global warming, the species’ range expansion towards Northern Europe started in the 1960s, and the northernmost populations are currently found in Northern Germany (Ott 2007, Brockhaus 2015). During his postdoctoral studies, Lieven Therry investigated the phenotypic divergence across an age-gradient and its impact on ecosystem functioning using 11 sites from Portugal to the Netherlands (Figure 33) and 3 complementary approaches: a monitoring of phenotypic traits and experiments on F0 and F1 individuals from these natural populations.

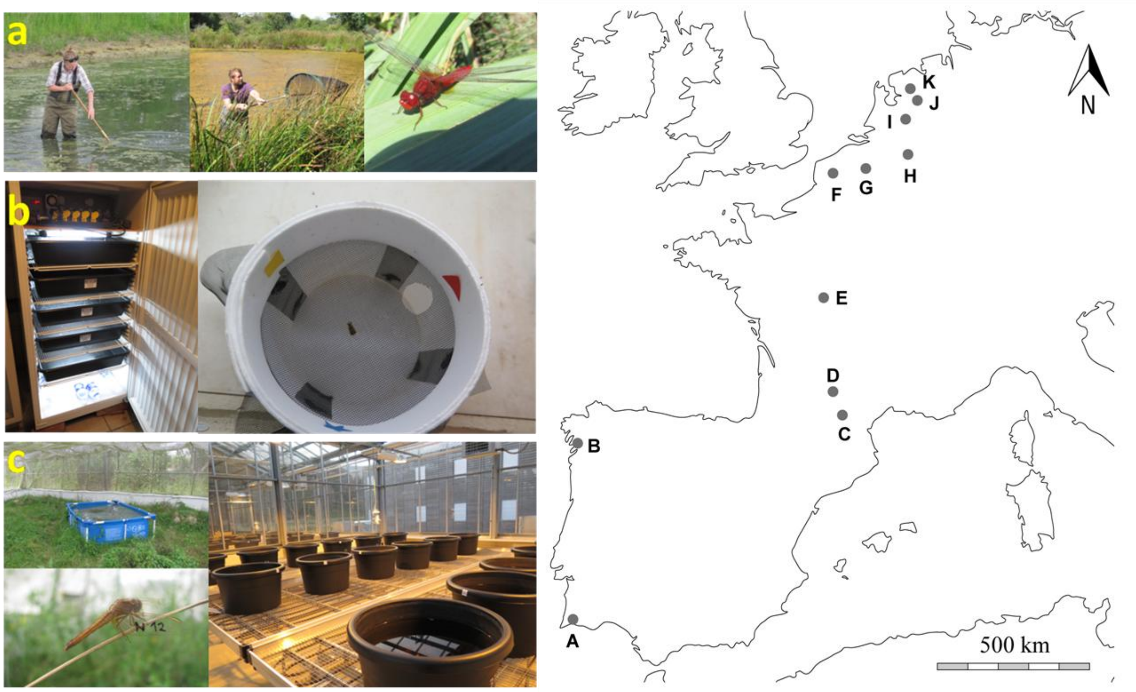


Figure 33: A series of sampling and experiments on the range expanding dragonfly *C. erythraea*. Left: some impressions of the experiments (a: collecting larvae and egg clutches across Western Europe; b: breeding and laboratory experiments; c: dispersal experiment and heated mesocosm experiment); right: sampling scheme in Europe.

In 2015, we collected larvae from 9 populations from southern France to central Germany and measured activity at a lower (19°C) and higher (25°C) temperature, larval darkness and larval size, before rearing the larvae in common garden until adulthood. We found that larvae at the expanding front, in northern populations, were darker and displayed covariations between darkness and activity and between darkness and body size missing in southern populations (Figure 34, Raffard et al. 2020). While the difference in larval darkness match a common difference with latitude in ectotherms improving thermoregulation in colder climates, the correlations suggest the emergence of alternative strategies in time-limited northern populations from individuals with a higher activity level and a better camouflage through darker coloration, to less active larvae benefited from an energy-saving strategy by reducing the investment in body darkness, a costly trait to produce, and increasing their body size. Our findings imply that phenotypic architecture is associated with the northward range shift, potentially differentially shaping fitness consequences and ecological interactions in southern versus northern populations.

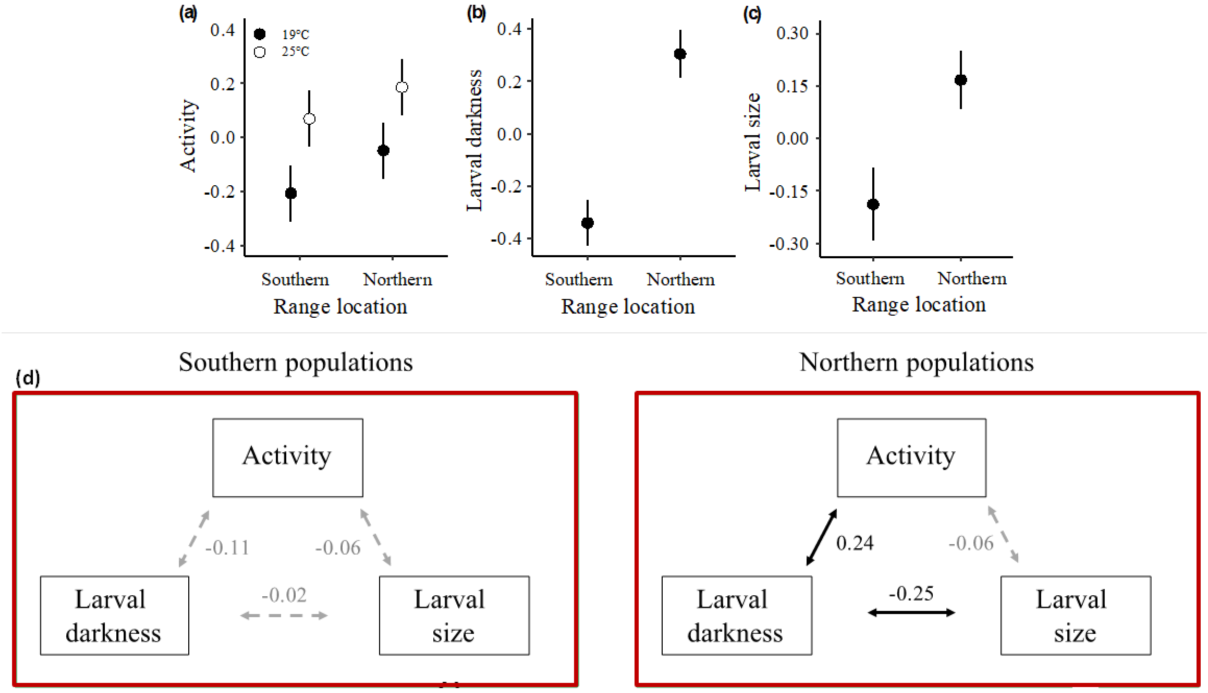


Figure 34: Means (± 1 SE) for larval activity (a), larval darkness (b), larval size (c) and coefficients of traits correlation (d). From Raffard et al. 2020.

The observed phenotypic differences between northern and southern populations may result from plastic responses to the variation in environmental conditions across the range and/or from the genetic architecture of populations resulting from founder effects, genetic drift or natural selection. Therefore we further performed a genomic screening of individuals across the range, currently being analyzed by Miguel Baltazar-Soares, and two experiments on F1 individuals to study the genetic and environmental drivers of phenotypic divergence. Egg clutches were collected from 8 populations from southern to northern Europe (12 clutches per population), brought to the lab and, after hatchling, larvae were further reared under 2 thermal conditions, an optimal one (28°C) and a sub-optimal one (24°C). These larvae were used to measure for thermal reaction norms in growth rate for all populations and then their impacts on ecosystem functions and community structure using a mesocosm set-up (see section ii). The split-plot common garden allowed to test whether the larvae growth rate varied with developmental temperature and with the latitude of mothers' origin. Growth rate of larvae greatly differed among populations, but not linearly with latitude (Figure 35, Therry et al. 2019) and was slightly higher at the highest rearing temperature. It suggests a genetic contribution to the growth rate driven by local conditions rather than by a founder effect in northern latitudes. We indeed found that climatic conditions in the populations of origin, modeled through the degrees-days (i.e. number of days above 8°C during larval development), explained larval growth rate better than the latitude (Figure 35). Colder conditions create a time constraint for larval growth rate. In ectotherms, individuals in populations encountering time stress typically evolve a genetically determined higher growth rates, so called countergradient variation (Kivelä et al. 2011). Time stress takes place at higher latitudes in temperate seasonal environments, whereby the growth season length decreases with increasing latitude; but also at lower latitudes where life-cycle length decreases due to a shift from an univoltine to a multivoltine life-cycle (Johansson 2003). Our results indeed show that the thermal constraint for development is the driver of variation in growth rate among populations.

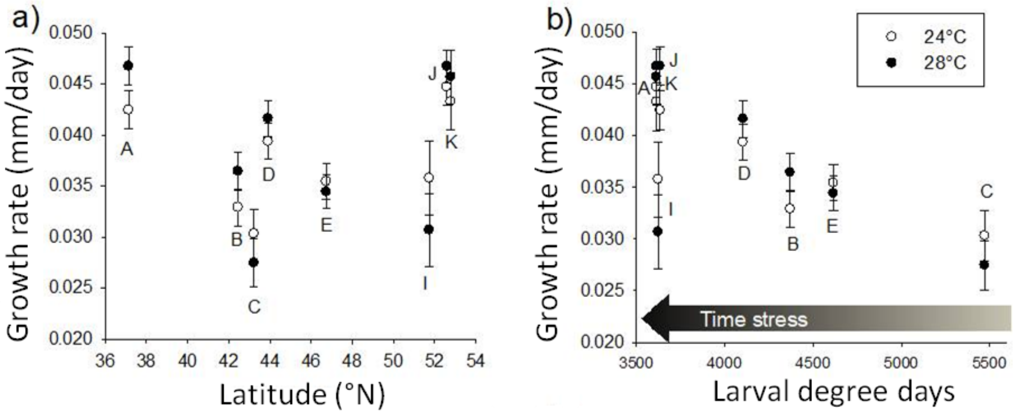


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Figure 35: Covariation of growth rate with latitude (a) and with population specific degree-days available for larval growth (b) when reared at 24°C versus 28°C. Given are population means with 1 SE.

ii. Consequences on invasion dynamics and native communities

I also aimed at predicting the consequences of a phenotypic bias at the invasion front on the invasion dynamics and the impacts on native communities. I first built on my postdoctoral studies on mosquitofish with a modeled developed with a PhD student, Sean Fogarty. This modeled was inspired by a verbal model that we published in Clobert et al. (2009) and Cote et al. (2010). In this scenario, colonizers are individuals with a specific phenotype (e.g. behavioral syndrome) that first establish new populations, and these newly colonized populations are then reinforced by joiners, individuals with a different phenotype from the colonizers. The immigration by joiners brings the newly established population towards its carrying capacity and may drive colonizers to leave and colonize new habitats. Our prediction was that the phenotypic heterogeneity and its link to dispersal strategies may accelerate the range expansion of invasive species. Sean, Andy Sih and I mathematically formalized this idea using sociability as a focal trait. We used a spatially explicit simulation model involving a network of patches and varying for the population's behavioral composition. The species was composed of two distinct types of individuals that differ in their fitness and dispersal responses to density (Cote and Clobert 2007, Cote et al. 2008). Asocial individuals have a relatively high fitness at low densities, including a relatively small Allee effect, and social individuals have a higher fitness at high local densities and are outperformed by asocial individuals at low densities. Individuals further exhibit fitness-dependent dispersal, dispersing at higher rates as their expected fitness decreases. It manifests as a density-dependent dispersal differing between social and asocial individuals. Three compositions were tested: all social individuals, all asocial individuals, or a mix of the two. The composition influences the spread and the impact of invader (here simply modeled as the total population density, Figure 36).

A outlined above, invasions is a multistage process; a successful invasion requires a species to get to a new area, establish, grow locally, spread, and grow regionally. Ecological theory and empirical research suggest that different traits are favored in different stages of this process. Our model showed that the problem of trade-offs in invasions can be solved by the within-species variation of traits.

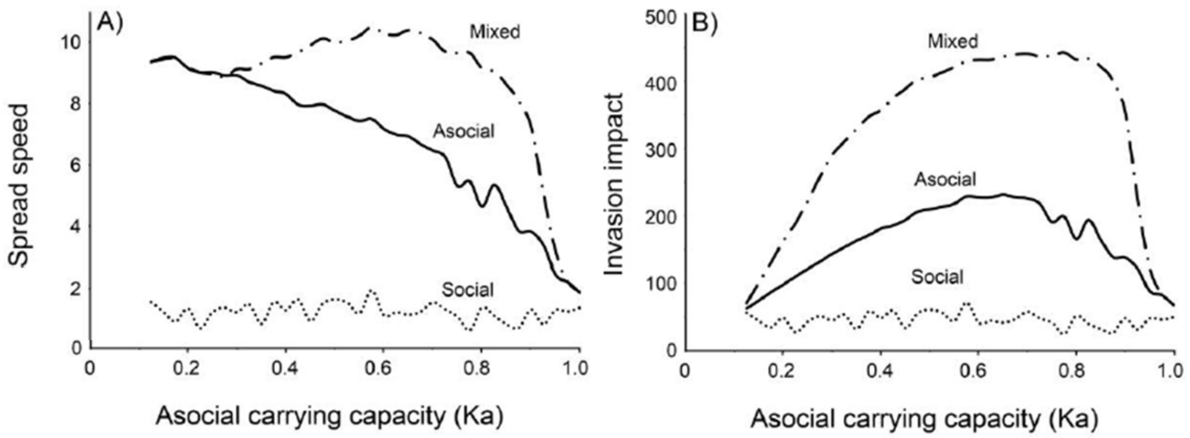

Figure 36: Spread speed (A) and invasion impact (B) during invasion for the three behavioral mixes as a function of asocial carrying capacity. When Ka is smaller, types are more dissimilar. Spread speed is measured as the rate of patch establishment. Invasion impact is measured as the total population size in the network. From Fogarty et al. 2011

A mix of social types increases the speed and the impact of invasions above a monotype of either social or asocial types alone (figure 36). Social types that do poorly at low density spread slowly because they grow slowly within each new patch they encounter, leading to long time lags between the establishments of each successive patch. This type does, however, eventually grow to high densities within each patch. In contrast, asocials spread more quickly than socials as a result of their higher growth rate at low densities, allowing for quick establishments and shorter lags between establishments of new patches. However, this type is unable to grow to high densities in each patch. A mix of types allows for both faster spread than asocials alone and for socials to grow to high local densities more quickly than they do alone. Within-species variation in density-dependent traits may influence the dynamics of invasions. In addition, along with our experimental results on mosquitofish and results on other species (e.g. Pintor et al. 2008, Groen et al. 2012, Hudina et al. 2014, Myles-Gonzalez et al. 2015), the model suggest that an invasion front may be led by individuals with a specific behavioral type. This specific behavioral type may confer upon range expanding species an advantage on native competitors (Duckworth and Badyaev 2007b), against native (and naïve) predators and a larger impact on native prey (Pintor and Sih 2009). For example, in mosquitofish, less social individuals survived better to novel predators at low density (Table 1).

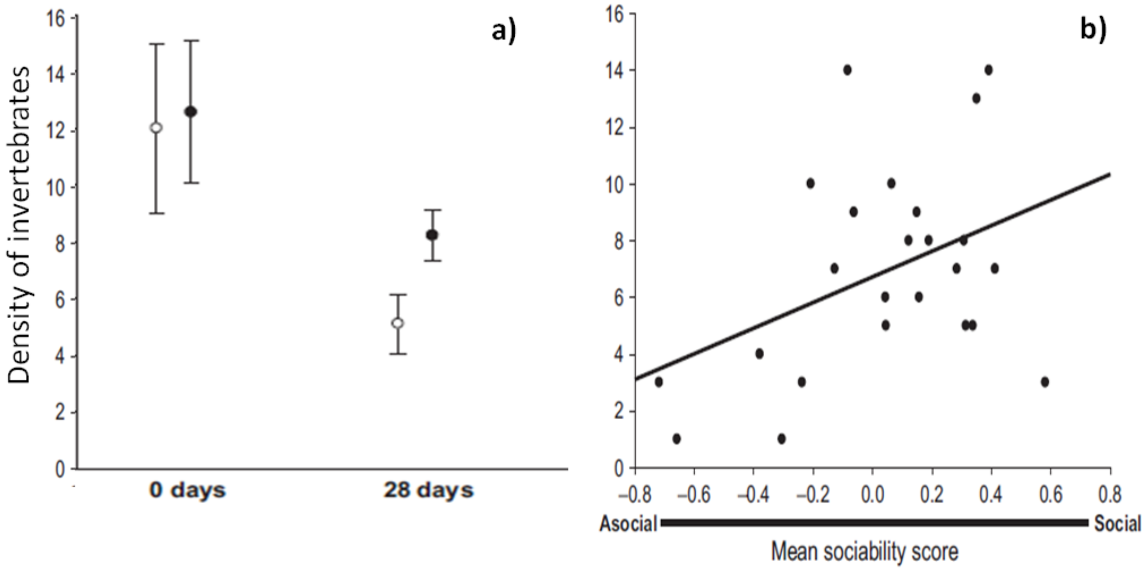

Figure 37: The density of invertebrates at 0 & 28 days in relation to a) group dispersal type (dispersers vs. residents) and b) group mean sociability score (for 28 days only). Shown are mean numbers of invertebrates sampled in mesocosms (± SE for a) containing groups of dispersers (open circles) or residents (filled circles). From Cote et al. 2017a.

In addition, we studied the potential impact of phenotypic biases at the leading front on prey communities using mesocosms containing at low density either individuals previously identified as dispersers or non-dispersing individuals (Cote et al. 2017a). Dispersers reduced prey abundance more than non-dispersers during the first 4 weeks after introduction, and the disperser's social types are likely drivers of these differences (Figure 37). However these differences in prey communities disappeared after 8 weeks suggesting prey community resilience against predation in these mesocosm ecosystems. Overall, the behavioral dispersal syndrome in mosquitofish may alter their interaction with predator and prey species and therefore the functioning of native communities and ecosystems compared to random dispersal.

My interest on the topic therefore pointed towards the potential consequences on community and ecosystem functioning. Given my limited knowledge on these topics, I started to collaborate with Julien Cucherousset and Simon Blanchet. The first step was to formalize the ecological consequences of phenotypic variation by coining the concept of functional syndrome (Raffard et al. 2017). Most studies have focused on the ecosystem effects of a single phenotypic trait (e.g. morphology, body mass) despite the fact that individuals can simultaneously vary in multiple phenotypic traits (Sih et al. 2004). Therefore, for his master research, Allan Raffard provided an integrative understanding of the effects of individuals on ecosystems. From a functional perspective, phenotypic traits have been classified as functional effect traits and functional response traits (Violle et al. 2007). Functional effect traits determine how and to what extent an organism influences energy flow and matter transformation in an ecosystem and functional response traits determine how an organism responds to environmental conditions (Díaz et al. 2013). We introduced the concept of 'functional syndrome' (Raffard et al. 2017) as the association between correlated suites of response and effect traits (Figure 38) through metabolic and stoichiometric constraints (Brown et al. 2004, Leal et al. 2017).

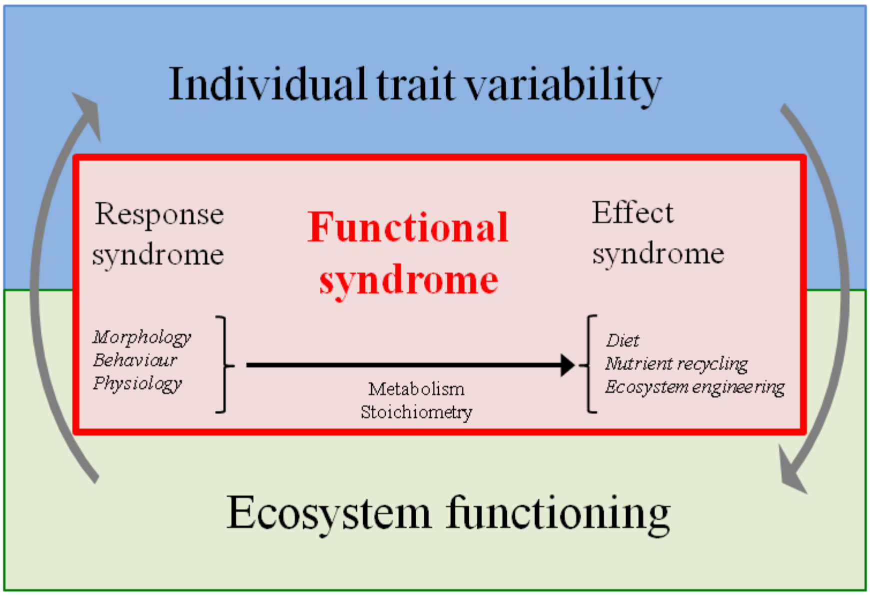

Figure 38: Conceptual representation of the functional syndrome, the association between response and effect traits, and examples of response traits, effect traits and underlining mechanisms. From Raffard et al. 2017.

We further investigated such a syndrome using the invasive red-swamp crayfish (*Procambarus clarkii*) as the model species. We monitored individuals over nine months and repeatedly quantified several response and effect traits. In brief, we showed that the variability among individuals of almost traits was stable and structured according to covariations among functional response traits and among effect traits (Figure 39). The resulting response and effect syndromes further covary directly and through body mass (Figure 39). This functional syndrome may drive ecological effects during invasion. We indeed showed this syndrome would have ecological effects on a key ecosystem process (i.e. whole-lake litter decomposition) to a level similar to those induced by doubling population size (Raffard et al. 2017). In invasion ecology and more generally in ecosystem ecology conspecifics should not be considered as functionally identical (Raffard et al. 2017).

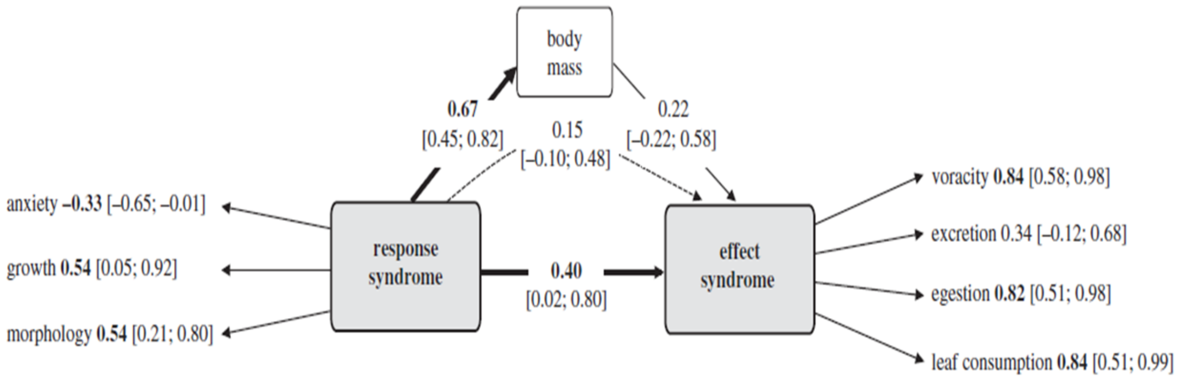

Figure 39: The functional syndrome in the invasive red-swamp crayfish. This structural equation modeling shows estimates of covariations between each trait and its latent variable (effect and response syndromes) and direct and mass-mediated covariations between the two latent variables. From Raffard et al. 2017.

Two additional projects therefore aimed at quantifying the ecological consequences of intraspecific trait variation and spatial divergence in invasive species on community structure and ecosystem processes. The first one is the master 2 project of Tristan Juette. We tested whether the variation in boldness, the tendency to explore a novel and risky environment, within groups of the invasive largemouth bass *Micropterus salmoides* influences prey communities and ecosystem functioning using an experimental approach. Four behavioral compositions were tested and mesocosms were monitored for 6.5 weeks. Groups of three individuals were made of bold individuals, shy individuals, individuals of intermediate level or one individual of each previous type, hereafter called mixed. Behaviorally-heterogeneous populations (i.e. mixed) used the habitat differently than behaviorally-homogeneous populations (Figure 40a). Individuals from bold, intermediate and shy groups were detected more often in water surface (i.e. where the inputs of allochtonous prey occurred) than individuals from mixed groups. This result may indicate either a higher complementary in resource use in mixed groups, with one individual using allochtonous resources and the other individuals using pelagic and benthic resources, or a higher social promiscuity among individuals of similar behavioral type. Growth rate also significantly differed between treatments (Figure 40b) with bold individuals growing more as expected (Biro and Stamps 2008).

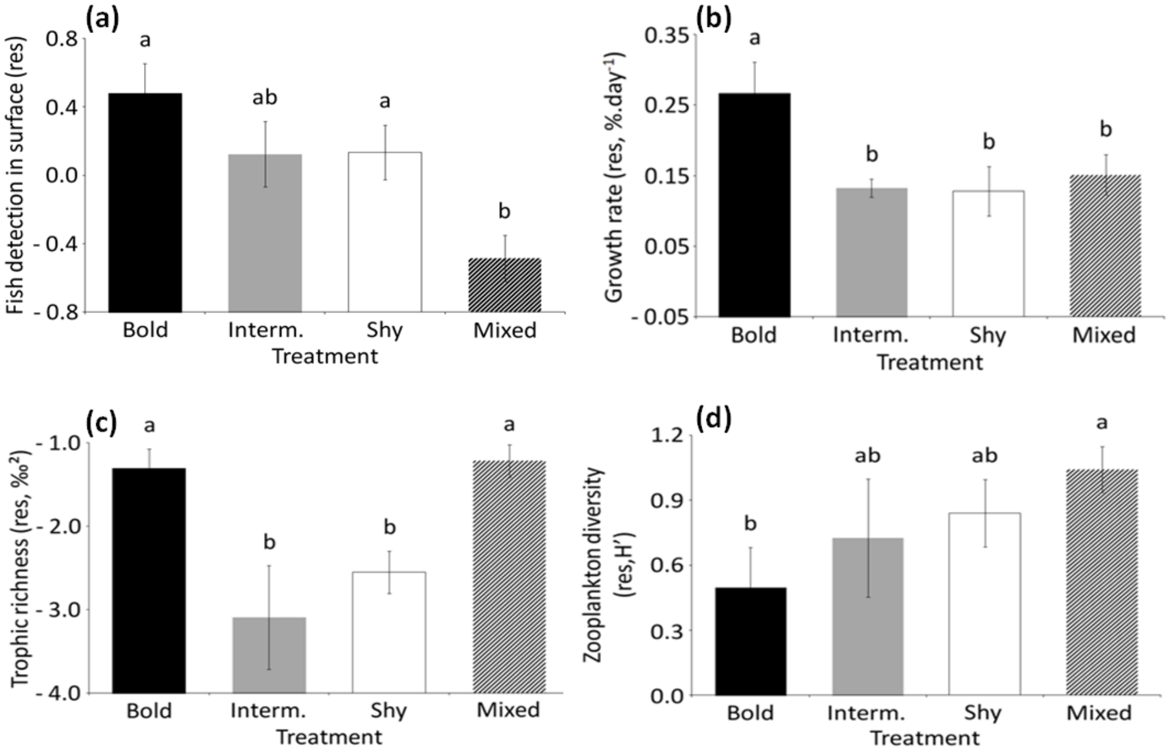

Figure 40: Ecological differences among groups of largemouth bass varying for their level of boldness (mean ± SE): (a) the probability of detecting a fish on the surface, (b) the mean growth rate in the group, (c) the trophic richness (a proxy of individual trophic specialization) and (d) the diversity of zooplankton at the end of the experiment.

Using stable isotope analyses, we found that bold and mixed populations were composed of individuals with a specialist diet (i.e. higher trophic richness) while intermediate and shy populations were composed of generalist individuals (Figure 40c). In the pelagic food chain, the behavioral composition modified the diversity, but not the biomass, of primary consumers (i.e. zooplankton, Figure 40d) but we did not detect a cascading effect on pelagic primary production (phytoplankton). Overall, Tristan's results show that animal boldness, a trait often observed to vary during range expansion and invasion, may alter the structure of prey communities.

The second project is a follow-up of the growth rate experiment on the range-expanding dragonfly *Crocothemis erythraea* (Figure 41). We used the larvae from four populations, one in Portugal, one in South of France, one in Central France and one in the Netherlands, that were reared from the egg stage on either 24°C or 28°C (see above) to test the relative effects of intraspecific trait variation in larvae and thermal conditions on the dynamics of freshwater community and ecosystem functioning (Therry et al. 2019).

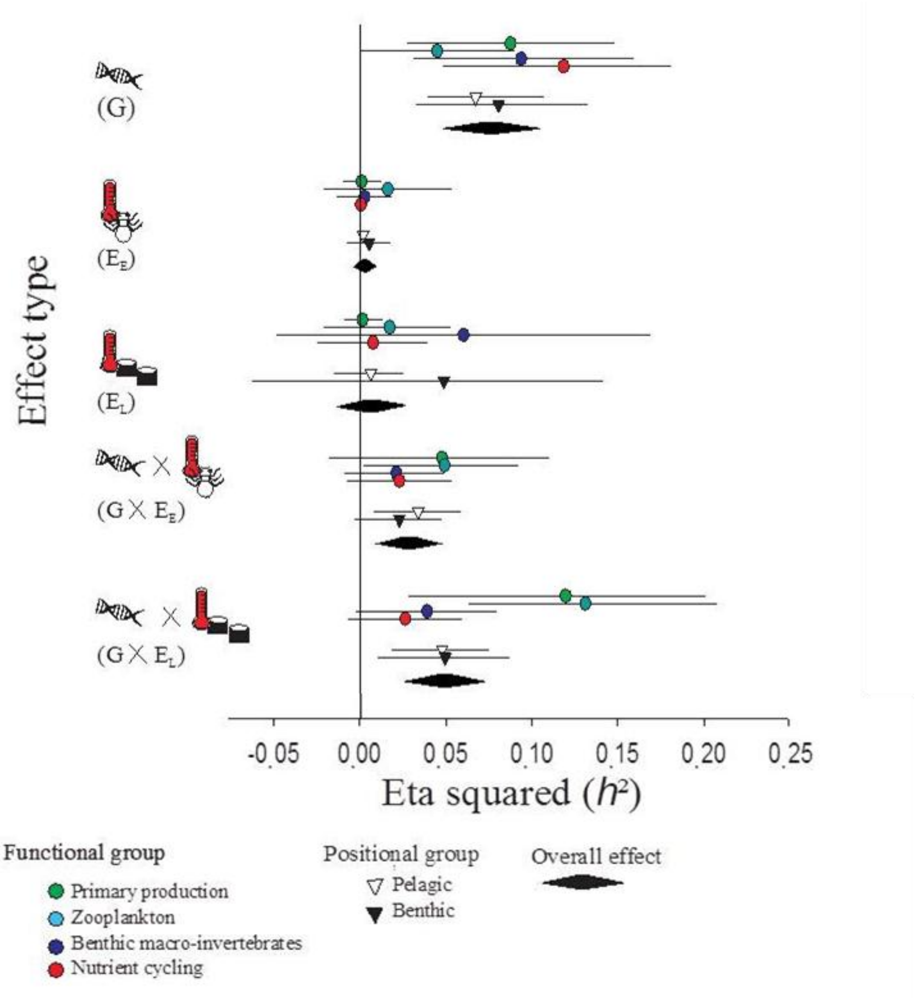

Figure 41: Eta-squared effect sizes for the genetic (G), early developmental environment (EE), late developmental environment (EL) and interactive (G × EE and G x EL) contributions to the effects induced by larvae on the community and ecosystem properties. From Therry et al. 2019

Using experimental mesocosms, we manipulated intraspecific trait variation arising from genetic (G), early developmental environment (EE, 24°C or 28°C) and late developmental environment (EL, in the mesocosms, 14°C or 18°C) contributions in a full factorial design. The genetic contribution is manipulated through the maternal population of F1 larvae reared from the egg stage in the lab. It is noteworthy that traits expressed in F1 can still be affected by non-genetic— yet inherited—processes such as maternal effects (Danchin et al. 2011). We showed that intraspecific trait variation arising from genetic effects has the strongest consequences on community and ecosystem dynamics relative to trait variation driven by the thermal environment (EE and EL, Figure 41). Importantly, the ecological effects of trait variation due to genetic effects were partly modulated by thermal conditions (G × EL, and to a lesser extent G × EE interactions) and varied among ecological response variables (Figure 41). However, the genetic contribution was not related to the population latitude. Intraspecific trait variation along an expansion gradient can result from variation in environmental conditions across the range (e.g., abiotic conditions, population or community structure) and/or from the genetic architecture of populations resulting from founder effects, genetic drift or natural selection. Our results suggest that the ecological consequences of a phenotypic and genotypic divergence among populations are unlikely due to a founder effect on the genetic architecture but rather to the adaption to local conditions or to genetic drift.

Conclusions and perspectives

Over the last 10 years, I oriented my research towards a more holistic understanding of global change impacts. I am in the process of diversifying my research focus from population ecology to community and ecosystem ecology and my research tools from phenotypic biology to molecular biology and microbiology. My objective is to expand my research towards both a microscopic and a macroscopic viewpoint of biodiversity and ideally to cover the impacts of global change from genes to ecosystems. More than biodiversity dimensions, this scaling allows me to address the question of global change impacts through an ecological perspective, an evolutionary perspective and the interactions between the two. It has now long been recognized that ecological and evolutionary dynamics can influence each other, even on short contemporary timescales, coining the term eco-evolutionary dynamics. It refers to changes in ecological factors leading to genetically or non-genetically heritable change of phenotypic distribution in a species, or to heritable change in phenotypic distribution leading to changes in ecological factors (Pelletier et al. 2009, Schoener 2011). When interactions between ecology and evolution are reciprocal, they lead to eco-evolutionary feedback loops (Post and Palkovacs 2009), which can deeply modify the functioning of communities and ecosystems (Matthews et al. 2011). While any evolutionary study a fortiori investigates eco-evolutionary dynamics, my background and interest in intraspecific variation colored my studies on ecological processes with an eco-evolutionary perspective.

With PhD students (Elvire Bestion, Felix Pellerin and Emma Fromm), postdoc (Laurane Winandy and Luis M San Jose), and colleagues (*e.g.,* Lucie Zinger, Robin Aguilée, Joël White, Staffan Jacob, Murielle Richard), we used the Metatron to perform short-term (1-2 yrs) to long-term (6 yrs) experiments on the impacts of climatic conditions on the common lizards, the community of species interacting with this apex predator and the ecosystem they inhabited. We demonstrated that a warmer climate has a strong impact on life cycle and population age structure of this species, with a faster growth rate, an earlier reproductive onset, and an increased mortality rate. This faster pace of life, also supported by results in natural populations (Rutschmann et al. 2016b, Dupoué et al. 2022), may result from plastic changes in life history traits (*e.g.,* growth rate), selection for fast life style (*e.g.,* age at first reproduction), or from plastic and selective effects on phenotypic traits tightly linked to individual life styles. The faster pace of life may encompass a suite of other phenotypic traits (Reale et al. 2010), in particular thermal traits (i.e. skin coloration and thermal preference) which have been found to respond to climatic conditions through plasticity and, to a lower extent, through selective processes. The first main objective (**Objective 1**) is to disentangle those explanations thanks to our 10 year-long monitoring of individuals phenotype and survival complemented with a 1) full pedigree and RAD-sequencing for the last 6 years, 2) a dataset of temporal changes in allele frequency in experimental and natural populations and 3) a monitoring of telomere dynamics to quantify physiological exhaustion (Figure 42).

These changes may go along with changes in species interacting with common lizards. Indeed, we repeatedly showed that warmer climate reduced microbial diversity in lizards’ gut (Bestion et al. 2017b, 2019b, Fromm et al. In preparation). We further showed that this change is correlated with changes in lizards’ diet breadth with warmer climates (Bestion et al. 2019b). If microbiota and diet changes are maintained over longer periods of time, we can expect top-down effects of this apex predator on invertebrate communities and microbial meta-communities inhabiting their gut. These changes may further influence plant communities (*e.g.*, changes in the proportion of herbivorous and predatory invertebrates) and microbial communities at other trophic levels (*i.e.*, invertebrates’ gut and soil microbiota). Alternatively, the changes observed in lizards may have resulted from changes in invertebrates, plants and microbial communities. For example, microbial communities in invertebrates’ guts might have been influenced by warmer climates and have had consequences on lizards’ gut microbiota. The community structure of plants might also have changed invertebrates’ activity pattern and influenced lizards’ diet through plastic or selective changes. These bottom-up and top-down effects are not exclusive and further create positive and negative feedbacks between climate effects at different trophic levels in ecological networks. My second objective (**Objective 2**) is at 1) studying the changes in the taxonomic and functional structure of invertebrates, plants and microbial communities and the impacts on ecosystem functioning and 2) teasing apart the top-down and bottom-up effects in observed ecological changes.

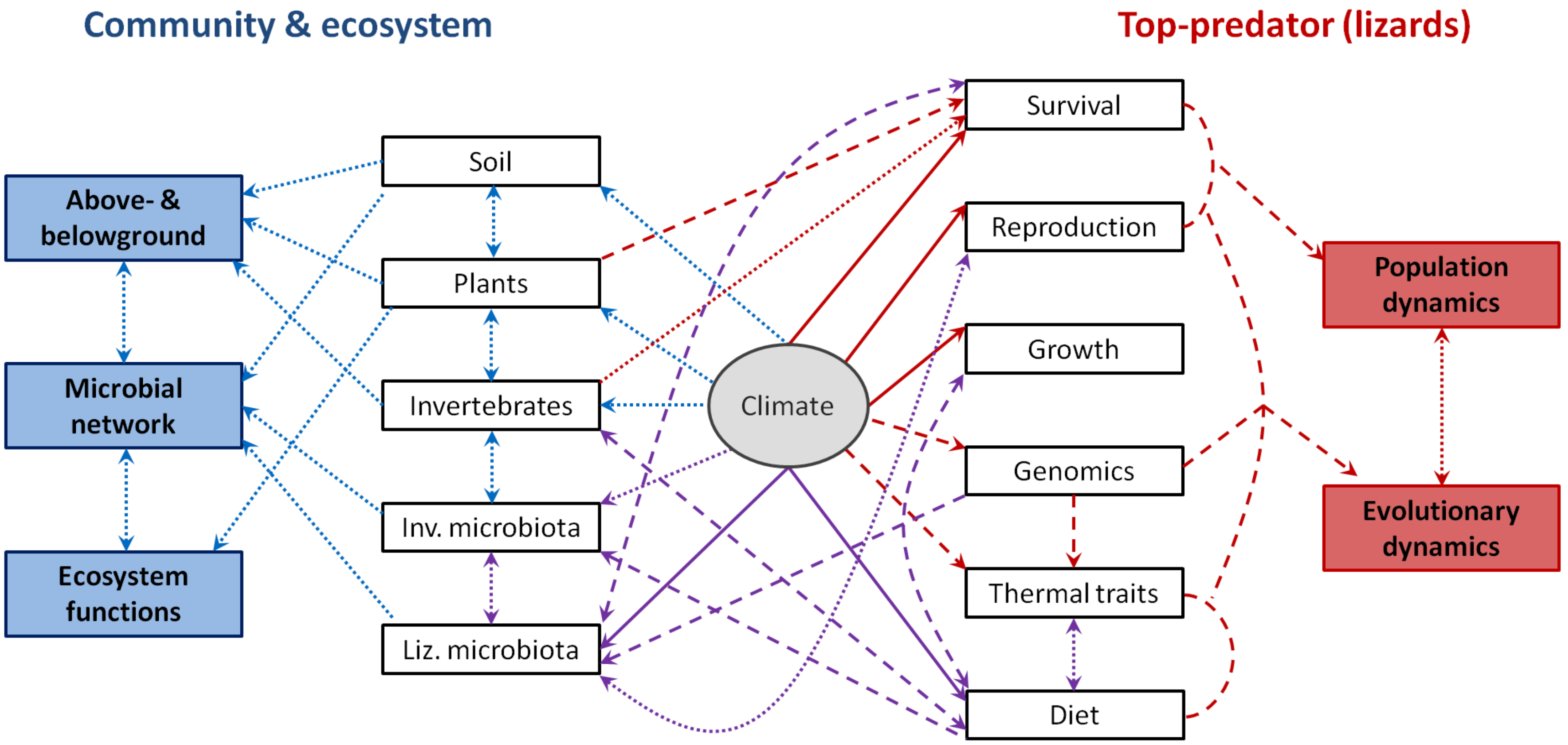

Figure 42: Conceptual sum-up of my ongoing projects. Relationships are categorized as (supposedly) understood (solid lines), partially understood relationships (dashed lines) and not yet understood (dotted lines). Colors indicate whose project this relationship belong to. Red = Luis, Félix and Elvire's project, purple = Emma's project, blue = Léa's project. Arrows show expected directionality of effects, double-arrowed lines being reciprocal effects. Inv. = invertebrates and Liz. = lizards.

Previous results suggest that eco-evolutionary dynamics may potentially be at play, considering phenotypic changes are at least partially heritable. It is however difficult to tease apart the two sides of the eco-evolutionary coin (*i.e.,* the influence of ecological dynamics on evolutionary dynamics and conversely) because of the nearly natural context of our experiments. We will therefore develop additional experimental approaches to better understand the feedbacks between changes in evolutionary and ecological dynamics (**Objective 3**).

i. Objective 1: Eco-evolutionary impacts on the apex predator

Intra- & intergeneration plasticity and selective gradients (Luis' and Elvire's projects)

This project is led by Luis, with the help of Elvire and Félix, and aims at investigating the evolutionary processes underlying observed changes (Figure 42). On the short term, we observed plastic changes in two main thermal traits, skin darkness and thermal preference, and a relatively weak differential selection. Our first goal is to study whether those plastic and selective responses are consistent on the long-term or fluctuate over time. Our climatic treatments indeed vary with external climatic conditions and may lead to fluctuating section and plasticity through 1) fluctuating differences in temperature between treatments which were shown to vary between 1.2°C and 2.0°C (mean daily temperature) and between 2.6°C and 3.1°C (maximum daily temperature) over the years and 2) fluctuating annual mean climatic parameters influencing ecological dynamics (*e.g.,* prey populations) and absolute thermal value in each climatic treatment. For example, in warm climates, summer daily temperatures varied between 26.4°C and 28.4°C and between 30.1°C and 32.3°C, mean and maximum temperatures respectively. As for thermal performance curves, species responses to temperature is a non-linear process in which their performance increases up to a thermal threshold (*i.e,* thermal optimum) and decline above this threshold. The shape of this non-linear dependency to temperature may further vary among age classes, sexes and fitness related trait. For example, the thermal optimum largely varies among biological processes (e.g., 30.2°C for gut-passage rate and 34.2°C for sprint speed, Van Damme et al. 1991). The costs-benefits balances of warm climates and the differential plastic and selective effects may therefore vary with the respective thermal conditions in both climatic treatments, leading to fluctuating effects over the years. An important step will therefore be to investigate whether phenotypic plasticity is adaptive or not. A main challenge is to predict trait's optimum because 1) the fitness-phenotype relationship varies with age, 2) the phenotypic plasticity interferes with our estimate of selective gradient and 3) thermal conditions do not linearly impacted fitness and fitness-phenotype relationships as explained above. In our short-term study, we found that phenotypic plasticity on skin darkness improve individuals' survival (Bestion et al. Submitted). Our experiment provides a complete longitudinal monitoring coupling an extremely low rate of missing capture (< 1%) and an extremely high rate of successfully encoded traits for all individuals, from birth to death, over 10 years. This larger database will allow us to better estimate selective gradient on traits and hopefully traits plasticity.

Genetic and environmental determinants of traits

The response to selection, the strength of phenotypic plasticity, as well as eco-evolutionary dynamics, will depend on traits genetic and environmental determinants. The second objective is therefore to better estimates the genetic and non-genetic determinants of thermal traits and of climate-dependent traits' plasticity. While we estimated traits' heritability on the short-term (Bestion et al. Submitted), a larger database will allow us to improve our estimates of traits variation due to genetic, maternal and environmental effects and to provide such estimates for traits plasticity (Nussey et al. 2005). In our 2011-2017 database, mother and father identities are known in 99.3 % and 92.3% of the cases, respectively, mean maternal and paternal sibship sizes are 3.7 and 4.3 juveniles, respectively, and the maximum pedigree depth is 5 generations. We can now add 4 more years to this database.

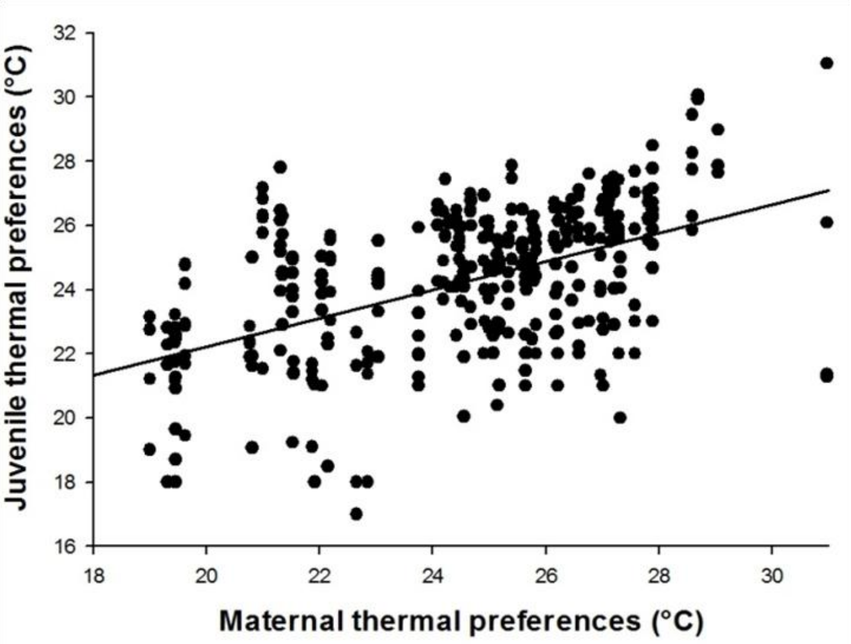

Figure 43: Correlation between maternal thermal preference during gestation and juvenile thermal preference at birth

On top of genetic variation, I am interested in non-genetic inheritance (Danchin 2013) and more particularly maternal effects (Sheriff et al. 2017). Common lizards are live-bearers with no parental care but with important maternal effects influencing offspring phenotype. Maternal hormonal levels, ectoparasite loads, nutritional status, thermal and water conditions as well as predation risk influence juvenile locomotion, basking behavior, activity morphology and dispersal (Sorci et al. 1994, Massot and Clobert 2000, Meylan and Clobert 2004, Bestion et al. 2014, Rozen-Rechels et al. 2018). As only 50% of juveniles survive their first summer (Meylan and Clobert 2005), juveniles have little time to plastically adjust to their environment and maternal effects might thus be a determining factor for juvenile fitness. With Elvire and Laurane, we developed several projects on maternal effects in common lizards. We found that an exposure to predation risk on gestating females influenced juveniles' natal phenotypes, with juveniles having a longer tail, preferring colder temperatures and dispersing more from natal habitats (Bestion et al. 2014), and personal and social uses of predation cues (Bestion et al. 2014, Winandy et al. 2021), and that vegetation structure in maternal habitats strongly influence juveniles activity levels and survival in habitats of varying vegetation structure (Bestion et al. 2022). While the project is not yet completed, we further studied the influence of maternal effects in juveniles’ acclimation to warmer conditions.

Thermal preferences in gestating mothers and neonates were correlated (Figure 43) and mothers’ thermal preferences plastically changed with climatic treatments even during gestation the following years (*i.e.,* 8 months after climatic treatments, Figure 9, Bestion et al. Submitted). We therefore expected maternal climatic treatments to influence natal thermal preferences and more generally thermal phenotype. In a short-term experiment, we applied a split plot design in which clutches of each mother were divided in two and released in warm or present-day climate. Juveniles from mothers that had experienced warmer environments had lower thermal preferences and became darker after one year when they were themselves in warmer environments (Figure 44). The effect of warmer climate on juvenile darkness (Figure 10) thus appears to be reinforced when maternal and juvenile environments match (Bestion and Cote In preparation), suggesting a role of the coherence between juvenile and maternal environments (*i.e.,* environmental predictability) on the strength and the adaptiveness of maternal effects (Burgess and Marshall 2014). This echoes the differences of warming impacts on darkness between adults and juveniles and the diversity of benefits and costs of a darker color in a warmer environment. On one hand, a darker color increases heating efficiency and may lead to a damaging overheating during heat waves (Roulin 2014). On the other hand, a darker color is a protection against skin damages induced by higher UV radiation encountered in zones with warmer and less cloudy climates (Roulin 2014). A potential explanation could therefore be that temporary warmer climates lead to paler skin to prevent overheating costs, as found in adults, while a consistently warmer climate lead to darker skins to prevent more serious structural damages. However, further analyses with the full database are needed to estimate traits' variation explained by (grand)maternal environments and fitness benefits of such intergenerational effects and to confirm or disconfirm this speculation. Another step would also be to investigate the proximate mechanisms of this maternal effect and its interaction with juveniles' climate. While I have not been running physiological studies for a long time, I hope that our current analyses on gene expression, using a TagSeq approach (Lohman et al. 2016) and led by Luis, will allow us to identify putative mechanisms underlying maternal effects.

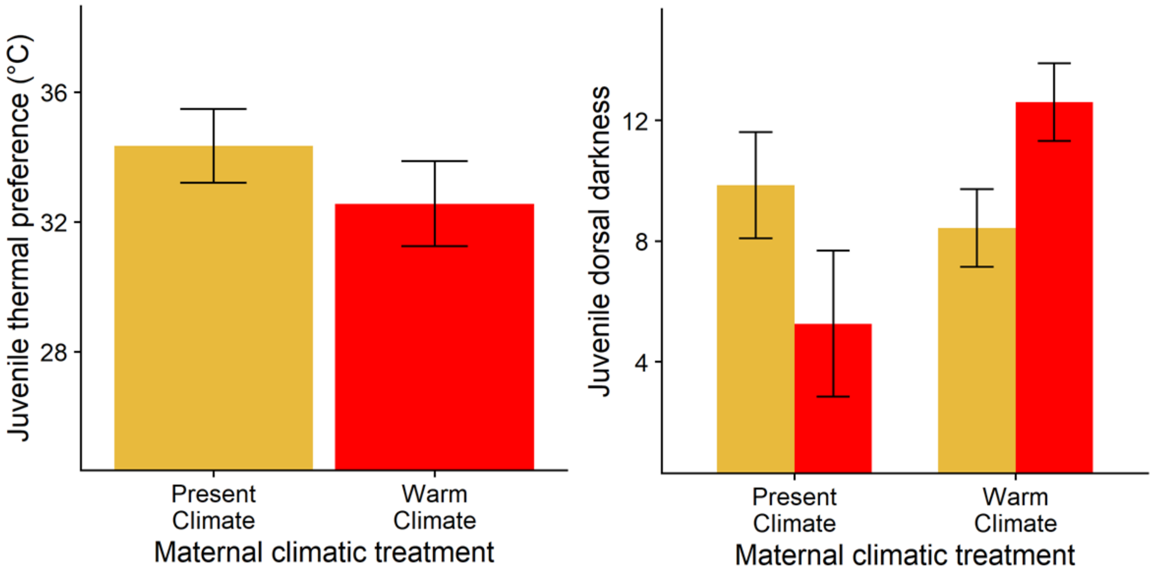

Figure 44: Juvenille thermal preferences at birth and dorsal darkness after ~1 yr in present (yellow) and warm (red) climates depending on maternal climatic treatments. Means ± SE are shown.

From ontogeny to senescence

We repeatedly observed that warmer climates increase juvenile growth rate, reduce the age of maturity, decrease adult survival and may lead to populations made of younger individuals (Bestion et al. 2015a, Pellerin et al. In preparation). Interestingly, the advanced onset of reproduction is only partially explained by the accelerated growth rate and cannot be explained by immediate effects of thermal conditions, manipulated ~5-7 months before mating season. This suggests a change in pace-of-life strategy towards an accelerated life style which can result from selection of or persistent plasticity towards faster life style. Aside from estimating natural and sexual selection on age at first reproduction, a related question is the influence of warmer climates on the ontogeny of phenotypic traits and senescence rate.

In warmer climates, the proportion of one year-old individuals reproducing is largely increased. As a consequence, we could expect a faster development of phenotype directly and indirectly influencing mating behavior, sexual selection and gestation. Among traits monitored, it may encompass behavioral traits, such social behaviors and thermal preference, and morphological traits, such as body size and jaw size. A faster development of these traits may facilitate the access to reproduction in young individuals, while the investment in early reproduction may divert resources from self-maintenance processes and have detrimental consequences at older ages (Monaghan et al. 2008, Bouwhuis et al. 2010). A long-standing unaccomplished objective is to study the age dynamics of phenotypic traits and reproduction parameters, including clutch size and number of partners, to estimate the climate-dependent ontogeny and senescence pattern of phenotypic traits, and their sexual dimorphism, and reproductive traits. In warm climates, I expect a steeper relationship of traits with age, both on the ascending (*i.e*,. development) and descending (*i.e.*, senescence) sections, a stronger sexual dimorphism in young individuals, an increase of reproductive outcome at an earlier age, a shorter reproductive time window and a lower life expectancy. Our result will allow us to better predict changes in pace of life and physiological exhaustion that could strongly influence climate-dependent population dynamics and selective gradient. To this end, we recently implemented, thanks to a collaboration with Jean-François Le Galliard and Andreaz Dupoué among others, our longitudinal monitoring with a monitoring of telomere length. Common lizards in endangered populations display shortened telomeres from birth (Dupoué et al. 2017) and recent results suggest that the acceleration of pace of life may be involved in this pattern (Dupoué et al. 2022). An objective will therefore be to monitor intra- and intergenerational effects of warmer climates on telomere attrition and to study the role of growth rate and reproductive onset on these changes.

Changes in allele frequencies in experiments and in natural populations (Luis' project)

Along with the monitoring of phenotypic traits, we obtained the SNPs from RAD seq data, aligned to an annotated common lizard's genome (Yurchenko et al. 2020), for the lizards in the Metatron for the short-term experiment (2012) and for the long-term experiment (2015, 2018 and 2021). Luis will lead the study and analyze gene-environment and gene-phenotype associations (GEA and GWAS) and temporal changes in allele frequencies with climatic treatments between 2015 and 2021 (Figure 42). Using data from 2012, he already studied changes in allele frequencies over 1 year using 3 warm and 3 present-day populations focusing on genes involved in skin darkness (Bestion et al. Submitted). On the 15 SNPs positively associated with skin darkness, the changes of allelic frequency were not significantly different between climatic conditions. However, changes were all in the same direction and the low number of populations might explain the lack of significance. The next step is therefore to run similar analyses on more populations.

We further generating RAD seq data for 437 lizards from 10 natural populations from the Cevennes Mountains in 2004-2005 and in 2014-2015 (~20 ind/pop/year). These populations are part of the 22 populations monitored for nearly 20 years (Figure 45) and characterized for the biotic (vegetation and invertebrate community) and abiotic (minimal and maximal temperature, precipitation, altitude) conditions and for the lizard population characteristics (population abundance, parturition date). Interestingly, the 22 populations are ranked along a PCA axis of extinction risk encompassing abundance changes between 2005 and 2017-2018, parturition dates and climatic parameters.

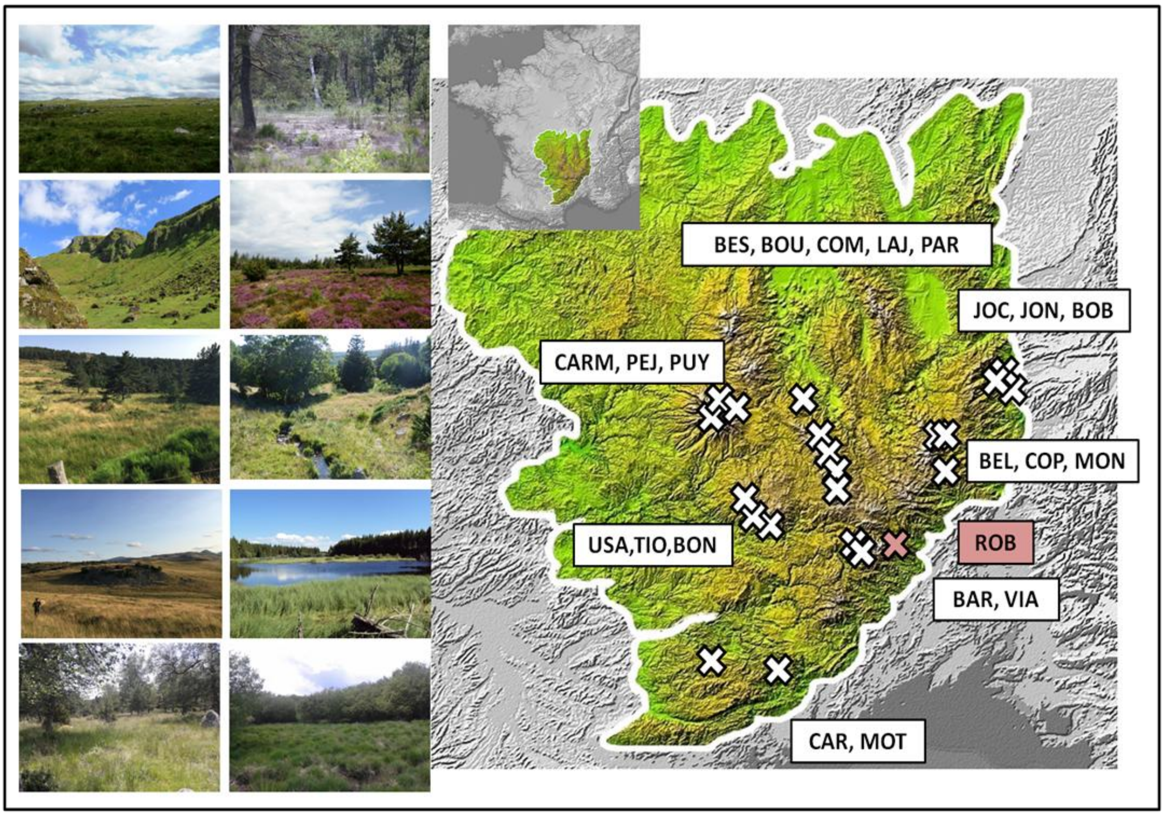

Figure 45: 22 populations of common lizards in the Cevennes Mountain, from Rutschmann et al. 2016

The dynamics of these populations have been strongly impacted by past climatic change (Rutschmann et al. 2016b, Massot et al. 2017). Luis is currently finishing the analyses and first results show changes in populations' allele frequencies over time and along environmental gradients. Our next steps are now to study 1) the link between changes in allele frequency between 2005 and 2015 and abundance changes during the same period and after 2015 and 2) the influence of identified genes on individual survival in experimental populations. The combination of experimental and long-term population monitoring approaches will allow us to isolate the sole effect of climate warming and to understand and predict whether genomic changes are fast enough to override the decline in population growth rate (Bay et al. 2017, 2018). Finally, we complement our population survey with more populations thanks to a biodivoc project, led by Raphaël Leblois and Simon Boitard and that we co-manage Pierre de Villemereuil, Jean-François Le Galliard, Luis and I for the common lizards. For this project, we will sample 225 females from 15 populations along the extinction risk axis and run a haplotagging approach (Meier et al. 2021) to additionally build demographic history for these populations and detect signs of selection.

Common garden experiment

This last sampling will give us the opportunity to run a common garden experiment with Luis, Pierre, Jean-François and Théo Bodineau (Jean-François’ PhD student). We will release juveniles from the 225 females in the Metatron by splitting clutches among 24 enclosures of either of present-day, intermediate or warm climates. Juveniles will be monitored for phenotypic traits (*i.e.*, thermal preference, metabolic rate, water balance, skin darkness, telomere length) and life history traits for 2 years. We will quantify the additive and interactive influences of populations of origin and climatic conditions on phenotypic development and life history strategies, estimate the selective gradients and the degree of plasticity and thus predict the adaptive potential of each population to future warming. This project will also allow us to investigate climate effects mediated by community structure and eco-evolutionary feedbacks (see below).

***ii. Objective 2:* Community structure and ecosystem functioning in warmer climates**

Temporal dynamics of below- & aboveground communities

We will investigate climate-induced changes in community structure in mesocosms with and without predators (Figure 42). On the 24 mesocosms used (12 warm and 12 present-day), only 16 mesoscosms contained lizards populations since 2015 and almost every year since 2012. However the abundances of lizards varied with experimental design, local conditions in mesocosms and climatic treatments. We can investigate the interactive effects between climatic treatments and lizards abundance to estimate direct effects of climate on community structure from indirect effects mediated by the lizards as an apex predator We started to monitor plant and invertebrate communities in 2012) and kept monitoring the changes of taxonomic and functional diversity at different levels of the food web (producers, detritivores, & consumers, Figure 46). From 2015, we collected soil samples to estimate decomposers community.

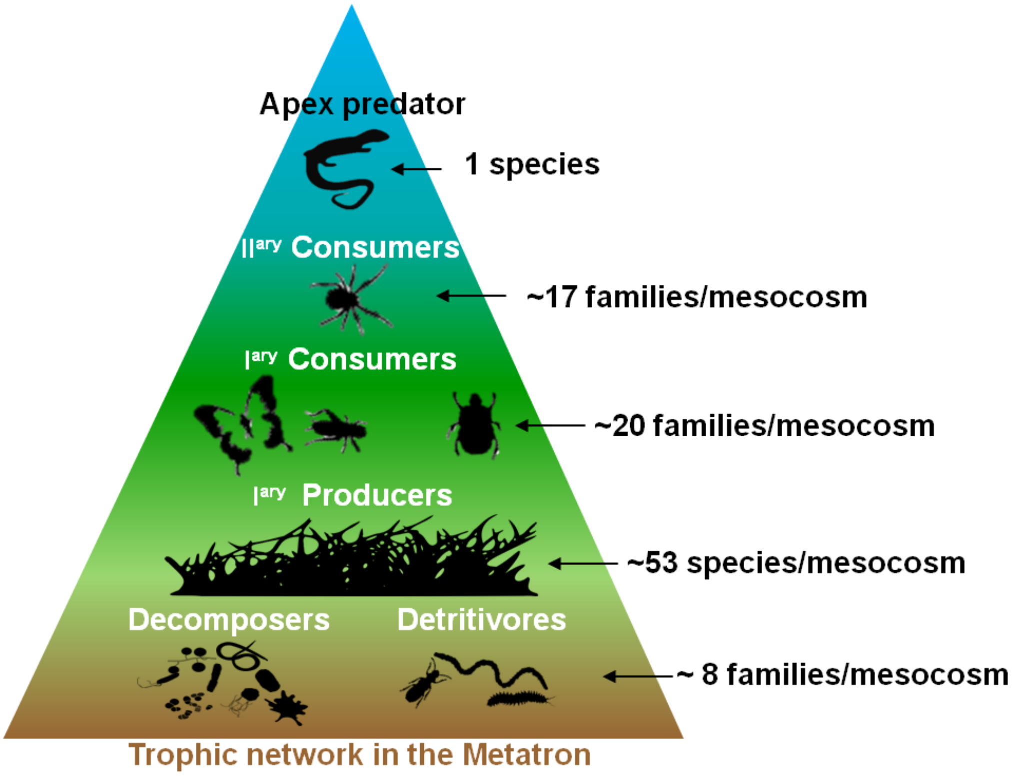

Figure 46: Schematic representation of the mesocosm food web.

The monitoring will be carried on until 2022 and we will estimate the abundance and the taxonomic diversity for different functional groups for invertebrates (annually, *e.g.*, detritivores, herbivores, predators) and for plants (every three years, *e.g.*, C3 grasses, non-leguminous forbs, leguminous). With Lucie Zinger, we are currently analyzing the communities of soil eukaryotes (i.e. fungi, protists & soil invertebrates) and prokaryotes with DNA metabarcoding and Illumina sequencing on samples from 5 different locations per mesocosm since 2015.

A new postdoctoral researcher, Léa Beaumelle, will investigate the influence of the climatic conditions and the abundance of top predators on the dynamics of aboveground (plants and invertebrates) and belowground communities (Figure 42). While plant and invertebrates richness are only slightly and temporary different between climates (Figure 20), the differences go in opposite directions or are stronger in mesocosms without lizards (Figure 47b) and in mesocoms without lizards (Figure 47a). More importantly, the analyses should investigate effects at the functional group levels for invertebrates, given lizards prefer predatory than herbivorous invertebrates (Figure 16), and all plants should not react similarly to warmer climates (Martin et al. 2019)

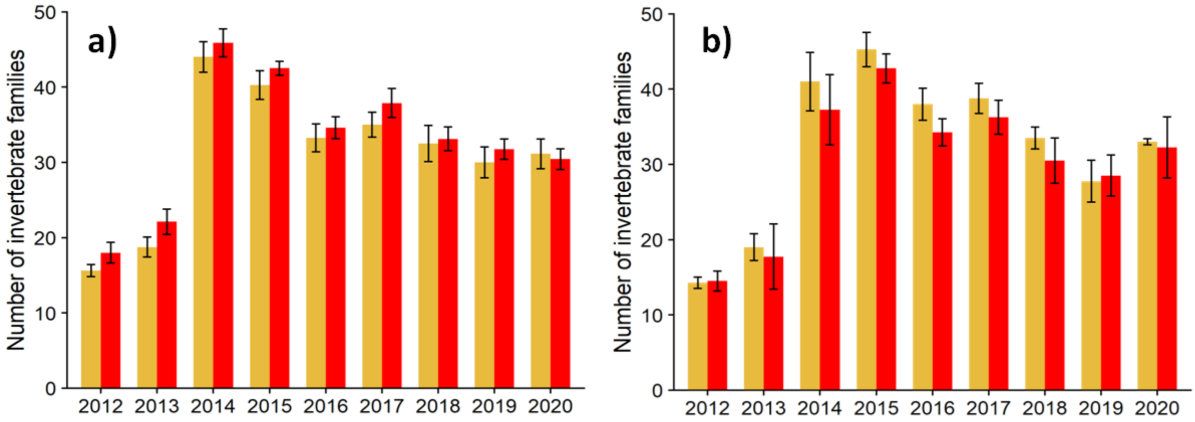

Figure 47: Number of invertebrate families in mesocoms with lizards (a) and without lizards (b) in warm (red) and present-day climates.

Existing databases (plants: Martin et al. 2019, Kattge et al. 2020, microbiota: Madin et al. 2020, invertebrates: Bennett et al. 2018, Herberstein et al. 2022) will help us study changes in functional traits with climatic treatments. For example, the difference in plant species diversity observed after 2 years of treatments (*i.e.*, in 2014, Figure 20) resulted from an effect of warmer climate on species more sensitive to water availability (Figure 48). The reduced effects of climates on plant diversity disappeared over time since then (Figure 20) may however suggest no further effect on species sensitive to water availability or changes in functional diversity in plant community (e.g. larger relative abundance of xero- on hygrophilous species).

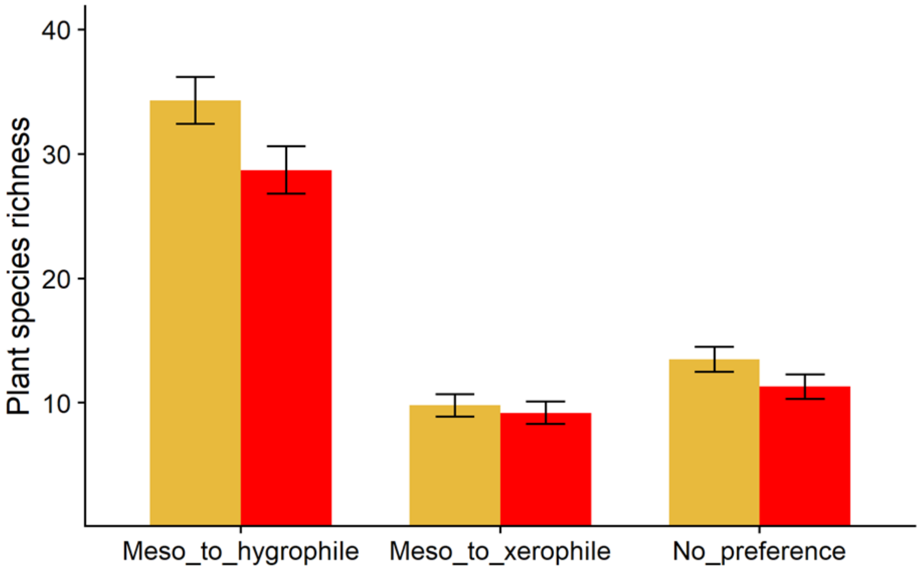

Figure 48: Number of plant species in mesocoms with lizards (a) and without lizards (b) in warm (red) and present-day climates depending on their sensitivity to water.

We are further running stoechiometry and stable isotopes analyses from soil to lizards. Léa will use available data on community monitoring and stable isotopes analyses to study how climatic conditions could influence food webs structure and the strength of species interactions occurring in mesocosms depending on lizards’ abundances. Given the changes of lizards’ diet with climate, we expect climate-dependent top-down effects to influence the architecture of food webs as well as the phenotype of species at lower trophic levels. Interestingly, while invertebrate communities are estimated at the whole mesocosm level, plant species are identified regularly (2011, 2014, 2017 & 2021) at the mesocoms level and on the 5 quadrats (1 m²) where the soil samples were collected from 2015. It will allow us to study covariations between soil and plant communities among and within climates over time.

Invertebrates’ phenotype

We are also investigating phenotypic changes in invertebrates to predict the consequences on ecological networks. First, we quantified the body size of invertebrates collected since 2015 on pictures. We will investigate changes in size structure within the ecological networks, a potential widespread response of species to warmer climates (Brose et al. 2012, Kalinkat et al. 2015). We expect a decrease in body size with warmer climate among and with species resulting in changes in species diet breadth and interaction links. However, we expect these effects to strongly depend on the presence and abundance of top-predators. The loss of top predator may theoretically decrease the average body mass of species and change the predator-prey mass ratio (Brose et al. 2017). However, in our experiments, climatic conditions influence lizards' age structure and body size on top of their abundance. Even if effects fluctuate over time, we expect overall a lower abundance, younger individuals and age-specific bigger individuals (Bestion et al. 2015a, Pellerin et al. submitted). Lizards' diets and feeding rate vary with age, body size and abundance (Avery 1966, González-Suárez et al. 2011, Bestion et al. 2019b). It is therefore difficult to predict the effects of lizards on lower trophic levels in warmer climate. For example, spiders are among the preferred prey species and this preference is strengthened in warmer climate (Figure 16). However, predating spider species can be risky for small juveniles as spiders may intentionally or not predate juveniles (personal observation). There is likely a size threshold above which juveniles more easily predate spiders. The accelerated growth rate in warm climates may help juveniles achieving this threshold at a younger age. Our 10 year-long database and structural equation modeling will hopefully help us teasing part the relative effect of age structure, body size and abundance on prey preference and climate-dependent changes in community composition.

Second, Elvire's CNRS research project aims at investigating differences in thermal phenotype and antipredator responses for various invertebrate species at different trophic levels. She is currently running phenotypic assays to quantify thermal performance curves on the metabolism of predatory, herbivorous and detritvorous invertebrates (*e.g.*, spiders, leafhopper, and woodlouse) from all Metatron mesocoms and we already have pictures to quantify invertebrates' darkness. In 2023, she will complement her study with similar measurements on invertebrates from climatic common garden (see above) to study the differences of thermal phenotype of invertebrate species with climatic conditions right after climatic manipulation or 2-3 generations after the manipulation in common garden and the role of top-predator in such changes. Third, we are also currently searching for funding to hire a PhD student to investigate differences between climates in species activity levels and responsiveness to predator cues (*i.e.,* lizards). We expect a strengthened predation pressure by lizards and so anti-predator responsiveness on spiders in comparison to other invertebrates in warm climates. Overall, we will be able to study whether climate-dependent changes in thermal traits in lizards and in invertebrates covary and, by comparing between mesocoms with and without lizards, predicting whether such potential covariances results from similar selective and plastic processes in lizards and in invertebrates or from climate-dependent changes in predation pressure (Segar et al. 2020).

Lizards' gut microbiota: relative influences of ecological and evolutionary drivers

A third objective, central in Emma's PhD, is to better understand the repeatedly observed differences of lizards gut microbiota between climates (Figures 18-19). The first step is to study the evolutionary drivers of microbial changes (Figure 42). We now have 10 years of data on microbial changes induced by climatic conditions along with a full pedigree and genomic data (see above) and life history and thermal traits. Emma's goal is to use the longitudinal monitoring to investigate microbial plasticity over the lifetime and depending on local conditions, selective gradients of microbial community structure on survival and reproduction, and genetic determinants (heritability and SNPs). It will allow us to estimate the evolvability of gut microbiota. We will particularly be interested in different aspects of microbial diversity. Until now and similarly to most studies, we focused on alpha diversity (e.g., species richness and Shannon index). However, alpha diversity poorly describes the structure and functionality of gut microbiota, given the functional heterogeneity among bacterial species (Johnston and Burnet 2016, Reese and Dunn 2018), which should be the main driver of host fitness (Worsley et al. 2021) and microbial sensitivity to climate. For example, in three different datasets, we found a lower microbial alpha diversity in lizards from warm climates. However, when analyzing taxa differentially abundant between climates, we found some discrepancies between our three datasets. In Bestion et al. (2017), we found a decrease of the Lachnospiraceae and Bacteroidaceae families relative abundance in warmer climates which can be deleterious for hosts. Emma's results are in partial agreement with this result. Firmicutes diversity is significantly lower after 3 years of warm climate, but the relative abundance of Lachnospiracea (members of the Fimicutes phylum) was higher in warm climates, and overall differentially abundant taxa between climates were different among years (Figure 49). The discrepancy may result from lower alpha diversity influencing relative abundances in remaining taxa or from a neutral skimming of taxa with warming. We therefore plan on studying the plasticity, selection and heritability on beta diversity and functional diversity thanks to existing databases (Madin et al. 2020) and to compare our results with a neutral model in order to tease apart random skimming from functional selection and then to better predict the mechanisms and consequences of alpha diversity changes.

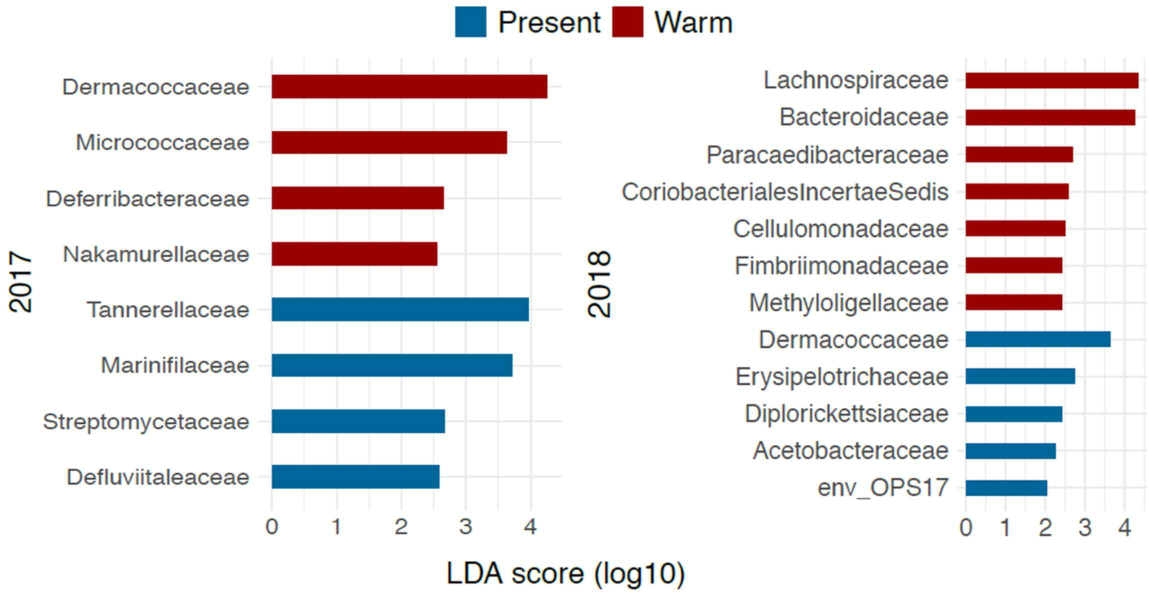

Figure 49: Linear discriminant analysis (LDA) scores of differentially abundant family between warm and present-day and warm climate. The p-value threshold was fixed at 0.005 and LDA score >2.

The second step is to investigate ecological drivers of microbial changes (and so of evolutionary processes). Changes in gut microbiota may result direct effect of bacterial thermal environment (*i.e.,* host body temperature), nutritional sources (*i.e.,* host energetic balance and diet) and transmission among hosts (*i.e.,* social and sexual contacts). Luckily, in our databases, we have or will have the information on lizards' climatic conditions, population density, sexual partners, and diet. Moreover we are currently analyzing the gut microbiome of major groups of detritivores and primary and secondary consumers, the potential prey of lizards. Emma will analyze the relative influences of social and sexual interactions, lizards diet and invertebrates' microbiota. In addition, we have run side experiments manipulating the number and identity of sexual partners in controlled mating assays and of social partners in cattle tank experiment. We will run this year an additional side experiment manipulating thermal conditions in the lab and food provided to lizards (*i.e,* spiders, crickets or woodlouses). Her goal is to confront correlative results from the databases and from side experiment to search for more likely drivers of microbial changes.

As a final step, we will collect microbiota samples from females captured in the 15 Cevennes populations for the common garden. Our goal is to explore variation along altitudinal and climatic gradients to compare patterns observed in experimental studies and in natural populations and have a realistic idea of climate impacts on lizards gut microbiota.

Soil ecology : aboveground-belowground interactions and biodiversity-ecosystem functioning

Thanks to more recent collaborations (*e.g.*, with Lucie Zinger), I started to consider a piece of understanding far from my primary interest (i.e. lizards interaction network) and so far from my expertise. As explained above, I started to collect soil samples since 2015 (5 replicates per mesocoms, once a year) to monitor changes in belowground communities (*i.e.*, micro- and mesofauna) and chemical composition. We are currently analyzing soil communities, with Lucie and Léa, soil stoichiometry and stable isotopes, with Jérôme

Mathieu and, in 2021, have obtained data on main soil functions (package Biofunctool, Thoumazeau et al. 2019), with Alain Brauman, on the same 5 locations than soil communities. We estimated decomposition rates from meso and microfauna (*i.e,* lamina baits and tea bags), labile C and mineral Nitrogen, and respiration in situ and ex situ using metabolic profiles on 5 substrates. As stated above, on the same 5 locations, we also quantified plant community (species presence and relative abundance) and in 2021 plant biomass. Over the last 8 years, we therefore have 120 sampling points for soil communities every year and for plant community every 2-3 years (*i.e.,* three time points).

Independently of climatic treatments, we therefore have a relatively large dataset to study spatial and temporal covariations between aboveground and belowground taxonomic and function diversity (Wardle et al. 2004) and likely the influence of specific plant functional groups (*e.g.,* leguminous, Poacaeae) on soil microbial diversity (Griffiths et al. 1992, Bardgett et al. 1999, Figure 42). Of course, we further plan on analyzing the effects of climatic conditions, treatments and continuous parameters, over the last 10 years on the mean position along each diversity axis (*i.e.,* aboveground and belowground) and on the strength of covariations. I expect some covariations, between aboveground and belowground diversities or between a functional group and microbial diversities, to be altered by warmer and potentially stressful conditions through concordant or discrepant changes in the structure of above- or belowground community or through changes in the variation of diversity among local communities. The plan is then to add the aboveground invertebrate community and lizard abundances (only estimated at the mesocosm level) and their gut microbiota in a path analysis (Figure 42) to have the whole picture of changes in ecological networks and predict interconnections between observed changes through top-down and bottom-up effects. Indeed, changes in the belowground network can influence aboveground herbivores through *e.g.,* changes in plant performance or nutrient content (Goverde et al. 2000, Bonkowski et al.

2001), with subsequent consequences on predatory invertebrates and lizards performance. On the contrary, changes in lizards diets and foraging rates may influence the abundance and diversity of species at different trophic levels. For example, a preferred consumption of predatory invertebrates compared to herbivorous invertebrates (Figure 16) may lead to a cumulated decrease in predation pressure on those herbivorous invertebrates and therefore a stronger herbivory. We expect to investigate such knock-on effects by confronting the monitoring of temporal dynamics at different trophic levels and estimating element fluxes with stoechiometry and stable isotopes analyses. Along with these analyses, the common garden experiment starting in 2022 will include mesocosms treated with an intermediate climate for two years with a monitoring of soil, plant and invertebrate communities. As these mesocosms will have been treated with warm and present-day climates for several years, we will be able to measure the ecological resilience of these communities.

The final step will aim at studying the covariation between plant and soil community diversities and ecosystem functions (*i.e.*, decomposition, respiration, plant biomass), how the biodiversity-ecosystem functioning vary among and within mesocosms and with climatic conditions (Gonzalez et al. 2020) and hopefully predict the causal effects of plant function changes on belowground processes (Cavender-Bares et al. in press).

iii. <u>Objective 3:</u> Eco-evolutionary feedbacks

The first two objectives will allow us establishing climate-induced changes in evolutionary and ecological dynamics. Both changes can result from direct effects of warmer climates on apex predator (i.e. lizards) phenotype and on ecological networks or from indirect effects of ecological networks on apex predator phenotype and vice versa. These two mechanisms are not mutually exclusive and the latter mechanisms belong to the eco-evolutionary dynamics framework. Eco-evolutionary dynamics refers to changes in ecological factors leading to a heritable change of phenotypic distribution in a species, or to heritable change in phenotypic distribution leading to changes in ecological factors (Pelletier et al. 2009, Schoener 2011). When interactions between ecology and evolution are reciprocal, they lead to eco-evolutionary feedback loops (Post and Palkovacs 2009), which can deeply modify the functioning of communities and ecosystems (Matthews et al. 2011, Segar et al. 2020).

A last objective is to estimate the strength of eco-evolutionary dynamics to investigate whether the effects of climates on ecology and evolution can be perpetuated and reinforced through cyclical eco-evolutionary interactions. The correlative aspect of my first objectives prevents from precisely estimating the eco-to-evo and evo-to-eco interactions. We are currently developing direct experimental tests of both interactions. This year, in 2022, we are finishing the long-term warming experiment and starting the common garden experiment described above. We will have on one side lizards and invertebrates from warm and present-day climates with potentially different phenotype and on the other side mesocosms of warm and present-day climates and with varying lizard abundances for the last 10 years.

Therefore the plan is first to recreate simplified ecological networks in small indoor mesocosms with one prey species from detritivores, phytophagous and predatory groups, variable plant species and homogeneized soil (Figure 50). Species will be chosen from Metatron inventories to match ecological dynamics in our mesocosms. We will add to these mesocosms groups of lizards from warm or present-day climate Metraton mesocosms and estimate the impacts of lizards, and their climatic origin, on lower trophic levels, from consumers to primary producers, on microbial communities and on soil functions. The experiment can be run on lizards freshly issued from the Metatron or on the offspring from these lizards, maintained in small cattle tanks for a year, to better disentangle stable (potentially evolved) and temporary phenotypic differences between climate and their impacts on ecological networks. Thanks to Elvire's project, this experiment will also be run with spiders fro warm and present-day climate and allow us to test for evo-to-eco effects at different trophic levels.

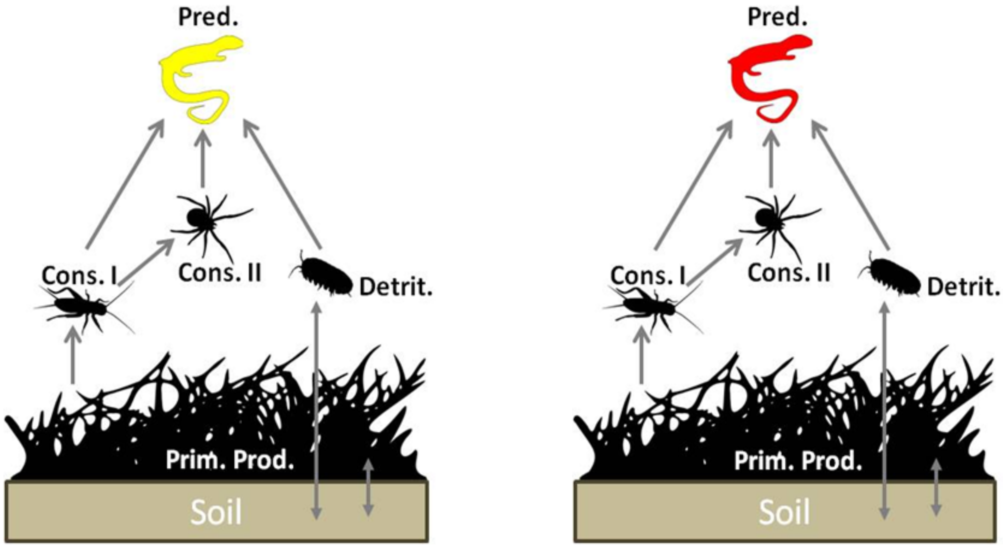

Figure 50: Experimental setup for impacts of lizards'phenotype on ecological networks in a simplified network. Yellow and red lizards are from Metatron mesocosms with present-day and warm climates resp.

Second, with the common garden experiment, we will run a mirrored experimental design to study the effects of climate-induced ecological changes on lizards' phenotypic changes. As explained above, the common garden experiment will use mesocosms treated with warm and present-day climates for several years and treated with an intermediate climate for two years from 2022. We will add juveniles from natural populations for two years and quantify lasting indirect effects of past climatic treatments on lizards' phenotype and life history traits. After two years, these juveniles will likely reproduce and we will be able to measure effects of past climatic conditions on newborns through transgeneration eco-to-evo effects. For example, we recently demonstrated that the community structure of primary producers, summarized in a metric encompassing vegetation cover, vegetation height and plant richness, in maternal habitats could influence the natal phenotype of juveniles and subsequently their survival prospects. Mothers from denser vegetation produce more active juveniles while survival prospects is positively related to natal activity levels in denser vegetation only (Bestion et al. 2022). While we are not sure vegetation structure is the causal factor, this adaptive maternal effect suggests potential evolutionary feedback of climate-induced ecological changes. Finally, by comparing the effects from our long-term experiment with these last two experiments, we will be able to predict the reciprocity of evo-to-eco and eco-to-evo effects and so the eco-evolutionary feedback loop induced by climate warming.

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Zeigler, S. 2013. Predicting responses to climate change requires all life-history stages. - Journal of Animal Ecology 82: 3–5.

Zeuss, D. et al. 2014. Global warming favours light-coloured insects in Europe. - Nat Commun in press.

Zhang, P. et al. 2018. The effect of temperature on herbivory by the omnivorous ectotherm snail <Emphasis Type="Italic">Lymnaea stagnalis</Emphasis>. - Hydrobiologia 812: 147–155.

Zhou, Z. et al. 2020. Meta-analysis of the impacts of global change factors on soil microbial diversity and functionality. - Nat Commun 11: 3072.

Curriculum Vitae

Professional experiences in Research Institutes

2011-ongoing	**Research associate CNRS** at the department Evolution & Diversité Biologique at the University Paul Sabatier, Toulouse (France).
2007-2010	**Post-doctoral position** at the department of Environmental Science and Policy at the University of Davis, California (USA) on the project “Personality traits and the spread of invasion in an invasive mosquitofish (*Gambusia* sp)”. Fyssen Foundation fellowship and AXA postdoctoral fund. Supervision: Prof. Andrew Sih.
2006-2007	**Post-doctoral position** at the Biogeosciences department at the University of Bourgogne (France) on the project "Immune activation and oxidant-antioxidant activities in the zebra finch (*Taeniopygia guttata*) ". Supervision: Dr. G. Sorci and Pr. B. Faivre.
2003-2006	**PhD student position** at the Ecology Department of the University Pierre and Marie Curie (France) on the project "Socially acquired information in the common lizard (*Lacerta vivipara*)". Supervision: Dr. J. Clobert and Dr. P.S. Fitze. Awarded with honours.
2002-2003	**Master research** at the Ecology Department of the University Pierre and Marie Curie (France) on the project "Effects of carotenoïds and corticosterone on the condition-dependant coloration in the common lizard (*Lacerta vivipara*)". Supervision: Dr. J. Clobert and Dr. P.S. Fitze. Awarded with honours.
2001	**Master research** at the Ecology Department of the University Pierre and Marie Curie (France) on the project "Effects of stress and leptin in basking behaviour and body temperature in the common lizard (*Lacerta vivipara*)". Supervision: Dr. A. Dufty and Dr. J.-F. Le Galliard.

Education

2003-2006	Ph.D. Biology at the University Pierre and Marie Curie (France)
2002-2003	M.Sc Biology at the University Pierre and Marie Curie (France)
2001-2002	Maitrise Biology at the University Paris Sud (France)
2000-2001	License Biology at the University Paris Sud (France)
1998-2000	DEUG Biology at the University Denis Diderot (France)

Teaching, supervising activities & other responsibilities

Supervision:

Postdoctoral fellow	**Luis-Martin San Jose** (2021-ongoing)
	Laurane Winandy (2016-2021 with D. Legrand until 2018)
	Jordi Salmona (2016-2017)
	Lieven Therry (2015-2017, with S. Blanchet)
	Oscar Brusa (2014)
PhD Students	**Emma Fromm** (2021-2024)
	Félix Pellerin (2015-2018 with Robin Aguilée)
	Elvire Bestion (2011-2015)
Engineers	**Bénédicte Lalot** (2022, technician)
	Anne-Sophie Bennoiston (2021, research engineer)
	Lucie Di Gesu (2014-2015, 2017, 2019-2022, study engineer)
	Elodie Darnet (2019-2022, study engineer)
	Luis-Martin San Jose (2019-2020, research engineer)
	Nicolas Canto (2015, study engineer)
	Fia Finn (2014-2015, study engineer)
	Aimeric Teyssier (2013, study engineer)
2nd year Master	**Emma Fromm** (2020-2021)
	Clément Le Potier (2018-2019)
	Félix Pellerin (2014-2015)
	Allan Raffard (2014-2015)
	Lucie Di Gesu (2013-2014)
	Tristan Juette (2012-2013)
	Aimeric Teyssier (2011-2012)
	Béranger Waterschoot (2011-2012)
	Fanny Delpierre (2006-2007)
1-4th year students	63 students

Teaching:

2011-ongoing	**Behavioral ecology**: 2nd year master BEE, Toulouse
2006-2007	**Teaching assistant:** Ecology, Statistics (2nd to 3rd year students in Biology)
2003-2006	**Teaching assistant:** Biology, Ecology, Behavioural Ecology (1st to 4th year students)

Other responsibilities:

2019-ongoing **Member** of the platform committee at the SETE

2018-ongoing **Member** of the Structure in charge of animal well-being (SCBEA) at the SETE

2017-2020 **Co-head** of the *Processes of Adaptation* team in the laboratory Evolution & Biological Diversity

2015-2017 **Manager** of the *Processes of Adaptation* team in the laboratory Evolution & Biological Diversity

2016-ongoing **Scientific head** of the *Metatron* experimental system (http://themetatron.weebly.com/) in the Station of experimental and theoretical ecology

2016-ongoing **Member** of the organization committee of the 2017 French Landscape Ecology Conference

2012-2014 **Co-organizer** of Seminars in the laboratory Evolution & Biological Diversity

Research activities

Research themes :

- ✓ Habitat fragmentation, Invasion biology, Climate change
- ✓ Intraspecific phenotypic variation (behaviour, coloration, physiology)
- ✓ Dispersal processes linked to behavioural ecology and population dynamics
- ✓ Socially acquired information
- ✓ Ecophysiology of the stress-response, Carotenoid-based coloration, oxidative stress

Publications :

(ISI, h-index = 36, Sum of the Times Cited: 4771, 6 ISI highly cited articles)
(Google Scholar, h-index = 39, Sum of the Times Cited: 6724)

68) Bestion, E., Teyssier, A., Rangassamy, M., Calvez, O., Guillaume, O., Richard, M., Braem, A., Zajitschek, F., Zajitschek, S., & **J. Cote** (2022). Adaptive maternal effects shape offspring phenotype and survival in natal environments. **American Naturalist**. In press.

67) Dupoué, A., Blaimont, P., Angelier, F., Ribout, C., Rozen-Rechels, D., Richard, M., Miles, D., Villemereuil, P. de, Rutschmann, A., Badiane, A., Aubret, F., Lourdais, O., Meylan, S., **Cote, J.**,

Clobert, J., & Le Galliard, J.-F. (2022). Lizards from warm and declining populations are born with extremely short telomere. **Proceedings of the National Academy of Sciences USA**. In press.

66) Raffard A., Bestion E., **Cote J.**, Haegeman B., Schtickzelle N. and S. Jacob. (2022) Dispersal syndromes can link intraspecific trait variability and meta-ecosystem functioning. **Trends in Ecology and Evolution**. DOI:https://doi-org/10.1016/j.tree.2021.12.001

65) Le Balle R., **Cote J**., Fernandez F.A.S. (2021) Evidence for animal personalities in two Brazilian tortoises (Chelonoidis denticulatus and Chelonoidis carbonarius) and insights for their conservation. **Appl Anim Behav Sci** 105400. https://doi.org/10.1016/j.applanim.2021.105400

64) Winandy L., Di Gesu L., Lemoine M., Jacob S., Martin J., Ducamp C., Huet M., Legrand D. & **J. Cote**. 2021. Maternal and personal information mediates the use of social cues about predation risk. **Behavioral Ecology**. In press. doi: 10.1093/beheco/araa151

63) Cayuela H., Besnard A., **Cote J.**, Bonnaire E., Pichenot J., Schtickzelle N., Bellec N., Joly P. & Jean-Paul Léna. 2020. Anthropogenic disturbance drives dispersal syndromes, demography, and gene flow in amphibian populations. **Ecological Monograph**. 90(2): e01406

62) Michelangeli M., **Cote J.**, Chapple D. G., Sih A., Brodin T., Fogarty S., Bertram M. G., Eades J. & B. B. M. Wong. 2020. Sex-dependent personality in two invasive species of mosquitofish. **Biological Invasions**. 22: 1353-1364.

61) Raffard A*, Therry L.*, Finn F., Kock K., Brodin T., Blanchet S. & **J. Cote**. 2020. Does range expansion modify trait covariation? A study of a northward expanding dragonfly. **Oecologia**. 192(2): 565-575. * denotes co-first authors.

60) Baltazar-Soares M., Blanchet S., **Cote J.**, Tarkan A., Záhorská E., Gozlan R., Eizaguirre C. 2020. Genomic footprints of a biological invasion: introduction from Asia and dispersal in Europe of the topmouth gudgeon (*Pseudorasbora parva*). **Molecular Ecology**. 29 (1): 71-85.

59) Bestion E., Soriano-Redondo A., Cucherousset J., Jacob S., White J., Zinger L., Fourtune L., Di Gesu L., Teyssier A., & **J. Cote**. 2019. Altered trophic interactions in warming climates: consequences for predator diet breadth and fitness. **Proceedings of the Royal Society B-Biological Sciences**. 286: 20192227. Journal cover.

58) Bestion E., **Cote J.**, Jacob S., Winandy L. & D. Legrand. 2019. Habitat fragmentation experiments on arthropods: what to do next? **Current Opinion in Insect Sciences**. 35: 117-122. https://doi.org/10.1016/j.cois.2019.07.011

57) Brodin T., Fogarty S., Sih A. & **J. Cote**. 2019. Personality-dependent survival of the invasive mosquitofish: being social can be deadly. **Aquatic invasions**. 14(3): 465-477.

56) Winandy, L., **Cote, J.**, Gesu, L. D., Pellerin, F., Trochet, A., & Legrand, D. 2019. Local predation risk and matrix permeability interact to shape movement strategy. **Oikos.**, 128(10): 1402-1412. doi: 10.1111/oik.06403

55) Therry L.*, **Cote J.***, Cucherousset J., Finn F., Buoro Y. & S. Blanchet. 2019. Genetic, plastic and environmental contributions to the impact of a range-expanding predator on aquatic ecosystems. **Journal of Animal Ecology**. 88: 35-46. Special issue Eco-evolutionary dynamics. * denotes co-first authors.

54) Pellerin F., **Cote J.**, Bestion E. & R. Aguilée. 2019. Matching habitat choice promotes species persistence under climate change. **Oikos**. 128(2): 221-234.

53) Jacob S., Laurent E., Haegeman B., Bertrand R., Prunier J.G., Legrand D., **Cote J.**, Chaine A.S., Loreau M., Clobert J. & N. Schtickzelle. 2018. Habitat choice meets thermal specialization: competition with specialists may drive suboptimal habitat preferences in generalists. **Proceedings of the National Academy of Sciences USA** 115 (45): 11988-11993.

52) Fronhofer E.A., Legrand D., Altermatt F., Ansart A., Blanchet S., Bonte D., Chaine A., Dahirel M., De Laender F., De Raedt J., Jacob S., Kaltz O., Laurent E., Little C., Madec L., Manzi F., Masier S., Pellerin F., Pennekamp F., Schtickzelle N., Therry L., Vong A., Winandy L. & **J. Cote**. 2018. Bottom-up and top-down control of dispersal across major organismal groups. **Nature Ecology & Evolution** : 1859–1863. Highlight: https://www.nature.com/articles/s41559-018-0720-2.

51) Saastamoinen M, Bocedi G, **Cote J**, Legrand D, Guillaume F, Wheat C, Fronhofer E, Garcia C, Henry R, Husby A, Baguette M, Bonte D, Coulon A, Kokko H, Matthysen E, Niitepõld, K, Nonaka E, Stevens V, Travis J, Donohue K, Bullock J & M del Mar Delgado. 2018. Genetics of Dispersal. **Biological reviews**. 93: 574-599.

50) Raffard A., Lecerf A., **Cote J.**, Buoro M., Lassus R. & J. Cucherousset. 2017. The Functional Syndrome: linking individual trait variability to ecosystem functioning. **Proceedings of the Royal Society B-Biological Sciences.** 284 (1868).

49) **Cote J**, Brodin T, Fogarty S & A Sih. 2017. Non-random dispersal mediates invader impacts on the invertebrate community. **Journal of Animal Ecology**. 86(6): 1298-1307.

48) Bestion E, Jacob S, Zinger L, Di Gesu L, Richard M, White J & **J. Cote**. 2017. Climate warming reduces gut microbiota diversity in a vertebrate ectotherm. **Nature Ecology & Evolution**. 1: 0161.

47) **Cote J.**, Bocedi B., Debeffe L., Chudzińska M.E., Weigang H.C., Dytham C., Gonzalez G., Matthysen E., Travis J., Baguette M. and A. J. M. Hewison. 2017. Behavioral synchronization of large-scale animal movements – disperse alone, but migrate together? **Biological Reviews**. 92(3): 1275-1296.

46) **Cote J.**, Bestion E., Jacob D., Travis J., Legrand D. & M. Baguette. 2017. Evolution of dispersal strategies and dispersal syndromes in fragmented landscapes. **Ecography**. 40(1): 56-73.

45) Legrand D., **Cote J.**, Fronhofer E., Holt R.D., Ronce O., Schtickzelle N., Travis J. & J. Clobert. 2017. Eco-evolutionary dynamics in fragmented landscapes. **Ecography**. 40(1): 9-25.

44) Caplat P., Edeaar P., Dudaniec R.Y., Green A.J., Okamura B., **Cote J.**, Ekroos J., Jonsson P.R., Löndahl J., Tesson S.V.M. and E. Petit. 2016. Looking beyond the mountain: dispersal barriers in a changing world. **Frontiers in Ecology and the Environment**. 14(5): 261–268, doi:10.1002/fee.1280.

43) Bestion E., Cucherousset J., Teyssier A. and **J. Cote**. 2015. Non-consumptive effects of a top-predator decrease the strength of the trophic cascade in a four-level terrestrial food web. **Oikos**. 124(12): 1597-1603. DOI: 10.1111/oik.02196.

42) Bestion E., Teyssier A., Richard M., Clobert J., and **J. Cote**. 2015. Live fast, die young: experimental evidence of population extinction risk due to climate change. **Plos Biology**. 10.1371/journal.pbio.1002281. Highlights: Sciencedaily, phys.org, Tech Times (English), Le Monde, RTBF , CNRS, UPS (p 16-17) (French).

41) Bestion E., Clobert J., and **J. Cote**. 2015. Dispersal response to climate change: scaling down to intraspecific variation. **Ecology Letters**. 18(11): 1226-1233.
Highlights: http://www.nature.com/nclimate/journal/v5/n10/full/nclimate2817.html

40) Jacob S., Bestion E., Legrand D., Clobert J. and **J. Cote**. 2015. Habitat matching and spatial heterogeneity of phenotypes: implications for metapopulation and metacommunity functioning. **Evolutionary Ecology**. 29(6): 851-871.

39) Cucherousset J., Fried G., **Cote J.** & Renault D. 2015. Biological invasions and ecosystem functioning; assessment of the ecological impacts driven by invasive species. **Revue d'Ecologie.** 70:49-52.

38) Bonnot N., Verheyden H., Blanchard P., **Cote J.**, Debeffe L., Cargnelutti B., Klein F., Hewison M., Morellet N. 2015. Inter-individual variability in habitat use: evidence for a risk management syndrome in roe deer? **Behavioral Ecology**. 26(1): 105-114.

37) Bestion E., Teyssier A., Aubret F., Clobert J. and **J. Cote**. 2014. Maternal exposure to predator scents: offspring phenotypic adjustment and dispersal. **Proceedings of the Royal Society B-Biological Sciences.** 281.

36) Juette T., Cucherousset J. and **J. Cote**. 2014. Animal personality and the ecological impacts of freshwater non-native species. **Current Zoology**. 60(3): 417 - 427.

35) Teyssier A., Bestion E., Richard M. and **J. Cote**. 2014. Partners' personality types and mate preferences: predation risk matters. **Behavioral Ecology**. 25(4): 723-733.

34) **Cote J.**, Fogarty S., Tymen B., Sih A. and T. Brodin. 2013. Personality-dependent dispersal cancelled under predation risk. **Proceedings of the Royal Society B-Biological Sciences**.280 : 1773.

33) Trochet A., Legrand D., Larranaga N., Ducatez S., Calvez O., **Cote J.**, Clobert J. and M. Baguette. 2013 Population Sex Ratio and Dispersal in Experimental, Two-Patch Metapopulations of Butterflies. **Journal of Animal Ecology**. 82: 946-955.

32) Dardenne S., Ducatez S., **Cote J.**, Poncin P. and V.M. Stevens.2013. Neophobia and social tolerance are related to breeding group size in a semi-colonial bird. **Behavioral Ecology and Sociobiology**. 67: 1317-1327.

31) Legrand D., Guillaume O., Baguette M., **Cote J.**, Trochet A., Calvez O., Zajitschek S., Zajitschek F., Lecomte J., Bénard Q., Le Galliard J.-F. and J. Clobert. 2012. The Metatron: an experimental system to study dispersal and metaecosystem dynamics for terrestrial organisms. **Nature Methods**. 9: 928-933.

30) **Cote, J.**, Fogarty, S. and A. Sih. 2012. Individual sociability and choosiness between shoal types. **Animal Behaviour**. 83: 1469-1476.

29) Sih A., **Cote J.**, Evans M., Fogarty S. and J. Pruitt. 2012. Ecological implications of behavioral syndromes. **Ecology Letters.** 15(3): 278-289. ISI highly cited article.

28) Pruitt J.N., **Cote J.** and M.C.O. Ferrari. 2012. Behavioural trait variants in a habitat-forming species dictate the nature of its interactions with and among heterospecifics. Functional Ecology. 26: 29-36.

27) **Cote, J.**, Fogarty, S., Brodin, T., Weinersmith, K. and A. Sih. 2011. Personality-dependent dispersal in the invasive mosquitofish: group composition matters. **Proceedings of the Royal Society B-Biological Sciences**. 278(1712): 1670-1678.

26) Hoset, K.S., Ferchaud, A.-L., Dufour, F., Mersch, D., **Cote, J.** and J.-F. Le Galliard. 2011. Natal dispersal correlates with behavioural traits that are not consistent across early life stage. **Behavioral Ecology**. 22:176-183.

25) Fogarty, S., **Cote, J.**, and A. Sih. 2011. Social personality polymorphism and the spread of invasive species: a model. **The American Naturalist**. 177(3): 273-287.

24) **Cote, J.**, Clobert, J., Brodin, T., Fogarty, S. And A. Sih. 2010. Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. **Philosophical Transactions of the Royal Society B: Biological Sciences**. 365: 4065-4076.

23) **Cote, J.**, Meylan, S., Clobert, J. and Y. Voituron. 2010. Carotenoid-based coloration, oxidative stress and corticosterone in common lizards. **Journal of Experimental Biology**. 213: 2116-2124.

22) **Cote, J.**, Fogarty, S., Weinersmith, K., Brodin, T. and A. Sih. 2010. Personality traits and dispersal tendency in an invasive mosquitofish (*Gambusia affinis*). **Proceedings of the Royal Society B-Biological Sciences**. 277: 1571-1579. ISI highly cited article.

21) **Cote, J.**, Clobert, J., Montes Poloni, L., Haussy, C. and S. Meylan. 2010. Food deprivation modifies corticosterone-dependent behavioural shifts in the common lizard. **General and Comparative Endocrinology**. 166: 142-151.

20) **Cote, J.**, Sorci, G., Arnoux, E. and B. Faivre. 2010. Age-dependent allocation of carotenoids to coloration versus antioxidant defences. **Journal of Experimental Biology**. 213: 271-277.

19) **Cote, J.** and J. Clobert. 2010. Risky dispersal: avoid kin competition despite uncertainty. **Ecology**. 91(5): 1485-1493.

18) Dreiss, A.N., **Cote, J.**, Federici, P., Clobert, J. and M. Richard. 2010. Age-specific response to change in population density and sex-ratio. **Behavioral Ecology**. 21: 356-364.

17) Fitze, P.S., **Cote, J.** and J. Clobert. 2010. Context-dependent mate choice in female common lizards Lacerta vivipara. **Oecologia**. 162: 331-341.

16) Fitze, P.S., **Cote, J.**, Isaksson, C., Andersson, S, Rossi, J.-M. and J. Clobert. 2009. Carotenoid-based colours reflect stress response in the common lizard. **PloS One**. 4(4): e5111. doi:10.1371/journal.pone.0005111.

15) Clobert, J., Le Galliard, J-F., **Cote, J**., Meylan, S. and M. Massot. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. **Ecology Letters**. 12: 197-209. ISI highly cited article.

14) **Cote, J.**, Dreiss, A. and J. Clobert. 2008. Social personality trait and fitness. **Proceedings of the Royal Society B-Biological Sciences**. 275: 2851-2858.

13) **Cote, J.**, Le Galliard, J.-F., Rossi, J.-M. and P.S. Fitze. 2008 Environmentally induced changes in a carotenoid-based coloration of female lizards: a comment of Vercken et al.. **Journal of Evolutionary Biology**. 21 : 1165-1172.

12) **Cote, J.**, Boudsocq, S. and J. Clobert. 2008. Density, social information and space use in the common lizard (*Lacerta vivipara*). **Behavioral Ecology**. 19(1) : 163-168.

11) Fitze, P.S., **Cote, J.**, Martinez-Rica J.P. and J. Clobert. 2008. Determinants of male fitness: disentangling between intra- and inter-sexual selection. **Journal of Evolutionary Biology**. 21(1): 246-255

10) Le Galliard, J.-F., **Cote, J.**, and P.S. Fitze. 2008. Lifetime and intergenerational fitness consequences of sexual aggression by males – can females compensate for a bad start? **Ecology**. 89(1): 56-64

9) **Cote, J.**, Clobert, J. and P.S. Fitze. 2007. Mother-offspring competition promotes colonization success. **Proceedings of the National Academy of Sciences USA**. 104(23): 9703-9708.

8) **Cote, J.** and J. Clobert. 2007. Social information and emigration: Lessons from immigrants. **Ecology Letters**.10: 411-417.

7) **Cote, J.** and J. Clobert. 2007. Social personalities influence natal dispersal in a lizard. **Proceedings of the Royal Society B-Biological Sciences**. 274: 383-390. ISI highly cited article.

6) **Cote, J.**, Clobert, J., Meylan, S. and P.S. Fitze. 2006. Experimental enhancement of corticosterone levels positively affects subsequent male survival. **Hormones and Behavior**. 49: 320-327.

5) Le Galliard, J.-F., Fitze, P. S., **Cote, J.**, Massot, M. and J. Clobert. 2005. Female common lizards (*Lacerta vivipara*) do not adjust their sex-biased investment in relation to the adult sex ratio. **Journal of Evolutionary Biology**. 18(6):1455-1463.

Book chapters :

4) Bestion E. & **J. Cote**. Species responses to climate change: integrating individual-based ecology into community and ecosystem studies. 2018. In *Encyclopedia of the Anthropocene* (ed Dominick DellaSala and Mike Goldstein). Elsevier. Volume 2: 139-147. doi: 10.1016/B978-0-12-809665-9.09801-3

3) Rehage J., **Cote J.** & A. Sih. 2016. The role of dispersal behaviour and personality in post-establishment spread. In *Biological Invasions and Behavior* (ed J. Weis and D. Sol). Cambridge: Cambridge University Press.

2) **Cote, J.**, Clobert, J., Brodin, T., Fogarty, S. and A. Sih. 2014. Personality traits and spatial ecology in non-human animals. In *Geographical Psychology* (ed J. Rentfrow). Washington, DC: American Psychological Association.

1) **Cote, J.** and J. Clobert. 2012. Dispersal syndromes in the common lizard: personality traits, information use and context-dependent dispersal decisions. In *Dispersal. Causes and consequence*s (eds J. Clobert, M. Baguette, T. Benton, J. Bullock & S. Ducatez). New York, NY: Oxford University Press.

Oral communications :

Invited speaker at the Eawag Kastanienbaum. Luzern, Switzerland. December 2019. "Ecological and evolutionary impacts of warmer climates on a lizard species: a semi-natural experiment".

Invited speaker at the Ten years with CanMove conference, Lund, Sweden, February 2018: "Dispersing in a landscape of fear: experimental approaches".

Invited speaker at the symposium "E2-Moves: From individual movements to eco-evolutionary consequences/dynamics" at the British Ecological Society conference, December 2017: "Species responses to climate change: accounting for intraspecific variation in dispersal".

Oral Presentation at Functional Ecology Conference, Montpellier, France, March 2017: "Climate change reduces gut microbiota diversity in a vertebrate ectotherm".

Invited speaker at the Dipee (CNRS, Toulouse France, December 2016). "Behavioral syndromes and biological invasions".

Keynote speaker at the Ecology & Behaviour conference (Lyon, France, June 2016). "Ecological implications of dispersal syndromes: the example of an invasive fish".

Invited speaker at the Department of Ecology and Environmental Sciences (Umea University, Sweden, March 2016). "Impacts of climate change on a temperate ectotherm: from individuals to the community".

Invited speaker at the Department of Ecology and Evolution (University of Lausanne, Switzerland, February 2016). "Impacts of climate change on a temperate ectotherm: from individuals to the community".

Invited speaker at the Centre for research on Biodiversity (UC Louvain, Belgium, October 2015). "Impacts of climate change on a temperate ectotherm: from individuals to the community".

Invited speaker at the Symposium "Putting personality on the map: New perspectives on person-environment links" (ECP, Lausanne 2014, Switzerland). "Personality and spatial ecology in non-human animals: The example of the invasive mosquito-fish".

Invited speaker at the Symposium "Evolution et implications de la variation comportementale intra-spécifique » (SFECA, Dijon 2013). "Population personality composition effects on ecosystem functioning".

Invited speaker at the Centre de Recherche sur la Cognition Animale, Toulouse, France (March 2013). "Personality-dependent dispersal: the example of an invasive fish".

Invited speaker at the Max Planck Institute for Ornithology, Seewiesen, Germany (February 2013). "Personality-dependent mate choice: predation risk matters".

Invited speaker at the Symposium on "Causes and Consequences of Organism Dispersal" (Jan 30th –Feb 1st 2013), Lund, Sweden. "Personality-dependent dispersal: the example of an invasive fish".

Invited speaker at the INRA Behavioral Ecology network, Toulouse, France, June 2012. "The Ecology of Personality Traits".

Invited speaker at the Evolution and Biological Diversity Department, Toulouse, France, March 2010. "Personality-dependent dispersal and the spread of an invasive fish, the mosquitofish".

Oral Presentation at 31st International Ethological Conference (IEC), Rennes, France, August 2009: "Personality and individual's ability to invade in the mosquitofish".

Invited speaker at the Center for Population Biology, University of California, Davis, USA, February 2009. "Heterogeneity in dispersal syndromes and the dynamic of spatially structured populations".

Oral Presentation at 4th European Conference on Behavioural Biology (ECBB), Dijon, France, July 2008: "Personality and individual's ability to invade in the mosquitofish".

Invited speaker at the Evolution and Biological Diversity Department, Toulouse, France, March 2008. "Individual variation in dispersal decision and habitat choice in common lizards".

Invited speaker of the Evolutionary Ecology Department, Bern, Switzerland, October 2007: "Individual variation in dispersal decision and habitat choice in common lizards".

Oral Presentation at 11th European Society for Evolutionary Biology (ESEB 2007), Uppsala, Sweden, August 2007: "Social personalities influence natal dispersal and fitness outcomes in common lizard (*Lacerta vivipara*)".

Oral Presentation at 11th International Behavioural Ecology Congress (ISBE 2006), Tours, France, July 2006: "Kin competition promotes colonisation success".

Invited speaker at Institut de Recherche pour le Développement, Bondy, France, May 2006. "Natal dispersal : Causes, mechanisms and consequences".

Oral Presentation at Meeting "Ecology and Behaviour", Strasbourg, France, March 2006: "Kin competition promotes colonisation success".

Oral Presentation at Meeting "Ecology and Behaviour", Chizé, France, March 2005: "Public information and emigration: Take a look at immigrants".

Oral Presentation at the scientific week of the Ecology Department, Paris, France, October 2004: "Experimental enhancement of corticosterone levels positively affects subsequent male survival".

Peer, Institutes and Media Interest

Media general interest:

Newspaper **La Forêt**.
Newspaper **Geo**.
Newspaper **Sciences & Vie Junior**.
Radio show "MAP vous explique". **RTBF**. Belgium National radio Channel.
Radio show "Curieux de Nature". **France inter**. National radio Channel.
TV show 'Les Héros du climat". **France 2**, National Channel.
Newspaper "Au métatron, le réchauffement climatique en action". **Charlie Hebdo**.

Experiment tracks lizards and butterflies through climate change. **Reuters**, UK.
Une nature en cage. Highlighted research of the **National Center of scientific research**, France.
L'impact du réchauffement sur les espèces se confirme. **Exploreur newspaper** U. Toulouse 3.
TV show "Télématin". **France 2**, National channel. Video not available anymore.
National evening news. **France 3**. Video not available anymore.
National evening news. **TF1**.
Changement climatique: ça chauffe pour les lézards. **La dépêche du midi**.
Ca surchauffe pour les lézards. **20 Minutes**.
Radio show "Information". **France Inter**.
Newspaper. Insectes à chacun sa personnalité. **Sciences & Vie**.

Specific interest in particular publications:
Bestion et al. 2019 Proc. Roy. Soc. B was featured in 1 scientific website, 20minutes and the CNRS.
Fronhofer et al. 2018 Nat. Ecol. Evol. was featured in Nature Ecology and Evolution.
Bestion et al. 2017 Nat. Ecol. Evol. was featured in Nature Climate Change, Science and 6 scientific websites and radio show.
Bestion et al. 2015 Plos Biol was featured in Plos Biology and in 7 scientific websites.
Bestion et al. 2015 Ecol Lett was featured in Nature Climate Change.
Bestion et al. 2014 PRSB was featured in Sciences et Avenir.
Legrand et al. 2012 Nat Meth was featured in Nature methods and Science.
Cote et al. 2010 PRSB was featured in Nature and in Conservation Journal.
Cote and Clobert 2007 PRSB was featured in New Scientist.

Outreach (general public, educational purposes):
Seminar Regional and Natural park (2015) ''Experimental approaches in the study of climate change : the common lizard as an example''
Book "Prix Le Monde de la recherche 2016" from Cedric Villani, Claire de March, Julien Jouganous, Barine Bézagu, Rémi Louf, **Elvire Bestion**. Eds Le Pommier.
Outreach article for secondary school teachers on planet-vie.ens.fr (in French)
Troisième "rencontre eXploreur" sur le Centre Universitaire de l'Ariège (2019), **E. Bestion**. ''Lézards menacés par le changement climatique : expérience dans le métatron''

Reviewing:

(151 articles for 39 journals since 2007 and 22 grant proposals since 2010)

Ecology Letters - Hormones and Behavior – Journal of Herpetology – Ethology – Behavioural Processes – Naturwissenschaften – Animal Behaviour – Functional Ecology – Animal Conservation – Journal of Experimental Zoology Part A - Journal of Comparative Psychology - Behavioral Ecology- The American Naturalist – Behavioral Ecology and Sociobiology – Journal of Animal Ecology – Acta Oecologica – Oikos – Behaviour – Current Zoology – Physiological and Biochemical Zoology –

Climatic Change – Evolution – Ecosphere – Ecography – Scientific reports – PloS One – The American Naturalist – Movement Ecology – Biological Invasions – Journal of Experimental Biology - Frontiers in Ecology and Evolution – Nature Ecology & Evolution – Oecologia - Limnology & Oceanography - Proceedings of the Royal Society B – PCI – Ecology & Evolution –TREE – Freshwater Biology – Journal of Mammalogy – Science of the Total Environment

Review of research proposals for the *Council for Earth and Life Sciences of the Netherlands* (2 proposals), the *National Science Foundation* (NSF, USA, 3 proposals), *Chercheur d'Avenir Languedoc-Rousillon* 2011 (1 proposal), the *Graduate Women in Science* (GWIS, 1 proposal) Fellowship, the *Research Foundation Flanders* (Fonds Wetenschappelijk Onderzoek - Vlaanderen, FWO, 4 proposals), the University *of Nottingham Research Fellowship Scheme* (1 proposal), the *Fonds de la Recherche Scientifique* (FNRS, Belgium, 1 proposal), *Kentucky Science and Engineering Foundation* (USA, 1 proposal) and the *Natural Environment Research Council (NERC, UK, 2 proposal), Netherlands Organisation for Scientific research (Netherlands, 2 proposals), Mardsen Fund (New Zealand, 1 proposal), Poland National Science Centre (Poland, 2 proposals), National Research, Development and Innovation Office (Hungary, 1 proposal), Swiss National Science Foundation (SNF, Switzerland, 1 proposal).*

Editorial activities:

Associate Editor for Ecology Letters since 2019
Subject Editor for Oikos since 2017
Associate Editor for BMC Ecology 2012-2018
Review Editor for Frontiers in Ecology and Evolution 2015-2018

Committees:

Member of 14 PhD committees (2016-ongoing)
Member of 5 PhD defense jury (2016-ongoing)
Member of 2 selection committees for assistant professor position (Lyon-1 2011 & Paris Sorbonne 2021)

Funded projects

Current grants:

2019-2024: Altered eco-evolutionary feedbacks in a future climate, *funding:* ERC Consolidator Grant (1983565 euros, **PI**).

Past grants:

2019-2020: Molecular basis of responses to climate change: an experimental evolution approach, *funding:* FRAIB (8966 euros, **PI**).

2014-2017: Contribution de la génétique à une Trame verte plus fonctionnelle en Région Midi-Pyrénées, *funding:* Contrat de Recherche Laboratoires-Entreprises (141000 euros, **Participant**, PI : M. Baguette).

2013-2017: Heterogeneity of patterns and processes along biological invasion successions, *funding:* Biodiversa research fund (675000 euros, **Co-Pi** with S. Blanchet, J. Clobert, French part: 284000 euros).

2013-2017: Fragmented populations and dispersal syndromes: from genes to metapopulations dynamic, *funding:* Young researcher ANR research grant (240000 euros, **PI**)

2014-2016: Transgenerational consequences of human-induced phenotypic changes on ecosystem functioning, *funding:* IDEX Université de Toulouse (55300 euros, **Participant**, PI: J. Cucherousset).

2012-2013: Do animal personalities affect ecosystem functioning? An integrative experimental approach, *funding:* Fyssen foundation research grant (35000 euros, **Participant**, PI: J. Cucherousset).

2011-2012: Personality traits and heterogeneity in habitat preferences: consequences for spatially structured populations, *funding:* Fyssen foundation research grant (30000 euros, **PI**).

2007-2010: Personality traits, new insights for ecological invasion, *funding:* Fyssen foundation fellowship for postdoctoral scholar (32400 euros, **PI**), AXA research fund for postdoctoral scholar (76000 euros, **PI**)

Awards:

2018: Prime d'encadrement doctoral et de recherche

2010: Award for excellence in postdoctoral studies at UC Davis 2010

July 2009: Animal Behavior Society travel grant for International Ethological Conference 2009 ($2000)